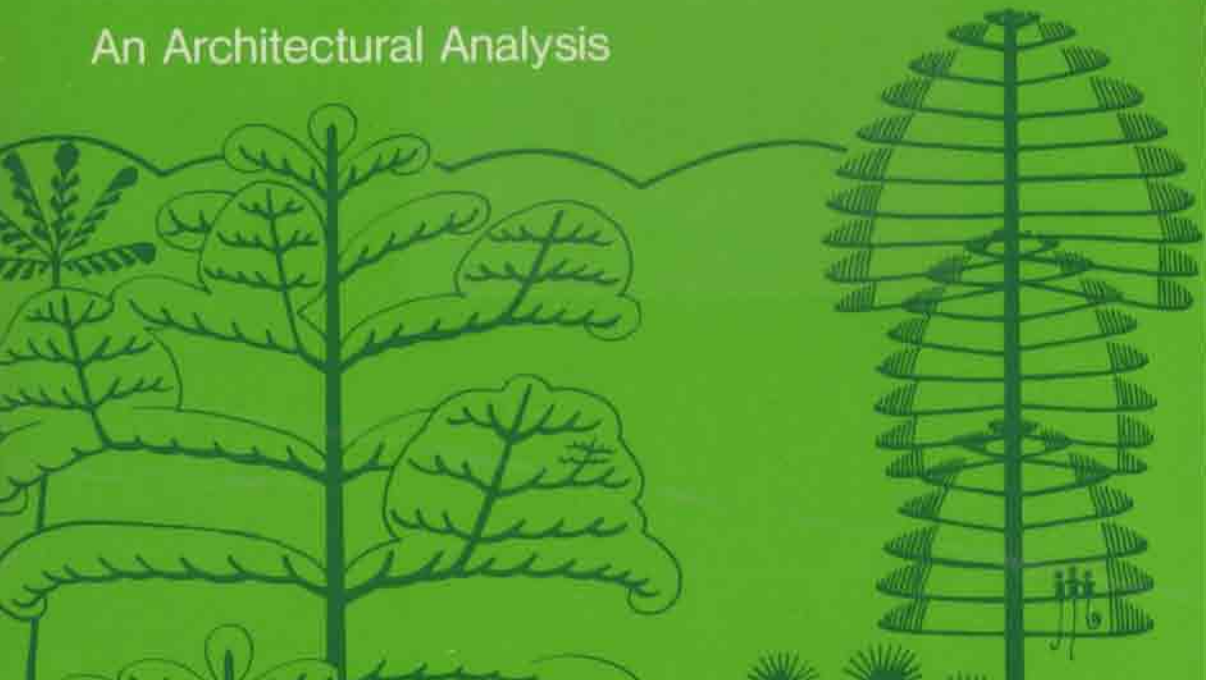
F. Hallé R. A. A. Oldeman P. B. Tomlinson

Tropical Trees and Forests

An Architectural Analysis



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An Architectural Analysis

With 111 Figures

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Jadis
les arbres
étaient des gens comme nous
mais plus solides
plus heureux
plus amoureux peut-être
plus sages
c'est tout

J. PRÉVERT

Gedaagde, bodemvaste boschgenooten
boomen die'k, wel vichtig jaren lang
boom wete; en, zoo hooge als nu geschoten
gezien hebbe, op zoo menig wandelgang
wat ben ik, arme miere, u bijgeleken
die sta en u aanschouwe, o hooge boomenreken

GUIDO GEZELLE, "*Eeuwelingen*"

Botany needs help from the tropics;
its big plants will engender big thinking

E.J.H. CORNER

Preface

This book is not an exhaustive survey of known information in the manner of a text-book – the subject is much too big for this to be possible in a relatively concise volume – but presents a point of view. We are concerned ultimately with the analysis of tropical ecosystems, mainly forests, in terms of their constituent units, the individual trees. Many different approaches are possible in the analysis of tropical forests. A simple one is to treat the trees as obstacles which in a military sense intercept projectiles or are a hindrance to foot soldiers (ADDOR et al., 1970). A similar approach might be adopted by an engineer confronted by a forest which has to be removed to permit road construction. The timber merchant is concerned with the ability of a forest to yield saleable lumber. The interest here is in the size of the larger trunks with some concern for the kinds of trees.

At a less destructive level the scientist aims to comprehend the forest from many different points of view. The forester himself, in conjunction with the taxonomist, will wish to analyze the floristic composition of the forest and perhaps account for species diversity in an evolutionary time scale (e.g., FEDOROV, 1966; ASHTON, 1969). The evolutionary biologist in his turn may be concerned with reproductive strategies in forest trees (e.g., BAWA, 1974), especially in a comparative way.

The approach adopted by the ecologist offers the greatest scope, since he may combine several different methods of analysis. Much research has gone into the physiognomy of tropical forests, size distribution of trees, stratification, diversity in relation to soil type or soil moisture content and has been summarized recently by ROLLET (1974). Phenological studies of tropical forests have produced a great deal of data which reveals the extent to which flowering, fruiting and leaf fall may or may not be seasonal (e.g., COSTER, 1923; HOLTTUM, 1940, 1953; cf. also LIETH, 1970). The production ecologist is interested in the forest as an efficient system for light interception and yield of dry matter, both in a relative and a comparative way (e.g., KIRA, 1978; KIRA et al., 1964, 1969; MONSI et al., 1973; BERNARD-REVERSAT, 1975). Photosynthetic efficiency in terms initially of leaf and branch orientation but ultimately in competitive ability is another stimulating approach which is summarized in the description of trees as "crafty green strategists" (HORN, 1971).

A universal tendency in these approaches is to treat trees as equivalent units – as taxonomic, physiological, reproductive units and so on. Much less attention has been given to the trees in the forest as individuals. This is our approach. However, we do not merely regard trees as individuals at one point in time, but as genetically diverse, developing, changing individuals, which respond in various ways to fluctuations in climate and microclimate, the incidence of insects, fungal and other parasites but particularly to changes in surrounding trees. The tree is then seen as an active, *adaptable* unit and the forest is made up of a vast number of such units interacting with each other.

In order to understand the adaptive strategies of the tree in the forest we must first, in a rather paradoxical way, remove it from its natural habitat and study it in isolation, more or less free from the natural accidents to which it is otherwise subjected in a competitive environment. Isolated in this way one can study the tree from the point of view of the geneticist and developmental morphologist. The tree develops from a seed which carries the genetic information which will determine its form. It is only by studying the form of the tree expressed in a more or less optimal environment that its genetic potential is clearly revealed. Briefly, we find out what the tree can "do". This leads, therefore, to the recognition of what has been termed the "architecture" of the tree (HALLÉ and OLDEMAN, 1970), a concept which is elaborated in great detail in this book. The concept of architecture involves the idea of form, implicitly containing also the history of such a form. The lifelong succession of developing forms in a plant is revealed by the concept of the architectural model and its reiteration.

By examining large numbers of species in a comparative way, we are led to the recognition of the existence of similar developmental plans among taxonomically dissimilar trees. Much of this book is, therefore, a description of these developmental "models" as established by HALLÉ and OLDEMAN, and this provides a framework to which we can attach a great deal of information about the growth of trees in the tropics. Recognition of the existence of similar constructional principles (architectural models) in a great variety of trees (and our survey has been as cosmopolitan as we could make it) implies that the "strategy" of a tree differs from species to species. What significance, in fact, does architecture have for the success of the tree in a natural environment?

Here we must return to the forest, away from our optimalized environment which has been so productive of new information. We have learned how a tree is capable of growing, by virtue of its genetic make-up. Now we can ask the question, how, in fact, does it grow in the vigorously competitive environment of the forest itself? This leads to the recognition of ways in which a "real" tree is constructed in a natural stressed environment, as distinct from an "ideal" tree, growing precisely according to its genetic plan and not subject to environmental stress. This is not to suggest that we are making a distinction between theoretical and practical information. Both circumstances exist, and trees function in both optimal and nonoptimal environments. The point will become clearly established that without a knowledge of the potential growth activity of the tree, it is impossible to recognize its actual growth expression. Once this is appreciated we are in a position to reassemble the living forest in terms of its developing units. From this it should be appreciated that our approach is a biological one in the purest sense.

Throughout the text we have stressed tropical examples and our ultimate aim has been to understand trees of the lowland, humid tropics. What is the reason for this emphasis? The answer is really quite simple. Taken in a very general sense the climate of the wet tropics is uniformly favorable for plant growth and allows the existence of an enormous species diversity. Consequently in this environment there is a wider array of growth expressions in woody plants than anywhere else in the world. If one seeks fundamental principles, it is clear that one should do so where they are freely and clearly expressed. Once an understanding of growth processes in tropical trees has been established, it then becomes possible to look at forests in the more constraining environments of temperate latitudes, where diversity is less and is directed towards survival amidst macroclimatic stress. One can understand a temperate forest better when one has grasped principles of tree growth in the tropics, but scarcely the reverse.

Unfortunately, botanical history has inverted this logical sequence. Consequently a degree of justification for our approach has to be introduced via our initial thumb-nail sketch of the floristic diversity of the tropics. For the same reason we have attempted to provide some background in morphogenetic terms for our subsequent analysis of tree architecture, since our approach is often different from that of a temperate forester for whom responses to seasonal climates seem so important in tree growth. This is by no means intended as a complete review of organogenesis in woody plants of the tropics, but it should serve to clarify further our point of view. Frequently, of course, a topic can only be discussed with examples of temperate tree species in mind because no information is available about tropical species.

Our greatest problem, and one which is encountered by all who have tried to describe tropical vegetation to an audience which has never visited it, is that the majority of plants are likely to be unfamiliar to the reader. We have used examples of common or commercially valuable trees, where appropriate, especially in the introductory chapters. We have otherwise made frequent reference to existing accounts of the more common tropical species, and to the earlier account of HALLÉ and OLDEMAN (1970), but in order that this book may carry as much new information as possible most of the illustrated examples are new. If the reader still retains a sense of the monstrous, the fabulous or the unreal in using this book he should try to make a mental reversal of the situation, which is botanically more appropriate. How strange is the temperate tree, leafless for a large part of the year, with such marked synchrony in its development, its brief period of extension growth, its ability to flower only once each year and with its peculiar annual radial increments of growth in the wood. Here is a bizarre object indeed! Organizational understanding of woody plants must come to terms with growth principles in parts of the globe where they are most readily comprehended, that is in the tropics. It is our intention to make the future investigators' task an easier one by presenting a rational basis for future research.

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In general the willing support of our differing institutions has been of great benefit during a task made difficult by our wide geographical separation and the continuing need to carry out our normal duties. We are thankful that our publishers have been patiently appreciative of this circumstance.

January, 1978

FRANCIS HALLÉ
ROELOF A.A. OLDEMAN
PHILIP B. TOMLINSON

Note: Since frequent reference is made to HALLÉ and OLDEMAN (1970), for conciseness this is referred to as "H.O., 1970" in the text.

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Chapter 1 Introduction

A. What is a Tree?

I. Definitions

The reader may find the concept of a "tree" used in this book a very generous one. On reflection we see that a tree is not easily defined or at least is definable in many different ways. Trees, in fact, are no longer the property of botanists, since to a mathematician a "tree" is a system in which any two points are connected via only one possible pathway (i.e., the system is not a reticulum and lacks loops). In this very general sense one may find trees in many disciplines – in heraldry as a genealogical chart (a family tree), in geomorphology as the tributaries of a stream system, in cybernetics as a decision-making process, each providing an example of a mathematical tree. The dichotomous key on page 84 is an example of such a tree. The mathematical concept of tree may have useful analytical and predictive purposes (Oohata and Shidei, 1971; McMahon and Kronauer, 1976) and is helpful in constructing computer programs by which botanical trees may be mimicked (Rashevski, 1944; Legay, 1971; Franquin, 1970; Lindenmayer, 1971).

However, our concern is with botanical trees, which are still susceptible to a variety of definitions. Usually these involve size (a tree is not a shrub, nor a herb) as well as physiognomy (existence of a major axis or trunk). The most rigid definitions are provided by foresters (e.g., Little, 1953, p. 5) – trees are "woody plants having one erect perennial stem or trunk at least three inches (7.5 cm) in diameter at breast height ($4^{1}/_{4}$ ft) (1.5 m), a more or less definitely formed crown of foliage, and a height of at least 12 ft (4 m)". This is a pragmatic definition used by a professional group for whom a tree is considered mainly as the source of merchandisable timber. By this definition a tree only has one trunk, but we will see that this is not necessarily a constant feature. An ecologist is likely to define a tree, in terms of a plant's competitive ability, as a unit capable of casting shade on other plants. An anatomical definition would be concerned with the rigidity of the plant, i.e., its ability to produce lignin, and might even be restricted to plants whose trunks are mainly made up of secondary tissue, produced by a vascular cambium ("wood" in a general anatomical sense). Thus a palm might be excluded because its trunk is primary; a banana is a "giant herb"; both, however, fit the forester's definition of a tree given above, as does *Alpinia boia*, a giant ginger whose aerial shoots arise from an underground rhizome. Lianes are usually excluded because they are not self-supporting, but some woody epiphytes do conform because they can reach the required proportions, even if by unconventional ways.

From this it is clear that our concept of a tree is angiosperm-centered (with the conifers thrown in for good measure), i.e., based on the method of construction of a tree exemplified by an oak, a rubber tree, or a pine. However, if we add a dimension of geological time we can appreciate that this concept is too limited, since the fossil record demonstrates many other, initially successful, attempts at tree-making, e.g., *Lepidodendron*, calamites, seed-ferns, in which branching patterns and anatomical principles are sometimes different from those in angiosperms (see p. 263). Although largely extinct, a few of these "ancient ways" still persist as in the cycads or, on a lesser scale, in horsetails (*Equisetum*). The tree-ferns and most woody monocotyledons (e.g., palms) represent examples of trees based on primary, not secondary, construction and it is likely that these monocotyledons are a relatively recent experiment in tree-making.

From this brief consideration of tree diversity it is evidently unwise to offer rigid definitions where they are not needed. Consequently in this book our concept of a tree is implied in the plants discussed, ranging from the oil palm, *Cycas*, *Cyathea*, the paw-paw, banana, dragon tree, to commercial crops of the tropics like coffee, cocoa and rubber and to forest giants like *Koompassia*, kapok, and sand box tree. We do not forget, however, the slender treelets of the forest undergrowth, especially as they tell us so much about the diversity of growth expression in woody plants. Even woody epiphytes, which may never develop a recognizable trunk, have to be considered.

II. Tree Making

If we broaden our concept of a botanical tree in this way so that it encompasses the diversity of large plants in tropical ecosystems it is of interest to consider the different ways in which plants become trees. The elements of a tree (Fig. 1) are crown, trunk or bole, and roots. The last, incidentally, never enter into the definition of a tree, although they are implicit in its growth.

In the generally considered case crown, trunk, and root system are synchronous in their development, maintaining a constant proportion in parts. This method of construction is represented diagrammatically in Figure 1 A and is, of course, the basis for the pipe model theory of tree form (SHINOZAKI et al., 1964). The developmental basis for this constructional method is the ability of the trunk to increase in diameter as it grows in height. In an alternative situation the crown may be developed first, at soil level, and with it much of the root system. Subsequently the crown is erected by extension of the trunk, which maintains a constant diameter (Fig. 1 B). This is the method of tree construction based on primary growth which characterizes the palms and tree ferns. A variant of this is seen in the proliferation of trunks and crowns by basal branching, which has the advantage of making initial use of an existing root system (Fig. 1 C). Multiple-stemmed palms, like the date, exemplify this and provide, incidentally, an example of a many-trunked tree.

Both these major categories are characterized by a relatively slow development of the crown. In a third category, trunk and a large part of the crown are essen-

Fig. 1 A–D. Four ways of making a tree. ▷

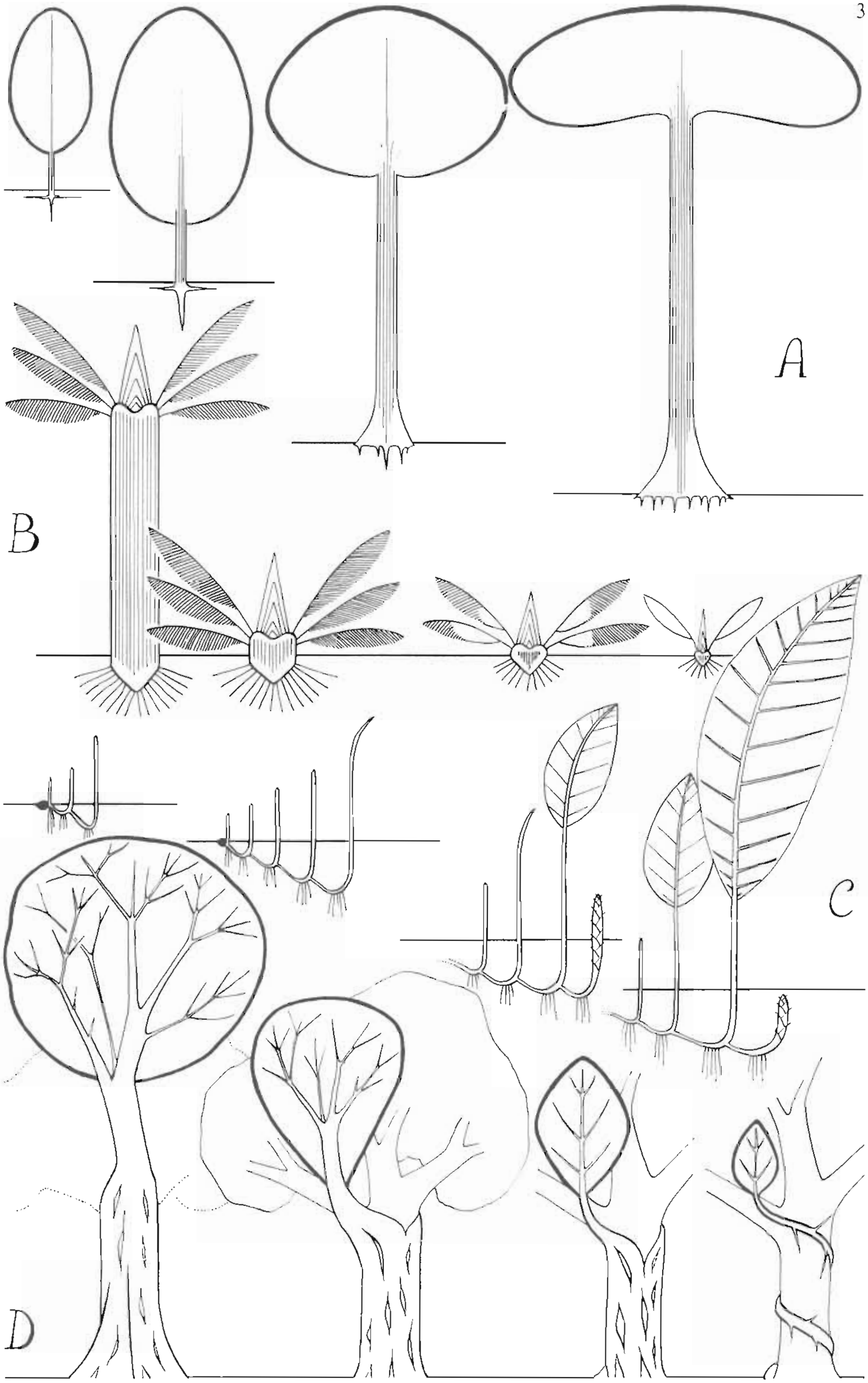
A Crown, trunk and root system develop synchronously.

B The crown and much of the roots develop first, at ground level, trunk extension comes later.

C Proliferation of trunks and crowns by subterranean branching.

D Germination on another tree, the "trunk" is largely formed downward by roots ("strangler").

A and *C* from left to right, *B* and *D* from right to left; *vertical lines* in *A* and *B* symbolize the vertical pipe systems (SHINOZAKI et al., 1964)


A
B
C
D

tially preformed, represented initially at soil level in a telescoped condition. Subsequently this "preformed tree" expands very rapidly. This method of tree construction is exemplified by the bamboos, growth is entirely primary and the system is again made possible by the existence of a previous root system (Fig. 1 C).

So far we have seen trees which are initiated at soil level; in a forest they gradually extend into the canopy. An uncommon, but yet distinct kind of tree is one in which the crown is made high up, within an existing canopy. This condition is represented by woody epiphytes, notably species of *Ficus* (Moraceae) which develop as a seedling in the crown of an existing tree. Here the trunk is initially the root system which grows in a downward direction and is at first not self-supporting. A free-standing tree is established only when the supporting host dies (Fig. 1 D).

It should be clear from this discussion that the understanding of plant form in the tropics is aided if we free ourselves from too constrained a definition of a tree. The notion of architectural model which is developed later in fact has as its basis a complete freedom from the concept of size in an approach to the understanding of constructional principles in plants.

III. Apical Meristems and Tree Construction

The aerial parts of trees are constructed by the activity of one or more primary (apical) meristems. We recognize here four major kinds of tree construction in meristematic terms as the basis for our subsequent description of architectural models. We do not mean to dismiss secondary (lateral) meristems (notably the vascular cambium) as insignificant, but such meristems owe their existence to the activity of primary meristems. There are many trees which lack secondary meristems, which are thus not essential in tree-making (p. 68).

The single apical shoot meristem of the seedling may give rise to a tree in four ways: (1) by its continued activity alone; (2) by multiplication to produce further meristems all of equal potential and, therefore, not differentiated into trunk and branch; (3) by multiplication to produce further meristems of unequal potential, some meristems giving rise to branches and one or more giving rise to the trunk; (4) by multiplication to produce further meristems of equal but mixed potential, i.e., each meristem giving rise first to a trunk segment, then to a branch segment, or even the inverse in certain examples.

This information is summarized in the key to architectural models (p. 84) but needs amplification here since basic concepts must be explained.

1. Trees Built by One Meristem

In this simplest condition the seedling meristem is the only aerial meristem active throughout the life of the tree, since it produces a single axis which remains unbranched in the vegetative state. This condition is exemplified by single-stemmed palms like oil palm and coconut, but also exists in dicotyledons. Vegetative shoot construction is monoaxial, all other trees are polyaxial (see p. 99).

2. Trees with Modular Construction

In such trees the seedling meristem proliferates by sympodial branching (rarely by true dichotomy, i.e., equal division of the shoot apex) with the new meristems repeating the construction of the parent meristem precisely in a morphologically qualitative sense. All meristems are alike and produce orthotropic shoots which are determinate, usually ending in an inflorescence but otherwise aborting in some way. Hence the tree is made up of a series of equivalent morphological units repeated indefinitely. We follow PRÉVOST (1967) in defining these units as *articles*, which we have translated as "modules" and we can refer to such trees as having a "modular construction". The use of this term has been amplified since PRÉVOST initially dealt with Apocynaceae only, but it is now evident that the same construction occurs in numerous families (PRÉVOST, 1978). The characteristics of a module are that of an axis in which the entire sequence of aerial differentiation is carried out, i.e., from the initiation of the meristem to the onset of sexuality which completes the development of the module. These processes are repeated in the next module, and so on. Most commonly modules form sympodia. In some trees a linear sympodium is developed, as in many cycads, and the tree is apparently unbranched. More usually two or more modules are repeated in the construction of a tree, which is then evidently branched. Such trees are represented by castor oil and cassava. In yet other examples the trunk is a single unit, the branch system alone being modular.

3. Trees with Trunk-Branch Differentiation

In this category meristems of the tree are no longer equivalent, since their differentiation leads to a distinction between trunk and branch. Thus trunk and branch are fundamental organizational features of the tree. The trunk has the principal architectural role, it determines the overall stature of the tree, is the central system of communication between roots and crown, and it maintains the mechanical stability of the whole organism. The trunk may be a monopodium produced by a single apical meristem, or a sympodium produced by a succession of apical meristems, each originating as a branch (relay axis) from the parent meristem, so that the trunk is made up of a succession of "relay axes". Branches are biologically specialized for photosynthesis and sexual reproduction, which functions are carried out in a great variety of ways.

This construction admits of a great many architectural possibilities, depending on the degree of differentiation between trunk and branch, i.e., whether branches are orthotropic or more or less plagiotropic. Examples of trees with a degree of differentiation between trunk and branch are numerous and include, among temperate trees, oak, maple, ash, and apple, and amongst tropical trees, mango, avocado, rubber, cocoa, coffee, as well as mahogany and many other timber trees.

4. Trees with Changes in Orientation of Axes

The final category is recognized in trees with meristems which give rise to axes which may be recognized as "mixed", since the same meristem contributes a trunk and a branch portion to the construction. This is possible because the geometric and physiological orientation of the axis changes during the activity of its meristem. The change may be primary, i.e., in the differentiation of the meristem which initially determines an orthotropic but subsequently a plagiotropic shoot. Otherwise, the meristem produces either an orthotropic or a plagiotropic axis which secondarily becomes reorientated.

Hence the constructional features which are the responsibility of two kinds of meristem in the previous category, are here achieved by a single kind of meristem. Tree construction then depends on the development of a succession of such meristems, produced as relay axes, a process which continues indefinitely. Examples include elm and beech among temperate trees and many leguminous trees in the tropics.

B. The Botanical World of the Tropics

The diversity of growth expression in tropical woody plants, which we will try to present in our account, originates for two main reasons. First, because tropical floras are extremely rich in numbers of species, especially of trees, as compared to temperate floras. Second, because tropical floras, especially those of humid lowlands, are less constrained climatically than temperate floras. Temperate trees develop in situations where their adaptive ability is directed towards survival in rigorous climatic circumstances, tropical trees are not so constrained. Competition in the contrasted kinds of environment therefore takes different directions and this is probably the basis for the different amounts of speciation which are preserved in the two regions. The subject clearly needs detailed consideration, but we can only deal with it in a very superficial way.

I. Distribution and Size of Flowering Plant Families

The floristic richness of the tropics has been repeatedly demonstrated (e.g., MARTIUS et al., 1840–1906). Here we provide some quantitative information to substantiate this emphasis.

The sharp segregation between tropical and temperate floras is evident even at the family level. Certain large and very natural families are well represented in both tropical and temperate floras. These include, amongst dicotyledons: Compositae (19,000 species), Euphorbiaceae (7500), Leguminosae (13,000), Rubiaceae (6500); and amongst monocotyledons Cyperaceae (4000), Gramineae (8000), Liliaceae (4500), Orchidaceae (20,000). Estimates of family size are only approximate and are intended to provide useful comparative values. Labiatae (4000) and Scrophulariaceae (4000) are marginal to this category since both are better represented in temperate floras; in the tropics they are often weeds. Within these cosmopolitan families (cosmopolitan in the sense of their representation, not by the distribution of constituent species) tropical and temperate groups are sharply contrasted. Temperate Leguminosae tend more often to be herbaceous and members of the subfamily Papilionoideae, in contrast to the woody, essentially tropical Caesalpinioideae and Mimosoideae. Rubiaceae in northern latitudes mainly belong to the herbaceous tribe Galieae (e.g., *Galium*) which does not represent the family well, since most Rubiaceae are woody plants with decussate leaves and interpetiolar stipules. Tropical Gramineae include the bamboos (subfamily Bambusoideae); such arborescent "grasses" are largely absent from temperate floras. Orchids in the tropics are typically epiphytic, not terrestrial like temperate orchids.

Taxonomic segregation of flowering plants between tropical and temperate regions is evident when one considers large families (of the order of 800 species or more). Annonaceae (2100) is a good example, since only one species in this family (*Asimina triloba,* a woody perennial herb of the southeastern United States) is wholly extratropical in its distribution. Other species in this family may range into temperate latitudes, but their distribution is largely tropical (e.g., *Annona glabra*). The Annonaceae may thus be described as a "large tropical family" with complete justification. The Palmae may be cited as a further example; few palms are extratropical and the boundaries within which most palms are distributed are represented approximately by the Tropics of Cancer and Capricorn themselves (MOORE, 1973). The palms are in fact symbolic of the tropics. Their altitudinal range is also limited, so that there are relatively few palms outside the lowland tropics. One can continue this analysis, appreciating that the number of temperate representatives of some families may be considerable. However, the list of large tropical families categorized in this general way is long and includes (with an estimate of species number):

Table 1. Large angiosperm families with predominantly tropical distribution

Dicotyledons	
Acanthaceae (2600)	Melastomaceae (3000)
Amaranthaceae (900)	Meliaceae (1400)
Annonaceae (2100)	Moraceae (1500)
Apocynaceae (2000)	Myrsinaceae (1000)
Asclepiadaceae (2000)	Myrtaceae (3000)
Begoniaceae (900)	Oxalidaceae (950)
Convolvulaceae (1400)	Piperaceae (1400)
Cucurbitaceae (900)	Rhamnaceae (900)
Flacourtiaceae (1300)	Rutaceae (1600)
Gesneriaceae (1800)	Sapindaceae (1500)
Guttiferae (900)	Simaroubaceae (1700)
Lauraceae (2200)	Solanaceae (2300)
Loranthaceae (1400)	Sterculiaceae (1000)
Malvaceae (1500)	Verbenaceae (2600)
Monocotyledons	
Amaryllidaceae (1100)	Iridaceae (1200)
Araceae (1800)	Palmae (2600)
Bromeliaceae (1700)	Pandanaceae (900)
Eriocaulaceae (1200)	Zingiberaceae (1300)

Such a categorization may run counter to ecological preferences. The Cactaceae (2000) are not easily accommodated because they are characteristic of dry areas.

To attempt the same thing for temperate families is more difficult, since many families which are well represented in temperate floras occur at high altitudes in the tropics. However, admitting a greater degree of flexibility one may include in a category of "large temperate families" the following:

Table 2. Large angiosperm families with predominantly temperate distribution

Dicotyledons	
Campanulaceae (2000)	Gentianaceae (1100)
Caryophyllaceae (2000)	Proteaceae (1400)
Crassulaceae (1400)	Ranunculaceae (2000)
Cruciferae (3000)	Rosaceae (3000)
Ericaceae (2500)	Umbelliferae (3000)
Monocotyledons	
None	

The generalization we have made is even more evident with this list, but it is safe to say that such families are poorly, if at all, represented in floras of the lowland tropics.

One can proceed further with this kind of arbitrary breakdown of families according to their size and distribution. Moderately large tropical families (400–800 species) of which we will encounter many examples in our subsequent discussion, include Anacardiaceae (600), Araliaceae (700), Bignoniaceae (800), Burseraceae (600), Celastraceae (850), Combretaceae (500), Ebenaceae (450), Icacinaceae (400), Lecythidaceae (450), Loganiaceae (500), Malpighiaceae (800), Sapotaceae (800), Theaceae (600).

This analysis can proceed further to smaller assemblages (see the later summary, p. 9) but the floristic disparity between the vegetation of tropical and temperate regions, evident at the family level, is already quite clear.

II. Tropical Floras as Tree Floras

Another conclusion which this very brief phytogeographic analysis permits is that tropical floras are rich in woody plants (Record and Hess, 1943). Most of the examples cited in the above lists of tropical families refer to families of trees (including woody climbers). Many are in fact almost exclusively woody (e.g., Annonaceae, Burseraceae, Combretaceae, Flacourtiaceae, Lauraceae, Lecythidaceae, Meliaceae, Myrsinaceae, Sapotaceae, Sapindaceae, Simaroubaceae, Sterculiaceae). Monocotyledons tend to be thought of as herbs, but they are well represented by trees in the tropics (e.g., Palmae, Pandanaceae). Temperate families, in contrast, tend to be herbaceous (e.g., Campanulaceae, Caryophyllaceae, Cruciferae, Gentianaceae, Geraniaceae, Onagraceae, Primulaceae, Ranunculaceae, Saxifragaceae, Umbelliferae).

The botanist who knows floras at high latitudes is often surprised to find that familiar herbaceous genera of temperate floras are, in fact, rather unrepresentative of their family as a whole, which often turns out to be woody and mainly tropical in its concentration. Examples include *Lythrum* (Lythraceae), *Hypericum* (Guttiferae), *Polygala* (Polygalaceae), *Viola* (Violaceae), *Verbena* (Verbenaceae), *Urtica* (Urticaceae), *Galium* (Rubiaceae). The family Violaceae provides a striking example since the familiar violets are not typical of the family as a whole, which is predominantly woody in the tropics, and the flowers are actinomorphic rather than zygomorphic (e.g., *Conohoria, Hymenanthera, Rinorea*). *Viola*, however, remains much the largest genus. It is also surprising to find how many type genera of large families are unrepresentative in this (and other) respects! The situation is frequently extended, so that several families which are encountered as herbs in temperate floras, are represented as trees in the tropics (e.g., Polygonaceae, *Eriogonum, Polygonum, Rumex*: temperate herbs, but *Coccoloba, Triplaris*: tropical trees; Papaveraceae: temperate herbs, but *Bocconia* species: tropical small trees; Gentianaceae: mainly herbs, but *Tachia, Lisianthius*: tropical shrubs).

If one assumes that herbs are derived primarily from trees, in an evolutionary sense, this may be expressed taxonomically even at the family level. The impression is often given that a temperate (herbaceous) family is the phylogenetic offshoot of a tropical (woody) family and suggests the universal tendency for trees which migrate on an evolutionary time-

Table 3. Tropical–temperate family pairs

Tropical–woody	Temperate–mainly herbaceous
Annonaceae	Ranunculaceae
Araliaceae	Umbelliferae
Bignoniaceae Caesalpinioideae Capparidaceae	Scrophulariaceae Papilionioideae Cruciferae
Chrysobalanaceae Cunoniaceae Ehretiaceae (=Boraginaceae *s.l.*)	Rosaceae Saxifragaceae Boraginaceae (=Boraginaceae *s.s.*)
Erythroxylaceae Guttiferae Moraceae	Linaceae Hypericaceae Urticaceae
Myrsinaceae Theophrastaceae	Primulaceae
Sapindaceae	Aceraceae (woody) Hippocastanaceae (woody)
Sonneratiaceae	Lythraceae

Table 4. Distribution of woody and herbaceous dicotyledonous families

Family size (species)	Large (800+)		Moderately large (400–800)		Moderately small (200 400)		Total
Generalized distribution	Tropical	Temperate	Tropical	Temperate	Tropical	Temperate	
Herbaceous	6	7	1	6	3	8	31
Woody	23	3	26	7	18	4	81
Total	29	10	27	13	21	12	112

Families with a high proportion of climbers have been accepted as woody.

Table 5. Relative composition of a tropical and a temperate flora. (After SCHNELL, 1971, Vol. I, p. 56)

Family	West Africa		France	
	Woody spp.	Herbaceous spp.	Woody spp.	Herbaceous spp.
Violaceae	37	3	0	13
Polygalaceae	7	24	3 (subshrubs)	10
Linaceae	12	1	0	16
Guttiferae	15	2	0	22
Euphorbiaceae	212	46	1 (subshrub)	62
Leguminosae	197	258	69	283
Umbelliferae	1	19	0	183
Boraginaceae (*s.l.*)	13	17	0	79
Rubiaceae	481	72	0	49
Totals	975	442	73	717
	1417		790	

Comparing only families represented in both areas.

scale from the tropics to survive in temperate latitudes only as herbs. Our current knowledge of the systematic affinities of families and their predominant growth habits suggests this kind of evolutionary change, as in the list of "family pairs" in Table 3, in which the families are taxonomically close, but generally show a tropical woody v. temperate–herbaceous correlation.

We have summarized information in Table 4 [data on families and distribution mainly from GOOD (1964) and CRONQUIST (1968)]. This serves to show the relative numbers of temperate, herbaceous and tropical, woody families.

To provide a more specific example we quote the values in SCHNELL (1971) which compare family representations for a part of West Tropical Africa comparable in area to that of France (Table 5). The figures are not directly comparable as an indication of the relative richness of the two floras, since many additional families in the tropical flora would not be represented in the temperate flora; were total figures provided, the imbalance would undoubtedly be greater.

III. Floristic Richness in Limited Areas

Precise examples of the high concentration of species in limited areas may produce astoundingly large figures. POORE (1968) in his analysis of an area 23.0 ha (57.6 acres) in extent, within the Jengka Forest Reserve in West Malaysia produced the following figures for trees, i.e., plants mostly with a girth greater than 91 cm (3 ft) at breast height. The term tree is here restricted to dicotyledons, except for one palm.

Families	52
Genera	139
Species	374

The commonest families were Dipterocarpaceae (32 species), Euphorbiaceae (27), Myrtaceae (23), Burseraceae (23), Lauraceae (22), Myristicaceae (21), Anacardiaceae (19), Sapotaceae (16), Leguminosae (15), Annonaceae (10). The figures are only approximate because a number remained incompletely identified and some were possibly new to science.

Under these circumstances, of course, the number of individuals of any one species was not large. The most abundant species was *Shorea acuminata* (94 individuals). No less than 137 species (almost 37%) were represented by a single individual. However, this does not exclude the possibility of a large number of individuals below the lower size class limit.

Under these conditions a reduction in the size of the plot reduces numbers of species, as would be expected. Nevertheless, ASHTON (1969) recorded as many as 12 species in six genera within a single family (Sapotaceae) in his analysis of a 241 × 121 m plot of mixed Dipterocarp forest in West Sarawak, where only trees exceeding two feet in girth were recorded. This degree of quantification has undoubtedly been repeated many times by forest botanists in the lowland tropics. Evolutionary biologists have, of course, discussed this richness extensively (e.g., in LOWE-MCCONNELL, 1969). We wish merely to establish the rich background against which we have worked. In contrast, ecological analysis in temperate forest is relatively simple; HORN (1975) for example deals with 13 tree species in New Jersey, so that a matrix of successional probabilities is easily constructed.

IV. Geographic Locations

In our survey of tropical tree architecture we have attempted to provide examples from as many different parts of the tropics as possible, but our selection inevitably must be biased towards species which reflect our personal experiences. We have throughout the text given only a very generalized picture of the distribution of the examples chosen, chiefly distinguishing between species occurring in the three main tropical regions of Africa, America and Asia. Where a species is significantly more restricted we have indicated this but still in a very generalized way, e.g., Guianas, West Indies, Madagascar, Borneo. In a work not primarily devoted to plant geography this provides a reasonable comparative basis.

V. Climate and Tree Growth in the Tropics

Tropical vegetation owes its great diversity to the range of climates that is to be found in the tropics, ranging from that of high mountains near the tree limit, to hot deserts with little rain and to the nonseasonal lowland tropics. Within the tropics, therefore, there are many climates unfavorable to plant growth for much or part of the year, and here vegetation shows a strong adaptive response to a rigorous environment.

In contrast, much of the lowland tropics is climatically very uniform, with high rainfall and temperatures suited to optimum plant growth throughout the year and with little or no seasonal fluctuation to which plants need adapt themselves. Records of such climates have been kept for many years in different parts of the tropics e.g., HOLTTUM (1953), GOUROU (1966). Under such circumstances microclimatic fluctuations tend to be of more ecological significance than macroclimatic fluctuations, despite the difficulties encountered in measuring them (CACHAN, 1963; CACHAN and DUVAL, 1963; ODUM and PIGEON, 1972).

The climate of Singapore provides an oft-cited example (HOLTTUM, 1953); the average annual rainfall is rather less than 250 cm, with no month having a mean rainfall less than 12.5 cm. "Dry months" are reckoned as those with less than 6.2 cm of rain, but only 21 have been recorded in 46 years, most frequently either February or July. The average difference between wettest and driest months is less than 5 cm. Humidity remains consistently high. The average temperature difference between coldest and hottest months is less than 2°C. The normal daily range of temperature (23–32°C) is a little less than the absolute temperature range (21–34°C).

In the lowland tropics where rainfall is regularly more than 150 cm per year and nonseasonally distributed, the dominant vegetation is rain forest, as in the Amazon Basin, tropical Africa, and much of southeast Asia and Melanesia (RICHARDS, 1952).

Our interest in this book is mainly with trees of such lowland forests. They are unique terrestrial environments because, being favorable for plant growth, survival of individuals is conditioned by competition without climatic stress. One can, therefore, witness a range of growth expressions established by endogenous interactions; exogenous influences are minimal. Leaf dimensions establish this point in a convincing way. In deserts, or forests with a monsoon or seasonally dry climate, or in temperate climates with a cold winter, woody plants tend to be either deciduous or have small leaves or leaflets, reflecting the restriction on leaf size and age imposed by periodic water shortage. In contrast numerous observers have commented upon the uniformity of leaf size in tropical forests (e.g., RICHARDS, 1952, p. 80)—what has been described as the "laurel"-type, i.e., within a size range 2,025–18,225 sq mm (usually about 10 cm long) with entire margins, a leathery texture, shiny surface and frequently a driptip when juvenile. However, this mesophyllous condition does include a range of leaf types. What determines this range, if not climate? In seeking answers to such a question we find that the primary diameter of the supporting axis is of considerable significance (p. 83), and one cannot discuss leaf size independently of a knowledge of the overall form of the tree. We can see that many *internal* correlations have to be looked for in explaining morphological features of tropical trees, when external influences, at least of climate, have been eliminated. We can ask the same question about leaf age. If leaf loss is no longer a necessary seasonal phenomenon, what factors determine the life span of individual leaves? This question is again briefly discussed elsewhere (p. 38).

Many of the points which relate to the biology of plants in the tropics can be approached from this point of view and one must attempt to dissociate oneself from the idea of a "norm" in entering into this discussion. It may even be that a knowledge of plant form expressed in uniformly favorable climates provides the standard for comparison. Thus one should not necessarily ask the question "Why do tropical trees so uniformly have entire leaves?", but "What factors determine the high incidence of leaves with dissected outlines in temperate trees?". Similar changes of outlook are needed in other disciplines, e.g., in physiology, in contrasting C_3 and C_4 photoassimilating mechanisms, in morphology, in contrasting syllepsis and prolepsis (p. 42).

Chapter 2 Elements of Tree Architecture

A. The Initiation of the Tree

I. Seedling Morphology

Successful establishment of the seedling is obviously essential to the development of the tree and remains the most critical phase in the life cycle of a plant (HARPER and WHITE, 1975). Mortality amongst seeds and seedlings is much higher than in any other ontogenetic phase. Seed predation is of acute interest to the population biologist since population structure of plants and animals is here closely interrelated (e.g., JANZEN, 1970b, 1971). When one considers that the single seedling meristem of a *Corypha* palm eventually produces about a quarter of a million fruits or seed meristems (TOMLINSON and SODERHOLM, 1975), of which only one is needed to replace the parent tree, the predator pressure and extreme seedling mortality is convincingly demonstrated.

Seedling morphology remains relatively stereotyped amongst plants but is still more diverse than the usual morphological division between epigeal (cotyledons above ground) and hypogeal (cotyledons below ground) germination suggests and is, of course, of prime value in systematics (DUKE, 1965, 1969; NG, 1973, 1978; BURGER, 1972; all of whom have provided extensive documentation of diagnostic features). Most seeds with large endosperm reserves have small, often poorly differentiated embryos and germination is hypogeal, the cotyledons usually remaining within the seed coat and never becoming erected and photosynthetic (i.e., germination is *cryptocotylar*, according to DUKE, 1965, who finds the older terminology etymologically unacceptable; his contrasted term is *phanerocotylar*). The cotyledons themselves may hold the seed reserves. Germination may still be hypogeal, as in avocado, but large fleshy cotyledons equally well may become erected and photosynthetic.

NG (1978) in his survey of Malayan forest tree seedlings emphasizes the function of the hypocotyl, rather than the behavior of the cotyledons, and finds room for an intermediate category "semi-hypogeal", represented most familiarly by durian.

The time of absorption of the endosperm (or perisperm) in embryo and seedling varies considerably. In some groups the method of germination and seed structure is stereotyped and follows taxonomic boundaries closely. In palms, seedlings are always hypogeal (GATIN, 1912) and only *Nypa* is biologically at all distinct, in its vivipary (TOMLINSON, 1971a). Annonaceae and Myristicaceae are equally uniform with endospermous seeds and hypogeal germination. However, the correlation between seed type and germination is, in fact, not necessarily constant. In coffee, for example, the seed is endospermous, but germination is epigeal and the cotyledons become photosynthetic. Quite closely related species may have dissimilar methods; in *Cordyline* (Agavaceae) for example, one group of species exemplified by *C. australis* is epigeal (TOMLINSON and FISHER, 1971), another group exemplified by *C. terminalis* is hypogeal (FISHER and

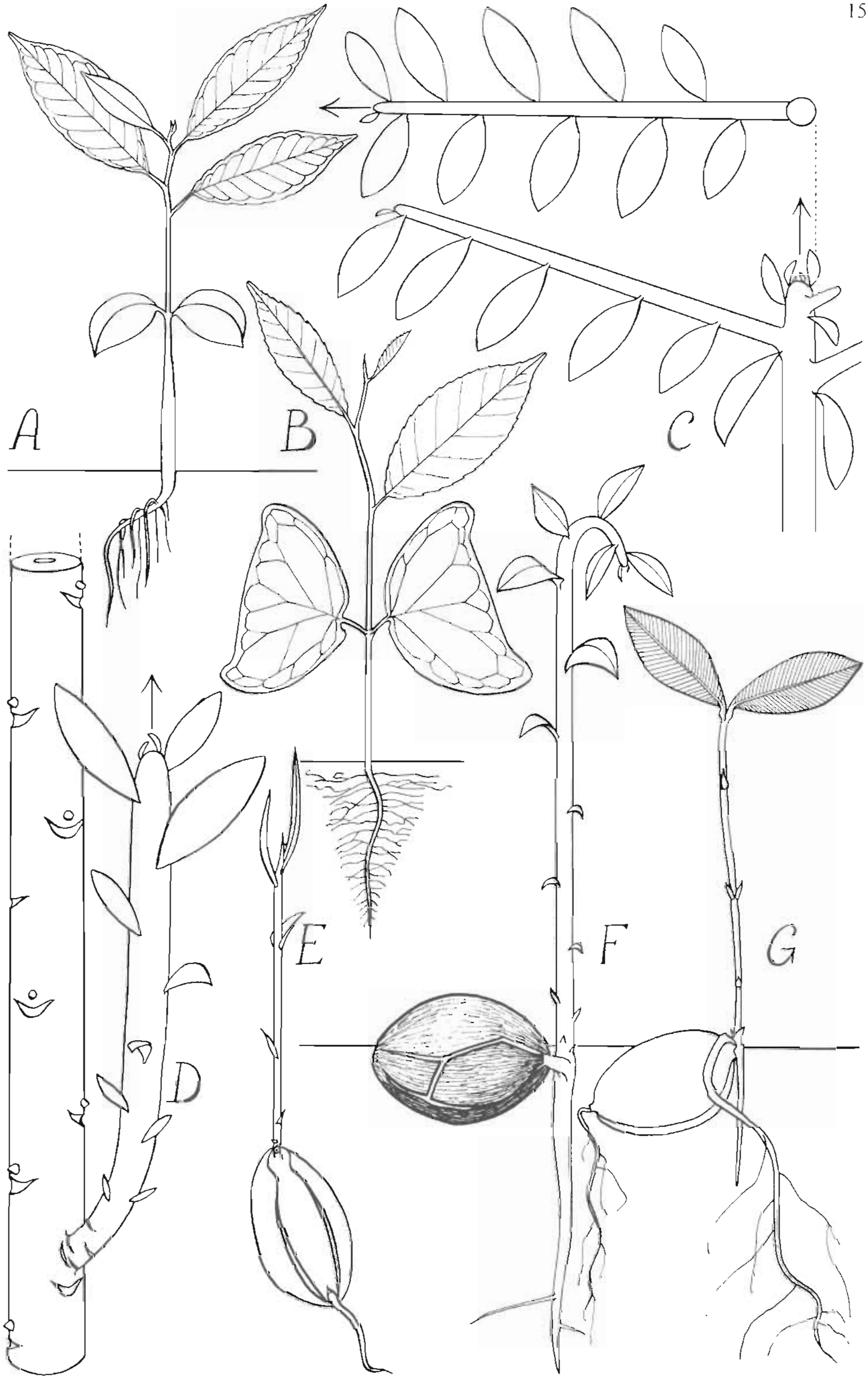
TOMLINSON, 1972). This might suggest a major biological difference, but in fact seed and embryo structure is very uniform in *Cordyline* and the two types of germination are not very contrasted. *Yucca* (also Agavaceae) provides a series of species with a similar range (ARNOTT, 1962). Amongst dicotyledons DUKE (1969) lists the following genera with different species showing contrasted germination methods: *Acer, Bauhinia, Caesalpinia, Clematis, Couratari, Lecythis, Ormosia, Passiflora, Phaseolus, Pithecellobium, Prunus, Pterocarpus, Quercus, Rhamnus, Rubia, Sapindus, Sophora, Sterculia, Terminalia, Theobroma,* and *Trichosanthes.*

A specialization of the germination process is described by JACKSON (1968) for *Butyrospermum paradoxum* (Sapotaceae) which is related to fire-adaptation (the "pyrophytic habit") in West African savannas. The plumule is buried by late extension of the cotyledonary axes, and this is described as "cryptogeal germination". A similar condition involving extension of fused cotyledonary petioles was later (JACKSON, 1974) described in several savanna species belonging to the genera *Combretum, Guiera, Quisqualis* (Combretaceae), *Gardenia* (Rubiaceae), *Lophira* (Ochnaceae), *Pterocarpus* (Leguminosae–Papilionoideae), *Piliostigma* (Leguminosae–Caesalpinioideae). It is interesting that germination of this type might otherwise be described as cryptocotylar or phanerocotylar depending on the species. The assumption is made in these studies that seed germination is always initiated at the soil surface and that the later burying is adaptive because the plumule is protected from fire.

Of significance in the subsequent organization of the tree is the nature of the axis above the cotyledons (the epicotyledonary axis). Here, a correlation between germination type and shoot organization is very evident. In hypogeal seedlings the epicotyledonary axis usually develops scale leaves, with a gradual transition to foliage leaves distally (Fig. 2E). This construction seems independent of whether the seed reserves are in the cotyledons or endosperm. On the other hand, epigeal seedlings lack scale and transitional leaves, the first leaves above the cotyledons are usually foliage leaves (Fig. 2A). This arrangement, with and without transitional leaves, parallels that found at the base of branches in relation to prolepsis (= hypogeal) and syllepsis (= epigeal), see p. 42. This close morphogenetic relationship between seed reserves and epicotyledonary shoot morphology deserves more detailed study, as it could provide clues to understanding morphogenetic processes in leaves generally.

Further examples suggest that the seed reserves supply growth hormones as well

Fig. 2A–G. Cryptocotylar and phanerocotylar ▷ germination, proleptic and sylleptic branching.
A Phanerocotylar seedling of *Anacardium excelsum* (Anacardiaceae; trop. America). (After DUKE, 1965, 1969).
B Phanerocotylar seedling of *Panda oleosa* (Pandaceae; W. Africa). (After de la MENSBRUGE, 1966).
C Sylleptic branch, seen laterally and from above; as phanerocotylar seedling, it has no reserves and depends immediately on photosynthesis. Note long basal internode (hypopodium, corresponding to the hypocotyl), and identical form of prophylls and leaves.
D Proleptic branch, seen laterally; growing after a period of latency it utilizes the reserves of the axis which bears it, like cryptocotylar seedlings use seed reserves; the basal internodes are short and bear scale leaves as in the epicotyl of cryptocotylar seeds.
E Cryptocotylar seedling of *Lecythis* sp. (Lecythidaceae; trop. America). (After DUKE, 1965, 1969).
F *Okoubaka aubrevillei* (Octoknemataceae; W. Africa), cryptocotylar seedling. (After de la MENSBRUGE, 1966).
G *Rheedia* sp. (Guttiferae: trop. America), cryptocotylar seedling. (According to DUKE, 1965, 1969)


A
B
C
D
E
F
G

as nutrients. In a number of trees the initial orthotropic phase is followed more or less abruptly by a plagiotropic phase and the switch may be controlled by the availability of seed reserves. In *Parinari excelsa* (Rosaceae) for example the length of the initial orthotropic phase (see p. 246) can be shortened by detaching the seedling from the seed before reserves are used up (HALLÉ, unpublished observation).

There has been much interest on the part of botanists in the control of germination by the fruit and seed, e.g., delayed germination by means of a thick endocarp (HILL, 1937); allelopathic responses of seeds to their own fruits (GARRARD, 1955) or the presence of inhibitors in seeds (ALEXANDER, 1966). Commonly the testa is the localized site of such an inhibitor.

A feature of woody plants which does not seem surprising in view of their subsequent habit is that the epicotyledonary axis is unbranched as in all the examples illustrated by DUKE (1965, 1969) and BURGER (1972). The subsequent organization of specialized meristems which, in all but monoaxial trees, determines the construction of the tree, comes later. In some trees with wholly modular construction the length of the epicotyledonary axis determines the length of the trunk of the tree (Leeuwenberg's model, p. 145) and the onset of branching may be much delayed.

With branching, however, the organization of the tree becomes more evident. Even so, in many trees a long period of development still may ensue before vegetative and reproductive maturity is reached. This is where the topic of juvenility can be raised.

II. Juvenility and Phases of Development

The existence of stages or "phases" in the development of individual woody plants analogous to the stages in the development of higher animals (i.e., juvenility, vegetative then reproductive maturity, and finally senility) has been recognized at least since the eighteenth century. This is largely because many trees as saplings show morphologically and physiologically distinct features which either are lost or change with age. The subject has been surveyed by SCHAFFALITZKY DE MUCKADELL (1959) – but see also BRINK (1962), MOORBY and WAREING (1963). Amongst the juvenile characters recognized, the most obvious is in leaf outline, but in addition one can list presence or absence of thorns (*Citrus*), leaf anatomy, rooting capacity (*Hevea*), branch angle, retention of monopodial growth (where sympodial growth characterizes the adult as in *Syringa*), retention of dead leaves (*Fagus*), anthocyanin content of young leaves or in fall coloring, phenological phenomena, grafting ability, growth vigor, etc. The list could be extended but most investigations relate to temperate trees. The economic significance of many of these properties has been frequently stressed, since they often relate either to rooting ability, as in *Hevea*, or to the onset of flowering which is important in many trees grown commercially for fruit.

There is an unfortunate zoomorphic bias in this kind of research which seems unnecessary when one considers the "open" method of growth of plants in contrast to the "closed" growth of higher animals. Thus juvenility should strictly refer only to those features found in the seedling and post-seedling stages of trees, although the recurrence of juvenile features in older plants is usually regarded as rejuvenescence, i.e., a return to juvenility. Is this, in fact, possible? Similarly, should one describe phase changes in plants as "ageing"? Perhaps this is a philosophical question, but it has occasioned a considerable degree of discussion (see MOLISCH, 1938). There is no a priori reason why perennial plants with their primary meristems should be involved in biochemical processes which lead to ageing and senility, as in animals. The basic problem is to decide to what extent there are age changes in plants with continuously active meristems or at least continuity of active meristems via branching of pre-existing shoots. Briefly, one may consider a one-year-old tree seedling in relation to the monopodial tall tree it eventually produces, say in 100 years. Are the apical meristems at the ends of the current-year twigs one year old or 100 years old? If 100, to what extent can they be "rejuvenated" by grafting or other means of propagation? The simplest answer is to assume that if one can restore juvenile features (morphological or biochemical) one has reversed an ageing process, but these questions have stimulated much research, as Schaffalitzky de Muckadell's review shows.

The situation in large trees has been expressed by the terminology which is made available (e.g., in BÜSGEN and MÜNCH, 1929; p. 51). MOLISCH (1922) coined the term "topophysis" for the organizational status of a meristem determined by its *position* and regardless of its age. Characteristic differences would then be those between orthotropic and plagiotropic shoots discussed elsewhere and for which VOCHTING's classic studies (1904) on *Araucaria heterophylla* have provided examples. MAGGS and ALEXANDER (1967) have described differences between regrown shoots and pruned shoots in *Eucalyptus cladocalyx* which are regarded as topophysic. Characters determined by age or progressive ontogenic processes are considered to be "cyclophysic". A good example is the successive decrease in the length of constructional units (modules) in plants like *Manihot* (Euphorbiaceae). However, a "periphysic" response is evident when the length is increased by a favorable climatic change (MÉDARD, 1973). The terms used by GOEBEL (1928–1933) to refer to the change from the juvenile to the adult stage, i.e., either a gradual one (homoblastic) or an abrupt one (heteroblastic) should be mentioned. This is most evident in changes in leaf form; species of *Acacia* provide striking examples.

The heteroblastic condition in trees of tropical islands like Madagascar, New Caledonia, Mauritius, Réunion is particularly notable (FRIEDMANN and CADET, 1976). In many species of the New Zealand flora for example, the difference of leaf shape in juvenile and adult phases is so pronounced that it is difficult to believe that a single individual is involved (COCKAYNE, 1928). Conversely, 51 species from 21 unrelated families show a very similar "divaricating", i.e., much-branched, habit as shrublets, morphological divergence coming sometimes when the adult phase is reached, usually abruptly (PHILIPSON, 1964).

In subsequent architectural descriptions, an appreciation of phase change is often relevant since it may signal the onset of the branching pattern which is characteristic of the tree. In many plants the adult phase may be considered to have begun when sexuality is first apparent, but maturity and sexuality are not necessarily synonymous. In many trees the position of flowers or inflorescences may be used by us to establish the architectural category to which a tree belongs, so that sexuality also is important in the vegetative growth dynamics of the tree. Otherwise the form of the tree is clearly established before flowering commences. The age to first flowering in Dipterocarpaceae, for example, is usually of the order of 20 to 30 years, as documented by NG (1966), by which time the tree is much-branched and well structured.

This consideration leads naturally to a discussion of the flowering process but this is deferred (p. 61) until further aspects of vegetative growth have been dealt with.

B. Apical Meristems and Buds

1. Terminal Buds

"A bud is an unextended, partly developed shoot having at its summit the apical meristem which produced it." ROMBERGER (1963) so defines a bud in the way which has been uniformly accepted and applied by morphologists who have in mind a clearly circumscribed organ. Subsequently we will on occasions prefer to use the term "meristem" for locating the primary growth centers of the shoot system. Buds, according to the above definition, are not necessarily always clearly circumscribed and are in fact most readily recognized in the dormant condition. They are particularly evident on the leafless twigs of deciduous species. On any one shoot there is a single terminal bud, usually together with one or more lateral buds which are the possible future terminal buds of higher branch orders. Here both terminal and lateral buds are delimited by specialized leaves (bud-scales) but additional protective structures or materials can be developed like hairs, latex, resins, varnish etc. Buds so delimited are common in evergreen, tropical species, e.g., many Meliaceae (*Swietenia*), some Lecythidaceae (*Bertholletia*) and their presence is always correlated with rhythmic growth. RESVOLL (1925) has commented on their existence in tropical evergreen *Quercus* species.

In many evergrowing shoots of tropical trees the same circumscription does not exist. Most woody monocotyledons like palms, pandans and larger Agavaceae, for example, have a massive crown consisting of the terminal cluster of evident foliage leaves enclosing a long series of leaf primordia in successive stages of development. No morphologically circumscribed "bud" set apart from the rest of the shoot is present. Dicotyledons with similar leafy crowns include *Carica* (Caricaceae), some Epacridaceae (*Dracophyllum*) and the rosette trees of tropical mountains in the genera *Espeletia*, *Senecio* (Compositae) and *Lobelia* (Lobeliaceae).

In trees which lack rhythmic or episodic growth, as defined on p. 25, a morphologically distinct terminal bud may be recognized when additional enveloping organs other than leaves are associated with developing primordia. These organs are most commonly stipules or otherwise modified leaf bases. Clearly such structures are protective, since any rigid struc-

Fig. 3A–E. Apical growth in a plagiotropic ▷ branch of *Tachia guianensis* (Gentianaceae, French Guiana); and *Viburnum* sp. (Caprifoliaceae, labeled *V. rhytidophyllum*, Central China, in the Botanic Garden of Montpellier), orthotropic axis.

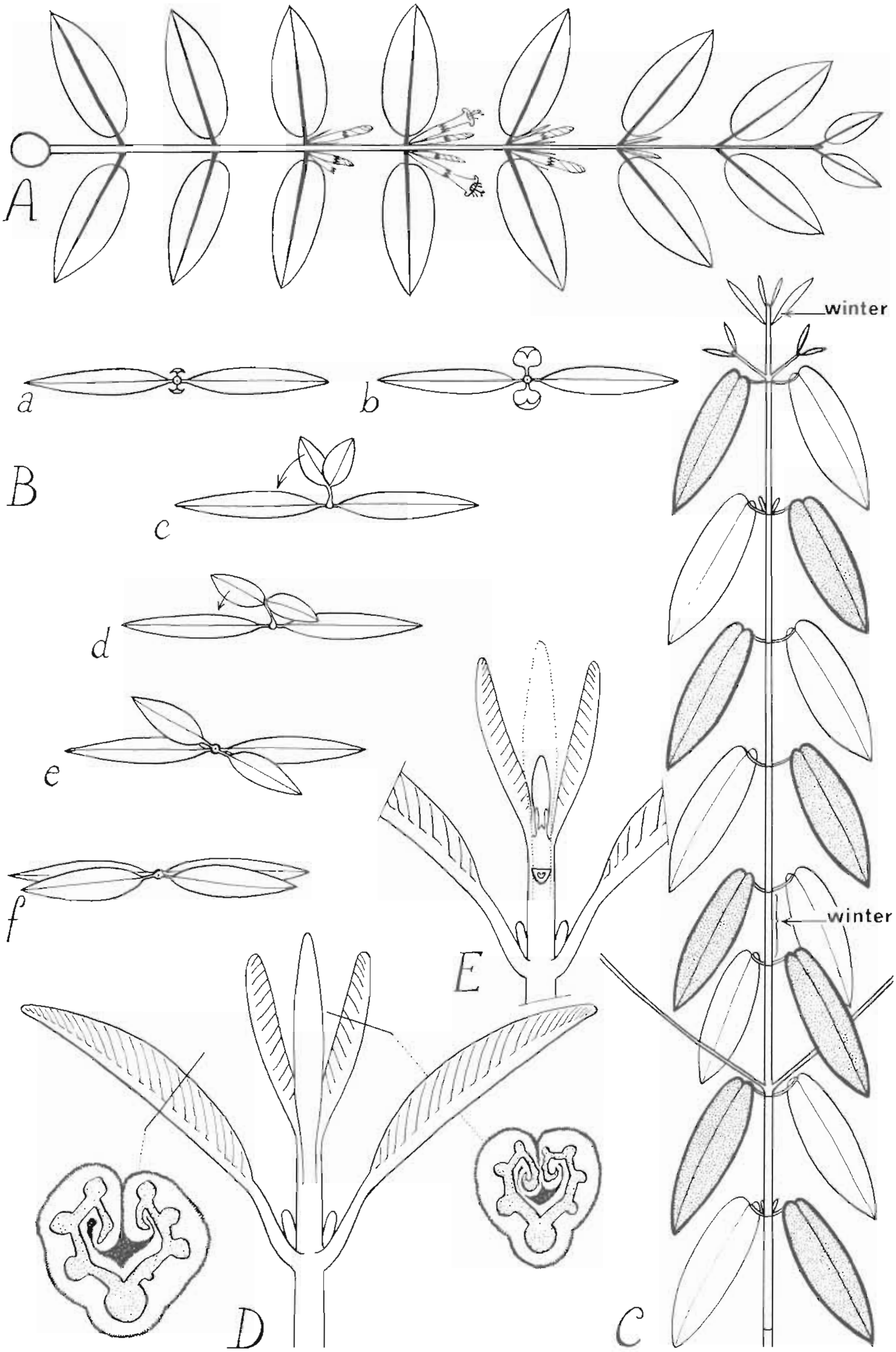
A Plagiotropic branch of *Tachia*, with secondary distichy, seen from above.

B The decussate leaves are brought into a horizontal plane by internode torsions, a process which is shown here in six stages (*a* to *f*), accompanied by leaf expansion.

C Orthotropic axis of *Viburnum* at the end of the winter. Internode length and poor vigor of the first expanded leaves after the winter discreetly suggest rhythmic growth; branching is clearly rhythmic. The leaves overwinter as arrested organs until circumstances again favor growth.

D Apex of the same axis at the same time; there is no differentiation of scale leaves; note spectacular indumentum on sections of leaves, which are longitudinally folded.

E Same apex, dissected. Several preformed leaf primordia are "protected" by the incompletely expanded leaves, but there is no differentiated bud structure. Hence the inappropriate name "naked bud" for apices so organized


A
winter
a
b
B
c
d
e
f
E
winter
D
C

ture which envelopes a delicate meristem and its associated primordia guards against excessive insolation, desiccation and the depredation of insects and other animal predators. For tropical trees the subject has been discussed briefly by POTTER (1891). He showed, for example, that the removal of enveloping stipules in *Artocarpus* (Moraceae) produce marked aberration in the later development of enveloped organs. Most stipules cover only organs younger than themselves, but STEIN (1975) describes stipule pairs in *Hymenaea* (Leguminosae) which cover their associated leaf, a condition considered by him to be unusual.

It is usual to contrast covered resting buds in temperate trees with so-called "naked buds", familiar in species of *Viburnum* (Caprifoliaceae) in which the overwintering terminal bud includes an outermost pair of visible, unexpanded leaf primordia (Fig. 3D). These expand and complete their development as the first foliage leaves of the renewal growth in spring. However, these primordia in the resting state have a dense indumentum and are not naked in a strict sense (Fig. 3E). Many buds without specialized enveloping organs which undergo a period of rest are similar, and although no extensive surveys have been made it seems clear that "naked" and "covered" buds are not necessarily sharply contrasted.

Several large families lack stipules almost entirely, e.g., Annonaceae, Apocynaceae, Asclepiadaceae, Bignoniaceae, Lauraceae, Melastomaceae, Meliaceae, Myrtaceae. Other families in contrast are characterized by diagnostic stipular patterns, with an obvious protective arrangement, like Magnoliaceae, Malvaceae, Moraceae, Rubiaceae, Sterculiaceae. The Leguminosae are characteristically stipulate, the stipules sometimes taking on a bizarre pattern, like the pinnately compound stipules of *Delonix*, or the leaflike stipules of *Sclerobium*, shown in Figure 4. In yet other families lateral stipules are inconspicuous and do not seem to have a marked mechanical function (e.g., Aquifoliaceae, Celastraceae, many Euphorbiaceae, Rhamnaceae, Ulmaceae). Such tiny organs may be involved in the close-packing requirements of the terminal bud and may be localized sources of protective mucilages or resins. However, they usually develop early, are highly tanniniferous and are caducous so they may render buds unpalatable to chewing insects, since tannins have been shown to have this function in oaks (FEENY, 1970).

In a number of tropical genera large and even massive stipules circumscribe sharply a part of the shoot as a bud, but the stipule abscises cleanly when an enveloped leaf enlarges: one or more conspicuous stipular scars are then left. The stipules of *Cecropia* and *Musanga* species (Moraceae) exceed 30 cms in length and are conspicuous fallen objects on the forest floor.

The tendency is for a closed cavity to be formed by the stipule or stipules, and the biology of the cavity is interesting. In trees with alternate leaves the stipule may be represented by a single, tubular structure, as in *Magnolia* and many Moraceae. In trees with opposite leaves there may be two structures tightly overwrapping to form a tube, notable in the Rhizophoraceae. The Rubiaceae perhaps provide the greatest diversity but still based on the central theme of a pair of interpetiolar stipules. These form a cap to the shoot which is pushed aside as the younger organs expand. Stipules may persist as nodal scales, abscise cleanly to leave a scar or degenerate into constituent vascular strands. In some Rubiaceae (e.g., *Hillia, Nauclea*) interpetiolar stipules are quite large and green and with a presumed considerable photosynthetic capacity.

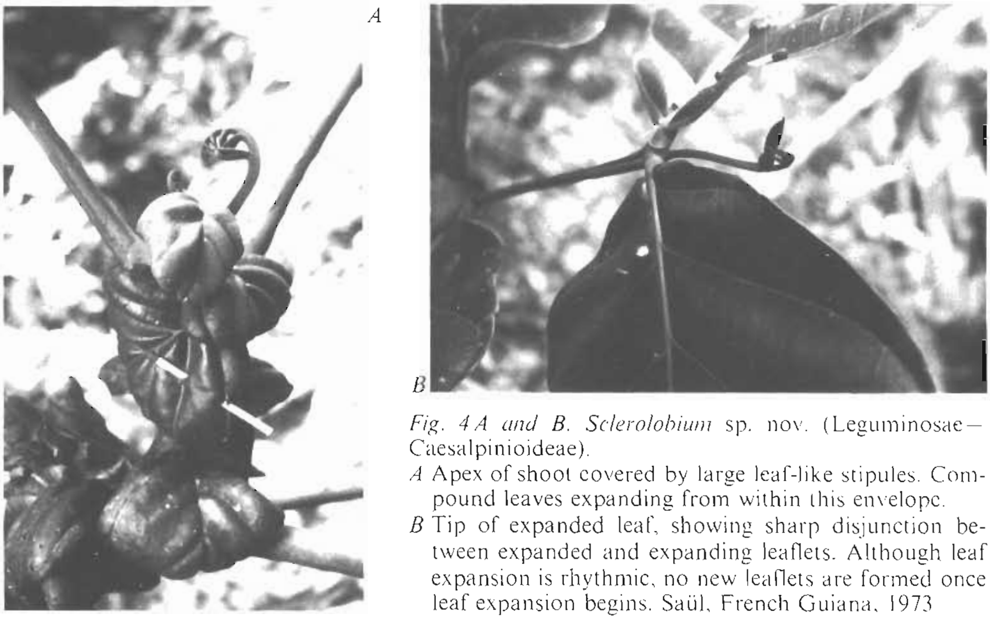


Fig. 4A and B. Sclerolobium sp. nov. (Leguminosae—Caesalpinioideae).

A Apex of shoot covered by large leaf-like stipules. Compound leaves expanding from within this envelope.

B Tip of expanded leaf, showing sharp disjunction between expanded and expanding leaflets. Although leaf expansion is rhythmic, no new leaflets are formed once leaf expansion begins. Saül, French Guiana, 1973

Paired, clasping, somewhat fleshy leaf bases characterize many Malpighiaceae and especially Guttiferae (e.g., *Clusia, Garcinia, Mammea*). Solitary adaxial stipules or grooved leaf bases are equally common; they occur on the massive shoots of many Araliaceae but are equally characteristic of the slender shoots of *Erythroxylon* (Erythroxylaceae). In a few Loganiaceae and especially in Dilleniaceae the petiole base is often winged and initially protects the terminal bud; subsequently it protects the axillant lateral bud. The student in the tropics soon learns to recognize woody members of the Polygonaceae like *Coccoloba* and *Triplaris* by their tubular ochreate leaf bases, but often fails to appreciate how this structure initially forms a cap to the terminal "bud". The organography of protective bud structures is diverse and tropical botanists have long used this diversity as a source of useful field characters in the identification of vegetative material.

A frequent biological phenomenon associated with enveloping structures of diverse morphological origin is the presence of secretory glands, often termed "colleters" (Lersten, 1974; Lersten and Curtis, 1974) which produce a mucilage or watery fluid bathing unexpanded organs. They can be found in the inner side of stipules (Rhizophoraceae, Rubiaceae), of clasping leaf bases (Guttiferae) and ochrea (Polygonaceae). Future research is needed to establish whether these merely lubricate primordia so that they do not dry out, or selectively encourage certain microorganisms. A peculiar biological situation is known in certain Rubiaceae (species of *Neorosea, Pavetta,* and *Psychotria*) in which this fluid may positively encourage the development of nitrogen-fixing bacteria which inhabit leaf nodules in a possibly symbiotic way (Horner and Lersten, 1968). Bacterial transfer from one leaf pair to the next is promoted by the stipular cavity. Van Hove (1972) in his study of *Neorosea an-*

dongensis (Hiern.) N. Hallé suggests that the bacteria are nurtured by secretions from the multicellular hairs which line the inside of the stipules. Bacteria do occur in other Rubiaceae which do not form leaf nodules [e.g., *Schumanniophyton problematicum* (A. Chev.) Aubr.]. Whether plants with leaf nodules can develop normally in the absence of bacteria has not been critically examined, possibly because of the difficulty of growing plants in axenic culture.

If such plants may be described as having "wet" buds, then "dry" buds are equally common in the tropics. Such may be exemplified by resting buds covered with a varnish-like substance. In many Apocynaceae (e.g., *Alstonia*, *Plumeria*) this may be akin to latex, but it is more resinous in some Rutaceae (e.g., *Amyris*) and Euphorbiaceae (*Drypetes*). This varnish cracks and flakes as the shoot later expands. Varnish-like secretions may accompany larger protective organs as in Combretaceae (bud-scales), Rubiaceae (stipules), *Ceriops* (Rhizophoraceae–stipules).

II. Bud Composition

The kind and number of primordia (leaf, branch, stipule) or "components" of terminal buds varies considerably, depending on the degree of "preformation", a topic which is discussed in some detail elsewhere. Some buds have few components, e.g., in *Rhizophora* (and related genera) terminal buds consistently have only three pairs of leaf primordia with associated stipules; branch and inflorescence primordia are sometimes also present (Gill and Tomlinson, 1971b). Low numbers of bud components probably characterize many evergrowing tropical trees. In contrast, Cremer (1972) found in *Eucalyptus regnans* that the terminal buds were represented by a highly complex, condensed shoot system, with as many as four orders of branches representing 27 embryonic shoots and as many as a total of 50 pairs of leaf primordia. It is interesting that *Eucalyptus* would be described as having "naked" buds in a morphological sense.

Bud morphology in general is most usefully discussed in a dynamic context, since terminal buds represent incipient but condensed shoot systems whose further development is conditioned by organized correlation within the whole tree. A further discussion of this topic occurs later when shoot extension is described with case histories at hand.

III. Lateral Buds

Axillary buds which undergo a period of rest usually develop protective devices similar to terminal buds. In most dicotyledons and even those which do not develop terminal buds scales, there is at least one pair of modified leaves or prophylls enveloping the meristem. Additional scales may occur, but only become visible when a long-dormant lateral bud finally expands (see prolepsis, p. 44). Long-persistent lateral buds, which become enveloped within the bark as secondary growth proceeds, are the potential sites of future epicormic shoots, or in cauliflorous trees, of inflorescences. Our subsequent discussion of architecture proceeds largely independently of any consideration of these "reserve buds", but they assume importance when the process of reiteration is described in a later section. The anatomy of resting meristems has been described by a few authors, but is not considered further here (cf. pp. 35 40 in Zimmermann and Brown, 1971).

Multiple lateral buds are common in woody plants, especially in the tropics, but the morphogenetic implication of this has been little considered by developmental morphologists. We may speak of a *primary bud complex* where several meristems are initiated separately within a single leaf axis. In dicotyledons the buds most commonly form a vertical series, as the serial bud complex common in many families (e.g., Bignoniaceae, Leguminosae, Oleaceae, Rubiaceae, Simaroubaceae). Serial buds may develop in either an acropetal (e.g., *Coffea*) or a basipetal (e.g., *Simarouba*) direction. Less commonly a transverse bud complex develops with two or more buds side by side in a horizontal plane as in some Icacinaceae. Geometrically less regular arrangements occur, e.g., in some Annonaceae. Where bud complexes occur in monocotyledons they are most usually transverse (e.g., Araceae). Some palms are notable for the development of several inflorescences at one node (e.g., *Arenga* spp., *Howeia*, *Morenia*).

Of especial architectural and morphogenetic interest are situations in which individual members of the bud complex at a single node have differential developmental potential. In *Coffea*, for example, the distal bud of each leaf pair on orthotropic shoots usually grows out as a precocious (sylleptic) branch, the additional (supernumerary or accessory) buds persist as reserve buds (VAROSSIEAU, 1940; MOENS, 1963). In *Rhizophora*, branching is diffuse and if it occurs, a node may bear either a (sylleptic) vegetative branch or an inflorescence. In the former circumstance a supernumerary dormant bud is above the developed branch, in the latter it is below. More specialized branch differentiation may occur at a single node when dormant buds occupy the same leaf axil as spines (e.g., *Citrus*) or flowering branches (e.g., *Bougainvillea*).

Diversity of complex nodal patterns needs to be studied in an architectural context since the distribution and kinds of lateral meristems can vary widely on different parts of one plant. This is obvious in the vegetative to reproductive phase change in plants (p. 61) or in shoot systems where there is marked polymorphism (p. 48). Seasonal changes along a single shoot may occur, as in *Fraxinus*, where the lower axils of each unit of growth bear single axillary meristems, whereas the upper ones subtend serial buds (GILL, 1971a).

Correlative processes govern the differential behavior of meristems, which in turn amplify the architecture of a tree. Organizational aspects of the development and function of lateral meristems become more evident when architectural models are described.

IV. Secondary Bud Complexes

A plurality of functional meristems at a single node may result from branching of an original solitary primary lateral meristem. One may then speak of a secondary bud complex which is essentially a condensed shoot system (cf. the discussion of short shoots, p. 59). The distinction between primary and secondary bud complexes is not always clear, since microscopic examination of developmental stages may be needed to resolve the precise morphological relationship between different meristems. In *Gossypium*, for example, the method of initiation of its paired buds was disputed until it was established that each leaf produced a secondary bud complex (ATTIMS, 1969; MAUNEY and BALL, 1959). *Acacia* species (Leguminosae – Mimosoideae), some Olacaceae (e.g., *Schoepfia*, *Ximenia*), some Myrsinaceae (e.g., *Rapanea*) provide examples. Commonly the secondary bud complex is long-lived and provides a site for continued flower-production. There may then be a transition to cauliflory.

Secondary bud complexes are striking in some bamboos and morphological study shows that the cluster of branches at a single node represents several successive branch orders. The biological advantage in such trees, with massive culms but slender lateral branches, is obvious here, since it leads to an enlarged photosynthetic area in a tree entirely primary in its construction.

The use of the term "bud complex" should not be confused with the expression "branch complex" introduced later. This relates to the expanded shoot system in which primary meristems interact in subtle ways, as in a plagiotropic branch complex.

C. Extension Growth in Tropical Trees

I. Introductory Remarks

Detailed studies on the periodicity of extension of shoots and renewal of leaves in dicotyledonous trees are surprisingly few. Only recently have specific studies which relate leaf initiation to shoot expansion been carried out, for example by CRITCHFIELD (1960) on *Populus*, CRITCHFIELD (1971) on *Acer*, GILL (1971a) on *Fraxinus*. Pioneer work in the tropics has been generalized and most of the accumulated data is basically phenological in its approach (e.g., COSTER, 1923, in the monsoon region of Java; HOLTTUM, 1953, in Singapore, and MEDWAY, 1972, in Malaya). The studies of KORIBA (1958) are equally generalized and essentially comparative in their approach. This work refers to periods during which species are visibly "flushing", i.e., exhibiting a crop of new leaves, usually associated with shoot extension. A framework within which more intensive studies may be carried out has been provided. Patterns of loss and renewal of leaves are diverse. Of interest are frequent records of nonsynchronous phenologies within a single tree, such that different parts of the crown have contrasted cycles. We offer a partial explanation of this in terms of reiteration later (p. 269).

More recent specific studies which have investigated the dynamics of shoot initiation and expansion in tropical trees include those by BOND (1942, 1945) on tea, *Camellia*; HALLÉ and MARTIN (1968) on rubber, *Hevea*; PUROHIT and NANDA (1968) on *Callistemon*; GREATHOUSE and LAETSCH (1969, 1973) and GREATHOUSE et al. (1971) on cocoa, *Theobroma*; BORCHERT (1969) on *Oreopanax*; HOLDSWORTH (1963), TAYLOR (1970, 1975), SCARRONE (1965) on mango, *Mangifera*; GILL and TOMLINSON (1971b) on *Rhizophora*. Of these the account of HALLÉ and MARTIN (1968) is particularly detailed and we will use it as a point of reference. In view of the limited amount of information, generalizations are difficult to make and our discussion largely considers case histories. Initially we also make little distinction between different kinds of axes and consider mainly orthotropic shoots, although for many trees this is an oversimplification (as in cocoa where there is marked differentiation of branches).

General observations allow us to distinguish two main patterns of growth:

1. Rhythmic growth, as defined by HALLÉ and MARTIN (1968) in which shoots have a marked endogenous periodicity of extension (Fig. 5A). This term may be regarded as synonymous with *episodic growth*, defined by ROMBERGER (1963), which mainly referred to temperate trees, or with *intermittent growth*, which is frequently used (e.g., KORIBA, 1958). The term "rhythmic" may imply a regular cycle though this is not intended.

2. *Continuous growth,* in which shoots have no marked endogenous periodicity of extension (Fig. 5B). This corresponds to the generally accepted usage of the term by H.O. (1970), and may be equated with Koriba's term "evergrowing".

These two contrasted types may be considered separately.

II. Rhythmic Growth

After a period of dormancy, the "flushing" of tropical trees, or bud burst in temperate trees, most strikingly demonstrates rhythmic growth. Rapid unfolding and expansion of leaves is then in contrast either to existing foliage or, in deciduous trees, to the previously leafless condition. In tropical trees the new flush may involve a veritable "pouring out" of the young leaves, the whole shoot system initially hanging limp, as in *Amherstia nobilis* and *Saraca taipingensis* among commonly cultivated trees. Sometimes flushing of leaves is so pronounced that from a distance the tree appears to be covered with blossom. Even where the new flush expands fairly slowly, color contrasts are often striking since the new leaves may be white (*Amherstia*), yellowish (*Elaeocarpus, Vochysia*), commonly reddish (e.g., *Mangifera, Cinnamomum, Eperua*), or pinkish to pale green (*Swietenia*). In the forest canopy in some parts of the tropics, flushing may produce seasonal color shifts clearly observable from an aeroplane, and readily confused with conspicuous flowering. Flushing largely indicates rapid expansion of preformed leaves. In many trees with essentially rhythmic growth expansion is less rapid and less obvious, so that the term may have limited application.

The morphological indication of rhythmic growth in the mature shoot system is a more or less pronounced segmentation of the axes, referred to by TOMLINSON and GILL (1973) as "articulate growth". In trees which develop bud scales successive increments are delimited by bud-scale scars, but otherwise there may be a series of short internodes or small leaves. For many trees with rhythmic growth the most conspicuous feature is the development of groups or tiers of branches and it is convenient to refer to the periodic production of branches in relation to rhythmic growth as *rhythmic branching* (Fig. 6).

Rhythmic growth and branching is of course clearly expressed in temperate trees, where episodic events are synchronous with seasons (Fig. 3C). We will begin our discussion with an example of rhythmic growth in a nonseasonal environment.

1. Rhythmic Growth in Hevea

Hevea brasiliensis Muell.-Arg. (Euphorbiaceae) is a large tree native to the forests of Amazonia but known widely in cultivation throughout the humid tropics as a source of latex for commercial rubber. Trees are normally grown from high-yielding clones, grafted onto vigorous rootstocks. The adult tree can reach a considerable size and specimens 50 m high with a basal trunk circumference of 9 m have been measured.

Rhythmic growth in rubber has been studied in seedling stocks by HALLÉ and MARTIN (1968). Epicotyledonary axes remain unbranched for upwards of a year, but show successive increments distinguished morphologically by the series of scale leaves, represented later by their scars. Rhythmic growth is endogenously controlled although its rate may be influenced exogenously, i.e., it may be speeded up by high light intensities, slowed or even temporarily halted by

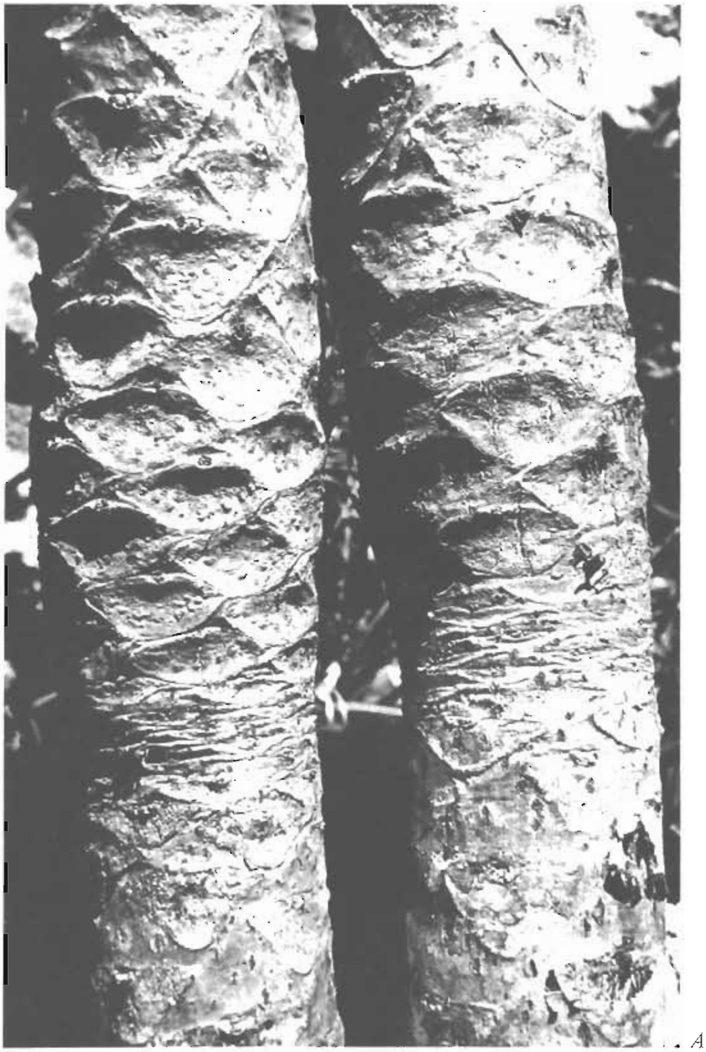


Fig. 5A and B. Morphological distinction between rhythmic and continuous growth.
- *A* Endogenous rhythmic growth, articulated trunks of *Cussonia bancoensis* Aubr. and Pellegr. (Araliaceae, Leeuwenberg's model), Adiopodoumé, Ivory Coast, with scale scars marking level of rest of terminal bud.
- *B* Continuous growth, trunk with uniform leaf scars of *Cyathea* cf. *cooperi* (Cyatheaceae, Corner's model), Sydney Botanic Garden

drought. The morphologically distinct growth increments may be referred to as "units of extension" (UE). Each consists of a basal series of scale leaves, separated by increasingly long internodes, followed by a series of trifoliate foliage leaves (Fig. 7C). There is an *abrupt* transition from scale to foliage leaves, which we can account for later, and the distal series of foliage leaves on the unit shows a progressive reduction in petiole length. An apical bud with enveloping bud-scales terminates the current increment. Such an axis therefore consists of a series of foliage leaf clusters, separated by leafless lengths of the axis, each cluster representing one "flush" of growth. Leaves persist about a year before they abscise.

Rhythmic growth in saplings produces on average six units of extension per year. Branching begins after about nine flushes, from the axils of the average-sized leaves of each cluster of foliage leaves (Fig. 7D), so that the branches are distinctly tiered.

Branches repeat the pattern of growth of the seedling shoot, with a certain dorsiventrality imposed by a pronounced tendency for branches of higher orders to be restricted to the lower side of the lateral shoot system. In young trees growth is synchronous in all active meristems, but this is lost with age, and flushes eventually become not only nonsynchronous but less frequent than on saplings. However, all axes retain the same morphology and constructional units. Flower spikes appear on older trees, in the axils of scale leaves towards the base of each unit of extension, on high-level branches (Fig. 7B).

Hallé and Martin's study of frequency of mitoses in the shoot apex of epicotyledonary axes shows that mitotic activity does not coincide with shoot extension and that there is, in fact, a distinct "unit of morphogenesis" (UM) whose chronological limits are determined by activity of the apical meristem

Fig. 6A and B. Examples of rhythmic branching in Massart's model.

A *Virola surinamensis* (Rol.) Warb. (Myristicaceae), Bélèm, Para, Brazil, the scars on the trunk left by a twining liane.

B *Coelocaryon* sp. (Myristicaceae), Gabon, West Africa, with spirally arranged leaves on the trunk, distichously arranged leaves on the markedly plagiotropic branches. (Photograph by N. HALLÉ) ▷

B

and are different from the limits of each unit of extension (Fig. 7B). This is shown diagrammatically in Figure 7A. The period of mitotic activity in the apical meristem occupies about 40 days, of which there are 30 days with frequent cell division and 10 days with virtually no divisions.

The onset of mitotic activity which signals the beginning of a UM coincides with the time of expansion of the first foliage leaves in the middle of the previous UE. The apical meristem initiates a series of scale-leaf primordia. These become the outermost scale leaves of the terminal bud which appears as the extension of the shoot ceases. This bud marks the completion of the previous UE. Even though the shoot system is latent because the terminal bud has been formed, this phase is in fact the time of most vigorous activity of the apical meristem, since the primordia of the foliage leaves of the next UE are now formed. With the completion of their initiation, mitotic activity ceases, the UM is completed and the terminal bud truly "rests". Bud burst and extension growth which mark the new flush begin before there is any marked renewal of mitotic activity in the apical meristem. The abrupt transition in leaf morphology between scales and foliage leaves marks the boundary between two successive UMs. One should note the independence between mitotic activity of the apical meristem and shoot extension: the time of maximum shoot extension coincides with a time of decreasing mitotic activity, which ceases completely before shoot extension is finished. Mitotic activity recommences before there is any morphological change in the bud.

One can briefly summarize the relation between initiation and expansion of appendages by saying that each cycle of initiation begins with foliage leaves and ends with scale leaves, but each cycle of extension begins with expansion of long internodes associated with scale leaves and finishes with short internodes associated with foliage leaves.

This analysis is significant in showing that a terminal nonextending bud is not necessarily in an inactive state, a condition we will find is quite common.

Less complete analyses of older shoots which develop branches have been made, but it seems significant that branches are proleptic and develop in the middle of a unit of morphogenesis, at a time when mitotic activity of the parent apex is high.

Some correlation between shoot extension and cambial activity is suggested by the observation that distinct growth rings are developed in the secondary xylem, each increment corresponding to one of the units of extension (Fig. 7B). On the other hand, there is no relation between

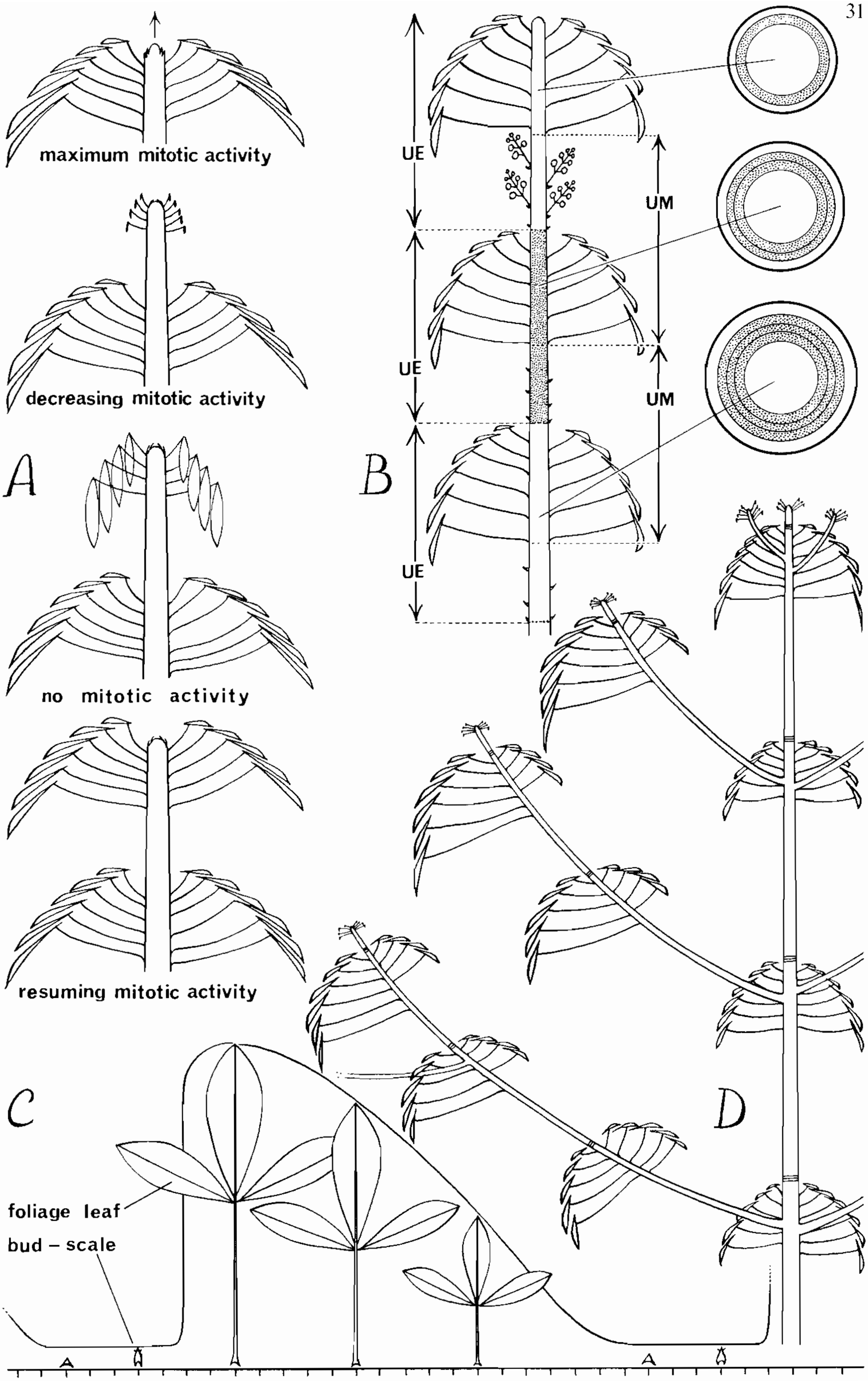
Fig. 7A-D. Rhythmic growth in *Hevea brasiliensis* – Euphorbiaceae. Amazonia. (After Hallé and Martin, 1968). ▷

A Diagram showing changes in shoot morphology during a single flushing cycle. *From top*: bud expansion, extension and early expansion of foliage leaves, later expansion of foliage leaves and continuing extension, and extension complete, bud passes into latent phase with final position of leaf blades. Note mitotic activity.

B Detail of apical units to show distinction between unit of morphogenesis (*UM*) whose limits are determined by a single period of activity of the apical meristem, and unit of extension (*UE*) which is the morphologically distinctive unit. Flowering branches in axils of scale leaves. Correlation between apical and cambial activity (on the right).

C Diagram to show sequence of leaves produced on a single unit of extension, beginning with protective bud-scales and passing via somewhat larger scales to foliage leaves.

D Rhythmic branching associated with rhythmic extension growth: branches of morphological equivalence to the trunk are borne in the axils of foliage leaves only


maximum mitotic activity
decreasing mitotic activity
A
no mitotic activity
resuming mitotic activity
B
UE
UM
UE
UM
UE
C
foliage leaf
bud – scale
D

shoot and root growth; this HALLÉ and MARTIN demonstrated by growing plants in such a way that the roots ran along an inclined surface which could be inspected readily. Root growth was always continuous, regardless of rhythmic growth of the shoot.

Endogenous rhythms seem to be an inherent feature of the shoot system of rubber because they are expressed quite regularly in uniform climatic conditions. Some attempt has been made to correlate the endogenous rhythmic activity of shoots of rubber with fluctuations in water stress. BORCHERT (1978) suggests that this is theoretically possible in a uniform environment, on the basis of a simulation study using computer techniques. HALLÉ and MARTIN's own experiments suggest that external water stress can influence rhythmic growth. They showed that in saplings, if about 65% of the surface of every leaf is removed, rhythm is suppressed and growth becomes continuous, producing a "lamp-brush" state which is sometimes also observed naturally.

2. *Preformation and Neoformation*

Rhythmic growth essentially of the kind exhibited by *Hevea* is common in temperate trees, but with a strong seasonal correlation. In most trees one flush of growth per year is developed, the actual period of overall shoot expansion varies but is relatively short; a matter of weeks (e.g., KOZLOWSKI and WARD, 1961). Some fluctuation in rate of growth may occur, in some conifers there is a late season burst.

Rubber also demonstrates a strong degree of *preformation*, i.e., the formation of a large part of a shoot in the primordial state with a period of rest prior to expansion. In rubber it is the unit of morphogenesis which is preformed in this way. Consequently there is a fluctuation in the number of primordia in the terminal bud. The opposite condition, *neoformation* involves the continued extension of primordia immediately after they are initiated, without any intervening period of rest. Consequently there is no build-up of numbers of appendages and bud composition does not fluctuate. This is the condition found in evergrowing shoots discussed later. Trees with rhythmic growth show varying degrees of preformation and neoformation. The terms are, of course, relative, since there is always a lag between initiation and expansion of the parts in any shoot.

Temperate gymnosperms, which have been much studied, provide particularly complex examples of preformation since each unit of extension may be formed within the terminal bud as much as two seasons in advance of the time it completes its expansion, as in *Pinus* species (e.g., SACHER, 1954). Primordia of lateral shoots and cones are also initiated very early. In other conifers the shoot is preformed almost a year in advance of its final expansion, e.g., Douglas-fir (*Pseudotsuga menziesii*, ALLEN and OWENS, 1972). Of particular interest are deciduous species. CLAUSEN and KOZLOWSKI (1970) showed that in *Larix laricina* in northern Wisconsin about half the basal needles are preformed, the remainder neoformed, but without needle dimorphism.

3. *Further Examples of Rhythmic Growth*

Amongst deciduous trees of the north temperate zone two contrasted types of shoot growth have been recognized. In the simplest, exemplified by *Fraxinus americana* (GILL, 1971a), the whole shoot of one season is preformed, i.e., initiated entirely in the previous year, and its primordia overwinter in the terminal bud (Fig. 8A). During the expansion of the

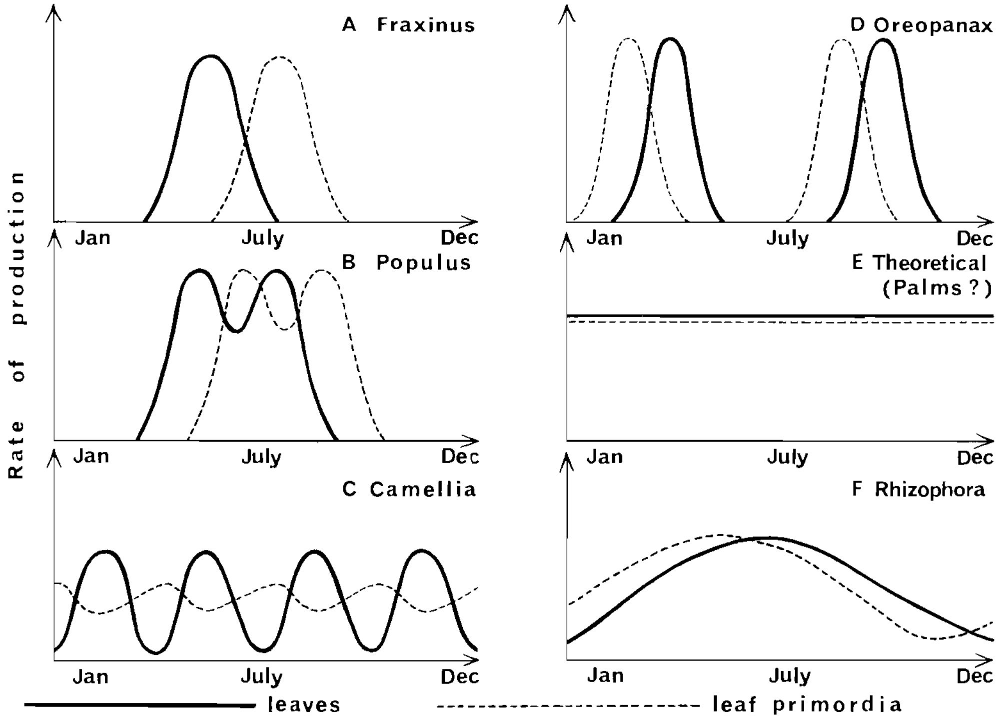


Fig. 8A–F. Relationship of leaf initiation and leaf expansion in various trees. (After Tomlinson and Gill, 1973; *E* here added). Data from the relevant papers cited, although the diagrams are not found in the original publications. To some extent these diagrams hence involve interpretation of the data. In each diagram the abscissa represents some measure of rate of leaf production, the ordinate one calendar year. *Continuous lines:* leaf expansion; *interrupted lines:* leaf initiation.

A *Fraxinus americana* (Gill, 1971a), USA. Leaves, initiated at the end of one growing season, do not expand until the next year. The number of leaves initiated equals the number expanding in the next season (determinate shoot).

B *Populus trichocarpa*, "long" shoot (Critchfield, 1960), USA. As in the previous example, but some leaves expand in the year of their initiation as a double flush of summer growth. Leaf number in the resting bud hence does not determine the number of expanding leaves in summer (indeterminate shoot).

C *Camellia sinensis* (Bond, 1942, 1945), Sri Lanka. Continuous leaf initiation, but not at a uniform rate, associated with (usually) four flushes of leaf expansion per year.

D *Oreopanax* sp. (Borchert, 1969), Colombia. Most foliage leaves initiated shortly before they expand, approximately two flushes yearly. Hence the resting bud contains a minimum of leaf primordia, not a maximum as in *A*.

E Theoretical curve for palms with continuous initiation and expansion, and constant numbers of initiated and expanded foliage leaves.

F *Rhizophora mangle* (Gill, 1971b), Florida, USA. Continuous leaf initiation and expansion with a seasonal change in rates correlated with climatic fluctuation. In nonseasonal climates possibly this species shows no change in rates of initiation and expansion (see *E*) shoot the only leaves which mature are those formed in the previous year. Late season activity of the terminal meristem continues after shoot extension has ceased and involves the formation of the following year's leaves. The term "determinate" has been used to describe this method of growth. Ecologically this fixity of leaf number in different parts of the shoot system is advantageous in that the amount of mutual shading is predictable,—of benefit in a tree with "multilayered" foliage (HORN, 1971).

In other temperate trees the shoot is not wholly preformed and shoots with appreciable heterophylly may develop (KOZLOWSKI and CLAUSEN, 1966). *Populus trichocarpa* described by CRITCHFIELD (1960) is a well-studied example. With reference to one kind of shoot (heterophyllous) each annual increment is produced in two distinct phases; the earliest is the result of expansion of preformed leaves ("early leaves") which had been initiated at the end of the previous summer and overwintered in the terminal bud; "late leaves" are produced by the apical meristem during the phase of summer extension of its parent shoot and they expand immediately, i.e., are neoformed (Fig. 8B). There is usually a distinct period during summer extension growth when shoot elongation ceases temporarily, corresponding to this change in leaf type. The morphological expression of this two-phase periodicity is an appreciable leaf dimorphism, with a distinction between early and late leaves. This periodicity refers to the long shoots; in short shoots leaves are entirely preformed (homophyllous). Sucker sprouts or their equivalent show only late leaves. An adaptive advantage of this mechanism is that there is no limit to the number of leaves formed in any one year by the amount of preformation, the system is very flexible.

At leaf fall abscission then involves leaves of two distinct ages: early leaves are more than a year old, late leaves are less than three months old. Species of *Acer* (e.g., *A. rubrum, A. pensylvanicum*) have a similar periodicity of leaf expansion on long shoots (CRITCHFIELD, 1971).

A summary of taxa with contrasted types of leaf developments, as provided by CRITCHFIELD (1960, 1971) is given in Table 6.

Table 6. Types of leaf development

Leaves wholly preformed	Leaves partly neoformed	
Acer, e.g., *A. platanoides*	*Acer*, e.g., *A. rubrum*, *A. pensylvanicum*	*Ligustrum* *Liriodendron* *Morus* *Paulownia*
Aesculus	*Betula*	*Populus*
Carya	*Castanea*	*Prunus*
Fagus	*Cercidiphyllum*	*Salix*
Fraxinus	*Ginkgo*	*Sambucus*
	Ilex	*Vitis*

Rhythmic growth with a different periodicity is shown by tea (*Camellia sinensis* = *C. thea*, Theaceae), studied in detail by BOND (1942, 1945). This information is of obvious economic importance since the young flush is the source of tea leaves. Extension growth proceeds by periodic "flushes" of up to four per year with intervening periods of dormancy ("banji"). The units of extension are marked by a fluctuation in the size and distribution of leaves; each includes seven leaves, i.e., two scale leaves, a transitional leaf, and four foliage leaves. The terminal bud visible in the banji condition is represented by two bud scales and a partially expanded ("fish") leaf which shows no later expansion; these leaves enclose a series of leaf primordia. Bond's measurements show that leaves are initiated continuously, but at a fluctuating rate (Fig. 8C). The rate is minimal at the time the rate of extension is most rapid, but becomes maximal during the phase of no extension. There is a build-up of unexpanded leaf primordia, with a maximum number just before a new flush begins, while the number is reduced to a minimum at the end of a flush. No measurements were made of rates of cell division in the shoot apex since apical activity was measured in terms of rate of primordia production, so that we do not know if there is a period of mitotic inactivity during the cycle.

Another tree with four (but unequal), flushes of growth per year is *Callistemon viminalis*, studied by PUROHIT and NANDA (1968). These authors noted no necessary correlation between the alternate periods of "rest" and extension and the seasonal climate, since a long period of rest in July and August coincides with annual maximum temperatures. The longest period of elongation is initiated in December, which is the coldest month. These authors detected appreciable histological changes in the shoot apex during the progression of the annual cycle, mainly indicated by changes in the activity of flanking meristems, but no statement about overall mitotic activity is made. It seems clear, however, from their description that during the longest period of "dormancy" (here meaning absence of elongation) there is still production of some leaf primordia which mature as scales. Built into this cycle is a period of expansion of lateral inflorescences, which corresponds to a phase of rapid overall shoot elongation; this produces the characteristic "bottle-brush" flowering shoot of this species. Flowering is here a complicating factor which we have so far avoided by discussing only vegetative shoots.

An unidentified species of *Oreopanax* (Araliaceae), studied by BORCHERT (1969) in a part of Colombia with a climate with two rainy seasons provides an example of rhythmic growth in which the build-up of leaf primordia occurs just before shoot extension. Leaves are typical of the family, palmately compound with long petioles and a clasping leaf base which encloses the normally inhibited axillary bud. Scale leaves which envelop the resting bud correspond to this basal portion, the distal part of the leaf remaining vestigial, as is shown by a gradual transition from foliage leaf to scale which occurs at the end of a period of shoot extension. In this species individual trees of a population are much out of phase with each other and almost all stages of a flushing cycle may be evident at one time, only in November are practically all buds dormant. Nevertheless, there are two peaks of shoot extension, one each corresponding to the wet seasons of March and November. The resting meristem is enveloped not by bud-scales but by reduced foliage leaves, so that one may speak of a terminal rosette rather than bud. Scale leaves are formed in some numbers towards the end of the previous cycle of initiation but remain enclosed within the resting rosette. With bud burst they complete their expansion and are a feature of the emerging bud. It is during this early phase of expansion that new foliage leaves are initiated. *Oreopanax* is thus unusual among our few case histories in that the resting bud includes a minimum and not a maximum number of foliage leaf primordia. Furthermore there is an abrupt transition from the last bud-scale to the first foliage leaf. Bud burst is here a slow process because of the absence of preformed leaves. The cycle of activity is represented in a generalized, comparative way by Figure 8D. BORCHERT concluded that rhythmic growth is endogenously determined, but there is some climatic influence. It is not known if mitotic activity ceases in the latent apex.

In cocoa, *Theobroma cacao* (Sterculiaceae), GREATHOUSE et al. (1971) and VOGEL (1975) have investigated rhythmic growth of plagiotropic branches in field and controlled conditions. The period of actual shoot elongation (about 12 days) occupies less than one quarter of each cycle of extension and results in the development of between 10 and 11 leaves. Since the number of leaves in the shoot tip remains relatively constant in the interflush period this shows that the apical meristem is inactive and that leaf initiation is therefore rhythmic. The results obtained suggest that leaf initiation starts before shoot extension begins, since there is a maximum leaf number (11 or 12) in the early flush which is categorized by bud swell. The shoot developed by each flush apparently consists of both preformed and neoformed leaves. Under controlled environmental conditions (12-h photoperiod and constant humidity) the shoot rhythm was shortened, from approximately 60 to about 26 days, but could not be eliminated, from which these authors conclude that rhythmic growth is determined endogenously. Later studies (GREATHOUSE and LAETSCH, 1973) showed that growth substances could influence the rate of shoot elongation but could not interrupt this endogenous rest.

A further case history is provided by *Quercus sessiliflora* (Fagaceae) which has been studied in natural and controlled environments by LAVARENNE-ALLARY (1965). She ascertained that this tree has a rhythmic extension with a period of apical activity of ten to fifteen days and a subsequent phase of extension of eight to fifteen days, which results in a cycle of twenty to thirty days comparable to that in *Hevea*. Rhythm is endogenous, but winter dormancy which needs a cold period to be broken in spring is superimposed. In nature, shoots of different age and different provenance (suckers, lammas shoots, seedling shoots) behave slightly differently in a quantitative way.

The case of *Citrus* (cf. REED and MACDOUGALL, 1937) is insufficiently documented to provide a basis for detailed comparison, which is surprising in view of the commercial importance of this rutaceous genus.

III. Continuous Growth

Trees in the tropics which show no evident shoot articulations have been described by KORIBA (1958) as "ever-growing", a term which needs some discussion. It implies that apical meristems undergo no "rest", or in the more precise usage of ROMBERGER (1963) "quiescence". However, because we know so little of the physiology of dormancy we must fall back on a knowledge of morphology alone. Absence of pronounced morphological segmentation of the shoot then becomes the most valuable criterion for continuous growth and a more or less continuous process of leaf production is involved. This is implicit in Koriba's description and is the type of shoot referred to by TOMLINSON and GILL (1973) as "nonarticulate", i.e., without regular change in leaf morphology. A more objective criterion for the recognition of continuous growth is the *constant* bud composition over a period of time, i.e., the same number of leaf components is maintained, unlike trees with rhythmic growth in which bud composition fluctuates according to regular patterns, as we have seen. The difference, of course, can only be established by periodic examination of buds.

The topic is best discussed by means of examples.

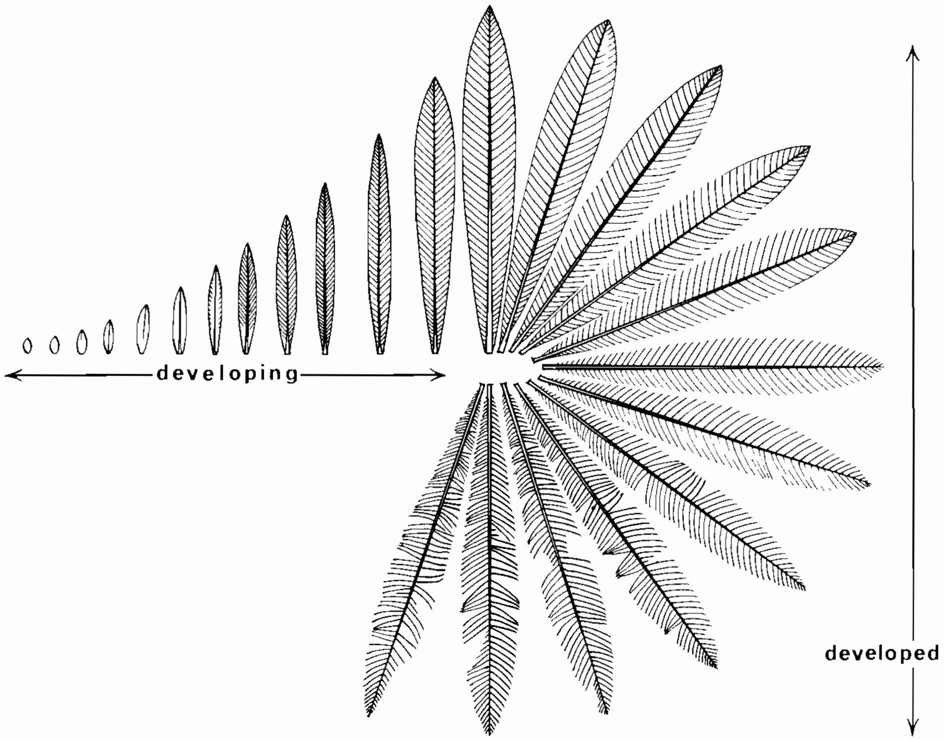


Fig. 9. Developing and developed leaves in the crown of a palm. (Based on Corner's diagram (1966, Fig. 12) of *Actinorhytis.*) Twelve developing leaves, the same number of expanded leaves, spacing at equal intervals of time and space according to age (cf. Fig. 7*E*). When a new leaf is initiated, the 12th developing leaf expands into the crown, and the 12th expanded leaf falls off

1. Palms

The family Palmae provides the best examples of shoots with continuous leaf production, with the coconut (*Cocos nucifera,* subfamily Cocosoideae) and African oil palm (*Elaeis guineensis,* also Cocosoideae) being the species studied in most detail. The composition of the crown is uniform, once the adult stage is reached, and there is a potential for continued initiation, expansion and final loss of leaves at a constant rate. In the reproductive phase axillary inflorescences must be added. For each new leaf initiated, the oldest leaf is lost and the crown includes a continuous series of leaves representing all stages of development, as shown in Figures 8E and 9. Consequently a measurement of the rate of expansion of leaves (or the rate of loss of leaves where they are abscised cleanly, as in coconut) together with a knowledge of total number of leaves in a single crown can be used to estimate leaf age and the length of time a leaf is at a particular stage of development.

In coconut, for example, about one new leaf expands each month, and since there are about 30 visible leaves and another 30 unexpanded leaves, the average life span, from inception to final abscission, is 60 months (five years), for about half of which time the leaf is visible (VENKA-

TANARAYANA, 1957). In the oil palm there are about 40 expanded and 40 developing leaves with a new leaf initiated or expanded each 16 days, giving values of about 22 months for the period in which a leaf is developing and the same value for its period of activity as an expanded, assimilating organ (REES, 1964; HENRY, 1955). CORNER (1966) suggests that these periods are always equivalent since he states that the numbers of unexpanded and expanded leaves are necessarily about the same (cf. Fig. 8E). More research is needed here.

The above figures quoted for two commercially valuable palms are average values, whereas the range of values varies widely according to climate and soil. For example, leaf expansion of coconuts in South Florida may almost cease in winter; fluctuation in the number of "spear leaves" in oil palm is correlated with the dry season in West Africa. One cannot by superficial examination of a palm decide whether it is vigorously producing new leaves or not. Nevertheless there is no regular alteration of periods of rapid growth with periods of quiescence which are endogenously determined, and which involve marked morphological changes in the crown, as in trees with rhythmic growth. Seasonal variation in inflorescence expansion and even initiation does occur in some palms, but this seems largely independent of leaf production.

2. *A Dicotyledon*

Rhizophora mangle L. (Rhizophoraceae) provides an example of an "ever-growing" dicotyledonous tree whose phenology has been studied by GILL and TOMLINSON (1971b) in the seasonal climate of South Florida. Since the tree is branched its growth is more complicated than the monoaxial palms described above, as interaction and competition between the numerous terminal meristems is possible. In *Rhizophora* the terminal meristem of each shoot consistently includes three leaf primordia (and their associated stipules) enclosed by the mature stipules of the youngest pair of expanded leaves to form a distinct terminal "bud". Stipules of all older leaf pairs abscise. Bud composition measured at intervals over a two-year period was shown to be maintained constantly at three pairs of leaf primordia, even in the seasonal climate of South Florida. Much as in palms, there is a continual production of leaves so that the expansion of each leaf pair "out of" the bud is matched by the initiation of a new leaf pair by the shoot apex. The chief variable in this process is the *rate* of leaf initiation and expansion, and there are evident differences in this rate between different shoots on the same tree. The process is directly influenced by climate so that in South Florida the rate of leaf production for a population of shoots on the same or different trees is slower in the (unfavorable) winter, compared with the (favorable) summer.

From the figures provided by GILL and TOMLINSON (1971b) the average rate of leaf production from all shoots measured was about one leaf pair every two months, with a minimum value (maximum growth rate) of three weeks and a maximum value (minimum growth rate) of three to four months. In view of this wide range, a single average value conveys a minimum amount of information, which contrasts with the situation in palms. The most frequent number of expanded leaves on a shoot is four or five pairs and this constancy is maintained by a close correlation between the rate of leaf expansion and the rate of leaf loss by abscission. In South Florida, for example, accelerated leaf production in summer is matched by accelerated leaf loss (Fig. 8F). This shows that leaf abscission, like leaf production, is an endogenously determined physiological process. Consequently leaves formed in the winter months (period of slow growth) have a greater life expectancy than leaves formed in the summer months (period of rapid growth); the range is of the order of six to twelve months, depending on the vigor of the shoot, with a maximum of 17 months. An average value of leaf life span, independent of any knowledge of the periodicity of shoot growth, once again conveys a minimum amount of information.

From these data it is evidently difficult to establish units of extension and morphogenesis, as is possible for trees with rhythmic growth. It is not known if there is a phase of mitotic inactivity during the plastochrone whereby one could differentiate growth phases. Morphologically the obvious unit of extension is the internode itself, but a larger unit is provided by the disposition of branches.

D. Phyllotaxis and Shoot Symmetry

I. Primary Orientation

Most discussion of leaf arrangement in plants is concerned with the primary orientation of leaf primordia during their early ontogeny (phyllotaxis) and less concern is given to secondary orientation of leaves during and even subsequent to their expansion by twisting of both internode and leaf axis. For purposes of architectural analysis both are significant but shoot symmetry is the most relevant parameter in leaf orientation strategies. Leaf arrangement must then be thought of as the most visible symptom of shoot symmetry. Geometrical patterns, which result from regular leaf arrangements and which may be subject to detailed mathematical analysis are not our concern (e.g., DORMER, 1972, Chap. 4; CHURCH, 1920; LOISEAU, 1969; CROIZAT, 1960).

Leaves may be borne singly or in multiples (usually pairs, i.e., decussate, less commonly whorls of three or more). When borne singly leaves are either *distichous*, i.e., alternate on opposite sides of the stem, or *spiral* with the angular divergence, expressed fractionally, giving an estimate of the steepness of the spiral. Leaf contact parastichies may be more useful in interpreting numerically complex spirals and may indeed be informative of growth changes (e.g., REES, 1964, in his study of the oil palm).

Leaves when opposite are almost invariably *decussate*, i.e., with successive pairs mutually at right angles. Secondary orientation will frequently produce a more dorsiventral or radially symmetric pattern. This last case is commonly seen on the terminal short shoots of branches which are plagiotropic by apposition. In the Rhizophoraceae the leaf arrangement is *bijugate*, i.e., in pairs with an angle of about 65° between successive pairs so that radial symmetry results in a shoot with a superficially decussate phyllotaxis.

Of most significance architecturally is the contrasting leaf arrangement on trunk and branch observed in many trees (see for example the discussion under Roux's model, p. 200). This contrast shows that the overall symmetry of the shoot is the most significant strategical aspect of tree organization. Primary leaf orientation may not be very relevant.

II. Secondary Orientation

In architectural terms erect shoots usually show radial symmetry, horizontal shoots usually show dorsiventral symmetry. Spiral and decussate arrangements confer radial symmetry on a shoot, a distichous arrangement confers dorsiventral symmetry. In many trees the phyllotaxis of the adult parts is constant for all shoots; erect shoots with a spiral or decussate leaf arrangement preserve the radial symmetry of their primary leaf orientation but may lose it on their horizontal shoots by secondary orientation or by differential growth of leaves (e.g., *Anisophyllea disticha*) (Fig. 11) so that we may speak of secondary dorsiventrality, a topic discussed in detail by MASSART (1923). These secondary changes which can reorientate either the blade or the whole leaf can be due to twisting of petioles (e.g., *Coffea*), to differential elongation of petioles (*Acer*), or to the activity of pulvini (e.g., *Theobroma* and other Sterculiaceae, many Leguminosae) or to the twisting of internodes (horizontal shoots with decussate leaves; many Myrtaceae) or from various combinations of these processes. Individual leaves then become orientated into a position appropriate for presumed maximum photosynthetic activity, i.e., at right angles to the incident light, which in the forest is mainly from above. The leaves on horizontal shoots are then always arranged in one plane, regardless of their primary orientation in the bud.

Secondary dorsiventrality is achieved very commonly in many members of the Rubiaceae in which leaves are predominantly decussate (but sometimes verticillate, i.e., whorled), but in which all leaf pairs on horizontal shoots rotate into one plane by twisting of internodes, as in *Coffea*. A series of illustrations which show this realignment in *Tachia guianensis* Aubl. (Gentianaceae) is shown in Figure 3A, B.

In the gymnosperms a spiral or whorled leaf arrangement is constant, but on horizontal shoots a marked dorsiventrality is achieved by secondary leaf orientation (*Abies, Picea*), sometimes with the addition of anisophylly (e.g., *Tsuga canadensis*).

Radial symmetry is sometimes reached by an unusual phyllotaxis. In monocotyledons the distichy is often twisted (spiro-distichous), this being so pronounced in species of *Cordyline* (Agavaceae) that a radial symmetry results. In *Pandanus* the phyllotaxis is essentially $^1/_3$, but this is not precise and mutual shading of leaves is reduced by additional twist, hence the common name "screw-pine" for such plants. Distichous leaves are rare in the orthotropic shoots of woody monocotyledons, but where they occur and are large the shoots are very striking (e.g., *Ravenala* and other Strelitziaceae; a few palms like *Oenocarpus distichus* and *Wallichia disticha*). In many bamboos the tall culms have a distichous leaf arrangement. Distichy is uncommon in erect shoots of dicotyledons; Annonaceae possibly provide exceptions, others are to be looked for in young *Campnosperma* trees (Anacardiaceae), most of the species of the genus *Erythroxylon* (Erythroxylaceae), and some Myrtaceae.

E. Branching: Dynamics

As a background to later descriptions of tree architecture some description of general principles and especially the standardization of terms is attempted here.

1. Branch Order Terminology

The nomenclature used to describe orders of branches in trees needs some clarification. In botanical terms a branch is, topographically, always one order higher than the axis on which it is inserted. Ordinal numbers are used to describe branch orders, i.e., first, second, third etc. The starting point for the series need not be known so that we speak of the nth order, n+1st order, n+2nd order and so on. Otherwise it is usual to consider the trunk of the tree as the starting point, order zero. This system is simpler than the use of classical numbers (primary, secondary, ternary etc.) and is certainly to be preferred to daughter, grand-daughter etc. axis which has been used (e.g., CREMER, 1972).

In botanical usage, the order of branches has a chronological connotation, the third order develops from and therefore is younger than the second order, the second younger than the first, and so on. The developmental sequence may not always be evident in an adult structure, however, and this can cause confusion if not recognized. In monopodial systems the analysis of branching is usually simple, and order number corresponds to the developmental sequence. In sympodial systems, however, this does not follow, and one has to distinguish between two systems of nomenclature, the *absolute* order, which refers to the developmental sequence in a morphological sense and is contrasted with the *relative* or *visible* order which refers to construction as it is directly observed. A sympodial system may appear to be unbranched (linear sympodium) whereas developmentally several orders of branching may be involved. Monocaulous but polyaxial trees described later provide an example of this (p. 99). In architectural terms (and in most other ecologically useful analyses) it is the relative order of branching which is described, since it is the overall construction which is significant. The periodic displacement or abortion of a terminal bud and its substitution or replacement by a lateral bud is of little significance in ultimate configuration, although of considerable morphological and physiological interest. In such overall usage progressive abscission or loss of branches rapidly obscures developmental relationships in a large, repeatedly branched organism.

The number of visible orders of branches is not large in trees, WILSON (1966) indicates a maximum of five for *Acer rubrum* which may seem low when one considers that in the normal pattern of growth each axis branches once each year. This is a reflection of how branching becomes less frequent in higher orders. In a range of species analyzed by OOHATA and SHIDEI (1971) the numbers vary between five and six, but seven seems to be a maximum in *Eucalyptus* (HOLLAND, 1969). The larger numbers seem characteristic of small-leaved species (e.g., *Leptospermum, Tamarix, Chamaecyparis*). The high number of nine orders of branching recorded by LÖHR (1965) in *Taxus baccata* (Taxaceae) represents an upper limit, although eight branch orders are recorded by MÜLLER and NIELSEN (1965) for *Macaranga spinosa* and *Strombosia pustulata*. In the large paniculate inflorescences of hapaxanthic palms five is probably a maximum number of branch orders which develop entirely by primary growth and which are therefore determinate (e.g., *Nannorrhops*, TOMLINSON and MOORE, 1968; *Metroxylon*, TOMLINSON, 1971b; *Corypha*, TOMLINSON and SODERHOLM, 1975).

It is interesting to recognize that there may be a high degree of branch preformation in the terminal buds of certain trees; for example, CREMER (1972) has recorded up to three orders of recognizable branches in developing buds of *Eucalyptus*.

A frequently used method of analysis of branching systems in trees which contrasts with the above developmental system derives originally from HORTON's (1945) analysis of stream orders in geomorphology (e.g., STRAHLER, 1964; MCMAHON and KRONAUER, 1976). This is a valuable system, especially in terms of the comparative data it produces (e.g., OOHATA and SHIDEI, 1971; HOLLAND, 1969) but it should not be confused with classical botanical terminology. This method reverses the numeration of branch orders by treating the ultimate units of the system (recognized because they themselves bear no further branches) as the *first order* of the system. The axes these are inserted upon represent the second order, which becomes visible when all first-order branches are removed, and so on. The great value of this method is that it is completely objective, since it does not depend on any a priori distinction between a parent and derivative axis, which is necessary in orthodox botanical analysis. However, it does mean that the two systems are not directly comparable and can, if applied to the same tree, lead to different analytical results.

No confusion should arise if one refers simply to "branch orders" for the chronological or developmental system (with the qualification of "absolute" or "relative" as occasion demands) and to the "Strahler order" where this contrasted system is applied.

II. Syllepsis and Prolepsis

1. Definitions and Descriptions

Two generally contrasted types of lateral branching occur in the shoots of woody angiosperms, but they have been inadequately distinguished by morphologists so that a somewhat lengthy discussion of the topic is needed. Branching may be according to one of two alternative developmental processes.

1. Syllepsis is the continuous development of a lateral from a terminal meristem to establish a branch, without an evident intervening period of rest of the lateral meristem (Fig. 2C). Branches so developed are referred to as *sylleptic branches*. They are always part of the normal differentiation sequence of a tree when it is conforming to its architectural model (sequential branching, p. 273). In many trees syllepsis is a useful criterion for recognizing sequential branching within the model, as distinct from other branching patterns not determined by the architectural model (i.e., reiteration, p. 274).

2. Prolepsis is the discontinuous development of a lateral from a terminal meristem to establish a branch, with some intervening period of rest of the lateral meristem (Fig. 2D). Branches so developed are referred to as *proleptic branches*, which may or may not form part of the normal sequence of differentiation which characterizes an architectural model. In some trees both syllepsis and prolepsis are a normal feature of branching in a tree conforming to its model (e.g., cocoa). On the other hand where regeneration of part of the tree occurs from a latent meristem this is, by definition, prolepsis.

This developmental distinction between two kinds of branching can be stated most succinctly by saying that a sylleptic branch is synchronous in its development with its parent axis (Fig. 10), but a proleptic branch is not, although in both instances, of course, the initiation of the branch meristem is an event developmentally continuous in time with the activity of the parent meristem. In most trees of higher latitudes in the northern hemisphere, for example, there is an age difference of one year between a branch and the axis on which it is inserted, because superficially visible lateral meristems usually overwinter as dormant lateral buds. The time lag may be even longer where buds do not become visible within a year, or where buds remain dormant

Fig. 10. Sylleptic branching illustrated in *Vismia augusta* Miq. (Guttiferae, Roux's model), Orapú River, French Guiana. This represents the first pair of branches produced by the trunk axis, marking the end of the seedling stage. The lateral meristems in the axils of the uppermost leaf pair are developing contemporaneously with the parent shoot

more than one year as with those that produce epicormic shoots by reiteration. The concept that current-year shoots do not produce extended branches is often regarded as a "norm" for tree growth. It is not, but merely represents one particular state which is predominant in Europe, North America and Northern Asia. Unfortunately this concept has lead to considerable confusion in terminology as we shall explain below.

The definitions of syllepsis and prolepsis given above are developmental ones, but in the majority of examples a simple morphological difference between the resulting branches allows one to distinguish them at a glance.

Sylleptic branches lack basal bud-scales and have an extended basal internode (hypopodium) generally below the first leaf or pair of leaves; this leaf (or leaf pair) is of a size and shape more or less normal for adult foliage, i.e., there is no morphological "reduction" of prophylls and there is virtually no transition in leaf shape along the shoot (Fig. 2C). Although this statement is a valid rule for most aerial shoots, it has to be qualified somewhat when species with large or dissected leaves are considered, or when rhizome branching is discussed, since in the former something of a transition in leaf size along a branch may be present, and in the latter, of course, scale leaves may be the normal condition throughout the rhizome.

Proleptic branches have one or more basal bud-scales (often arranged in pairs) and usually with a series of transitional forms (transitional in both size and shape) towards the adult leaf (Fig. 2D). The transition may not be gradual and a distinction between preformed and neoformed leaves may be evident. The morphological features of proleptic shoots are clearly seen in the bursting of lateral buds in temperate trees in spring as branches start to elongate, but the same process is rather common in tropical trees (e.g., many Bignoniaceae, Burseraceae, Leguminosae, Meliaceae, Moraceae). Bud-scales are caducous once branch expansion begins so that they are soon represented only by their scars. Normally it is the scars of these basal bud scales by which one recognizes a proleptic branch (Fig. 2D).

The development of leaves as bud-scales reflects one example of the production of leaf primordia by the lateral meristem prior to its becoming dormant (or at least latent) and in the strict sense of our definition it may be suggested that the meristem and the organs developed on it prior to the onset of dormancy are sylleptic. This refinement is misleading, however, as the contrasted states are always clear in terms of *branches*. Bud-scales undergo little or no further differentiation in the direction of leaves once branch expansion begins, i.e., they themselves are not at an arrested state of development. They themselves, though diminutive, play important functions in the protection of dormant meristems from frost, drought, and insects, and may also be essential as photoreceptors. Visible leaf primordia which do overwinter in an arrested state of development which is completed subsequently are known in temperate trees, notably species of *Viburnum* (Caprifoliaceae, Fig. 3C). An articulated morphology, in which growth increments are separated by bud-scale scars, is then not evident. A transitory state of rest even in nonseasonal climates is probably quite common in the leaf primordia in terminal buds of tropical trees. Were the same kind of rest to occur in a lateral meristem and be associated with internodal elongation, in the normal manner of shoot growth, then a shoot with proleptic growth would have sylleptic morphology. This rarely occurs, but has been seen in *Citharexylum fruticosum* (Verbenaceae) in South Florida, for example.

2. *Historical Usage of the Terms*

Syllepsis and prolepsis are here adopted (according to the suggestion of TOMLINSON and GILL, 1973) as terms to distinguish two very real processes, but their usage now differs somewhat from the original definitions of SPÄTH (1912), who introduced them. We have retained SPÄTH's terminology despite this shift in meaning, because one of his terms, "syllepsis", is exactly what is needed; "prolepsis" has to be redefined. The point stressed here is that the restricted view of a "norm" for tree growth, which is still prominent today, has to be changed. SPÄTH, as a temperate forester, was concerned with the late-season flushing of shoots of temperate trees which, as supposedly exceptional states, he and other workers have tended to regard as an "abnormal" phenomenon. This has led to their description, variously in different languages, as "lammas or St. John shoots, pousses de la St. Jean, Johannistriebe, Sint Jansloten", referring to the saint's day (June 24) or lammas tide (August 1) which approximate to their occurrence. This suggestion of abnormality is based on the concept of one flush of shoot growth per year as a norm, familiar only in temperate trees where extension growth is closely synchronized with season.

SPÄTH's definitions are quoted (in translation) in full:

> "Sylleptic shoots are such as develop regularly on a leafy unmodified shoot, without consideration of the season, during continuous extension growth of the terminal bud from newly formed lateral axillary buds – mostly without forming bud scales first – therefore without a preceding rest period and developing independently of other factors. Therefore they belong to the normal shoot system of the plant, but they are to be found frequently and regularly in young plants only and may be lacking occasionally in old ones.
>
> True proleptic shoots are those which develop irregularly on a leafy unmodified shoot, without consideration of the season after complete conclusion of extension growth, therefore from already closed (almost always terminal) buds after an appreciable resting period. Therefore they do not belong to the normal shoot system of the plant."

These definitions indicate that no distinction is made between activity of terminal and lateral buds, i.e., the terms do not relate only to branch "prolepsis". SPÄTH thus clearly means "precocious" breaking of a bud which would "normally" be expected to overwinter, a sense in which it is still commonly used, especially with reference to specialized shoot systems like that of *Pinus* e.g., RUDOLPH, 1964). "Syllepsis" as defined by SPÄTH refers to branching exactly in our usage. Now that we have a more cosmopolitan understanding of tree growth and especially now that we can appreciate that synchronization of shoot extension with season is neither a necessary, nor the most common condition for tree growth, as tropical observation demonstrates, we can apply SPÄTH's terminology strictly to branch expression in the way we have established on p.42 without treating it as a special case. This leaves the field clear for "lammas shoot" and its equivalents to describe a normal but only infrequently expressed phenomenon. We thus invert the whole of the philosophy behind the forester's thinking, by saying "temperate trees are anomalous, lammas shoots of various kinds are normal phenomena of growth."

This case is particularly instructive as it indicates how important the understanding of tropical trees is to the development of a clear set of terms about growth in all woody plants. CHAMPAGNAT's (1954a) term "rameaux anticipés" (precocious branches), now substituted by sylleptic branches, can be put in a more general context, as such branches are only precocious in relation to the restricted norm for *Alnus*, the genus which he studied, as well as many other temperate trees.

We have employed the terms syllepsis and prolepsis freely in our discussion of architectural models, since it is by their application that their usefulness becomes evident. One cannot, in fact, proceed very far in a study of the growth of tropical trees without needing such contrasted terms. They are immediately helpful in the understanding of branch differentiation, considered later.

3. *Apical Dominance*

The concept of prolepsis and syllepsis as alternate functional states of the same meristems is easily demonstrated. CHAMPAGNAT (1954b) in his observations of branches in *Alnus glutinosa* demonstrated that meristems which on normal shoots remained dormant (i.e., would have been potentially proleptic branches) were on vigorous sucker shoots induced to develop as sylleptic branches.

In the experiments of NEVILLE (1969) on *Gleditsia* an appropriate treatment induced premature bud break and consequently produced the morphological features of a sylleptic branch in a shoot which otherwise would have become proleptic.

Once it is grasped that lateral meristems have these alternative developmental possibilities, it becomes of interest to seek explanations for the underlying physiological mechanisms. There is some information to show that syllepsis (at least in some species) is correlated with rapidity of shoot growth, i.e., the greater the rate of extension of a shoot, the greater is the likelihood of its lateral meristems developing by syllepsis. Examples where this is known have been provided by CHAMPAGNAT (1954b) for *Alnus*, GILL (1971b) for *Avicennia*, GILL and TOMLINSON (1971b) for *Rhizophora*. It is suggested in the data provided by FISHER (1978) for *Terminalia*. It is illustrated by BROWN et al. (1967) for *Liquidambar* (their Fig. 5). This correlation led TOMLINSON and GILL (1973) to suggest that the switch from a "lower" state which determined prolepsis of a lateral meristem, to another "higher" state which determined syllepsis is conditioned by a "threshold" which in turn is determined by growth "vigor" of the parent shoot. Once this vigor is exceeded, the balance is tipped from the lower to the higher state. This hypothesis is illustrated diagrammatically in Figure 90. It provides an alternative to explanations of branching solely in terms of "apical dominance", i.e., the production by active terminal meristems of growth substances which clearly inhibit the development of lateral meristems in many plants. The complexity of organizational mechanisms of branching in woody plants has been made evident in the discussion on the subject by BROWN et al. (1967) which led to their suggestion that apical dominance should really be thought of as "apical control" in woody plants. The effects of apical control are described by the term "acrotony", well-established in the European literature (e.g., TROLL, 1937). "Basitony" is an appropriately contrasted type of behavior whose physiological basis seems complex (CHAMPAGNAT, 1978). Comparative morphological evidence from the study of tropical trees can play a significant role in distinguishing carefully between contrasted physiological mechanisms.

One reason for our lack of understanding of syllepsis is its infrequency in the woody plants of cooler latitudes in the northern hemisphere. In eastern North America, for example, a selected area in central Massachusetts (Harvard Forest) shows one example (*Cornus alternifolius*, Cornaceae) of a tree with sylleptic branching as a normal feature of its architecture amongst about 40 native woody species. As one moves further south one meets progressively more examples [e.g., *Liquidambar* (Altingiaceae), *Liriodendron* (Magnoliaceae), *Sassafras* (Lauraceae)]. BROWN et al. (1967) made the observation that it is the neoformed lateral branch meristems, i.e., those initiated in the current year, which are sylleptic in *Liquidambar* and *Liriodendron*. In South Florida, which has a predominantly West Indian tree flora, a high proportion of tree species (about 20%) show syllepsis. Exceptions must be made for specialized sylleptic shoots, spines, tendrils and flowering axes which are determinate (e.g., *Bumelia*, *Crataegus*, *Prunus* species, *Ulex*, *Ximenia*). These examples of syllepsis are excluded from later discussion since they are not architecturally significant, although they are of physiological interest.

Branching in inflorescences is exclusively sylleptic, even in temperate trees.

It seems an obvious conclusion from this type of evidence, and from general observation, that syllepsis is a feature of many woody dicotyledons in the tropics; one might regard it as a tropical phenomenon. However, South temperate woody floras may show a relatively high incidence of woody species with sylleptic branching. The good representation of tropical families like Araliaceae, Avicenniaceae, Bignoniaceae, Elaeocarpaceae, Icacinaceae, Lauraceae, Meliaceae, Monimiaceae, Moraceae, Myrsinaceae, Sapindaceae, and Sapotaceae in the New Zealand flora (ALLAN, 1961) is one element which complements this morphological observation.

In the foregoing discussion we have not considered herbaceous plants in which syllepsis is much the most common method of branching. This is largely the consequence of shoot construction being carried out by them in one growing period.

III. Continuous and Diffuse (Intermittent) Branching

In the previous discussion of shoot growth, distinction was made between rhythmic (episodic) and continuous growth and some mention was made of the types of branching associated with them. Where growth is rhythmic, branching is closely correlated and branch tiers are produced (either by syllepsis or prolepsis) which bear a precise relationship with the rhythm of growth extension of the parent axis, i.e., their position is predictable with a high degree of certainty (Fig. 7D). Where shoot growth is continuous, however, two conditions exist. In the simplest situation, all leaves subtend sylleptic branches and the branching pattern can be said to be continuous. This is the condition found in Roux's and Cook's models, for example. In a less simple situation (less simple because it is unpredictable), branching may be diffuse or intermittent, i.e., discontinuous, since branches appear at intervals which bear no obvious relation to morphological features of the shoot. An example would be *Rhizophora* which produces tiers of branches although its growth is described as continuous in the sense that obvious dormancy of the apical meristem does not occur (GILL and TOMLINSON, 1969, 1971b). However, it can be objected that the discontinuity of branching is itself a manifestation of rhythmic growth and that there can be no condition intermediate between rhythmic and continuous branching. GILL and TOMLINSON (1971b) themselves demonstrate that vegetative branching in sapling axes of *Rhizophora* is correlated with vigor, i.e., the more rapidly growing the shoot, the more likely it is to branch, and this they suggest is related to an internal feedback mechanism (see also OLDEMAN, 1974a). Nevertheless there is no way in which the pattern of branching of *Rhizophora* can be anticipated on the basis of simple morphological evidence. This seems a useful criterion by which its branching pattern can be categorized (albeit in a negative fashion). It therefore seems useful to retain a term such as diffuse or intermittent branching and this is adopted in subsequent description.

RACIBORSKI (1901) analyzed branching patterns in a number of tropical species, but he did not make a clear distinction between orthotropic and plagiotropic shoots. Nevertheless his study represents a pioneer venture since he described many patterns unfamiliar to the temperate botanist. It now becomes possible to place his work in an architectural context.

The obvious need in the future is for well-worked-out examples by means of which general principles can be clearly established. In view of the subsequent descriptions of architecture, which rely so extensively on branching patterns, the seriousness of this deficiency in fundamental knowledge should be quite clear.

F. Branch Polymorphism: Long Shoots

I. Orthotropy and Plagiotropy

From the time of SACHS (1879) and even earlier (FRANK, 1868) the difference between erect and horizontal aerial shoots in plants has been circumscribed using several criteria as follows:

1. Orthotropic shoots, i.e., shoots which are erect, with essentially radial symmetry, phyllotaxis spiral or decussate, branching three-dimensional, axis negatively geotropic, often nonflowering.

2. Plagiotropic shoots, i.e., shoots which are more or less horizontal with dorsiventral symmetry (Fig. 11), leaves either distichous or secondarily arranged in one plane, branching two-dimensional, axis diageotropic, often flowering.

This is perhaps a broader usage of the terms than originally envisaged by SACHS, but examination of common tropical trees will demonstrate that divergence between shoots on a single tree is very common. Thus the erect axis in coffee bears decussate leaf pairs, branches continuously and usually lacks flowers. The horizontal branches remain little- or unbranched, are dorsiventral by virtue of the secondary orientation of leaf pairs so that they all lie in one plane, and bear numerous axillary flower clusters. Coffee thus provides a clear example of shoot dimorphism and we may speak of there being *differentiation* among different apical meristems which produce the contrasted types of shoot. Examples of this marked degree of axis differentiation are described in detail later (e.g., under Nozeran's, Massart's, and Cook's models).

In some examples the degree of differentiation is pronounced and strongly fixed so that it is not possible for a single meristem to undergo a change from one kind of symmetry to another. In cocoa, for example, erect shoots have spirally arranged leaves, horizontal shoots have distichously arranged leaves and the sequence of production of these two kinds of axis in the development of the tree is very precise. In the common weed-tree genus *Trema* (Ulmaceae), species of which are widely distributed in the tropics on disturbed sites there is a similar differentiation between orthotropic shoots, with spirally arranged leaves, which bear a regular sequence of lateral axes, with distichously arranged leaves. Further examples can be found in conifers, as the classic work of VÖCHTING (1904) on *Araucaria heterophylla* (=*A. excelsa*) has shown. Here the fixity of organization of different branch orders was demonstrated by experimentally rooting detached axes. Even when growing independently of the trunk such branches retained a horizontal orientation. RACIBORSKI (1901) has discussed some aspects of branch differentiation in tropical trees, while MASSART (1923) has provided detailed descriptions of some of the more striking examples.

In contrast, it is a familiar observation in most temperate trees and in many tropical trees that a horizontal branch orientation is imposed by the activity of a dominant leader, a continued form of the "apical control" discussed by BROWN et al. (1967). Should the leader be cut off to the level of a branch, the response can be a rapid change from the horizontal

Fig. 11. Anisophyllea sp. cf. *A. disticha* Baill. (Rhizophoraceae or Anisophylleaceae) as an example of extreme dorsiventrality in a plagiotropic branch. The leaf arrangement is described as distichous but there is marked leaf dimorphism with a series of small leaves on the upper surface of the branch and large leaves towards the lower surface (cf. CORNER, 1952, p. 122)

to the vertical and the branch substitutes for the missing leader. In this case we now recognize that plagiotropy is induced in the meristem of the branch axis but in a reversible manner. So, if we can speak of differentiation of meristems, we can also recognize the process of dedifferentiation, much as one uses the term for organization at the cellular level. It is useful to recognize that the "organizational level" which an axis meristem achieves may be low or high, depending on the degree to which the axis produced deviates from the orthotropic condition. Strictly orthotropic axes may be said to have a low level of differentiation, irreversibly plagiotropic branches have a high level of differentiation. The stability of these two contrasted levels is pronounced, but in intermediate or less stable systems there is a marked tendency for meristems to fall towards the lower level of differentiation, i.e., there is a strong tendency towards orthotropy. Our later concept of architecture is developed from the recognition that different species of trees have different levels of total genetic organization, depending in turn on contrasted levels of differentiation between meristems. The most highly organized trees have the greatest degree of polymorphism of differentiation between shoot systems. These concepts are summarized in Table 7 and subsequent discussion provides specific examples. It is clear from this analysis that the basic division is one which distinguishes between "trunk axis" and "branch axis", with trees showing one trunk and many branches. We shall see later, however, that under a variety of circumstances trees can develop more than one trunk axis, a reaction to which they are more or less disposed by genetic organization.

1. Strict Orthotropy of Trunk Axes

The axis which forms the trunk in many trees provides the best example of an orthotropic shoot, recognized as the dominant leader. Commonly the leader is monopodial and of indefinite growth. Its extension may be either rhythmic or continuous. It should be emphasized that trees do not necessarily grow tall as the result of an orthotropic trunk axis, successive axes which are partly plagiotropic can produce growth in height, as is described under "mixed axes", p. 232. Where the trunk axis is potentially indeterminate in its activity its stability is high, but it may be lost accidentally. In such trees there are mechanisms for rapid replacement of a leader, either by substitution of an existing branch, or by rapid development of a previously latent meristem. In other trees the orthotropic trunk meristem is determinate and the trunk is a sympodium; *Alstonia boonei*, cocoa, *Gonocaryum littorale, Hura crepitans, Ochroma lagopus* provide examples.

2. Orthotropic Branches

Branches may exist at an orthotropic level of differentiation. The inherent orthotropic nature of their meristem is indicated by essentially radial symmetry (i.e.,

Table 7. Types of axis in woody plants (except mixed axes)

Axis types	Stability	Differentiation level	Phyllotaxis	Symmetry	Secondary leaf orientation	Branching	Origin
A. Trunk axes							
Strict Orthotropy (I)	stable	low	spiral or decussate	radial	little	common, continuous or rhythmic	mainly by prolepsis
B. Branch axes							
Orthotropy (II)	stable but sometimes masked	low	usually spiral or decussate				
Reversible plagiotropy (I)	unstable	low		dorsiventral	little		
Irreversible plagiotropy (II)	stable	high	distichous or decussate		much	infrequent diffuse or rhythmic	mainly by syllepsis
phyllomorphism	stable	high			much		

spiral phyllotaxis). However, a branch usually grows away from the trunk and hence its orientation during the initial phase of its development is not vertical but more or less askew. This asymmetry is most pronounced at the base of an orthotropic branch axis, because the apex gradually assumes a vertical direction of growth at a certain distance from the trunk. The proximal segments of such axes could be mistaken for more or less plagiotropic organs because their asymmetry which, at first, only results from secondary leaf orientation, is accentuated with age by differential secondary development on the upper and lower surfaces (Fig. 12A).

Early growth may be erect, as in the current-year lateral shoots of pines, for example, in which a more or less horizontal position is gradually adopted when they grow away from the trunk later. It may also be horizontal or askew as soon as the branch starts growing, as in most tropical dicotyledons. The inherent orthotropy is convincingly demonstrated when the branch is released from the influence of the controlling leader. Likewise isolated cuttings of such branches can directly restore an orthotropic trunk axis. Analysis of this level is, of course, very simplistic, because little is known of the mechanism of this apical control (Brown et al., 1967) although a precise hormonal balance is involved.

Confusion with the very specialized plagiotropic organization of complex branches may arise easily at the distal parts of an orthotropic branch system, in the periphery of the crown. A first-order orthotropic branch bears a second-order axis in a hypotonic position (i.e., on its lower surface) at the curve where it straightens up. The second-order lateral grows askew in its turn before it becomes upright and the third-order branch, which originates hypotonically at the curve of the second-order one, behaves in the same manner. However, these axes become smaller as the branch order becomes higher, and their vertical extremities are progressively less important in comparison with the outward directed bases. *Physiognomically* there is a marked convergence between such distal, peripheral parts of orthotropic complex branches and branching complexes showing plagiotropy by apposition as in "Terminalia-branching", discussed later (p. 56). The distinction can be made immediately, however, by the observation of the top of the trunk, where the different origin of such complexes is not as yet masked by secondary phenomena.

The fundamental difference between the two procedures should be understood in order to comprehend the distinction between architectural models based on this criterion (Rauh's model, p. 221, and Aubréville's model, p. 182). From the center towards the periphery of an orthotropic branch system the axes become less massive and less vigorous. The branches of *Rhizophora mangle* provide a good example. Initially, i.e., near the top of the trunk, the meristem shows its orthotropic character and produces a suberect shoot with fairly complete radial symmetry. However, after the production of several lateral branch orders the symmetry of the distal axes becomes markedly dorsiventral. It also becomes progressively more difficult for the axial meristems to function in a perfectly orthotropic way.

If this process were to be explained in terms of plagiotropy induced through apical control by the trunk axis, there would be an inconsistency in the fact that the further a meristem is from the parent trunk, the more "plagiotropic" it becomes, whereas apical control might be expected to diminish with distance. Tentatively it seems more logical to assume that a purely orthotropic differentiation sequence is not able to cope with the extension of a branch system beyond a certain branch order. In such a system, branch order and branch age thus become important in establishing the degree of imperfection in the orthotropy of a meristem whose behavior is adjusted to that of adjacent meristems functioning in concert. Probably, the whole process can be compared with phenomena such as pauperization (p. 276) and fragmentation (p. 261) in models.

In terms of the ecology inside the tree crown, axes at the periphery must grow out from under a denser leaf canopy than branches which originate directly near the top of the trunk. This increases the distance between the base of such peripheral axes and the free space where their leaves can function. Moreover, the whole branch system becomes heavier by secondary thickening and its lever arm increases by extension growth; hence it gradually is lowered into and below a horizontal level. Any new peripheral axis then has to grow following a large arc before it can reach a vertical position. Because such axes most often are not very vigorous, they rarely can become erect.

The orthotropic branch system and the modular complex which characterizes Terminalia-branching are compared in Figure 12A and B. The contrast between the bankruptcy of the orthotropic differentiation sequence in the first case, and the well-programmed process creating a plagiotropic complex in the last instance—which is here stressed as an architectural criterion—can be observed immediately in this illustration.

3. Plagiotropic Branches (Reversible)

The base of orthotropic branches, although they are not vertical and show some secondary leaf orientation, are not plagiotropic but possess some superficial resemblance to plagiotropic axes. Moreover, orthotropic branches grow vertically upwards as soon as they can do so and even in the presence of the leader. Plagiotropy is manifest only when the secondary dorsiventral orientation of the leaves is pronounced and is accompanied by a more or less discreet anisophylly, whereas

Fig. 12A–F. Orthotropy and plagiotropy in ▷ branches.

A Orthotropic branch complex. All axes morphologically equivalent to the trunk, though functionally not so. Note gradual decrease of internode length on each axis and of axes towards the periphery of the crown (*inset*). Such decreases are not preprogramed and probably only the result of a conflict between gravity and orthotropic differentiation in branch building. They are not to be confused with the highly developed modular construction of *B*; the difference can be ascertained by examination of the tree top and its young branches (*inset*).

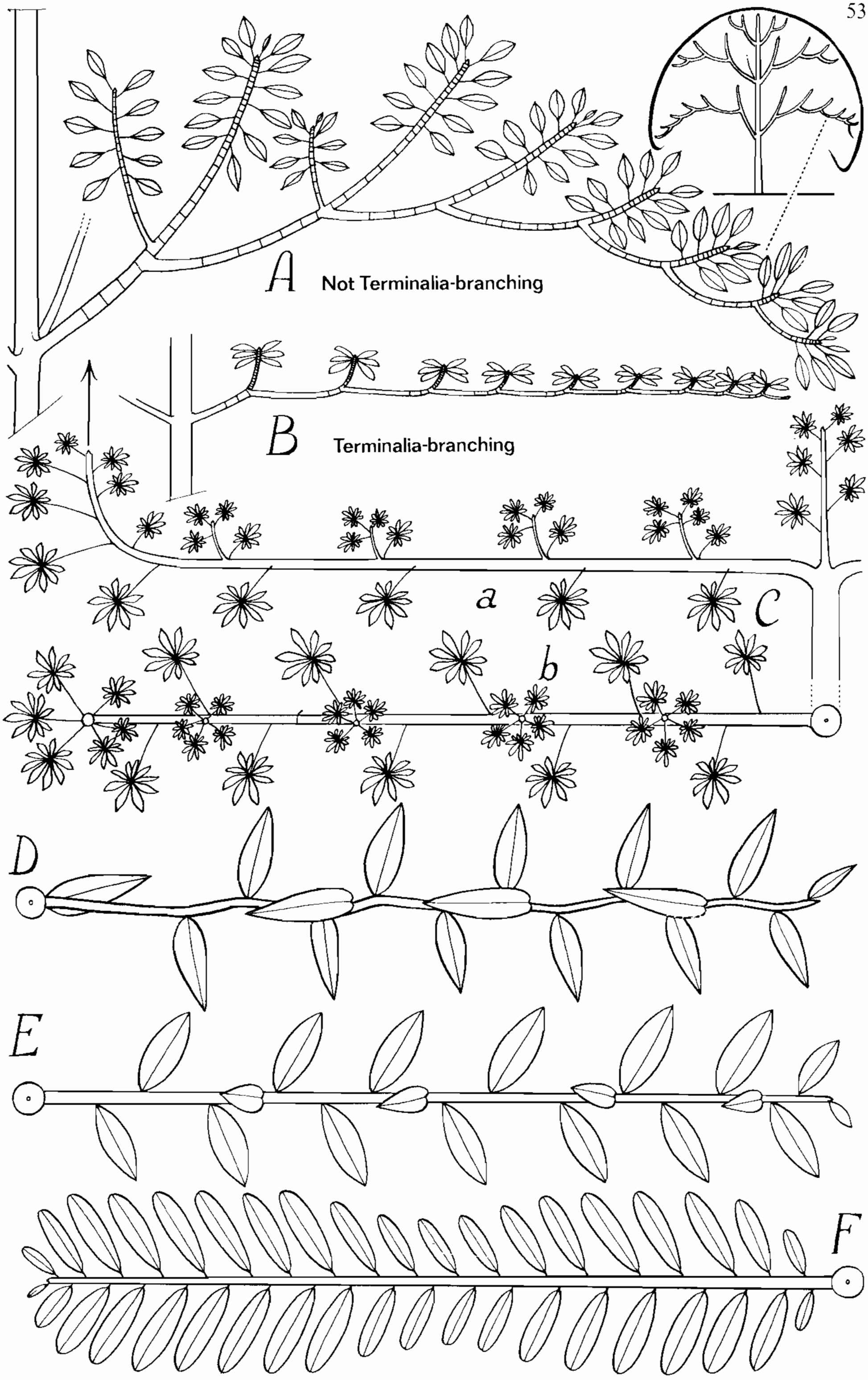
B Modular branch with plagiotropy by apposition ("Terminalia-branching"). Abrupt decrease of internode length after the basal part of each module, decrease in module size from center to periphery proportionally small. Not to be confused with orthotropy in *A*.

C Secondary and reversible plagiotropy in a branch of *Ceiba pentandra* ("Kapok tree", Bombacaceae, pantropical); leaf size differentiation and secondary orientation of internodes; apical part vertical and radially symmetrical. Lateral view (*a*) and from above (*b*).

D Secondary and reversible plagiotropy in a branch of *Ocotea guianensis* Lauraceae, Guianas); leaf orientation and internode orientation; apex less evidently orthotropic than in *C*.

E Same as *D*, but accompanied by leaf dimorphism, in *Ocotea splendens* (Lauraceae, Amazonia, and Guianas).

F Complete and irreversible branch plagiotropy with distichy originating in or very near the apex. This branch shows rhythmic extension as is often found in myristicaceous trees


A
Not Terminalia-branching
B
Terminalia-branching
a
C
b
D
E
F

the axis itself assumes an orientation which is markedly closer to the horizontal than to the vertical even near the top of the trunk.

It still is relatively easily reversible by removing the adjacent trunk meristem. This reversal may be slower than the change in an orthotropic branch released from its leader. Because leaf orientation is secondary and primary phyllotaxis is spiral, whereas axes with this kind of plagiotropy often grow out vertically when young and lower themselves towards a horizontal level a little later by secondary growth, the top of the trunk of a tree with such branches may sometimes bear a remarkable likeness to the top of a tree with young orthotropic branches (H.O. 1970, Fig. 57: *Ocotea splendens*).

The branch tiers of *Ceiba pentandra* (Bombacaceae, Kapok tree) provide a good example (Fig. 12C). Initially, the meristem of the branch shows its radially symmetric character and during a short period it produces a suberect shoot. However, the axis soon begins to lower itself into a horizontal plane and at the same time its dorsal leaves remain rather small and the lateral and ventral ones become larger. The different axillary products later accentuate the plagiotropic character of the branch system. However, when in nature the apical meristem of the trunk dies or the tree is decapitated the end meristems of the branches very soon lose their plagiotropic differentiation and construct erect axes with spirally arranged leaves.

In the genus *Ocotea* (Lauraceae) there are species with orthotropic branches (*O. rubra*), with reversibly plagiotropic branches without evident anisophylly (*O. guianensis*, Fig. 12D) and with both plagiotropy and anisophylly (*O. splendens*, Fig. 12E). In all species of *Ocotea* that we have seen, however, branch differentiation is late, and reversible by decapitation of the tree.

Observation of such plagiotropic axes in nature alone is sufficient to establish a convincing case for apical control determining their differentiation. As soon as the leader meristem ceases to exist the plagiotropy of these branches also disappears.

4. Plagiotropic Branches (Nonreversible)

In many trees plagiotropy is expressed by the lateral meristem from the time of its inception, there is no initial orthotropy; the plagiotropy of the branch is not then usually reversible by manipulation (Fig. 12F).

A classic example of this degree of branch differentiation was provided in the experimental work of VOCHTING (1904) on *Araucaria heterophylla* (Araucariaceae). He rooted first-order branch complexes severed from the parent trunk and even after five years the plagiotropic response remained unaltered. Plagiotropy in this species is interesting because it does not depend on primary leaf orientation which is spiral on all shoots. VOCHTING also rooted detached second- and third-order branches, which retained their organization and posture without change. From this, one can conclude that the meristem of the branch has plagiotropy imposed upon it from its moment of inception.

Similar results have been obtained for coffee by CARVALHO et al. (1950) and *Hydnocarpus* (Flacourtiaceae) by MENDES (1950).

Irreversible plagiotropy is most pronounced when it is accompanied by a change in phyllotaxis so that orthotropic shoots retain a spiral or decussate leaf arrangement in contrast to the distichous leaves of the plagiotropic shoots. We have mentioned the genus *Trema* (Ulmaceae), which shows this contrasted morphology well. Dedifferentiation of a kind is shown by the tendency of the distal part of older branches to become erect, as may be seen in mature individuals of *Trema occidentalis*, where there is even reversion to spiral phyllotaxis. In some Annonaceae (*Xylopia*) the distal erect portion of a dedifferentiated shoot retains the distichous leaf arrangement (OLDEMAN, 1974a). This tendency shows that there exists in some species a certain degree of instability of the apical branch meristem, conditioned by its age.

5. *Phyllomorphic Branches*

In the most highly specialized examples of plagiotropy in branches there is no instability. No standard manipulative procedures will change branch organization and orientation. In the tropics there is a biological group of trees, described later under Cook's model (p. 206) in which the plagiotropy of the branch system is so rigid and is combined with a number of other features, notably determinate growth, that the branch resembles a compound leaf–the "phyllomorphic branches" of CORNER (1953–1954). As branches they originate in the axil of an often reduced or scale-like leaf on the trunk, they have either distichous or decussate phyllotaxis but with pronounced dorsiventrality, and they may bear flowers. Growth may be either monopodial or sympodial. Leaf-like characters include determinate growth, limited life span (i.e., they eventually abscise as a unit) and lack of further visible branching. *Castilla elastica* (Central American rubber tree, Moraceae) provides a good example. The morphology is expressed strikingly in the genus *Phyllanthus* (Euphorbiaceae) which ranges widely in stature, some species are small herbs, others are low trees.

In summary, we can appreciate from the comparison of a wide range of species that plagiotropy and orthotropy are contrasted states but with a range of intermediate conditions. The extremes are stable, but there is otherwise a strong tendency towards the orthotropic state. Where shoots of both kinds occur on a single tree we can appreciate differentiation between meristems, but in less stable meristems dedifferentiation may occur. Our later descriptions of architectural models and their reiteration will provide numerous examples illustrating these concepts.

II. Branch Complexes and Sympodial Growth

Although initiated as a single lateral meristem, a branch may proliferate; the proliferated structure still continues to function as a lateral unit for which we will use the term *branch* (or *plagiotropic*) *complex*. Branching within such a complex may be monopodial or sympodial.

Monopodial branching seems to be most common in axes which have distichous phyllotaxis, the resulting branches themselves are also arranged distichously so that dorsiventrality is maintained in all branch orders. This is common, for example, in cocoa, nutmeg, (*Myristica fragrans*, Myristicaceae), many species of *Diospyros* and *Phyllanthus* and in members of the Annonaceae. The relationship is not strict, many conifers have a rigidly expressed dorsiventrality of the branch complex but spiral phyllotaxis. Most Rubiaceae have a decussate leaf arrangement, but frequently also branch complexes with pronounced plagiotropy.

Sympodial branching of plagiotropic branch complexes occurs in two possible ways (using the terminology established by KORIBA (1958) but slightly modified and restricted to branches):

1. Substitution growth ("substituting growth" of KORIBA), the replacement of a terminal by a lateral meristem, after the terminal meristem has either aborted or, more usually, has become determinately differentiated as a terminal flower or an inflorescence.

2. *Apposition growth* ("apposing growth" of KORIBA), the displacement of a terminal meristem, which continues its vegetative growth, by an axillary meristem promoting the further extension growth of the branch complex (Fig. 12B). Because the evicted terminal bud continues its vegetative growth, usually as a short shoot, the successive units of the sympodial system remain clear.

To distinguish these two types of growth it is useful to refer to *plagiotropy by substitution* vs. *plagiotropy by apposition.*

Substitution growth by regular abortion of the shoot tip has been little studied in tropical trees. KORIBA specifically mentions it for *Xanthophyllum curtisii* (Polygalaceae) and it appears to occur in Dipterocarpaceae. In contrast, substitution of a seasonally aborted terminal by a lateral bud is familiar in a number of temperate trees; ROMBERGER (1963, p. 62) has provided a partial list which includes 17 genera, of which *Ailanthus, Catalpa, Celtis* and *Diospyros* may be cited here as taxa with the closest tropical affinities. In taxa with alternate leaves the morphologically lateral substitution meristem comes to occupy a pseudoterminal position and "pseudomonopodial" is a term sometimes used to describe such branching (e.g., in *Betula, Corylus, Salix*).

Substitution growth below a terminal flower or inflorescence occurs in a diversity of ways. Where there is delay in the development of the replacement shoots (i.e., where their development is proleptic) the morphological relationships are clear. Otherwise, development is by syllepsis; if the vegetative portion of each sympodial unit is then short and terminal inflorescences follow each other in rapid succession, the sympodial construction may no longer be obvious. In *Gossypium hirsutum* (Malvaceae), for example, each renewal shoot ends in a single flower and otherwise consists of only two vegetative leaves, one a prophyll, the other a foliage leaf which subtends the next unit and so on. This rapid succession of units in substitution growth seems significant in the reproductive strategy of the tree, since flowering becomes almost continuous. Other specialized examples are discussed on p. 174.

Apposition growth in some tropical trees is expressed in a stereotypically programmed way, commonly referred to as "Terminalia-branching", from the genus (family Combretaceae) in which it is so strikingly expressed. We comment upon it extensively elsewhere (Aubréville's model on p. 182) but describe its essential features here after FISHER (1978). *Terminalia catappa* provides the commonest and most widely distributed example. The orthotropic trunk grows rhythmically and branches monopodially to produce tiers of lateral branches, each branch of a tier developing as a plagiotropic complex. Growth of the complex may be described as horizontal, though in effect the sylleptic branch axis is at first orientated obliquely upward, but becomes progressively displaced toward and even below the horizontal.

After its first, limited, horizontal growth the apical meristem of the branch is reorientated and becomes erect whereupon further extension of the branch complex comes from a lateral meristem (Fig. 12B) which eventually repeats the eviction process. Commonly two lateral meristems are developed from one parent unit, these grow out in the horizontal plane at a fairly precise angle to each other so that the branch complex proliferates and fills the plane. Each evicted terminal meristem continues to function as a short shoot with congested internodes, showing rhythmic growth and seasonal flowering. It is convenient to speak of "displacement" of terminal by lateral shoot in a morphological sense, although physiologically this is misleading since the terminal meristem has normally turned erect before the replacement shoot is much developed, so that the development of the lateral is not a prime determining influence.

The lateral replacement shoot as a repetition of the first unit is sylleptic in its morphology, with a long basal internode. Four or five leaves are produced distally on the horizontal part of the axis before its apex has turned erect; the renewal axis or axes of the next generation arise in the axils of the third and fifth leaves but always on the lower surface. The individual shoot units of this system may be regarded as essentially orthotropic since leaves are spirally arranged and each meristem rapidly adopts an erect position. However, the integration of equivalent units into a branch complex is of an almost industrial precision so that "plagiotropy by apposition" describes the branch architecture well. Control of this complex in a high degree is shown in the genus *Bucida* (Combretaceae). In *B. spinosa,* sylleptic laterals are often aborted early and function as short spines. In *B. buceras* and its hybrid with *B. spinosa* the organization of the complex is such that a major sympodium becomes evident in older parts, with regular dominance of alternately left or right branch at a fork. The angle between forks is quite constant and not determined by phyllotaxis, as might be expected. The length of units is carefully controlled so that the mosaic of leafy rosettes (terminal short shoots) is optimally spaced. Examination of such a shoot system will readily convince an observer that a high degree of organization exists.

Apposition growth of this type is rather common in tropical trees, and one soon learns to distinguish it from the configurations of peripheral axes in orthotropic branch complexes, where no real plagiotropy exists as an organized differentiation (Fig. 12A, B). *Terminalia* (and other examples described later under Aubréville's model) show plagiotropy. In contrast, in many genera the lateral orthotropic meristems in the outer reaches of the tree crown function imperfectly and gradually come to imitate plagiotropy by apposition; the resemblance is most striking in distal units (e.g., *Rhizophora, Bumelia*). A comparison of young with older branch complexes on a single tree discloses whether one is dealing either with an orthotropic branch complex or with plagiotropy by apposition. In temperate trees with more slender axes the distinction might be less clear. However, plagiotropy by apposition is essentially a tropical phenomenon.

III. Plagiotropy and Syllepsis

In trees with differentiated shoot systems, the chronological sequence of branch initiation is an evident factor in determining meristem differentiation. It seems clear in such examples that the processes of syllepsis and prolepsis control shoot organization in a remarkable way. Cocoa, as investigated experimentally by GREATHOUSE and LAETSCH (1969), demonstrates this correlation. It must be recalled that with syllepsis, a lateral meristem develops as a branch without rest, with prolepsis a lateral meristem undergoes a period of rest after initiation but prior to further development; morphologically the resulting shoot types are readily contrasted (p. 42). The seedling axis of cocoa is orthotropic, with spirally arranged leaves. This sapling is determinate, but shortly before the abortion of its terminal meristem, a pseudowhorl of branches ("jorquette") originates at the ultimate nodes. These laterals develop by syllepsis and each forms a plagiotropic complex (whose further development usually involves infrequent monopodial branching). Subsequent growth in height is achieved by a single meristem which is situated at a node below the branch tier, this develops by prolepsis (since it was initiated earlier but has rested) and the shoot it produces is orthotropic, repeating the organization of the original seedling axis, and so on. By pruning orthotropic shoots immediately below the jorquette it was shown that resting buds could be induced to develop as either plagiotropic shoots or orthotropic shoots. The majority of these induced shoots were orthotropic, with orthotropy becoming virtually certain in meristems which had been long dormant. Another way of stating this is to say that syllepsis results in plagiotropic meristems; prolepsis mainly results in a meristem producing an axis similar to the parent meristem. The rule is neither universal nor absolute, but seems a useful rule of thumb to be applied to numerous tropical trees.

The positional effects of meristems in relation to their developmental potential are even more subtle and differences may occur in meristems closely juxtaposed, e.g., in the same leaf axil. Commonly, one (rarely more) meristems may develop sylleptically and become plagiotropic, adjacent meristems may be capable only of prolepsis and become orthotropic. *Rhizophora* and *Phyllanthus* species provide examples, with distal members of serial buds in a single leaf axil developing sylleptically, proximal members of the same series remaining dormant but growing into orthotropic shoots should they develop. In *Goupia glabra* (Celastraceae) the order of development is the inverse. This close connection between polymorphism and syllepsis in part explains the uniformity of axis organization in most temperate trees, since we have established that syllepsis is rare in them.

Quite clearly this overview does little to resolve many of the questions raised, but does reveal the complex situation. Anatomical examination of nodes which develop lateral meristems of differing potential is likely to be informative. For example, CREMER (1972) showed that in *Eucalyptus regnans* the traces to the two dormant (accessory) buds at each node are inserted on the stele of the sylleptic branch which develops at the same node. Does this indicate that they are themselves second- and third-order branches of a sylleptic first-order branch? Developmental details are needed to fill in this void which becomes very evident when a comparative survey is made.

IV. Plagiotropy in Monocotyledons

Plagiotropic complexes do not enter into the construction of aerial axes in woody monocotyledons to any marked degree. The only conspicuous exception is found in those species of *Pandanus* with marked differentiation between trunk and branch, described later (e.g., Stone's model). Plagiotropy of aerial branches is found in some scandent monocotyledons like *Dioscorea, Freycinetia, Ripogonum*, and *Smilax*. The bamboos provide other examples and their special situation is referred to later (McClure's model).

Plagiotropy is, of course, a pronounced feature of the underground axes of many monocotyledonous trees, as in many palms and the bamboos. We have even included a description of a monocotyledonous "tree", *Nypa fruticans* (Palmae) in which the whole vegetative system is plagiotropic, but here we obviously stretch our definition of tree well toward the rhizomatous condition generally.

However, such examples of creeping and underground axes stress the point already made by the plagiotropic branches without distichy, displayed by gymnosperms, i.e., that neither orientation nor phyllotaxis are absolute criteria in establishing plagiotropy. It is evident that axes can be made plagiotropic in many ways, and that plagiotropy and its definition still form a challenging field for more thorough investigation.

G. Branch Polymorphism: Short Shoots

I. In Dicotyledons

Differentiation of the shoot system within one tree into long shoots and short shoots (dwarf shoots) produces a useful division of labor. The long shoots produce growth in height and their proliferation adds to the overall framework of the tree. Short shoots usually have a specialized function, often as photosynthetic units, but commonly also as localized sites for reproductive structures (e.g., cone-bearing axes in conifers, flower spurs in fruit trees). They may also function as spines. In subsequent descriptions of architectural models we have concentrated on the distribution of long shoots, tending to treat short shoots as ephemeral units equivalent to leaves. This, of course, represents a considerable over-simplification because some very complex strategies must govern the disposition of short shoots. One can suggest that short shoots represent an economizing in axis "expenditure" which is most successful in exposed situations or with the deciduous condition, but we know of no studies which specifically address this point. The topic is dealt with in detail by ZIMMERMANN and BROWN (1971, pp. 25–30) with a discussion of physiological control. They also use the term "short-shoot habit" to refer to trees with uniformly congested internodes, like cycads.

We have already dealt with the special condition of Terminalia-branching, which leads to the development of plagiotropic branch complexes. The individual *terminal short shoots* produced by progressive eviction of meristems here form a mosaic of long-lived leafy rosettes as an essential architectural feature of the tree. This arrangement is common in tropical trees; the genus *Cornus* provides some somewhat comparable examples among temperate trees.

Lateral short shoots, in contrast, are developed in both temperate and tropical trees. Such shoots may be clearly circumscribed on the branch system, or there may be a transition between long and short shoots. This occurs in *Acer*, *Fagus*, and *Ulmus*, for example, where both long and short shoots are borne laterally on a previous year's extension shoot, long shoots developing from distal nodes, short shoots from basal nodes, with intermediate nodes bearing shoots of intermediate length. However, the distinction between the two kinds of shoot need not necessarily be arbitrary, because WILSON (1966) in his careful analysis of shoot distribution in *Acer rubrum* (red maple) in New England defined the two as follows:

> "Long shoots: Branches that elongate more than 2 cm per year and normally bear lateral branches if more than one year old.
> Short shoots: Branches that elongate less than 2 cm per year and do not bear lateral branches."

Thus not only short or congested internodes characterize short shoots, but they also fail to branch vegetatively. Transposition of one kind into another is possible if the local environment of a shoot changes. WILSON established that short shoots occupy most of the volume of the crown and bear most of the leaves and flowers. Equally, short shoots are relatively short-lived in comparison with structural long shoots, though long-lived when comparing them with leaves; perhaps 20 years is an absolute maximum. However, NEVILLE (1970) experimentally established that short shoots in *Maclura pomifera* (Moraceae) possess an "immunity" to senescence; they stay physiologically young. Abscission of short (and long) shoots has aroused considerable curiosity (e.g., THOMAS, 1933; MÖLLER et al., 1954).

Gymnosperms with short shoots are evidently highly specialized; they include *Larix* and *Pseudolarix* (Coniferales) and *Ginkgo* (Ginkgoales) all of which are deciduous but have persistent short shoots, which replace the foliage leaves annually. In *Cedrus* and *Cathaya* short shoots are present but evergreen. In *Pinus* the short shoots (needle shoots) are determinate but last more than one season. In *Taxodium* and *Metasequoia* the majority of shoots are ephemeral and abscise in the fall, but morphologically they are not short.

Temperate angiospermous trees with a well-developed short shoot system are familiar in *Acer, Betula, Corylus, Fagus* and a number of rosaceous fruit trees like *Pyrus*. All are deciduous. *Berberis* provides a shrubby example which is evergreen. The limited life span of short shoots is demonstrated by their frequent precise abscission, often leaving a characteristic clean scar, as in *Populus*. The age of fallen twigs can easily be determined by counting series of bud-scale scars.

Lateral short shoots are not found frequently in tropical rain-forest trees, and it seems that the evergreen habit is not conducive to their development. One may contrast this with their more frequent occurrence on trees in tropical environments which are dry, disturbed, or otherwise exposed, as in species of *Acacia* (Leguminosae – Mimosoideae), *Bumelia* (Sapotaceae), *Ximenia* (Olacaceae). *Crescentia cujete* (calabash-tree, Bignoniaceae) provides another example; here the framework of the tree consists of few thick branches bearing long-lived, spirally arranged short shoots which become quite deeply embedded in the furrowed bark of older axes.

The numerous examples of spine shoots in trees, e.g., *Crataegus* (Rosaceae), and many Celastraceae are not discussed. They represent but one kind of organ modification which produces spines and their protective function is clear. Of interest are those examples where both spines and short shoots occur together: as in *Maclura pomifera* (Moraceae) investigated by NEVILLE (1970). Here the relationship between spines, short shoots and long shoots is developmentally complex.

II. In Monocotyledons

Axis polymorphism is not a major feature of arborescent monocotyledons, as we have mentioned earlier, and clearly circumscribed short shoots are not formed. One species of *Pandanus* (*P. gemmiferus*) develops short laterals on the trunk and branches which may be organs of propagation, functioning like bulbils (ST. JOHN, 1962). Peculiarly specialized aboveground branches are developed in species of *Cordyline* (Agavaceae), especially *C. terminalis*, as negatively geotropic scale-bearing and fleshy shoots ("aerial rhizomes"). Experiments by FISHER (1972) showed that these shoots can readily be induced to become erect leafy shoots by manipulative experiments and by application of growth substances. The reverse procedure, i.e., the conversion of leafy shoot into a rhizome has not been achieved. This suggests that aerial rhizomes exist at a relatively unstable level of organization. Their ecological significance is obscure, but they illustrate well the morphogenetic principles which underly the concept of differentiation.

Our discussion of short shoots is necessarily brief, but we clearly do an important topic scant justice. In differentiating between terminal and lateral short shoots, we have evidently made a distinction between two important leaf-bearing strategies. More detailed analytical work addressing itself specifically to this point would be welcome.

H. Abscission

This topic is not dealt with in this volume, although the process of loss of parts is obviously important in determining tree shape. We refer the reader for instance to the work of VAN DER PIJL (1952, 1953) who cites many examples and discusses their biology, and to ADDICOTT (1978), where principles are discussed from the point of view of the plant physiologist.

I. Inflorescence

In subsequent descriptions of tree architecture, the organization of shoots is discussed in terms of the distribution of flowers only when overall branching is so influenced. Only a few general comments on flowering in tropical trees are therefore admitted at this point.

The subject of the physiological control of flowering in tropical trees is a complex one and the literature on the subject much too extensive to be considered here. Coffee probably represents the best studied example (e.g., CANNELL, 1972).

1. Flowering and Shoot Construction

Most definitions of inflorescence are morphological (e.g., JACKSON, 1928) although RICKETT (1944) has pointed out that the term initially had a physiological meaning referring to the condition of flowering. Hence the term should have a dynamic meaning, i.e., an axis or plant "at inflorescence". We have continued to use the term in our descriptions in its usual morphological sense. Much of the elaborate morphological terminology for "inflorescences" refers to herbaceous plants. One general principle which does emerge if ontogenetic events are considered is that dicotyledonous flowering branches are essentially dichasial in construction, with axes tending to be developed in pairs, corresponding to the paired bracteoles of a decussate system, whereas monocotyledonous flowering branches are essentially monochasial with axes developed singly at a node corresponding to the solitary bracteoles of a distichous system. The ultimate units in monocotyledons are often cincinni, i.e., sympodial complexes with one-sided branches (e.g., many Scitamineae, Palmae, Commelinaceae). In contrast dicotyledonous inflorescences tend more often to have terminal units which are two- or three-flowered, e.g., Myrtaceae – Myrtoideae, many Rubiaceae.

VAN STEENIS (1963) has pointed out some of the problems involved in delimiting the inflorescence as a distinct morphological entity in woody plants. His definition, however, still remains essentially a morphological one, i.e., "a specialized fertile part (or parts) of an individual plant which post anthesis does not participate in the vegetative extension of the 'individual'." The problem remains which order of axis must one use as a starting point, i.e., what does one mean by a "part" of a plant?

We do not wish to enter into a lengthy discussion of morphological terms, but point out that for architectural purposes (i.e., in the analysis of the overall organization of a tree) two ontogenetically exclusive conditions exist depending on whether or not flowering ends further activity in the meristem that gave rise to the flowers: (1) *hapaxanthy,* when a shoot apical meristem becomes wholly transformed into a flowering axis after a period of vegetative growth, i.e., the hapaxanthic shoot is determinate and ends in an inflorescence; (2) *pleonanthy,* when a shoot apical meristem continues its vegetative activity while producing lateral flowers or flowering axes, i.e., the pleonanthic shoot is indeterminate, its activity not being limited by flowering. This condition is most obvious in monoaxial trees like single-stemmed palms. In *Corypha,* for example, vegetative growth ends with flowering; in coconut, by contrast, it does not and the palm continues its vegetative growth while flowering also continues. Dicotyledonous trees with modular construction most commonly have hapaxanthic axes, e.g., *Ricinus, Manihot* (Euphorbiaceae) in which each axis ends its growth by flowering, to be substituted by lateral axes as described under Leeuwenberg's model (p. 145). In mango (*Mangifera indica,* Anacardiaceae) the vegetative and reproductive phases are distinct events, some meristems produce determinate flowering systems at one time of the year, vegetative meristems are active at another time of the year.

Sometimes the distinction between terminal and lateral inflorescences is initially not obvious. In many genera of Myrtaceae – Leptospermoideae (e.g., *Callistemon, Melaleuca*) the vegetative axis develops what appears to be a terminal spike because its flowers are produced laterally on the distal part of a growing shoot which continues its growth without loss of the terminal meristem. In such axes periods of rest, vegetative growth and flowering are clearly set apart, all dependent on the activity of the same meristem (PUROHIT and NANDA, 1968). In avocado (*Persea americana,* Lauraceae) the tree in flower appears to develop conspicuous terminal panicles. However, they are not hapaxanthic shoots because subsequent growth demonstrates that the apical meristem of the flowering axis continues its activity vegetatively and that the "inflorescence" is made up of a series of lateral compound dichasia and is not determinate. This situation is found in many species with rhythmic growth where the flowers more obviously occur at the base of each unit of extension (e.g., *Swietenia, Hevea*). In such examples there may be, on a single individual, a series of transitional forms between axes which are floral basally, vegetative distally, and those in which the distal vegetative phase of growth is lost. Consequently, one has long shoots with lateral flowers and short shoots with "terminal" flowers. In morphological terms the limits to the structure which may be recognized as "an inflorescence" can only be defined in an arbitrary fashion. For example, if one contrasts related genera in Myrtaceae-Myrtoideae one finds that some (e.g., *Psidium* spp.) can be described as having solitary flowers in the axils of foliage leaves. In others (e.g., *Myrcianthes* spp.) the axillary units, still subtended by foliage leaves, are branched and represent compound dichasia, which individually may be described as "lateral inflorescences". In other species (e.g., *Eugenia*) the individual flowers are subtended by scale leaves and recognition of the suitable comparative unit depends on whether the supporting axis is determinate or indeterminate. Both conditions can occur in the same individual and the problem is to establish which axis order is an "inflorescence axis". The situation is often very clear if one examines the shoot system of a tree as a whole, when the site of origin of meristems which, directly or indirectly, bear flowers can be established on a developmental basis. The term "inflorescence" for a constructional unit may, however, remain difficult to apply, and confusion can occur in diagnostic descriptions.

II. Continuous Flowering

In pleonanthic axes with continuous (as opposed to rhythmic) growth it is possible to have continuous flowering, a condition approached by several commercial and ornamental shrubs in the tropics (e.g., in species of *Hibiscus*, Malvaceae; *Ficus* spp. Moraceae; *Allamanda*, Apocynaceae and in *Carica*, Caricaceae) but the strict condition is probably rare. Otherwise flowering is itself an episodic phenomenon, despite the continued vegetative activity of the meristem. Some palms flower seasonally, though production of inflorescences is continuous (e.g., *Sabal*). External conditions, notably photoperiod, may control such periodicity. In *Rhizophora mangle*, in South Florida, where the climate is distinctly seasonal, GILL and TOMLINSON (1971b) have suggested that the seasonal fluctuation in flowering intensity, which involves a peak in mid-summer, is in part influenced by climate and in part mediated by internal nutritional balance. *Rhizophora* is essentially ever-growing and ever-flowering, but shoot growth is slowed in winter by low temperatures and flowers are then less frequent. Measurements further show that the presence of developing viviparous seedlings reduces the likelihood of a shoot flowering until the propagules it bears have fallen.

III. Cauliflory

Ramiflory and cauliflory (the development of flowers on the older branches or trunk of a tree) is seemingly unconnected with the overall organization of the tree, except in so far as inflorescences or flowers originate in leaf axils on young shoots from primary meristems which remain dormant for extended periods before flowering is expressed. This primary positioning may be evident when the scar of the subtending leaf long remains visible, as in cocoa (LENT, 1966). Of interest in cocoa, however, is the observation that normally flowering cannot commence before the development of the first plagiotropic tier, i.e., there is correlative interaction between the two kinds of axis in this cauliflorous species. In contrast we have the situation recently described by PUNDIR (1972) in *Ficus glomerata* (Moraceae), one of the numerous species of cauliflorous figs. The first syconia develop distally from buds in the axils of leaves. Flower development continues from these same sites on older branches, apparently endogenously from dormant buds, i.e., the site functions as a bud complex. Subsequently buds can appear exogenously and produce syconia for several years before they die and are replaced by yet another adventitious bud.

In the cannon-ball tree (*Couroupita guianensis*, Lecythidaceae) MCLEAN THOMPSON (1952) has described the cauliflorous inflorescences as wholly adventitious in origin. The specialized biology of stoloniferous flowering branches from the base of a tree (geocarpy and "earth-figs" of CORNER, 1952) has been discussed by EVRARD (1964) in relation to *Paraphyadanthe flagelliflora* (Flacourtiaceae). *Duguetia rhizantha* (Annonaceae) described by FRIES (1959) is a comparable example. As EVRARD points out there is no known example of flowers arising directly on roots, since a stem must precede the initiation of floral primordia.

IV. Floral Phenology

Discussion of flower periodicity in tropical trees has largely centered on overall flowering of populations and forests and the literature is extensive (e.g., ALVIM, 1964; HOLTTUM, 1940, 1953; MEDWAY, 1972; KORIBA, 1958; KOELMEYER, 1959). This reflects the biological and ecological importance of the topic to workers concerned with overlapping periods of nectar availability in different tree species as related to food resources for populations of pollinating insects or, from the point of view of the plant, in relation to competition for available pollinators (JANZEN, 1967; GENTRY, 1974). Fruiting in turn may determine food availability for larger animals (MCCLURE, 1966; JANZEN, 1970b, 1971). Foresters on the other hand need to know flower and fruit periodicity in relation to times of abundant seed for harvesting, important in dipterocarps, for example, which flower only at wide intervals (BURGESS, 1972; JANZEN, 1974).

The topic is of obvious commercial value in tropical tree crops, particularly as it relates to climatic influences and to commercial timber species, where it relates to breeding programs.

In our present concern with the individual tree, periodicity of flowering is not of major architectural significance as is discussed by RIVALS (1966). In pleonanthic shoots, for example, flowering may coincide with shoot expansion (e.g., rubber, mahogany) or not (e.g., coffee). In hapaxanthic shoots the inflorescence may develop only after a period of rest, as in the rather exceptional case of mango. The way in which different seasonal periodicities may be imposed on different genera with identical shoot construction is well shown by LEMS (1962) in temperate members of the tribe Andromedeae of Ericaceae. In all the examples chosen, axes are determinate and end in flowering. However, in *Oxydendrum* one morphogenetic cycle is completed within a single growing season, i.e., flowering axes are initiated and complete their development between June and August. A new shoot cycle is begun each April. In *Pieris floribunda* flowers are initiated, undergo meiosis and complete pollen development in one summer, but do not proceed to anthesis until the following spring, having overwintered. A new cycle is then initiated in early summer. In *Lyonia mariana* the morphogenetic cycle is even longer, since shoots which are initiated in April proceed only as far as the differentiation of inflorescence (but not flower) primordia by winter. These primordia overwinter and complete their development the following summer as conspicuous lateral buds on the leafless shoots.

J. Radial Growth: Conifers and Dicotyledons

In dicotyledons and coniferous trees architecture is the direct result of the activity of primary meristems. Secondary changes which are determining factors do occur in some examples, mostly by the development of reaction wood (e.g., Koriba's model, p. 155, possibly in Troll's model, p. 242 and see also the description of *Tsuga*, p. 246). Aspects of secondary growth are, therefore, not emphasized in subsequent accounts, but some brief discussion is relevant, especially in relation to growth periodicity. In addition some consideration of volume change is necessary for an understanding of surface/volume relationships (p. 289). Temperate trees exhibit periodicity of both extension and radial growth, which is clearly correlated with seasonal fluctuations in climate. The two are interrelated via a complex hormonal balance which is still not very well understood (ZIMMERMANN and BROWN, 1971, p. 82). What is the interrelationship between these two types of growth in nonseasonal, tropical climates? We have already seen that primary growth may be either irregular, or with a rhythm which is independent of climate, or in some circumstances continuous. Evidence for cyclic activity of the vascular cambium in tropical trees which possess such a meristem may be sought in the distribution of growth rings.

I. Growth Rings

A consequence of the annual period of cambial dormancy in temperate trees is the development of distinct discontinuities, usually annual, in the secondary xylem so that successive growth increments are conspicuously differentiated as "annual rings". The essential feature of an annual ring, such that the increment of wood of one year can be sharply segregated from that of the next, is a precise boundary between late and early wood. Late wood, formed at the end of one increment, is characterized by radially contracted elements with thick walls and narrow lumina; early wood, formed at the beginning of the next increment, is characterized by radially extended elements with thin walls and wide lumina. The boundary between the two represents the period of cambial rest (usually winter) during which time no secondary derivatives are produced. This abrupt distinction is further emphasized in ring porous trees in which a majority of wide vessels is concentrated in the early wood.

Other sorts of growth rings can exist in temperate trees but these can usually be recognized as "false rings" because they lack the sharply discontinuous outer boundary of the "true ring". False rings can be induced directly by a variety of external circumstances of which drought, fire, frost, insect defoliation, and mechanical wounding are well recognized. A common but not exclusive feature is their discontinuity, the increments may be lens-shaped or may merge gradually with unmodified wood in a tangential direction.

Dendrochronology, or tree ring dating, is a highly developed branch of wood anatomy which is dependent on a skilled observer being able to determine the relative age of a wood sample from the number of annual rings. By cross-dating an absolute age can often be produced for long-dead samples. The width of a single increment is a sensitive measure of the average growing conditions for the year of its formation, so that paleoclimatological information of a kind can be extracted from comparative tree ring studies. Sensitivity is greatest in seasonally stressed environments and in trees growing close to the limits of their tolerance. Much of forest ecology in north temperate regions is dependent upon the ability of an observer to date and cross-date standing and fallen trees to the extent that successional processes may be put in an accurate chronological context (HORN, 1975). This may prove highly enlightening when coupled with known historical events (e.g., hurricanes, see OLIVER, 1975).

The forest ecologist in the tropics has to forego this crucial parameter since tree rings either do not occur, or if they do there is insufficient information to support an understanding of their periodicity. Temperate foresters are so accustomed to the reliability of tree ring dating that they may not appreciate that temperate trees represent a special case.

Wood anatomists are prone to refer to any discontinuity in the wood of a tropical tree as a "growth ring", which of course is true in a general sense, but the source of this discontinuity is rarely known and the use of "annual ring" is usually very misleading. There are limited discussions of the topic of growth rings in tropical trees, but developmental understanding is always deficient. Is the growth ring a structural element, or is it a consequence of differential distribution of substances like tannins which impart color to the wood, as is the situation in *Rhizophora*, for example? Is there an abrupt transition from one increment to another, suggestive of a period of cambial dormancy, or is the transition gradual, as in a "false ring"? Are the rings localized and lens-shaped? So long as such uncertainties exist, the tropical ecologist works at an enormous disadvantage; a simple but reliable method for determining the age of tropical trees would be of enormous benefit to him. As it is, one is forced to rely on the subjective ability of an observer to recognize growth rings, and different sets of data may not be directly comparable.

II. Growth Rings in Tropical Trees

Extensive surveys which provide information about the distribution of growth rings in woody plants of the tropics are few. That of COSTER (1927, 1928) is classical and oft-cited. He demonstrated the wide structural variation which was possible and made it clear that age estimation by means of growth rings was unreliable. He attempted to correlate the presence of distinct growth rings with periodicity of shoot extension and suggested that deciduous species most usually have marked growth rings. Of particular interest was his discovery that species may lack growth rings and yet the cambium may be periodically dormant.

Other studies have concentrated on the distribution of growth rings in a sampling of woody stems. MANICRE (1958, cited in ALVIM, 1964) indicates that for 60 species from the rain-forest regions of the Amazon Basin 21 (35%) showed "clear" growth rings, 13 (22%) had "poorly defined" rings and 26 (43%) showed no rings at all. In regions with more seasonal climates the incidence of trees with clear rings rises, those with poorly defined or no rings become fewer. CHOWDHURY (1964) gives a figure of 25% for trees with rings in India. He indicates the wide range of anatomical characters which he admits in his recognition of rings.

Even in a subtropical climate, the range of possibilities may be considerable. TOMLINSON and CRAIGHEAD (1972) surveyed the woody flora of South Florida, which has a predominant West Indian element and a minority of temperate species, but a markedly seasonal climate. The temperate species, as might be expected, show pronounced annual rings of growth, but so do a few tropical species, e.g., *Swietenia mahagoni*. The great majority of species (51 out of 87, or 59%) lack growth rings, using fairly rigorous criteria for the recognition of growth rings. One temperate species, *Quercus virginiana* (Fagaceae) falls into this category, although it is known to develop annual rings in the more northerly and greater part of its range. These authors made some attempt, by measurements of scarred trees, to establish frequency of growth rings and on this basis were able to recognize a group of trees (21 out of 87, or 24%) with non-annual growth rings. One special example in this category, *Avicennia germinans*, is discussed further below.

From this work, which is only preliminary, it is nevertheless clear that no generalizations can be made. Specific case histories need to be studied. The range of possibilities is wide so that one cannot predict the growth ring structure of the wood of a tree from a knowledge of shoot behavior, or vice versa. It is safe to say that ring porous trees are very rare in the tropics; *Tectona grandis* ("teak", Verbenaceae) is the most familiar example. Probably all ring porous trees are deciduous.

III. Cambial Activity in Tropical Trees

Studies of the periodicity of cambial activity in tropical trees are rare. RICHARDS (1952) cites only three articles on this subject, those of SIMON (1914) and COSTER (1927, 1928). At the present time one can add to these very little more (e.g., ALVIM, 1964; AMOBI, 1973, 1974; LAWTON and LAWTON, 1971; HUMMEL, 1946). AMOBI (1973) has established useful anatomical criteria for recognizing fluctuations in cambial activity. However, the subject should progress since there are now excellent recording dendrometers for humid environments which are extremely sensitive and reliable; the subject has been reviewed very completely by BREITSPRECHER and HUGHES (1975).

The above literature has a strong West African emphasis, and since this is a region with a distinct dry season it may provide a biased representation. An annual period of cambial activity is common in trees of that area, usually with the development of growth rings, but the sampling bias here seems to be towards deciduous species. Results by different workers may not necessarily be consistent with each other. For example, AMOBI (1973) records a period of cambial inactivity in *Bombax buonopozense*, but LAWTON and LAWTON (1971) include this tree in a group of species in which there was always "active phloem" present, but were unable to decide if the cambium itself remained continually active.

Nonannual periodicities in cambial activity which still result in discrete growth rings in the secondary wood are known for tropical trees. HALLÉ and MARTIN (1968) established a direct correlation between the periodicity of extension growth (usually six flushes a year; Fig. 7) and the number of growth rings in the axis of rubber saplings. The existence of trees in South Florida with nonannual growth rings has been recognized by TOMLINSON and CRAIGHEAD (1972).

A specialized, but pertinent example is provided in the study by GILL (1971 b) of *Avicennia germinans*. The stem anatomy of this tree is unusual in that alternating rings of secondary xylem and phloem tissue are produced, apparently by successive cambia. Ring width is very uniform. Measurements show that there is no seasonality to the production of these rings, their number is a direct function of the axis diameter. This is most readily observed when the base of sylleptic branches is compared with the axis on which they are inserted; although these are contemporaneous in development, the number of rings they exhibit is different. GILL suggests that ring development is under endogenous control.

The limited discussion of the subject does establish that careful studies of cambial activity in tropical trees still need to be done in great numbers. It is only after a wide selection of case histories have been reliably documented that general principles will emerge. Existing work on secondary xylem and phloem formation in temperate trees surely must serve as a guide, but rules which apply to certain groups of trees need not necessarily apply to all. The subject is of obvious commercial application since a knowledge of periods of cambial dormancy can be important in determining when grafting can be most easily effected. Another application might be the determination of the moment for the felling of commercial timber with a minimum risk of splitting of the bole.

K. Radial Growth: Some Variations

I. Trees Without Secondary Growth

Evolution in land plants has been directed both towards more efficient reproductive methods, e.g., the development of the seed, and towards a taller, much-branched habit. The former condition makes plants more efficient and adaptable in terms of dispersal, dormancy and establishment, i.e., as populations; the latter makes them more successful in intercepting light individually. Taller plants also shade out competitors. It is evident from our knowledge of the anatomy of extinct groups of plants that evolution of the tree habit was a gradual one and that a number of contrasted possibilities were exploited. Many of these groups "experimented" with some kind of secondary growth which culminated in the modern tree represented by the dicotyledonous hardwood or the conifer, both of which have ranged widely in a great diversity of ecotopes, temperate and tropical. Such trees possess a vascular cambium capable of producing secondary vascular tissues which augment and support the elaborated primary body. The cambium is supplemented by a phellogen, or cork cambium, which produces protective bark. Other trees lack the ability to produce secondary vascular tissues. Examples include palms, pandans, and some other arborescent monocotyledons, together with tree ferns, all of them almost exclusively tropical in their distribution. We discuss here the special constructional features which are a consequence of the limitations imposed on the plant body by the absence of secondary vascular tissues, and consider why they should be tropical.

1. The Palm-Habit

Apart from the true palms (Palmae) a number of other taxa have the same constructional features as palms, i.e., most species of *Phenakospermum*, *Ravenala*, and *Strelitzia* (Strelitziaceae), some Xanthorrhoeaceae (e.g., *Dasypogon*, *Kingia*), a few Bromeliaceae (notably *Puya raimondii*). These have vegetatively unbranched aerial stems bearing a crown of either large or numerous leaves. All species of *Pandanus* and *Sararanga* (Pandanaceae) are similar in that they lack secondary vascular tissues, producing massive axes by primary growth, but the aerial shoots are branched.

When one appreciates that such plants originate from seed-borne meristems with small apical tissue which is initially capable of very limited primary thickening growth, it is clear that the seedling axis itself is narrow. The development of the massive crown meristem which eventually is needed for the production of a wide primary axis is achieved by gradual ontogenetic change; successive nodes are progressively wider so that the adult diameter is achieved by a stepwise process. The formation of a primary trunk is therefore a protracted process.

"Establishment growth" was the term coined by TOMLINSON and ZIMMERMANN (1967) to describe the process of initial trunk development in palm seedlings, and the expression is useful in describing early stages of growth in all monocotyledons.

The process involves peculiar mechanical and physiological restraints imposed on the developing axis of a plant without secondary vascular tissues (HOLTTUM, 1955). An axis developing in this way is obconical and is obviously mechanically unstable. In most palms this instability is obviated by the initial development of the axis below ground level. Growth of the seedling itself is often specialized to bring about burial of the plumule. In many palms, for example, the cotyledonary organ elongates, so aiding the burial of the shoot apical meristem. Otherwise the burial process may occur later in ontogeny. In a number of palms the shoot grows obliquely downward for an extended period before becoming re-erected. The seedling axis then has a characteristic "saxophone" shape (e.g., *Sabal, Rhopalostylis*).

The radicle or seedling root in monocotyledons is always short-lived because it is capable only of primary growth, consequently no matter how much it can extend its absorptive area by distal branching, its attachment to the seedling axis represents a bottleneck and the seedling root alone cannot supply the increasing needs of an enlarging axis and crown. The obconically elongating axis, however, provides an increasing area for the insertion of numerous adventitious roots so that the potential bottleneck is by-passed.

In some palms (e.g., *Socratea* and related genera) and especially in many *Pandanus* species, the seedling axis does elongate, whereupon its obconical form is very obvious. Associated with this method of growth is a series of aerial adventitious roots which are of progressively wider diameter in proportion to the diameter of the axis. In addition to supplying the transport needs of the plant, these aerial roots also provide the mechanical support for the developing tree and the term "stilt root" or "prop root" which is applied to them is appropriate. In the larger species of *Pandanus* these aerial prop roots may exceed 10 cm in diameter; it must be remembered that these massive organs are wholly primary.

Increase in crown size of palm-like plants remains restricted by the width of the trunk which the young plant establishes, since it provides an axis of given diameter with fixed mechanical limits and a fixed cross-sectional area for conduction. Such plants, therefore, have either unbranched aerial axes, as in palms, or if there is branching, as in *Pandanus*, it is quite limited. In *Pandanus* there is either progressive reduction in branch diameter as the tree develops, or the branches are all much narrower than the trunk. Consequently the architectural convergence between such trees and those with secondary growth is the more intriguing, because their anatomical and physiological organization has little in common. As in plagiotropic branches, one here encounters once again comparable structural features brought into being by a fundamentally different internal pattern. The point deserves stressing because one of the essential points raised in this book is that such structural convergences, spurious though they may seem, represent a biological necessity for functional and competitive disposition and growth of organs in plants.

Many *Pandanus* species "short-circuit" the trunk as the pathway for conduction between root and crown by developing direct connection between branch and substrate via further aerial roots; such trees are typically low and spreading, e.g., *P. tectorius, P. candelabrum*.

Other methods of establishment growth are possible in monocotyledons, and TOMLINSON and ESLER (1973) have provided a description of some of these as they relate to the woody monocotyledons in the New Zealand flora. Not all of these necessarily lead to the development of trees.

2. Bamboos

Establishment growth in bamboos and, indeed, in many rhizomatous monocotyledons, involves the development of progressively wider aerial axes by sympodial branching of an underground rhizome system, each successive branch order being ultimately wider than the parent axis on which it originates until the axis diameter characteristic of the adult is achieved (see p. 3). In larger bamboos this can lead to the development of culms up to 30 cms in diameter and approaching a height of 30 m. TOMLINSON and ESLER (1973) have provided a description of establishment growth of this kind in *Ripogonum scandens* (Smilacaceae), a monocotyledon with twining aerial stems.

3. Tree Ferns

Larger ferns of the families Cyatheaceae and Dicksoniaceae lack secondary growth, but develop tall woody trunks up to 10 m high. Establishment growth is protracted in these plants, but the gradually widening basal part of the trunk is obscured by the massive fibrous network of slender adventitious roots which provide most of the tree's mechanical support. The stele of such trees is massive, but not very complex in its anatomy, although it is often supplemented by a well-developed medullary vascular system. Since tree ferns are subject to the same constraints as all trees with entirely primary growth, the trunk is normally unbranched and the terminal crown of leaves is large. Some do propagate by lateral stoloniferous offsets (HALLÉ, 1965).

A few monocotyledons, notably of the family Velloziaceae, have the same generalized construction as a tree fern, i.e., with an axis supported by fibrous adventitious roots, but they do not make plants much over 2–3 m high. The anatomy of the axis proper is, of course, fundamentally different from that of the tree fern, but still lacks secondary vascular tissues. *Microdracoides squamosus* (Cyperaceae, West Africa) is similar.

II. Arborescent Monocotyledons with Secondary Growth

One cannot complete a description of trees without mention of monocotyledons which do develop a secondary, vascular cambium (TOMLINSON and ZIMMERMANN, 1969). These are best exemplified by trees like *Cordyline, Dracaena, Yucca, Dasylirion,* and other genera included by HUTCHINSON in the family Agavaceae, but trees with a similar anatomy occur in Xanthorrhoeaceae (*Xanthorrhoea*) and mention has to be made of certain shrubby Iridaceae (*Witsenia, Klattia*). The secondary tissue in such plants consists of scattered vascular strands, and is quite unlike that of dicotyledonous trees. There is a close structural and developmental relationship between primary and secondary vascular bundles in such trees. This is sufficient to demonstrate that the developmental step from primary to secondary growth is not a large one (ZIMMERMANN and TOMLINSON, 1969, 1970). One might reasonably conclude from this that such plants are derived and specialized, but the possibility of their being ancestral cannot be ruled out entirely. An argument against this is the close similarity of the primary body in both types of arborescent monocotyledons and the observation that establishment growth is found in *Dracaena* and similar plants. *Cordyline,* in fact, shows a peculiar specialization of its underground organs in early stages of development (TOMLINSON and FISHER, 1971; FISHER and TOMLINSON, 1972; TOMLINSON and ESLER, 1973).

Such monocotyledons, in fact, although they would appear to have overcome the mechanical constraints of the primary tree, by virtue of their ability to form a secondary body, still retain many features of palm-like plants. They may be, as in *Yucca, Xanthorrhoea,* and *Dasylirion,* little-branched plants with few massive axes. *Cordyline* and some *Dracaena* species become relatively well-branched, but retain terminal tufts of strap-shaped leaves. The trunk may become quite massive as in *Dracaena draco* or basally swollen as in species of *Beaucarnea.* Undoubtedly one restraint put on their ease of elaboration is that the roots still remain entirely primary; the only exception being the genus *Dracaena.* Establishment growth leading to the formation of an obconical primary axis is easily demonstrated in such trees.

Architecturally, such plants have a quite limited capacity to develop much diversity, as is evident in later descriptions.

III. Cycads

Although cycads possess secondary vascular tissue, this is always limited in extent. Such plants consequently suffer from very similar constraints to those imposed on palm-like plants. Their physiognomy is, therefore, similar, although our later description demonstrates interesting specializations.

L. Root Systems in Tropical Trees

Root systems of tropical plants are so little investigated that no extended discussion is possible although there exist excellent summaries (e.g., SCHNELL, 1970, pp. 229–254; JENÍK, 1978). Here we mention a few major topics, but appreciate that lack of knowledge represents a serious deficiency in our later description of tree architecture. The deficiencies are even more obvious when root competition in forest trees is discussed (e.g., WILKINSON, 1939).

The existence of morphological and anatomical diversity in the roots of tropical trees has long been known (e.g., ADAMSON, 1910 on *Terminalia arjuna,* Combretaceae) but attention has inevitably focused on the more obvious aspects of root morphology of tropical trees, notably those resulting in the development of aerial roots, especially in mangrove species (TROLL, 1937). Buttressing, which is not strictly a root phenomenon, has been a major preoccupation (see p. 288).

A number of authors (e.g., OGURA, 1940) have drawn attention to the potential value of relatively accessible aerial roots in tropical plants as a source of general information about root growth and physiology. JENÍK has been a prime mover in this field (LONGMAN and JENÍK, 1974, p. 56–59; JENÍK, 1978). GILL and TOMLINSON (1975) have provided case histories chosen from diverse examples (e.g., *Rhizophora, Pandanus, Cissus, Ficus, Macrozamia*) and to this list tree ferns, numerous epiphytes and lianes could be added. Aerial root systems of woody plants are notable in swampy parts of tropical forests and have produced many descriptive studies (e.g., KERFOOT, 1963; JENÍK, 1967; KUBIKOVA, 1967; OLDEMAN, 1971). Pneumatophores seem particularly characteristic of palms in wet situations, as emphasized by OLDEMAN, (1969) in his study of *Euterpe oleracea* Mart. and DE GRANVILLE (1974) in the same species and *Mauritia flexuosa* L. The aerial root systems of mangrove plants provide a varied set of examples and the work of TROLL and DRAGENDORFF (1931) on *Sonneratia* in this field is outstanding as an example of an investigation of root architecture. Much of the research on mangrove roots has been anatomical-physiological in its approach, with an attempt to understand the functions of such aerial roots in terms of gas exchange [e.g., CHAPMAN, 1944 on *Avicennia germinans* (syn. *A. nitida*), Avicenniaceae]. GILL and TOMLINSON (1971a) have been concerned with the unusual growth of aerial roots in *Rhizophora mangle* in which the zone of extension exceeds 15 cm, compared with a very short extension zone in subterranean roots. This indicates how the freedom of the aerial environment can permit growth expression of distinctive kinds to occur in roots. An analysis of the underground system of *Rhizophora racemosa* by ATTIMS and CREMERS (1967) has stressed the importance of the capillary rootlets in these plants which otherwise lack root hairs. *Rhizophora* is of interest morphogenetically because the aerial root remains unbranched (unless damaged), but the same root meristem when it becomes subterranean is abundantly branched (GILL and TOMLINSON, 1977).

A universal feature of root systems in woody plants which is apparent in much of this work on tropical trees, as well as in temperate woody plants (e.g., WILSON, 1964; LYFORD and WILSON, 1964, on *Acer rubrum*) is that roots mainly grow horizontally. This needs emphasis since so much experimental work is done on the radicle of a few herbaceous plants (pea, bean, maize, tomato) in which a positive geotropic response is pronounced. This represents one possible orientation for roots, but should be contrasted with erect pneumatophores, arising from otherwise predominantly horizontal roots. Specialization of ultimate roots either in mycorrhizal association or in association with nitrogen-fixing microorganisms has been insufficiently studied in tropical trees.

Precise orientation with differentiation comparable to that between orthotropic and plagiotropic shoots in aerial parts is evident in many root systems with the "orthotropic" roots growing down and not up. Since roots bear no specialized appendages the range of morphological criteria used for shoots (p. 48) is not available. However, OLDEMAN (1971) found evidence of a regular disposition of root-organs on pneumatophore-bearing horizontal roots of *Eschweilera* sp. (Lecythidaceae). Orientation, i.e., vertical versus horizontal, for the moment remains the predominant diagnostic criterion.

A detailed experimental study of cocoa by DYANAT-NEJAD (DYANAT-NEJAD, 1971; DYANAT-NEJAD and NEVILLE, 1972) has indicated the extent of root organization. The seedling radicle is orthotropic and produces a series of plagiotropic laterals arranged in six series. It was shown experimentally that the plagiotropy of the laterals is induced precociously by the meristem of the orthotropic tap root. Destruction of the orthotropic meristem brings about its immediate replacement by one of the plagiotropic laterals, which becomes the new orthotropic "leader". Older laterals, however, retain their plagiotropic state, having become "fixed". We have here a system of "apical control" quite comparable to that in the aboveground parts of woody plants with induced plagiotropy (p. 50). In oak (*Quercus sessiliflora*, Fagaceae) on the other hand, replacement of a damaged radicle is entirely by the formation of an adventitious meristem, since existing laterals retain their plagiotropic state and show no dedifferentiation. This situation is comparable to that in the aerial roots of *Rhizophora* and *Pandanus* in which a damaged apex is replaced by a newly constituted lateral meristem. This seems a distinctive feature when considered in isolation, but the subterranean root system of woody plants generally seems to behave in the same way (LYFORD, 1975).

The existence of regular series of plagiotropic laterals in root systems suggests that it may be possible to recognize "architectural models" in root systems comparable to those in the shoot system, and JENÍK (1978) has made a preliminary attempt. According to LÉONARD (1957) laterals may develop in series of four (*Afzelia bella*) or six (*Gilbertiodendron splendidum* both in the Leguminosae-Caesalpinioideae) on the seedling root with a precise orientation in relation to the cotyledons, suggesting the expected relation with anatomy. The existence of tiers of laterals on the roots of *Lecythis* species provides an example of distinctive architecture.

Of particular interest are the correlations between root and shoot growth. HALLÉ and MARTIN (1968) showed that root growth in *Hevea* (rubber) is continuous in contrast to the rhythmic growth of the shoot system. This independence between root and shoot growth has been demonstrated for temperate trees by LYFORD and WILSON (1966) who showed that roots of *Acer rubrum* in Massachusetts could be made to continue growth in early winter, long after the shoot system had become dormant, by providing roots with localized warmth. A similar lack of correlation between root and shoot in the matter of cambial activity was also demonstrated by WILSON (1964), who showed in *Acer rubrum* that the distal parts of woody roots are often uniformly cylindrical over long distances, without any regular taper.

There is only scattered information about root suckers in tropical trees, although the phenomenon is probably quite extensive. Where it occurs it may characterize behavior in open or disturbed sites (e.g., *Trema*, Ulmaceae) and, according to CHIPP (1913) in *Musanga* (Moraceae). The subject is mentioned again briefly where reiteration is described.

Chapter 3 Inherited Tree Architecture

A. The Concept of Architecture and Architectural Tree Models

In the previous section features of morphology and growth of trees have been discussed, with a major concern for tropical species; parts and processes have been emphasized, but there has been little discussion of the overall organization of the tree. This aspect becomes the subject of the middle section of the book, in which, tree "architecture" is described in terms of "models" within an "architectural continuum". These terms have a special application in our usage and need an exact definition.

I. The Architectural Continuum

Organization in plants reflects the precisely controlled genetic program which determines their development. This organization exists in large, long-lived woody plants as much as in herbs, cryptogams and microorganisms where the organized whole is often very obvious. Organizational patterns in trees, however, have not received sufficient attention for three reasons. First, is the obvious problem of their size – they can be studied only in natural environments or arboreta. Trees cannot be stored in toto, as dried specimens in herbaria or museums.

Second, the range of expressed form is large only in the tropics; it is only by examining a variety of tropical species that the existence of a great diversity of growth patterns in woody plants can be appreciated at all. This is a point we have mentioned elsewhere, and it needs continual emphasis. Botanical science originated in temperate countries, with an initial preoccupation with the vegetation of temperate latitudes, and it still remains largely temperate-centered. Trees in a tropical forest have a range of growth form represented, for instance, by palms, pandans, mahogany, kapok, cocoa, coffee, sandbox, etc., not all of which have their counterpart in a pine, beech, oak or birch forest in northern latitudes. Studying organizational diversity in regions where it is minimal is least likely to produce valid generalizations.

Third, precise growth patterns of trees are much disrupted by exogenous, environmental factors, since most woody plants are long-lived and the opportunities for environmental disturbance are proportionately extended. Trees, unlike animals, have an "open" pattern of growth resulting from continued activity of growth centers (meristems) which are usually replaced readily if they are lost. Consequently any underlying regular pattern in the proliferation and spacing of primary meristems tends to be obscured by outside disturbances. The microclimatic environment of the tropical rain forest is relatively uniform and ecological disturbances are minimized, providing the best opportunities for recognizing endogenously determined growth patterns in trees.

The visible, morphological expression of the genetic blueprint of a tree at any one time is here referred to, as its *architecture*. The concept is static so far as there is no change implied in a *momentary* observation, as might be illustrated by the analogy of a building under construction that we look at every day; one single daily observation does not in itself clarify the dynamics of construction, whereas a series of such observations does. For a tree, the growth program which determines the successive architectural phases is here called its *architectural model*, or shorter, its model. The concepts of architecture and model can be illustrated diagrammatically by a series of figures (see illustrated key, p. 84), each one showing an ephemeral phase in the development of the tree, i.e., its architecture, real and observable at any one time. The model, in contrast, is an abstract concept, made visible only by a series of architectures. Therefore, when we speak about the "architectural model" of a tree, we refer to its plan of growth. Analyzing tree growth in this way, we find that many arborescent species have the same, other species different architectural models, and that these similarities and differences are not necessarily dependent on taxonomy. Difficulties are encountered because in its momentary architecture a tree may or may not *conform* to its model. Many gymnosperms conform very precisely to their genetic growth programs, so that their architectural model in part is evident because such trees are symmetrical – one need only think of *Araucaria*, *Pinus*, *Abies*, for example. A similar symmetrical architecture is common in many "pagoda trees" of the tropics (e.g., *Terminalia catappa*). Equally, however, many trees conform precisely to their model without necessarily being symmetrical; an architectural analysis has to be made before this can be appreciated. Trees described later under Troll's model (p. 242) exemplify this well.

The architectural model is also commonly obscured in trees because they suffer continuous environmental stress and accomplish constant adjustment to this stress.

Recognition of the architectural model of a tree is often difficult. The complete spectrum of architectural phases of a tree model is only expressed when the tree is grown from seed, and a cycle of architectural changes can be considered to be complete when a tree flowers and seeds are dispersed. Beyond this phase, the architecture of the tree continues via observable changes as the tree grows in size. However, the model is not usually "completed" in the sense that a building constructed from an architectural plan is completed, because the essence of the model is *change*. Only Holttum's model and the few rare branched hapaxanthic (= monocarpic) trees constitute an exception. Otherwise constraints are eventually put on growth by the energy limits of a natural environment.

Architecture is therefore not to be confused with *shape* or physiognomy, which is a static concept, not taking dynamic processes into account. Similarly architecture cannot be equated with growth habit, since this refers essentially to the ultimately expressed form of the organism (herb, shrub, or tree) and implicates size. Architecture does not involve size and diminutive herbs and giant forest trees may exhibit precisely the same architecture. *Phyllanthus niruri* (Euphorbiaceae), a weedy species of which flowering individuals may scarcely exceed 10 cm, has an architectural model identical with that of *Goupia glabra* (Celastraceae) a forest tree reaching a height of 50 m.

Diagrammatic illustration of the architecture of a tree is problematical because there is no static schematic method whereby continual change can be represented. A single drawing represents the level of architectural organization of one point in time, a series of drawings is better but still indicates a limited number of phases. It might be possible, were one to adopt the movie camera, to represent one dimension by motion, as ZIMMERMANN and TOMLINSON (1966, 1972, 1974) translated length into apparent motion in their analysis of vascular systems, or as BELL (1976) simulated spread of rhizome systems with computerized techniques. Our own two-dimensional single or serial illustrations of each model therefore are but the simplest possible graphical representations of growth.

It must be emphasized that this form of analysis is applicable to all organisms, not only trees. Any entity which has a structure which changes in time can be studied architecturally; there is an insect model, there are coral models, algal models, fungal models and also forest and vegetational models. We shall deal briefly in subsequent chapters with the subject of architectural models in lianes and herbs and show their frequent similarity to tree models. It is appropriate also to consider later the likelihood of evolution in kinds of architectural tree models.

Restricting one's attention to trees for the moment, methods have to be found of describing them and categorizing their models. The simple criteria used in architectural analysis are outlined below (p. 80). Using the methods described in the next section to investigate a large number of trees, including a majority of tropical species, it becomes evident that the variety of architectural models which can be discovered effectively forms a continuum, but with many contrasted extremes. An oil-palm and a rubber tree, for example, are architecturally widely divergent. The intervening architectural domain is not empty, but charting it would seem to be an impossible task were it not for the fact that many species show identical or more or less identical architectural models. The continuum is not uniform, we can find points of reference within it and these points are named by a system which is described later (p. 79). These named points of reference in the continuum of tree architecture may therefore be likened to centers of population on a demographic map, corresponding to towns of greater or lesser size separated by intervening, sparsely populated country. The named models provide semantic pegs on which a great deal of information about tree growth can be hung. Most trees which have been investigated over an extended period in their individual development can be confidently assigned to a named model, or much less frequently, to an approximate place between named models. This permits a sorting of the variety of tree architectures into rational order.

Two contrasted methods are available for establishing categories for models, first that of *typification*, which provides a taxonomic point of reference to which a given example may or may not approximate; second that of *definition*, which provides precise boundaries within which a given example may or may not be included. For reasons which are discussed elsewhere (p. 79) the second method is adopted, following H.O. (1970). The method has proved workable and we have been able to recognize 23 tree models, which is a manageable number. It is surely not without significance that, out of the thousands of tree species which exist, this small number of architectural models can be recognized, and it is useful to consider the adaptive significance, in an ecological sense, of different models. This is difficult because, as we have emphasized, an individual mature tree conforms only more or less precisely to its model. We have therefore to determine the degree of plasticity in individual development which each model permits, this process of adjustment is explained at some length in a later section of this book. Since the behavior of trees under stress in rigorous environments cannot be anticipated without a detailed understanding of architectural tree models, our apparent preoccupation in subsequent pages with the minority of trees showing an "ideal" growth is absolutely essential if we are to discuss trees in the forest.

The use of this term "model" should not be confused with that of modern cyberneticians who have, for example, a precise mathematical usage for the word "tree"; see LEOPOLD (1971). Our models are simple—they probably represent the most elementary analysis of plant form possible and they are qualitative. Recognition of this diversity by analysis and categorization of examples is surely beneficial to the advancement of the science of plant morphology.

II. Recognition and Study of the Architectural Models

The concept of architectural modeling is a dynamic one, since it refers to the genetic information which determines the succession of forms of the tree, analogous to the blueprint which is the plan of a machine. In order to understand architectural models, one has to observe trees as individuals at different ages, including at least the earliest part of their life and in as optimal an environment as possible so that the model is expressed freely. In fact, a tree ceases to be of value in architectural analysis once it is subject to some environmental "traumatism" which irreversibly alters its visible form. It may be objected that trees very rarely grow unstressed in ideal environments. Nevertheless, the concept of an environment without substantial physical disturbance is quite appropriate to the humid tropics where it is more nearly approached than in temperate forests. A treelet of the forest undergrowth, for example, is almost in an optimal environment climatically, although still subject to damage by insects, falling branches and browsing animals.

For the moment, observation of trees in a state as nearly ideal as possible may be compared to early studies in physics, when understanding of movement without friction or of ideal gases, was an indispensable preliminary to the correct interpretation of more complex natural situations. This is also true of the study of architectural models. The analysis of evident growth processes expressed by such phenomena as reiteration, readjustment, and miniaturization (p. 259) had to wait until clear ideas had been established about the elementary endogenous development of the model throughout at least one biological cycle (i.e., from seed to seed). Only this relatively simple condition is referred to in this central section of our book. If the reader is eager for knowledge of the growth of trees in natural environments and wearies of the initial description of the ideal state, we beg his patience, because other and perhaps ecologically more significant aspects of growth are considered in later sections. It is our main contention in this work that it is this disregard of inherent growth parameters of trees which has hampered a full understanding of their form.

Trees are generally long-lived and slow-growing, therefore protracted observation is necessary to follow the complete development of their successive architectural phases. This can be done by growing trees where they can be regularly observed. In the humid tropics cultivation of wild trees is no great problem. A rudimentary, insect-screened slat-house with concrete or wooden tubs, each containing a cubic meter of good soil, and with a water tap at hand, is sufficient to allow most trees to be grown until they flower and fruit for the first time. Seeds are collected in the field, together with a voucher herbarium specimen which in the tropics is essential for identification of the parent source, because taxonomic knowledge is so often at an imperfect stage. Seeds are handled according to size (cf. NG, 1973, 1978). Larger seeds are sown directly in pots, smaller seeds can be germinated on wet blotting paper in Petri dishes. The seedling is drawn or photographed for record purposes before being transplanted, either directly into one of the tubs, or after an intermediate stage in a flower pot. Drawn and written records of further development over as long a period as possible are kept, ending mostly when the young tree threatens to exceed the limits of the slat-house. When the tree flowers early, this method is ideal and a surprising number of species can be studied since many trees, even big ones, do flower at an early age. *Hura crepitans*, for example, is a forest giant which can flower first at a height of 2 m and so initiates the branching pattern by which its model can be recognized (p.158).

Tropical tree crops provide another source of information since often large populations of uniformly aged trees can be studied. Plantations are usually protected against pests and diseases, while nutrient and water deficiencies are avoided so that endogenously determined form can often be well observed. One has to be aware, however, to what extent propagation is clonal, by cuttings or grafting, as with rubber and mango. Propagation may involve only part of the model, as with plagiotropic branches of cocoa.

Plantations of commercial timber species can be important sources of information, especially as these usually involve propagation by seed. Ornamental trees or shrubs and many fruit trees are too often pruned or trimmed to leave their architecture intact and they also are usually grown from cuttings rather than seeds. Similarly plants in botanic gardens, although potentially a source of a great deal of information, may also have been pruned or maladjusted in transplanting. A botanic garden serving its true function as a research institute is probably the greatest potential source of information about architectural aspects of tree growth, provided the administration is sympathetic towards research on large numbers of species of woody plants. Too often, however, botanic gardens serve purely horticultural ends and neither the selection of material nor the objectives of science are well served.

Natural forest itself, of course, would appear to supply the largest source of information about tree architecture. In reality, the percentage of plants with an intact architecture and showing different developmental phases is small. More usually saplings and trees are damaged to the extent that their inherent form is obscured. In French Guiana, for example, between five and twenty intact trees may be found along 100 m of forest trail; moreover, most of these trees often belong to the same species. To find sufficient examples of intact architecture in another species 2 or 3 km of trail may have to be prospected.

In conclusion, although trees grown for other purposes may be a useful source of architectural information, the most reliable source is still plants grown from seed in reasonably controlled environments and so subject to a minimum of stress, and with regular records of growth features for lengthy periods.

III. Nomenclature

The concept of architecture in trees being new, the search for a system of naming the models by which trees could be categorized proved to be difficult. Nomenclature had to be simple, unambiguous and neutral, i.e., without reference to other botanical concepts. Neologisms, abbreviations and symbolism all were to be avoided since all have become a nuisance in scientific language. Any system of reference by number or letter could unintentionally imply a linear descent, while rearrangement or insertion of newly discovered models would be difficult. The series of models is quite large, so that to coin Latin names, as did RAUNKIAER (1934) for his biological life forms, would overburden the literature. It is for the same reason difficult to find a sufficient number of distinctive objects for comparison whereby one could refer to "candelabra-tree" for example, or use a term like "sword-tree" (CORNER, 1966). Four major criteria serve to separate models and synthetic words based on abbreviations for those criteria proved ugly and unpronounceable and were rejected.

From this it became clear that models should be named after something or someone. The obvious approach, and the one used initially in private correspondence, was to select the names of plants which illustrate clearly the principles of growth in each model. This would have produced perhaps, Oak model, Coconut model, Cocoa model or more scientifically *Quercus* model, *Cocos* model, *Theobroma* model. In practice this is unhelpful; generic names alone are insufficient since there are many genera – often quite well known – which include species belonging to different models (e.g., *Celtis, Cordia, Euphorbia, Pandanus, Phyllanthus, Theobroma*). Longer, more cumbersome names would therefore become necessary, like *Quercus sessiliflora* model, *Cocos nucifera* model, and *Theobroma cacao* model. Furthermore, models are cosmopolitan in their distribution but nomenclatural "types" are not: a tropical botanist would prefer a more familiar point of reference e.g., *Hevea brasiliensis* to *Quercus sessiliflora*. One obviously could not guarantee a universally familiar named set of reference points.

More serious botanical objections are the systematic and phylogenetic implications inherent in taxonomic nomenclature. Unwittingly this can lead a reader to make assumptions which are not intended about interrelationships between models. Furthermore, it seems fundamentally wrong to choose a taxonomic frame of reference for a system, the very contribution of which to biology is its independence from any existing systematic arrangement. Nor could it be said that a taxonomic reference would be helpful by virtue of its existing familiarity to botanists, because we have been able to complete a categorization of models only by including many uncommon species which, being tropical and rare, are unfamiliar to most plant scientists.

However, the strongest objection to a type system which is implied in the use of taxonomic nomenclature is its excessive rigidity. We repeat again that architecture refers to a continuum, out of which we have made a selection of points of reference as our models. To revert to a typification in nomenclature would be to obscure, if not destroy entirely the uniqueness of our approach. We appreciate that it is unhelpful to introduce a voluminous new vocabulary into botanical science, especially one which might grow with the discovery of new architectural models. Experience shows, however, that the actual models initially established (H.O., 1970) provide a sufficient framework. Access to newer and richer floras simply confirms the general applicability of a system established on more restricted examples. HALLÉ (1974) in his study of 76 species from 45 families in New Guinea found no new models. The only new models named in this book refer to ones previously anticipated on theoretical grounds (Stone's model, previously Theoretical Model III of H.O., 1970, p. 71) and to the inclusion of bamboo-like plants (McClure's model) by virtue of their unique construction. The risk of proliferation of new terms seems negligible. Moreover, the same framework is likely to prove useful in the analysis of other biological types such as herbs and lianes (see p. 251, 259).

The value of a taxonomically inspired nomenclature thus remains to be demonstrated while its disadvantages are manifest. The nomenclature used in this book as a satisfactory alternative does not necessarily mean that no better one exists, but ten years of thought given to the problem have not produced it.

In our nomenclature each architectural model is named after a botanist who has contributed to a knowledge of the model or has done morphological research on plants exhibiting the model. This leads to a simple, neutral, pronounceable nomenclature without abbreviation or neologisms. It is also a nomenclature with ample precedent, since scientific and everyday nomenclature is replete with words of patronymic origin. Thus we have physical units like ampere, volt, watt; the laws of Boyle, Charles, Gay-Lussac, Hooke; the cities of Edinburgh, Leningrad, Sydney, Washington; automobiles by Ford, Morris, Peugeot; the states of Georgia, Louisiana, Victoria; the country of Colombia; the continent of America. We can sail through the Straits of Magellan and Torres, or across the Tasman Sea to admire Mount Cook, fly over the Owen-Stanley range, walk over the Albert Bridge. We study at Duke or Stanford or Yale University – but preferably at Harvard! – or are trained at the Pasteur Institute.

Experience has shown that since the nomenclature refers to visible entities, it is eminently serviceable. One soon learns to recognize distinctive models like those of Leeuwenberg, Rauh, and Troll, by means of trees belonging to the same model, but which are not identical taxonomically.

IV. Recapitulation of Growth Criteria Used in Recognizing Models

Architectural models are recognized mainly by criteria which relate to primary (extension) growth. Radial growth from a vascular cambium which brings about secondary increase in thickness serves to stabilize the primary system, although in some trees secondary changes do influence the architecture (e.g., Koriba's model, Troll's model). Stabilization by secondary tissue is not indispensable, as is shown by trees either without a cambium or with little cambial activity, e.g., palms, cycads, tree ferns, and lianes. Absence of a cambium is chiefly expressed architecturally in a restriction of branching, which has been discussed in greater detail in relation to monocotyledons. Nevertheless, there are trees with a cambium which only retain a limited capacity to branch.

Life-Span of Meristems. This is the single most important functional character which determines models. In simple terms, a terminal meristem does or does not continue to exist. The architectural counterparts of these alternatives are hapaxanthy and pleonanthy in sexual terms, monopodial and sympodial growth in vegetative terms. Loss of an apical meristem (by abortion or differentiation as an inflorescence) does not necessarily result in visible branching.

A linear sympodium, in which substitution of a terminal meristem by a subapical meristem guarantees continued axial growth, may be physiognomically indistinguishable from a monopodium. In both cases a single trunk results. Horizontal branches, which are sympodial by apposition in many tropical trees, provide an example of sympodia with significance in the overall organization of the tree. It has not escaped us that in using contrasted morphological procedures as criteria for categorizing our models we may be recognizing fundamentally different biological strategies.

Differentiation of Vegetative Meristems. This term is difficult to define, except by example, but implies divergence in organizational abilities of the meristems produced by a single tree. It is best illustrated by contrasting alternative meristematic behavior in particular physiological or morphological states.

1. Sexual (determinate) vs. *vegetative* (indeterminate) differentiation. This process of sexuality is to be regarded as irreversible. It is best exemplified by the conversion of a vegetative axis into a terminal inflorescence, whereby the life span of the meristem is limited. The construction of this inflorescence i.e. whether it may be described as a spike, umbel, panicle, cincinnus, thyrse etc. is of no architectural consequence: it is the influence of sexuality on subsequent axis development which is important.

2. Plagiotropy vs. *orthotropy*. These are synthetic concepts uniting direction of growth with symmetry and in many cases phyllotaxis (Fig. 12). Orthotropic axes are erect and commonly with spiral or decussate phyllotaxis; they are radially symmetrical. Plagiotropic axes are horizontal and commonly with distichous phyllotaxis; they are dorsiventrally symmetrical. Normally these states are alternatives and a meristem determines exclusively one or the other condition. However, in the type of axis defined as "mixed" (see below) there is a change in time from one state to the other (usually from orthotropy to plagiotropy) along a single axis which is the product of a single meristem.

This emphasis on a particular kind of axial dimorphism is warranted because of its architectural importance in comparison with many other kinds of differentiation leading to axial polymorphism, e.g., long shoots versus short shoots, imposed differences in orientation of shoots, differences in phyllotaxis, leafy and leafless axes, axes which differ in leaf size, axis modification as tendrils, hooks or grapnels, glands, spines etc., none of which directly determine architecture, though they often determine its flexibility.

3. Rhythmic (*episodic*) vs. *continuous* growth. These alternate states distinguish meristems which are continuously functioning in a uniform state from those in which meristematic activity is temporarily suspended (a period of "rest"). The two states can be recognized by morphological features: axes developed by continuous growth show a quantitative equivalence of all internodes, leaves and lateral meristems: axes developed by rhythmic growth show a regular and endogenous alternation between series of short internodes bearing relatively reduced leaves, and series of long internodes bearing large leaves. Lateral meristems commonly contrast in their developmental potential so that branching also becomes rhythmic; syllepsis may alternate with prolepsis.

4. Chronology of branch development. This is necessary to recognize certain models. Growth of several equivalent lateral axes at one level on the parent axis may be followed at a later time by development of an adjacent meristem, sometimes differentiated from earlier branches, and always playing a different role in the subsequent architecture of the tree (see Prévost's model). On the other hand late specialization of one axis among a group of contemporaries initially all alike is important in recognizing Koriba's model. Here a time factor is introduced, which is appropriate since the model concept is dynamic. In fact, time is also one of the criteria used when distinguishing syllepsis from prolepsis (p. 42).

V. Size and Architectural Proportions – Corner's Rules

Size is one of the characteristics most often used to define trees (e.g., Aubréville, 1963; Little, 1953), but we have not taken it into account in our definition of the architectural model. We should not be overawed by the huge dimensions and parts of many tropical plants simply because our temperate experience leaves us unprepared to accept them, but should appreciate the range of possibilities embraced by a tropical flora. The range of leaf size in an oak or beech forest at high latitudes is much smaller than in a tropical rain forest at the equator. In dry regions, since the tendency is to reduce leaf area, the overall range is even smaller.

A scale leaf to most botanists is something ephemeral, often delicate and certainly small. The bud-scale of a horse-chestnut (*Aesculus hippocastanum*, Hippocastanaceae), sufficently large to be noted in elementary botanical teaching, is still only about 1 cm long. Contrast this with the woody, boat-shaped prophyll, over 2 m long and weighing about 2 kg, which envelops the inflorescence in certain cocosoid palms like *Attalea* and *Maximiliana*. It still has to be generally appreciated that this structure is a "reduced" leaf in relation to the foliage leaves of the palm, which are about five times as long. Even if it could injure a man if it fell from a height, this woody organ is as much a "scale-leaf" as the bud-scale of a temperate tree. Stipules in a number of tropical species, e.g., *Cecropia* spp., *Musanga cecropioides* (Moraceae) may be up to 30 cm long as is appropriate since the developing organs they envelop in terminal buds are proportionally larger. The size spectrum of plant parts, extended to include such examples, makes obvious that not size but its distribution according to certain proportions determined by architectural principles provides us with valid criteria to study form and function in plants.

The first step in building sizeable axes according to such proportions is primary meristematic growth, which essentially defines tree models. In this process architecture, surface, volume, and mass are interrelated within a single complex determined by four measurable parameters: primary diameter of the axis and internode length, both of which are related to volume and mass; leaf surface; rate of meristematic activity, which integrates the first three into an architectural pattern. Leaf volume can usually be neglected, as surface considerations outweigh all others, except in special circumstances, notably when leaves are very large (e.g., tree ferns, palms, some Meliaceae) or where they are not flattened, as in needle-leaves.

The four parameters are interdependent. An increase in rate of meristematic activity, for instance, is expressed in an increased rate of leaf production, resulting in turn in the coexistence of more living leaves with a larger surface to be irrigated by translocated water and to be emptied of photoassimilates. To maintain volume/surface relationships the primary diameter of the axis has to be augmented in order to increase transport over its cross-section, but then internode length has to decrease if volume per internode is to remain the same. If another parameter changes first, for instance during a decrease in internode length, primary diameter of the axis, leaf surface and meristematic activity rate, all three, also have to adjust to this altered condition.

Even without experimental research this principle can be demonstrated because it is expressed in the variety of shoot form which reaches its maximum diversity in tropical plants. An empirical formulation of this visible expression has been given by CORNER (1949, p. 390; see also the first attempt at a mathematical treatment by CHUAH, 1977), and we will subsequently refer to Corner's enunciation of principles as "Corner's rules" stated by him as follows:

> "The following two complementary principles occur with such regularity in the construction of flowering plants as

to appear susceptible of mathematical treatment:

a) Axial Conformity. The stouter, or more massive, the axis in a given species, the larger and more complicated are its appendages. Thus the stouter the main stem, the bigger the leaves and the more complicated their form, e.g., saplings of trees (some with compound leaves while the branches have simple leaves, as in *Artocarpus, Scaphium,* and some Proteaceae), or the stems of herbaceous plants like *Nicotiana* and *Helianthus,* or rosette Umbelliferae and Compositae with the large basal leaves diminishing in size and form to bracts.

b) Diminution on Ramification. The greater the ramification, the smaller become the branches and their appendages, e.g., in *Solanum,* the leaves, inflorescences, flowers, fruits, and twigs become smaller as the ramification increases; and in *Carica papaya,* the scarcely branched female inflorescences have a few large flowers whereas the highly branched male inflorescences have many small flowers."

The term "massive" in Corner's rules refers clearly to volume (stoutness) and more precisely to axial diameter; it generally conveys an impression of size.

Other principles concerning proportional relations between axes had been formulated earlier, notably when we think of the statement of Leonardo da Vinci (RICHTER, 1970, p. 393): "All the branches of trees at every stage of their height, united together, are equal to the thickness of their trunk below them." To which he added, "All the branches of a water (course) at every stage of its course, if they are of equal rapidity, are equal to the body of the main stream", which is probably a more significant statement. Of particular relevance is the further statement: "Every year when the bough of a plant (or tree) have made an end of maturing their growth they will have made, when put together, a thickness equal to that of the main stem." This is, of course, the basis of the pipe stem model of trees developed by SHINOZAKI et al. (1964). However, as ZIMMERMANN (1978) emphasizes, the situation is complicated by the physical problems of movement in small capillaries, since it is not only mechanics but hydraulic conductivity which must be considered. STEVENS (1974) claims, however, that LEONARDO's rule has been found inconsistent with models of rivers and blood vessels: "all branches united together exceed rather than equal the thickness of the trunk" (p. 96). Obviously in a stream system all volumes must be additive.

Our descriptions of architectural models certainly provide ample qualitative verification of Corner's rules, out of which may be cited here *Raphia* (Palmae) and *Aglaia* (Meliaceae), both of Corner's model, combining particularly massive trunks with particularly big leaves. The bamboos are interesting in that the large scale leaves on rhizomes and culms are not morphologically "reduced", since foliage leaves are never borne on massive axes and are always small.

Instructive examples are provided in the transition from vegetative to reproductive architecture in hapaxanthic palms like *Corypha, Nannorrhops,* and *Metroxylon,* where leaf and axis size are proportionately reduced on branches of successively higher order. Some quantitative data have been produced by TOMLINSON and MOORE (1968), TOMLINSON (1971b), and TOMLINSON and SODERHOLM (1975).

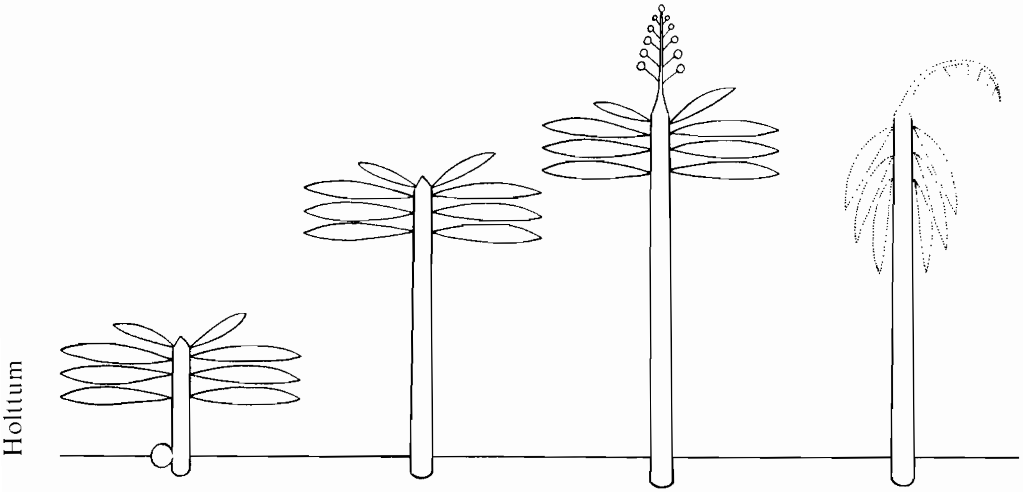
B. Illustrated Key to the Architectural Models of Tropical Trees

The models are not necessarily listed here according to the sequence they occupy in the text.

Note: Theoretical Model II defined (by H.O., 1970, p. 71) as an architecture resulting from growth of a meristem producing a sympodial modular trunk, with tiers of branches also modular and plagiotropic by apposition, has still not been recognized in a known example and has now been suppressed. It would occur in the key next to Aubréville's model from which it differs in its sympodial trunk.

1a. Stem strictly *unbranched* (Monoaxial trees) 2
1b. Stems *branched*, sometimes *apparently* unbranched in Chamberlain's model (Polyaxial trees) 3
2a. Inflorescence *terminal* . . . . Holttum's model (p. 101)

[1] e.g., Monocotyledon: *Corypha umbraculifera* (Talipot palm – Palmae)
Dicotyledon: *Solmreyia excelsa* (Rutaceae)



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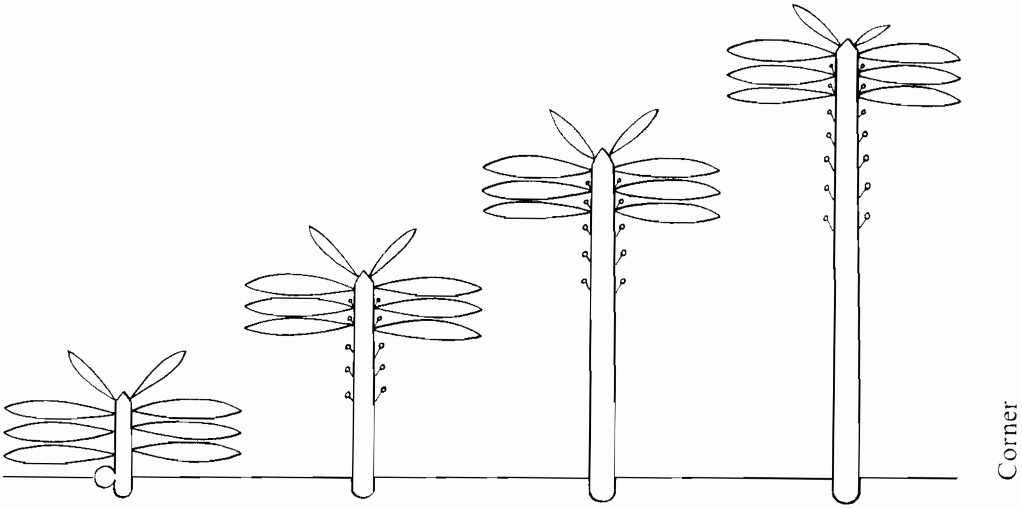
[1] Examples chosen, where possible, represent common species, especially those of commercial importance, which have a pantropical distribution and are likely to be familiar to the non-specialist. They are not necessarily the same examples described in detail later. Many of them are described and illustrated in H.O. (1970).

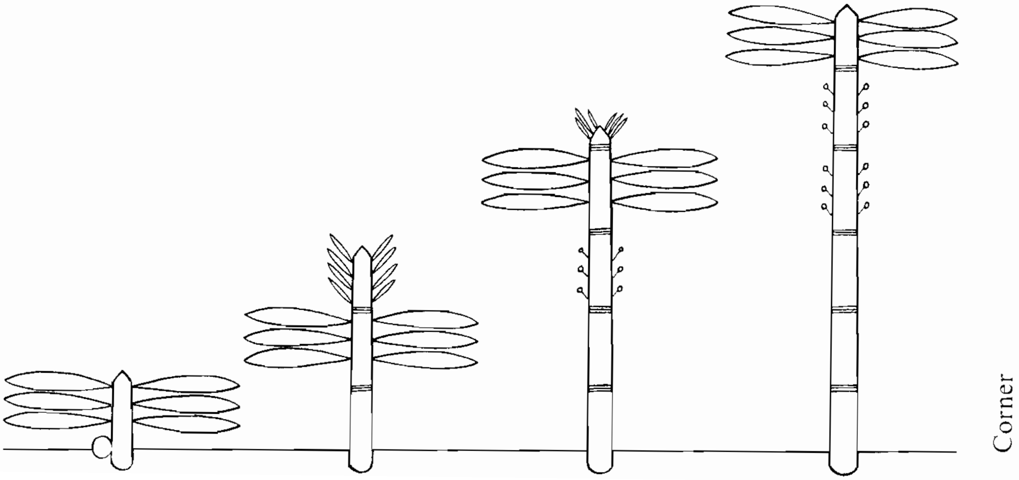
2b. Inflorescences *lateral* . . . . Corner's model (p. 109)
Growth continuous

e.g., Monocotyledon: *Cocos nucifera* (coconut palm – Palmae)
Elaeis guineensis (African oil palm – Palmae)
Dicotyledon: *Carica papaya* (papaya – Caricaceae)



Growth rhythmic

c.g., Gymnosperm: Female *Cycas circinalis* (Cycadaceae)
Dicotyledon: *Trichoscypha ferruginea* (Anacardiaceae)



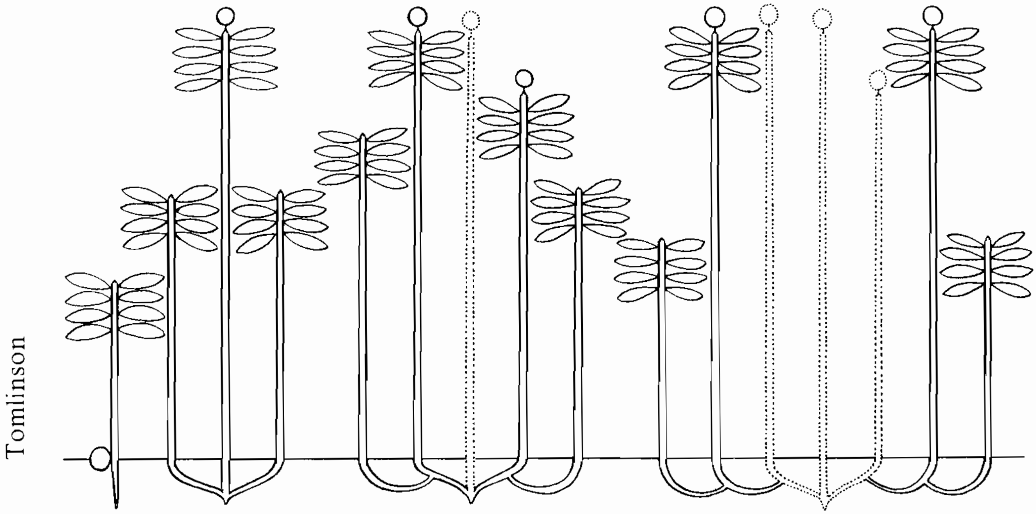
3a. Vegetative axes *all equivalent*, homogenous (not partly trunk, partly branch), most often orthotropic and modular 4

3b. Vegetative axes *not equivalent* (homogenous, heterogenous or mixed but always clear difference between trunk and branches) 7

4a. *Basitony*, i.e., branches at the base of the module, commonly subterranean, growth usually continuous, axes either hapaxanthic or pleonanthic
Tomlinson's model (p. 118)

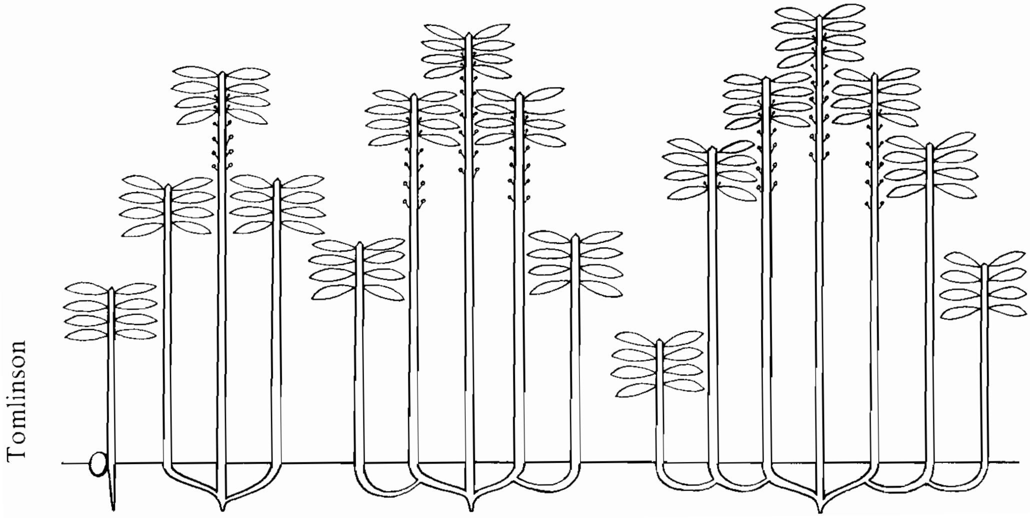
Hapaxanthy, i.e., each module determinate, terminating in an inflorescence

e.g., Monocotyledon: *Musa* cv. *sapientum* (banana – Musaceae)
Dicotyledon: *Lobelia gibberoa* (Lobeliaceae)



Pleonanthy, i.e., each module not determinate, with lateral inflorescences

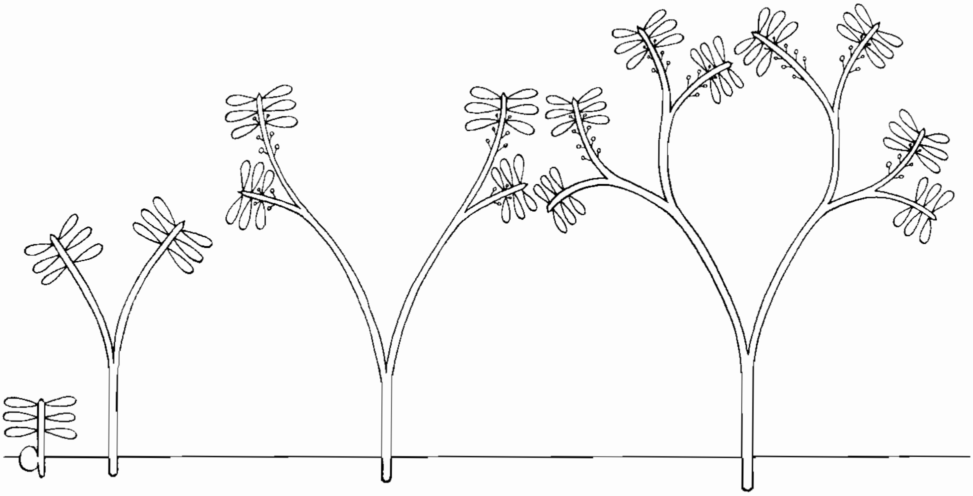
e.g., Monocotyledon: *Phoenix dactylifera* (date palm – Palmae)



4b. *Acrotony*, i.e., branches not at the base but distal on the axis 5

5a. *Dichotomous* branching by equal division of apical meristem
Schoute's model (p. 128)

e.g., Monocotyledons:
Vegetative axes orthotropic – *Hyphaene thebaica* (doum palm – Palmae)
Vegetative axes plagiotropic – *Nypa fruticans* (nipa palm – Palmae)

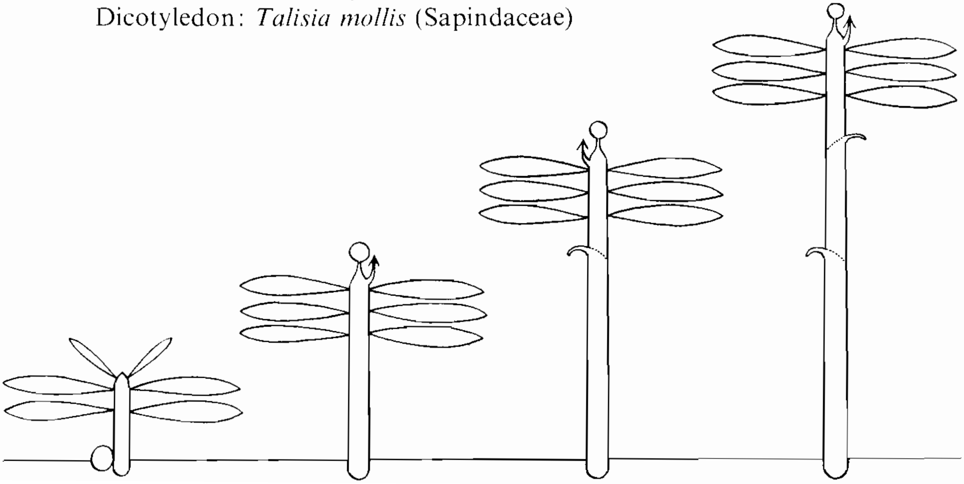


Schoute

5b. *Axillary* branching, without dichotomy 6

6a. *One branch* per module only; sympodium one-dimensional, linear, monocaulous, apparently unbranched, modules hapaxanthic, i.e., inflorescences terminal
Chamberlain's model (p. 133)

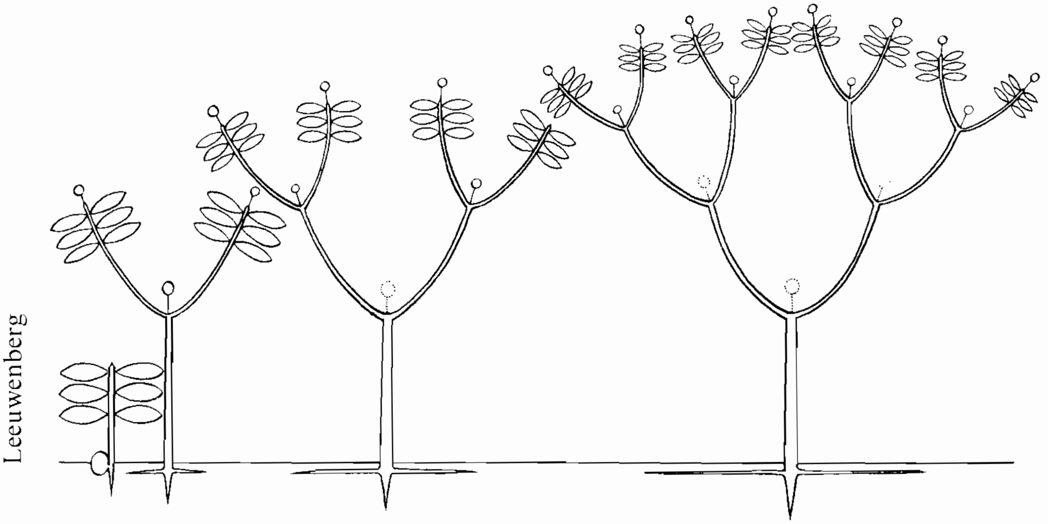
e.g., Gymnosperm: Male *Cycas circinalis* (Cycadaceae)
Monocotyledon: *Cordyline indivisa* (Agavaceae)
Dicotyledon: *Talisia mollis* (Sapindaceae)



Chamberlain

6b. *Two or more* branches per module; sympodium three-dimensional, nonlinear, clearly branched; inflorescences terminal . . . . Leeuwenberg's model (p. 145)

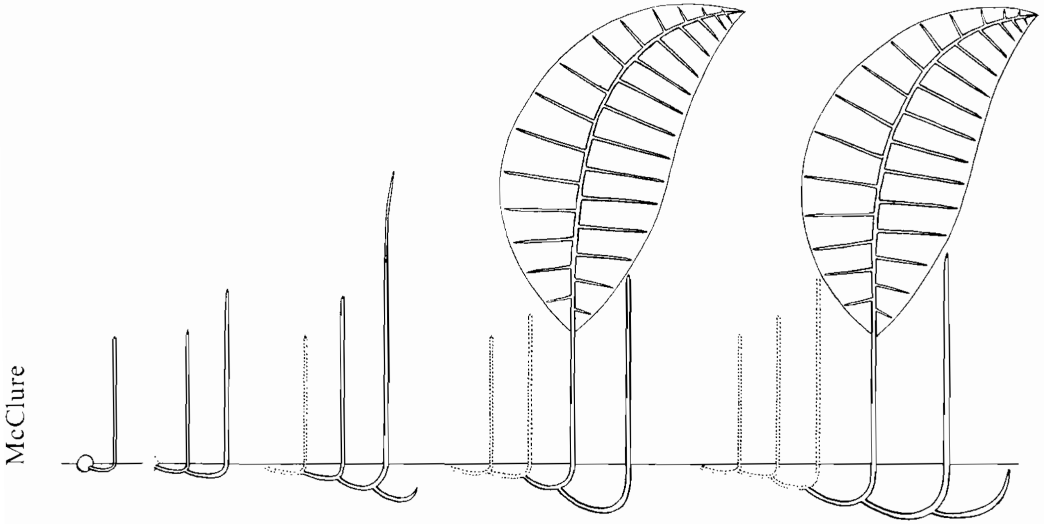
e.g., Monocotyledon: *Dracaena draco* (dragon tree – Agavaceae)
Dicotyledon: *Ricinus communis* (castor-bean – Euphorbiaceae)
Manihot esculenta (cassava – Euphorbiaceae)



7a. Vegetative axes *heterogenous*, i.e., differentiated into orthotropic and plagiotropic axes or complexes of axes 8
7b. Vegetative axes *homogenous*, i.e., either all orthotropic or all mixed . 18 (p. 94)

8a. *Basitonic* (basal) branching producing new (usually subterranean) trunks McClure's model (p. 139)

e.g., Monocotyledon: *Bambusa arundinacea* (bamboo – Gramineae – Bambusoideae)
Dicotyledon: *Polygonum cuspidatum* (Polygonaceae)



8 b. *Acrotonic* (distal) branching in trunk formation (never subterranean) . . . 9

9 a. *Modular* construction, at least of plagiotropic branches; modules generally with functional (sometimes with more or less aborted) terminal inflorescences . . 10

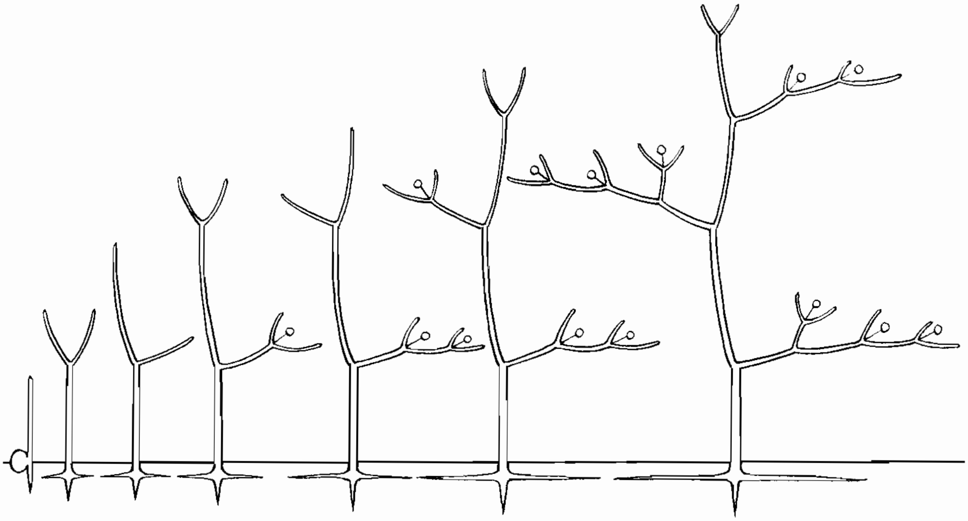
9 b. Construction *not modular*; inflorescences often lateral but always lacking any influence on main principles of architecture 13

10 a. Growth in height *sympodial, modular* 11

10 b. Growth in height *monopodial*, modular construction restricted to branches . 12

11 a. Modules *initially equal*, all apparently branches, but later unequal, one becoming a trunk . . . . Koriba's model (p. 155)

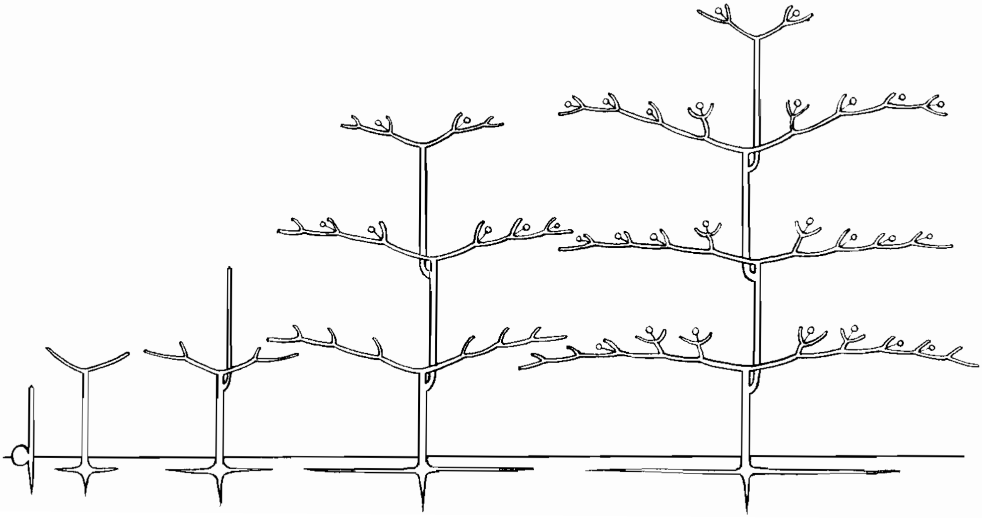
e.g., Dicotyledon: *Hura crepitans* (sand-box tree – Euphorbiaceae)



Koriba

11 b. Modules *unequal from the start*, trunk module appearing later than branch modules, both quite distinct . . . . Prévost's model (p. 161)

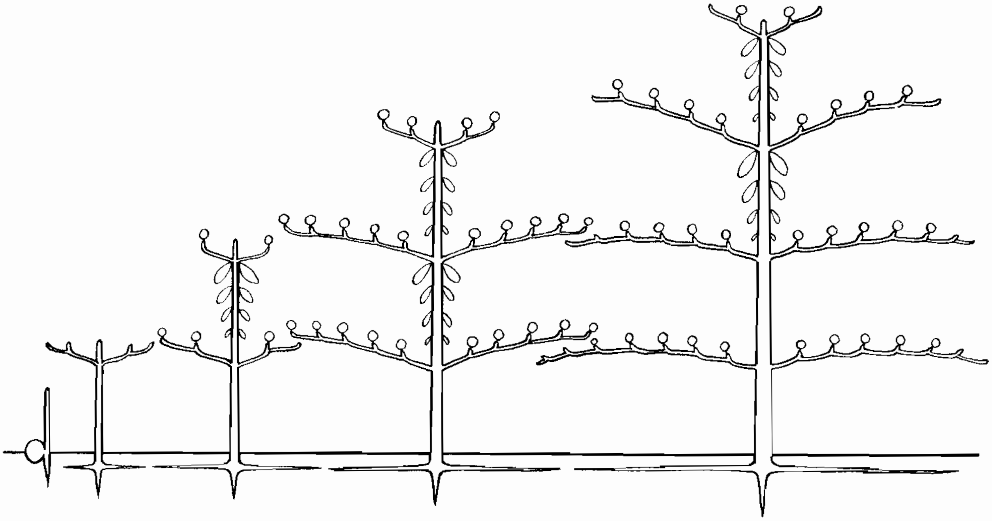
e.g., Dicotyledon: *Euphorbia pulcherrima* (poinsettia – Euphorbiaceae)
Alstonia boonei (émien – Apocynaceae)



Prévost

12a. Monopodial growth in height *rhythmic* . . . . . . Fagerlind's model (p. 167)

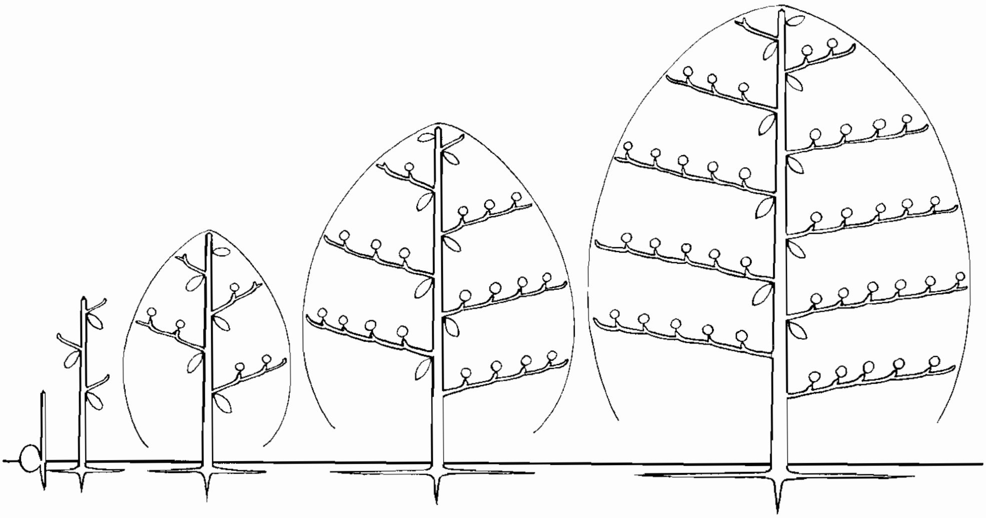
e.g., Dicotyledon: *Cornus alternifolius* (dogwood – Cornaceae)
Fagraea crenulata (Loganiaceae)



Fagerlind

12b. Monopodial growth in height *continuous* . . . . Petit's model (p. 173)

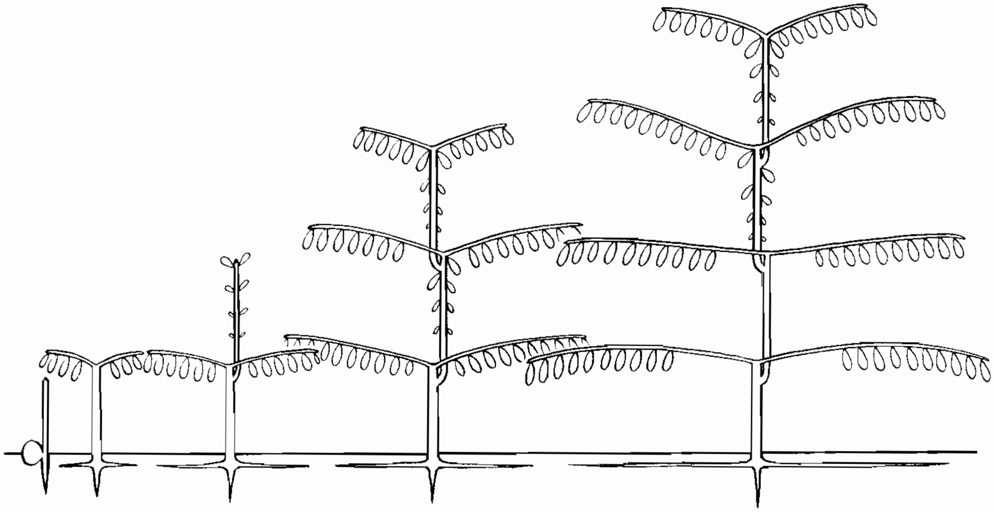
e.g., Dicotyledon: *Gossypium* species (cottons – Malvaceae)



Petit

13a. Trunk a *sympodium* of orthotropic axes (branches either monopodial or sympodial, but never plagiotropic by apposition) . . . . . Nozeran's model (p. 177)

e.g., Dicotyledon: *Theobroma cacao* (cocoa – Sterculiaceae)



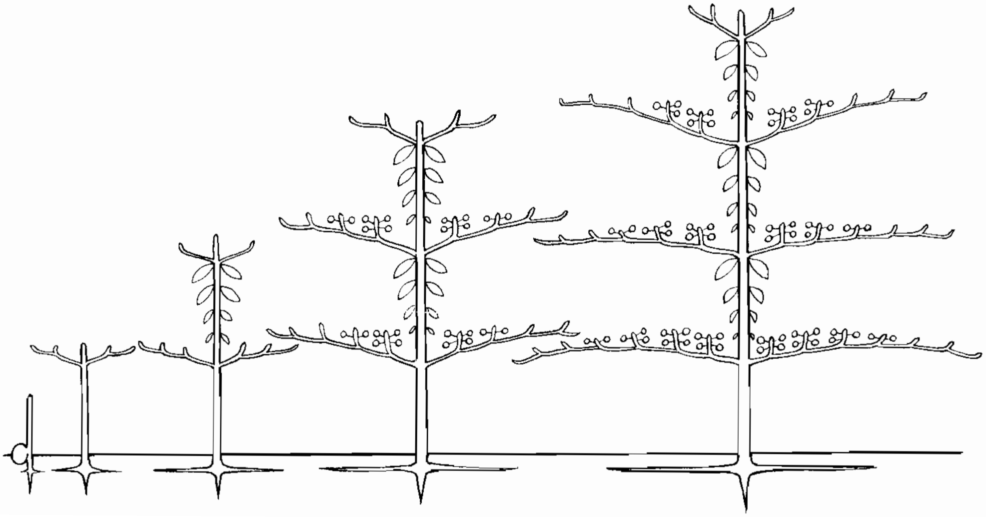
Nozeran

13b. Trunk an orthotropic *monopodium* 14

14a. Trunk with *rhythmic* growth and branching 15
14b. Trunk with *continuous or diffuse* growth and branching 16

15a. Branches *plagiotropic by apposition* . . . . Aubréville's model (p. 182)

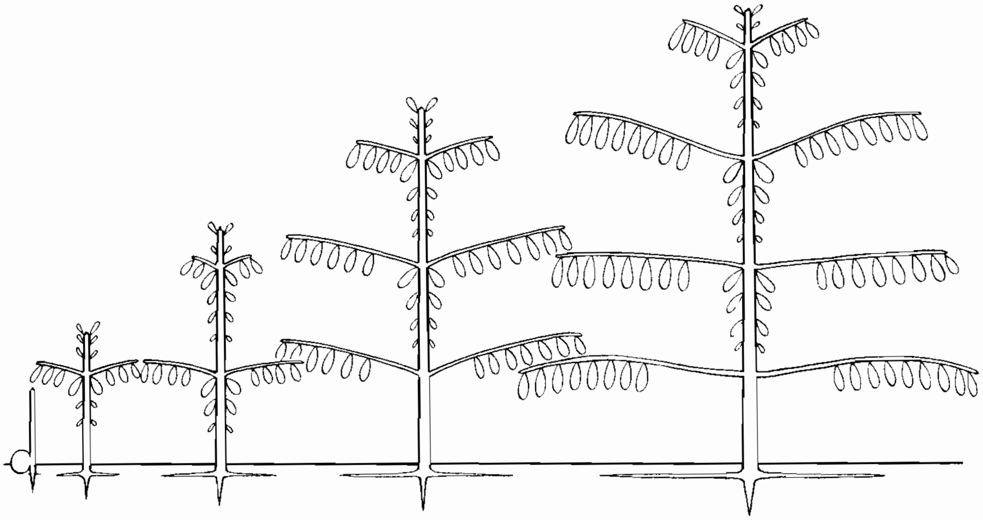
e.g., Dicotyledon: *Terminalia catappa* (sea-almond – Combretaceae)



Aubréville

15b. Branches *plagiotropic* but *never by apposition*, monopodial or sympodial by substitution . . . . Massart's model (p. 191)

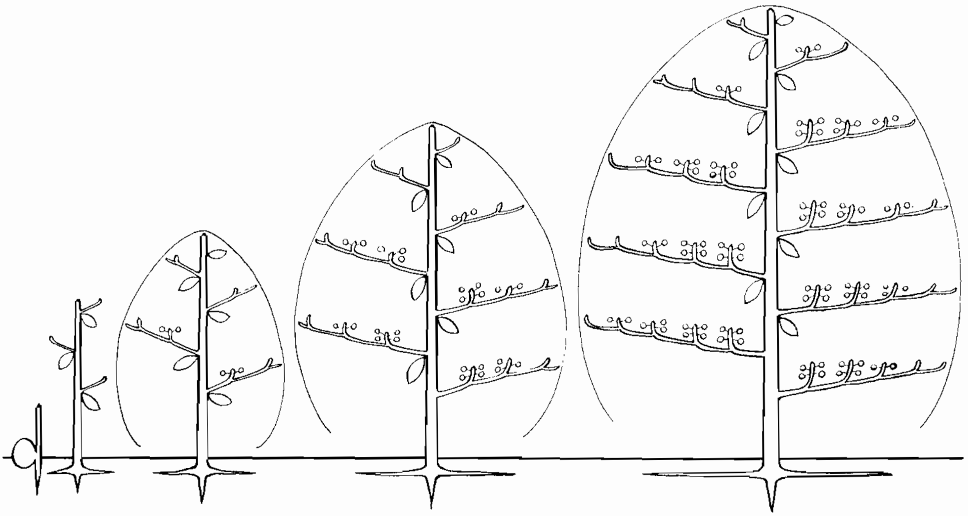
e.g., Gymnosperms: *Araucaria heterophylla* (Norfolk Island pine – Araucariaceae)
Dicotyledon: *Ceiba pentandra* (kapok – Bombacaceae)
Myristica fragrans (nutmeg – Myristicaceae)



Massart

16a. Branches *plagiotropic* but *never by apposition*, monopodial or sympodial by substitution 17
16b. Branches *plagiotropic by apposition* . . . . Theoretical model I (p. 92)

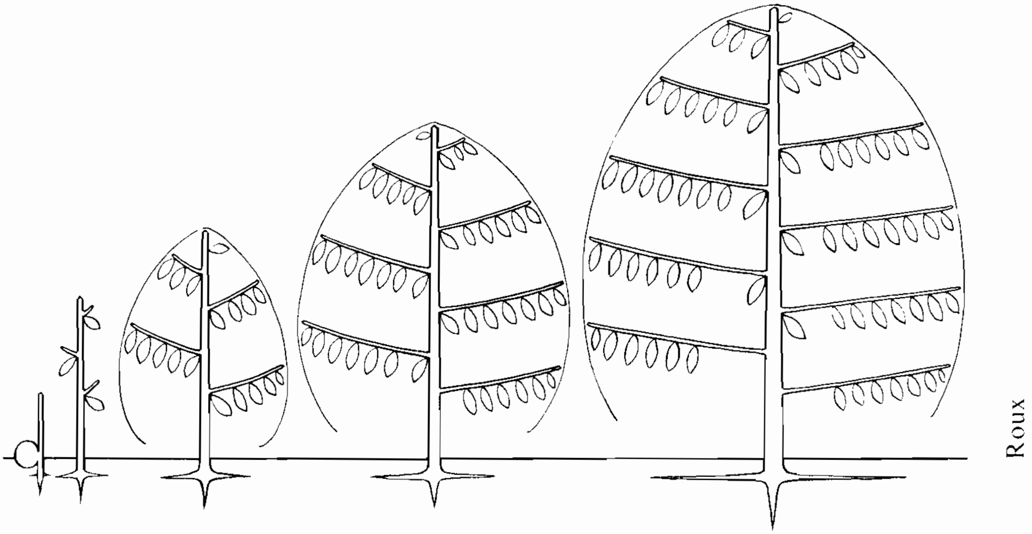
e.g., Dicotyledon: *Euphorbia* sp. (Euphorbiaceae)



Theoretical Model I

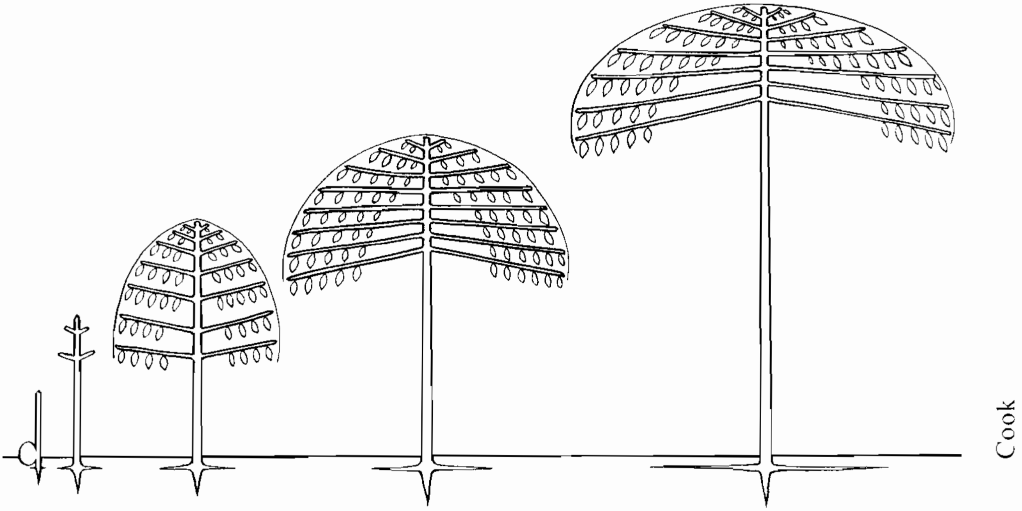
17a. Branches *long-lived*, not resembling a compound leaf . . Roux's model (p. 200)

e.g., Dicotyledon: *Coffea arabica* (coffee – Rubiaceae)
Bertholletia excelsa (Brazil nut – Lecythidaceae)



17b. Branches *short-lived, phyllomorphic*, i.e., resembling a compound leaf
Cook's model (p. 206)

e.g., Dicotyledon: *Castilla elastica* (Ceara rubber tree – Moraceae)

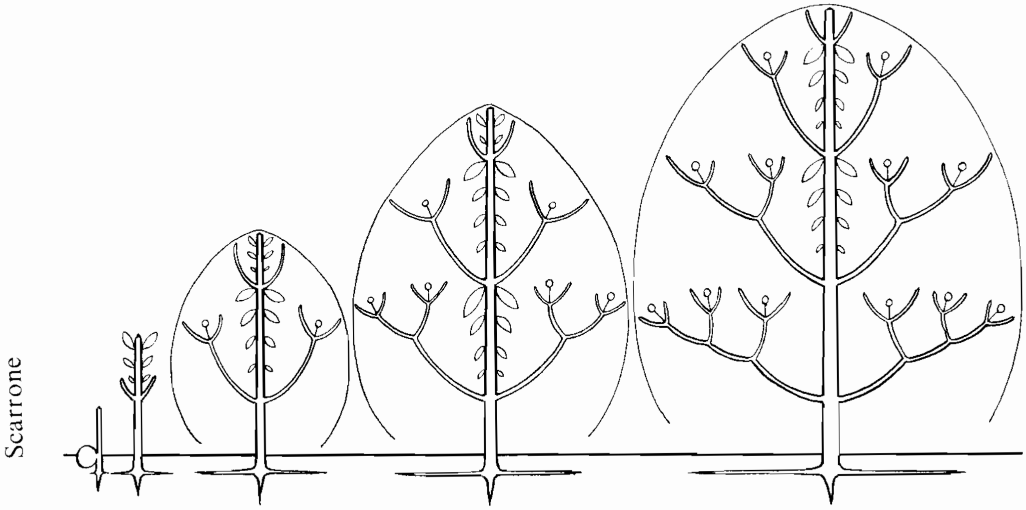


18a. Vegetative axes *all orthotropic* 19
18b. Vegetative axes *all mixed* . . . . 22 (p. 96)

19a. Inflorescences *terminal,* i.e., branches sympodial and, sometimes in the periphery of the crown, apparently modular 20
19b. Inflorescences *lateral,* i.e., branches monopodial 21

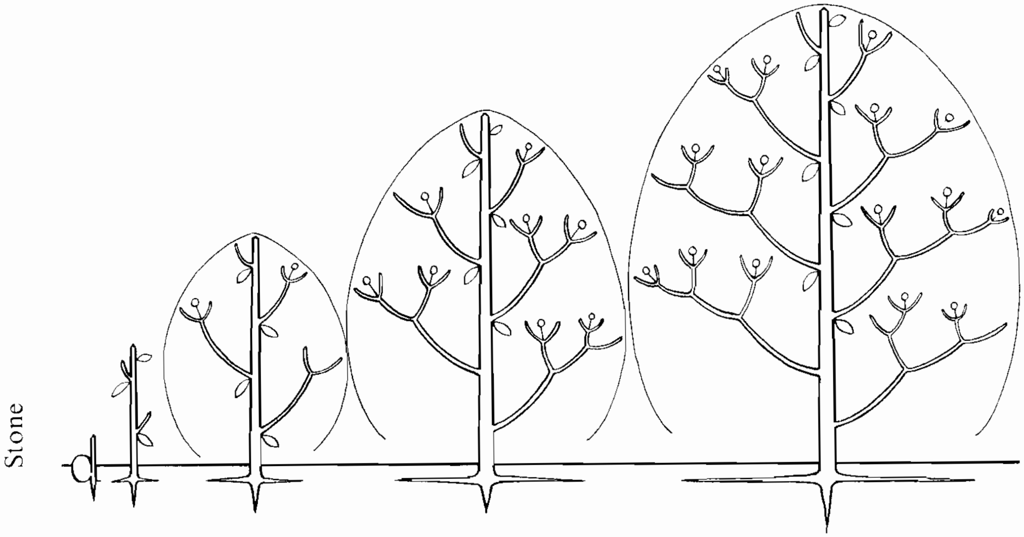
20a. Trunk with *rhythmic* growth in height . . . . Scarrone's model (p. 213)

e.g., Monocotyledon: *Pandanus vandamii* (Pandanaceae)
Dicotyledon: *Mangifera indica* (mango – Anacardiaceae)



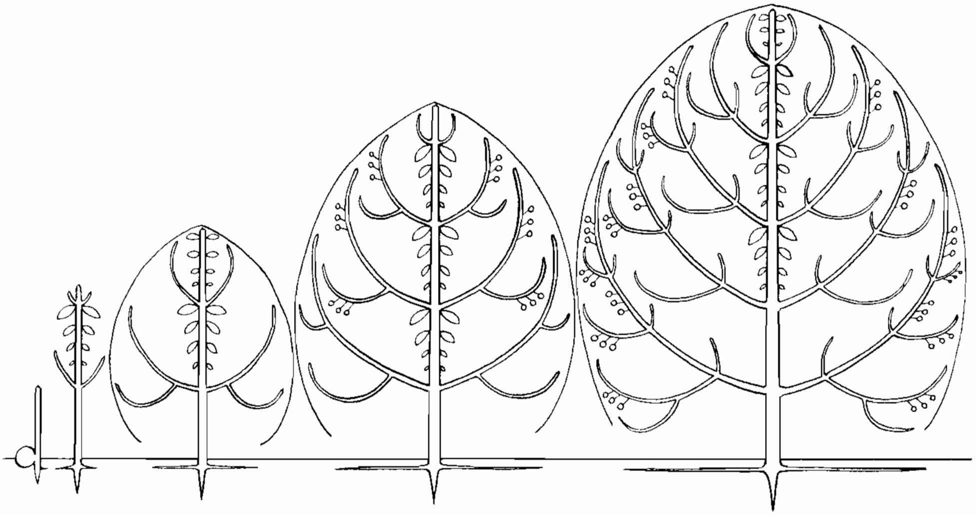
20b. Trunk with *continuous* growth in height . . . . Stone's model (p. 217)

e.g., Monocotyledon: *Pandanus pulcher* (Pandanaceae)
Dicotyledon: *Mikania cordata* (Compositae)



21a. Trunk with *rhythmic* growth in height . . . . Rauh's model (p. 221)

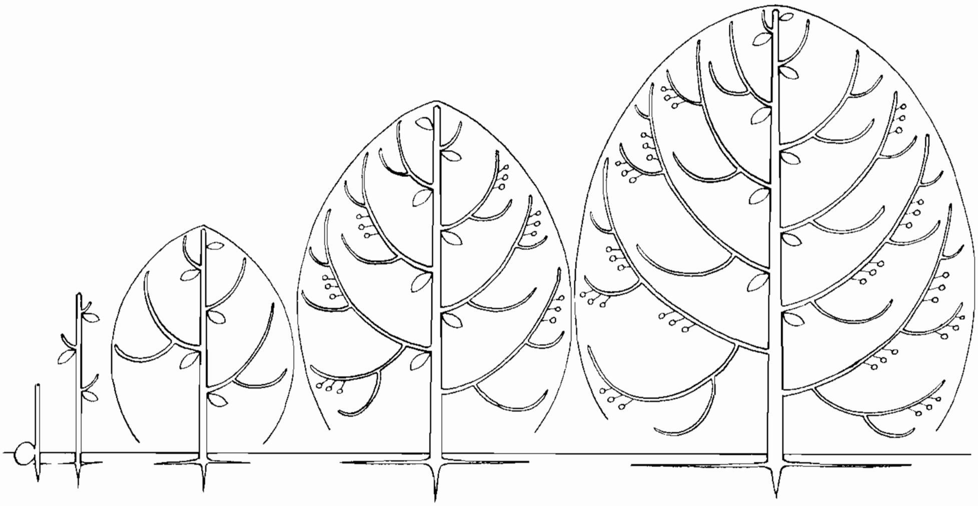
e.g., Gymnosperm: *Pinus caribaea* (Honduran pine – Pinaceae)
Dicotyledon: *Hevea brasiliensis* (Para rubber tree – Euphorbiaceae)



Rauh

21b. Trunk with *continuous* growth in height . . . . Attims' model (p. 228)

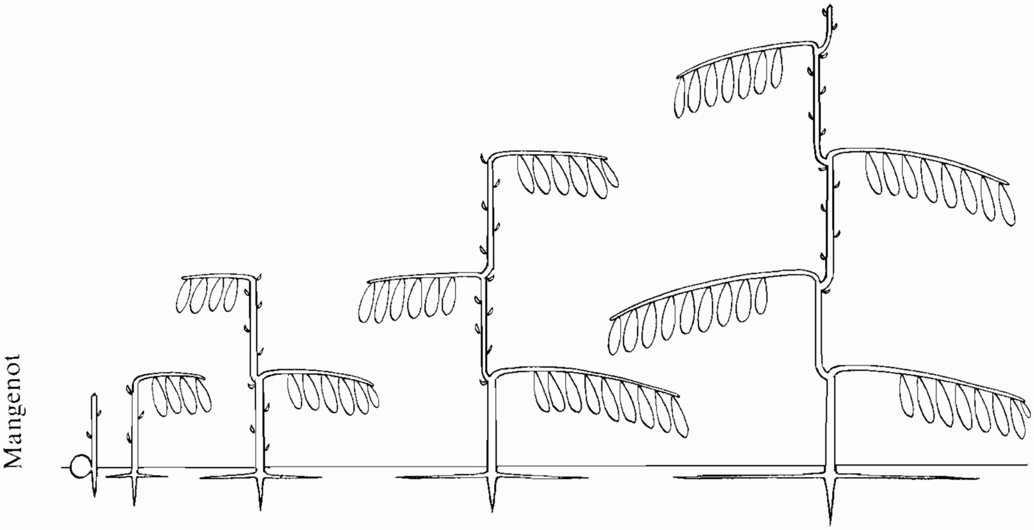
e.g., Dicotyledon: *Rhizophora racemosa* (Rhizophoraceae)



Attims

22a. Axes clearly *mixed by primary growth,* at first (proximally) orthotropic, later (distally) plagiotropic . . . . Mangenot's model (p. 233)

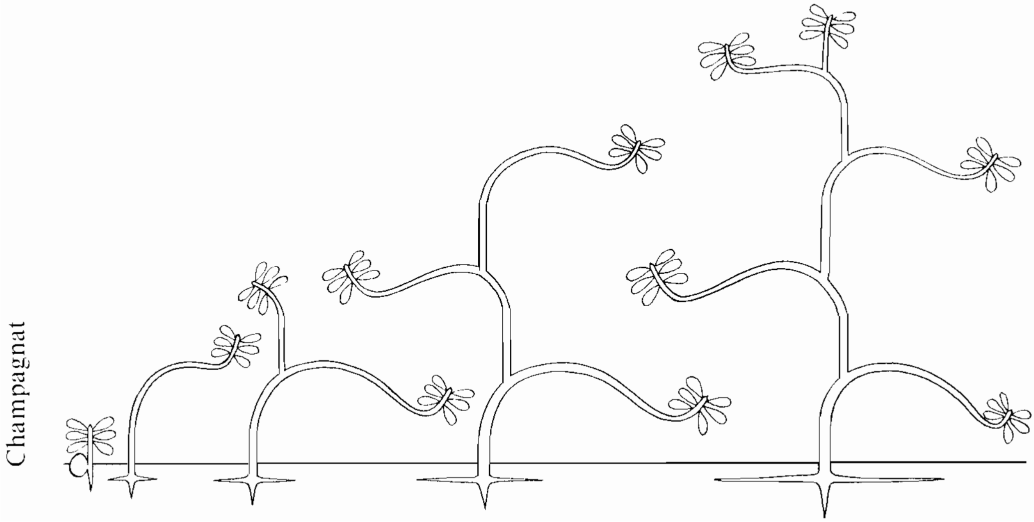
e.g., Dicotyledon: *Strychnos variabilis* (Loganiaceae)



22b. Axes apparently *mixed by secondary changes* 22

23a. Axes all *orthotropic, secondarily bending* (probably by gravity) Champagnat's model (p. 238)

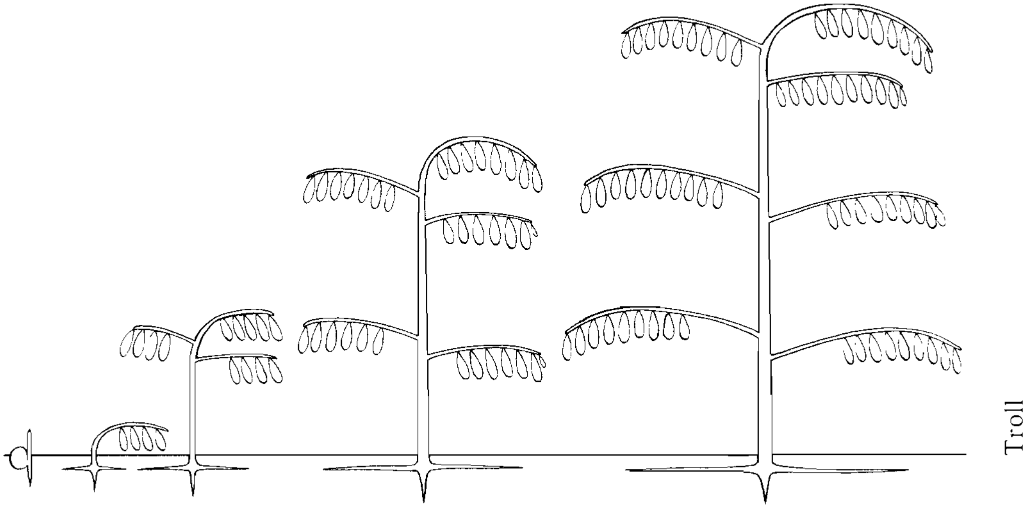
e.g., Dicotyledon: *Bougainvillea glabra* (Nyctaginaceae)



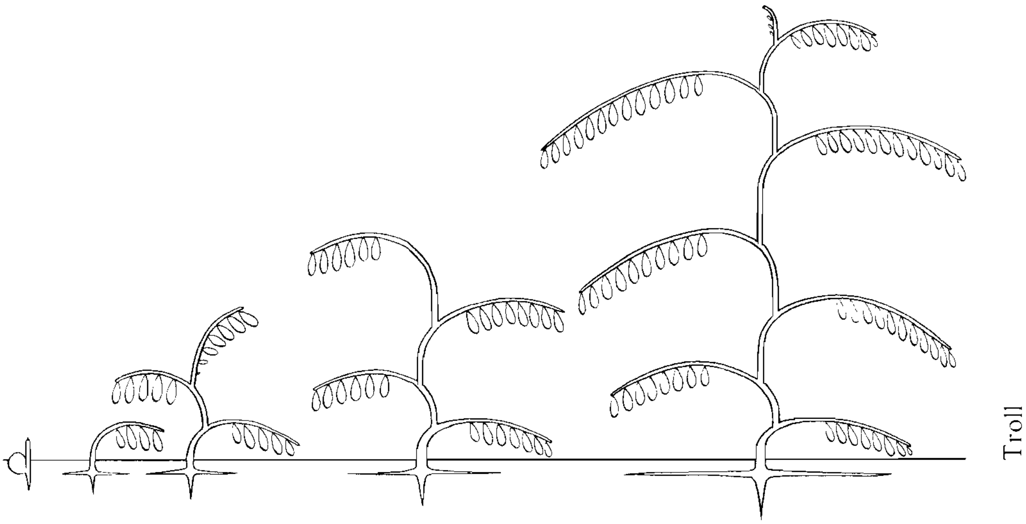
23b. Axes all *plagiotropic, secondarily becoming erect*, most often after leaf-fall
Troll's model (p. 242)

e.g., Dicotyledon: *Annona muricata* (custard apple – Annonaceae)
Averrhoa carambola (carambola – Oxalidaceae)
Delonix regia (poinciana – Leguminosae – Caesalpinioideae)

Trunk a monopodium (e.g., *Cleistopholis patens* – Annonaceae)



Trunk a sympodium (e.g., *Parinari excelsa* – Rosaceae)



C. Descriptions of Architectural Tree Models

In the following section the reader will find a definition and short description of each of the 23 architectural models we have so far recognized. Each model is illustrated initially by species which show the model well. In addition we have illustrated species which show a degree of variation *inside* the limits of the definition of the model. At this point, in so far as they are known, species with an architecture transitional between two models are often introduced as they serve to emphasize the existence of a continuum. A brief discussion of the ecologically adaptive value of each model is also introduced although it is clear that this topic is to a large extent speculative. The description of each model concludes with a concise list of species (by family) the morphogenesis of which remains inside the definition of the model. Usually the generalized geographic distribution of each species is stated, but where we are not sure of this, we indicate where we have studied the species in question. Our intention here is merely to provide a guide in a book which is not primarily biogeographic. In many instances we studied examples cultivated in botanic gardens, not in the wild; we indicate these by an asterisk (*). Where information is not original but has been provided by a colleague familiar with our system we have indicated this by a cross (+). A source of relevant bibliographic information is included as a literature reference where appropriate. This usually includes architectural information, but otherwise has appropriate illustration of habit or morphological detail. In many instances, our observations on wild plants are documented by herbarium specimens which have not been cited. Occasionally an incompletely identified plant is cited; here the herbarium voucher is indicated. Emphasis is given at all times to tropical species, but where their architecture has been studied by us, temperate examples are given since they will serve as useful points of reference for readers not familiar with the tropical examples. Lianes (indicated by an L) and herbs (indicated by an H) are included to a limited extent; their special properties and relationships are discussed briefly in separate chapters elsewhere. They serve to remind the reader that the architectural continuum is not in any way restricted to trees.

I. Illustrations of the Models – a Note of Explanation

Illustrations largely refer to species we have examined in greater or lesser detail and are based on field notes and sketches supplemented by photographs. Field diagrams have usually been drawn out accurately the same evening they were made, to allow correction to be made with material at hand. Exceptionally a few examples are reproduced from other people's accounts. Citation to this and other relevant literature is also given in the figure legend. Usually the geographical locality of the example as studied, rather than its overall range, is quoted in the legend since there is some reference to the general geographical distribution of each species in the lists of examples which follow the textual description of each model. Many examples have been examined solely in botanic gardens and this source is always indicated. Such commonly cultivated plants and many familiar wild species in which identification is not in doubt have not been documented with herbarium vouchers. Otherwise, a citation to a herbarium voucher is provided in the legend to the figure.

The illustrations represent the architectural model semi-diagrammatically, but at the same time in such a manner that concrete examples can be recognized. In some examples this necessitates a series of drawings showing different stages of architectural development. With few exceptions root systems are stylized. We realize that this is a serious omission, but the investigation of root architecture is so deficient that the few examples we have studied do not permit generalizations, although this has been attempted by Jeník (1978).

An effort has been made to illustrate examples of each model from the three main tropical regions, i.e., Africa, America, and Asia with Polynesia, in the hope that this cosmopolitan coverage will provide reference points for workers in all parts of the tropics. Where possible, the examples selected are different from those illustrated in H.O. (1970). This widens the scope of published examples. In some instances, however, a previously used example is repeated where it represents a species of major commercial interest or is particularly distinctive.

For convenience drawings at different magnifications are grouped on each plate. Although size is not of primary interest in architectural analysis (though obviously of ecological importance) scale is provided either by some reference object in the drawing (usually the figure of a man) or by some indication of maximum stature in the legend. Where different trees are shown at one magnification these are usually placed on the same line, representing the soil level.

Branch systems and phyllotaxis inevitably are both represented in two dimensions, although with very few exceptions (e.g., *Oenocarpus distichus* Corner's model) trees are three-dimensional in their branching and leaf arrangement. To assist the reader in a three-dimensional vision, the tree is often shown from two aspects mutually at right angles and organs outside the plane of the drawing may be stippled. Inflorescences are stylized, since it is the position of inflorescences which is architecturally significant, not their three-dimensional structure.

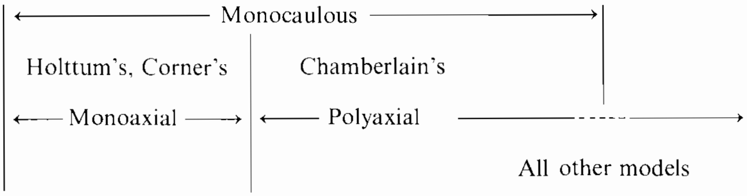
II. Monoaxial and Polyaxial Trees

The first two models describe vegetatively unbranched trees with a single terminal meristem. Clarification of the terms we use at this point is necessary. A distinction has to be made between trunk and axis, the former a *physiognomic* term, referring to the shape or general appearance of the tree and the latter a *morphological* term expressing a precise unit of construction. To separate these usages we have consistently made a distinction between (1) monocaulous and (2) monoaxial, as follows:

1. Monocaulous (monocaulescent), with reference to trees with a single trunk or visible stem of the plant (from the Greek *καῦλοσ* = stem or stalk). This may be the product either of one apical meristem or of several apical meristems which function in sequence. A complementary term is acaulous (acaulescent), without a trunk, as in plants with underground stems. Polycaulous (polycaulescent) we have not used since it means a "tree with several trunks", which is a contradiction to the usual definition of a tree. It should be used to describe shrubs; its only possible application in the subsequent description of models would be in Tomlinson's and McClure's models.

2. Monoaxial in a morphological sense refers to trees with a single axis (from the Latin *axis* = pivot, i.e., stem), where an axis is the product of a single apical meristem and so is an exactly circumscribed unit. The complementary term is polyaxial, i.e., a tree with several morphologically distinct axes, derived from more than one meristem. Polyaxial trees are usually visibly branched, but this is not always so, as is exemplified by Chamberlain's model where we have a monocaulous (apparently unbranched) tree which is polyaxial.

Using these criteria it is now possible to segregate the architectural models so that two morphologically distinct kinds of monocaulous trees are recognized:



The physiognomically monocaulous condition has been recognized by numerous authors, but with a variety of names, e.g., "Palmenform" and "Bananenform" of von Humboldt (1808), "Rosettenträger" of Reiter (1885), "tuft-trees" of Warming (1909), "rosette-trees" of Du Rietz (1931), "megaphytes" by Cotton (1935, 1944), "cabbage-trees" by Irvine (1961) and other English botanists, as trees with a "columnar growth habit" by Zimmermann and Brown (1971), or simply as plants which are "palmoid" (D'Arcy, 1973). Bremekamp (1936) distinguished three groups of Indonesian plants which are monocaulous; "pseudo-trees" (schijnbomen), "tree ferns" (boomvarens) and "ordinary palms" (gewone Palmen) the distinction being largely taxonomic. This taxonomic categorization may be replaced by one which recognizes the common features of massive primary stem, large leaves and short internodes which are functionally the most important characters. The apparent simplicity of monocaulous trees should not lead us to class them all as "primitive" (cf. Corner, 1949); many of them are highly specialized ecologically and morphologically. This is apparent when it is appreciated that two distinct conditions are represented depending on whether the trunk is sympodial or not.

Polyaxial Trees. Since most trees correspond to this definition and include numerous active meristems they are more complex than unbranched trees. Their models can conveniently be arranged in three groups.

The first group includes models with modular growth, as defined earlier (p. 4); their axes are all morphologically equivalent and orthotropic. A trunk is developed in two models only by activity of the seedling apical meristem and is a direct continuation of the epicotyledonary axis.

The second group includes the greatest variety of branched trees, those with a clear morphological distinction between trunk and branch axes. Each axis has one unchanging function in the branching pattern. The trunk may be monopodial or sympodial in its development, it is physiologically important in its monopoly of the translocation function; mechanically it supports the crown and is the backbone of the whole architecture. In the models with a high degree of differentiation between axes (Roux and Cook) the trunk plays little or no part in photosynthesis and except where cauliflory occurs, none in sexual reproduction. We emphasize that we are dealing with the *model* in this analysis, a mature dicotyledonous tree may develop several trunks by the process of reiteration described elsewhere (p. 269). It is useful to subdivide this group into a category of models with two kinds of axis, orthotropic and plagiotropic, and a category with only one kind, orthotropic.

A third group of branched trees possesses *mixed axes*. A mixed axis includes a basal trunk segment, and a distal, longer or shorter branch segment all produced by the same meristem. The trunk of the adult tree is a linear sympodium made up of proximal segments of successive axes. Sometimes this structural segmentation is correlated with physiological specialization (e.g., cauliflory).

The reader will find that repeated reference to the dichotomous key (p. 84) will illustrate how these characteristics of trunk growth and branch differentiation serve to define architectural models.

III. Plan of the Descriptive Arrangement

Descriptions of models are inevitably arranged in the following pages in a linear sequence of more or less increasing complexity. This linear arrangement is often helpful for comparative purposes but certainly should not be interpreted as an evolutionary sequence, or even a sequence representing an increase in level of specialization. Many of the early described models, though simple morphologically, represent a high degree of organization, as witness the remarkable transfiguration of the apical meristem in Holttum's model when the axis passes from vegetative to flowering state.

The general plan is as follows:

1. Monoaxial trees (with a *single* apical meristem; "unbranched trees"). Models of Holttum, Corner.
2. Polyaxial trees (with *more than one* apical meristem; "branched trees").
   a) Vegetative axes all equivalent and orthotropic. Models of Tomlinson, Schoute, Chamberlain, McClure.
   b) Vegetative axes differentiated into trunk and branch. (1) Axes *orthotropic* and *plagiotropic*. Models of Leeuwenberg, Koriba, Prévost, Fagerlind, Petit, Nozeran, Aubréville, Massart, Roux, Cook. (2) Axes all *orthotropic*. Models of Scarrone, Stone, Rauh, Attims.
   c) Vegetative axes mixed (at first either plagiotropic or orthotropic, subsequently orthotropic or plagiotropic). Models of Mangenot, Champagnat, Troll.

IV. Monoaxial Trees

Holttum's Model

Definition. The unique axis is provided by a single aerial apical meristem and always remains vegetatively unbranched. It passes through an initial vegetative phase of stem building, followed by a reproductive phase where the terminal meristem differentiates completely into an inflorescence. Since the tree becomes reproductive and dies once fruit maturation is complete and seeds are dispersed, the tree is, by definition, monocarpic[2].

The model is named after R.E. HOLTTUM (H.O., 1970, p. 18) who has provided a classic analysis of the growth limiting characteristics of monocotyledons (HOLTTUM, 1955) which includes descriptions of monocarpic forms. In general trees which conform to this model may be described as "palm-like", indicative of their generally massive proportions and large leaves

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[2] See the distinction between monocarpy and hapaxanthy made elsewhere (p. 62).

(Fig. 13). They are not numerous but occur in a range of families, mostly monocotyledons. Dicotyledonous examples of such trees have been found, but in this group the model seems to be particularly frequent among herbs.

Example. Corypha elata (Palmae – Coryphoideae) exemplifies the model (Fig. 14). This tree is native to India and Ceylon but it, together with the related *C. umbraculifera* (Talipot palm) is often cultivated as a botanical curiosity. The specimen in Miami, Florida investigated by TOMLINSON and SODERHOLM (1975) provides representative dimensions. This tree at full flowering when it was 44 years old from seed, had a total height of 19.3 m, the inflorescence itself 4.5 m tall, the vegetative axis alone was 14.9 m tall. The diameter of the trunk at the base was 0.86 m, tapering to 0.46 m at the base of the inflorescence. Two stages in the development of this large fan-palm are shown; Figure 14Ca represents the tree in mid-life during the adult vegetative phase, with the huge crown of leaves, each leaf almost 4 m long. From counts of the total number of leaf scars on the trunk it can be estimated that the tree examined produced an average of ten leaves per year. None of the leaves subtends a vegetative meristem so that the palm is incapable of vegetative branching. Flowering, represented by Figure 14Cb, involves a major transformation of the apical meristem whereupon inflorescential branching becomes prolific. Foliage leaves are progressively, but fairly abruptly, reduced in size to bladeless bracts which, together with some of the transitional foliage leaves, subtend thick lateral axes, the largest over 3 m long. Branching is repeated to as many as five visible orders with successive orders reduced in diameter; flower-bearing axes (rachillae) 20–30 cm long and 3 mm wide terminate branches of all orders. This applies even to the main axis which, since the inflorescence is a monopodium, can be traced from the vegetative stem, which at its base is represented by a trunk about 1 m in diameter, to the end of a terminal rachilla scarcely 2 mm in diameter. The whole of this axis, through its various phases is a product of the single meristem originating in the seedling.

Inflorescence expansion in the palm particularly examined was relatively rapid, occupying a period of about three months. Flowers are aggregated on rachillae in linear series which represent condensed cincinni. Anthesis of flowers was completed in less than one month, a surprisingly short period in relation to the total life span of the tree. Fruit ripening to the time when it fell spontaneously required a further year, even though fruits reached their full size in less than three months. Quantitative calculations of inflorescence dimensions provided some remarkably high figures and give some idea of the reproductive effort of the tree. It was estimated that there were between 3 and 15×10^6 functional flowers on the inflorescence and these produced about 3×10^5 fruits. The total length of flower-bearing axes (i.e., rachillae, themselves representing only a part of the branch system) was of the order of 5000 m. *Corypha elata* is exceeded in all its dimensions by *C. umbraculifera* – the adult foliage leaf of a Talipot palm is over 5 m long.

Other Examples

1. Monocotyledons. Some species of *Metroxylon* (Palmae – Lepidocaryoideae), the true sago-palm of the Old World tropics (Malaysia to the Pacific Islands) e.g., *M.*

Fig. 13. Holttum's model, *Metroxylon salomonense* (Palmae – Lepidocaryoideae) from the Solomon Islands. (Photographed in the Singapore Botanic Garden) ▷

salomonense (Fig. 13), and *M. vitiense* have the same general appearance as *Corypha*, if not the same stature (CORNER, 1966; MOORE, 1973), but are feather-leaved. Nevertheless the inflorescence of *M. vitiense* produces about a million flowers (TOMLINSON, 1971b). Single-stemmed species of *Raphia* (Palmae – Lepidocaryoideae) represent Holttum's model well. *Raphia* ranges from Madagascar through tropical Africa to Central America where it is represented by a single species *R. taedigera*. The hapaxanthic condition is not very obvious in *Raphia* because no extended terminal axis is developed to raise the flowering branches above the leafy crown (RUSSEL, 1965). Instead the long and rigid, but downwardly curved flowering branches, which develop in acropetal order, are subtended by distal and usually little modified foliage leaves. *Raphia regalis* (Fig. 14B), of equatorial Africa, is undoubtedly the most imposing member of the genus with leaves no less than 25 m long, which surely sets a record for the length of determinate leaves of any vascular plant[3]. These large leaves give stature to the plant, since the trunk is relatively short. In some *Raphia* species (e.g., *R. humilis* of the Cameroons) the inflorescence is somewhat differentiated, with distal foliage leaves reduced to distinct bracts.

Plectocomia griffithii (Palmae – Lepidocaryoideae) is of interest as a lianescent example of Holttum's model. It is probably the most massive of the rattan palms of the Malaysian tropics, since its stems exceed a diameter of 8 cm, but is unbranched and monocarpic (FURTADO, 1951). Most rattans are branched basally and conform to Tomlinson's model, and indeed *Plectocomia* has an incipient tendency to produce basal suckers, but Furtado reports that they always abort.

Puya raimondii (Bromeliaceae) the giant "puma" of the Bolivian and Peruvian Andes, contrasts markedly with the palms in habitat; it is localized at altitudes of 3700 4200 m in the Andean paramos (KINZL, 1949) but illustrates Holttum's model well (Fig. 14D). In the vegetative state the plant reaches a height of 3 m, with a short trunk and a crown of numerous lanceolate leaves (Fig. 14Da). In the reproductive phase (Fig. 14Db) the height of the plant is more than doubled by the dense paniculate inflorescence.

Several species of *Agave* and *Furcraea* (so-called "century plants", Agavaceae) mainly of the drier parts of Central America and the Caribbean represent this model well in so far as they lack the ability to sucker or become stoloniferous. They often propagate vegetatively by means of

Fig. 14A–D. Holttum's model. ▷

A *Sohnreyia excelsa* Krause (Rutaceae, from the Amazonian forest near Manaos, Brazil). The tree is 20 m high at flowering time (KRAUSE, 1921).

B *Raphia regalis* Beccari (Palmae, from the Meyah forest, Congo, *F. Hallé 1461.*) A nearly acaulous palm with a terminal inflorescence; the leaves, more than 25 m in length, are probably the largest in living angiosperms and here reach the forest canopy.

C *Corypha elata* Roxb. (Palmae, southeast Asia, from specimens cultivated in Bogor, Indonesia, and in Miami, Florida). *a* Vegetative phase; *b* reproductive phase; the tree is 44 years old and 19 m high; its terminal inflorescence 4.5 m high (TOMLINSON and SODERHOLM, 1975).

D *Puya raimondii* Harms (Bromeliaceae, Andes of Peru and Bolivia at an altitude of more than 4000 m, from photographs supplied by Basset Maguire). *a* Vegetative phase; *b* reproductive phase; the tree is 10 m high, with the terminal inflorescence exceeding the trunk in length (KINZL, 1949)

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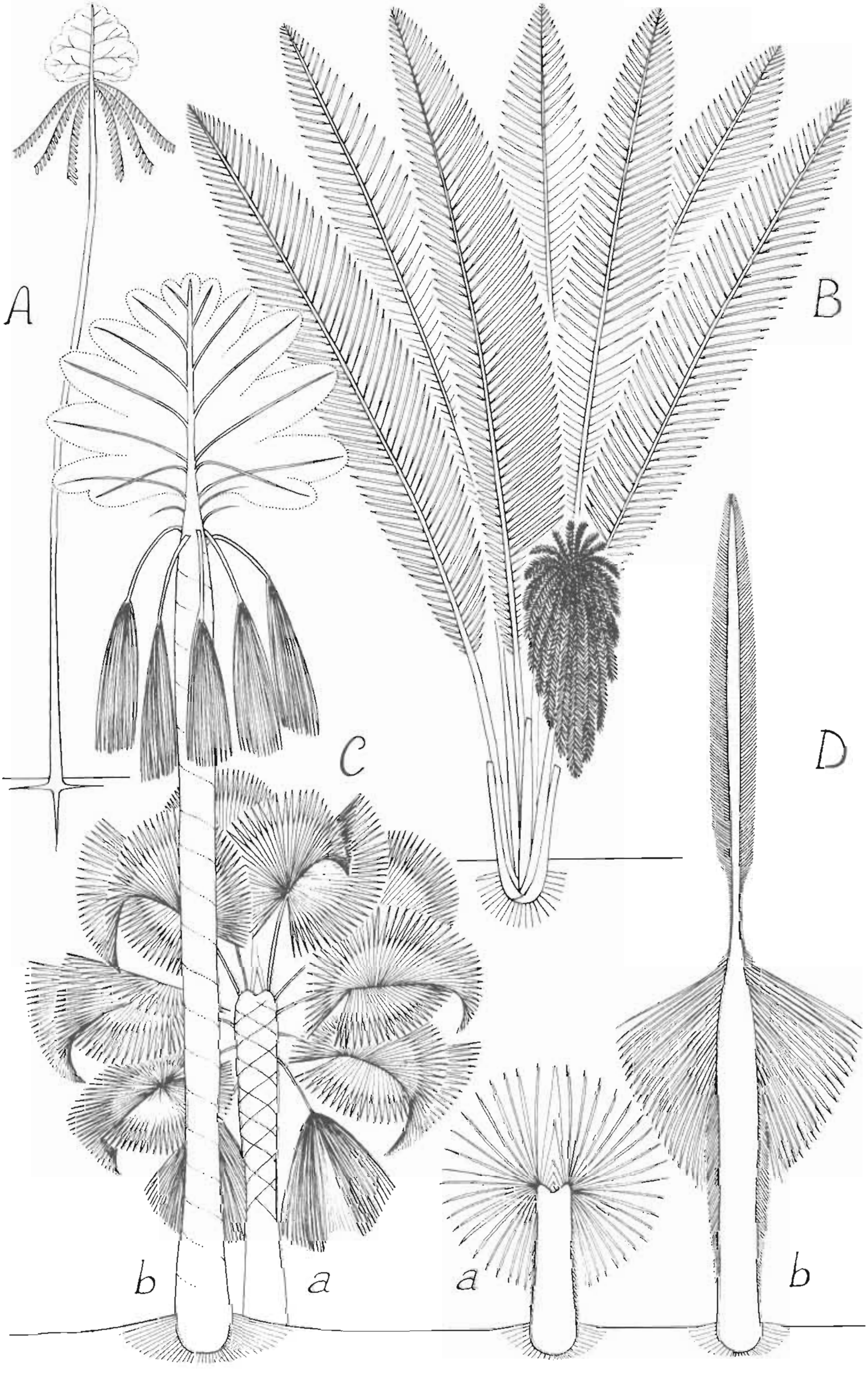
[3] They are possibly exceeded by the leaves of some climbing ferns, which are, however, indeterminate.


A
B
C
D
b
a
a
b

bulbils on the inflorescence, so it may be disputed that they are strictly monocarpic. The vegetative axis is usually short so the rosette of fleshy leaves remains at ground level, but some species produce a distinct trunk (e.g., *A. attenuata*). Holttum's model is further represented by species of *Ensete* (Musaceae, tropical Africa), a wild, usually monocarpic banana of distinctive physiognomy. *Ensete,* like *Musa,* may be arborescent by virtue of the overlapping leaf bases (forming a "pseudostem") but in *E. edule* the true trunk is well developed and edible as a kind of sago-tree.

2. *Dicotyledons.* Holttum's model is rare in arborescent dicotyledons but it is illustrated precisely by *Sohnreyia excelsa* [Rutaceae; Manaos, Brazil, (Fig. 14A)] as described by KRAUSE (1921). This plant may reach a height of 20 m, remaining unbranched, before producing a massive terminal inflorescence. The description by KRAUSE does not state if these dicotyledons lack lateral vegetative meristems completely. In this same family species of the genus *Spathelia* (Central America and the Caribbean) are also monocaulous and monocarpic (MENNINGER, 1967: MARIE-VICTORIN, 1948). Two further examples from different families include *Echium bourgeanum* (Boraginaceae) and other species of *Echium* from the Canary Islands (REISIGL, 1964). These species of bugloss reach a height of 4 m, the whole distal part of the axis being an inflorescence. *Lobelia deckenii* (Lobeliaceae) and some other arborescent *Lobelias* of the East African mountains from Ethiopia to Tanzania (COTTON, 1944) represent this model.

Harmsiopanax (Malaysian Archipelago), recently revised by PHILIPSON (1973), represents Holttum's model in the Araliaceae, not otherwise known for the family although common in the Umbelliferae. The tallest (*H. ingens*) reaches a height of 18 m, the remaining species being smaller (to 7 m). These species are monocarpic, but the possibility of branching is not ruled out. More information about the architecture of this genus would be useful, especially in relation to its stem anatomy.

Variations. The definition of this model is so restrictive that it would scarcely appear to admit variation, but certain palms, belonging exclusively to the subfamily Caryotoideae (MOORE, 1973) show a unique flowering condition which represents a departure from the strict pattern of the model. We represent this by *Wallichia disticha* (Fig. 17A). This palm of India and Malaya is unusual in its distichous leaf arrangement (all other caryotoid palms have spirally-arranged leaves). The palm remains in the vegetative state for an extended period (14 years in one measured example) before its shoot apex ceases to grow and the reproductive phase ensues. A terminal inflorescence results from extension of the distal internodes but with basipetal development of flowering branches. In other caryotoid palms the hapaxanthic condition is expressed in an equally distinctive way since previously inhibited lateral meristems in the axils of the foliage leaves expand as flowering branches, but mature in a basipetal, not an acropetal sequence. This reverses the order of their age and one finds distal branches with ripe fruits above branches which have still to flower. Monocaulous species of *Arenga* (e.g., *A. pinnata*) and *Caryota* (e.g., *C. urens*) conform to this pattern. There are exceptions to this rule of basipetal flowering in caryotoid palms, e.g., *Arenga obtusifolia* Mart. and *A. retroflorescens* Moore and Meijer, according to MOORE (1973).

Although demonstrably distinctive in a biological sense, Holttum's model shows considerable similarity to both Corner's and Tomlinson's models, next to be described. This is evident when one considers the number of genera in which different species illustrate two or even three models, notably in the palms where closely related species may be either hapaxanthic or pleonanthic and with or without basal suckers, all possible permutations exist. Examples of this intrageneric variation include *Arenga, Caryota, Metroxylon* and *Raphia,* while the Musaceae include the two genera *Ensete* (mainly nonsuckering) and *Musa* (suckering).

Strategy of the Model. The monocarpic character of the plants in Holttum's model does not favor individual longevity in comparison to the extended life span of most trees. *Corypha* at about 40 years probably represents an upward limit; most agavaceous "century plants", despite their common name, live only a few years (of the order of 10–15) before flowering. Biologically Holttum's model seems inferior in its single reproductive act after so extended a period of vegetative growth, so that it is difficult to account for its existence in a woody plant. However, measurements of biomass distribution in *Corypha elata* (TOMLINSON and SODERHOLM, 1975) suggest that about 15% of the total dry matter produced by the palm in its lifetime is diverted into seed production. Functionally this "strategy" bears comparison with annual herbs, in which Holttum's model can be found (and indeed may be common).

It is perhaps unfortunate that the word "strategy" is used with reference to sessile organisms like plants, implying as it does conscious action, but the term has such accepted use in population biology, especially with reference to alternative possibilities for population regulation via contrasted kinds of life history, that it is adopted here. Discussion of life history strategies is based on the "r" vs. "K" selection terminology elaborated by MACARTHUR and WILSON (1967; see also WILSON, 1975, p. 80–105). These parameters appear in the models for population growth which may be expressed by the logistic equation: $dn/dt = rN(1-N/K)$ where r = the intrinsic rate of increase of a population and K = the carrying capacity of the environment, i.e., the maximum number of individuals which can be supported by a given environment.

On the one hand, organisms have been contrasted as "r strategists" or "opportunistic species" which make use of a high reproductive capacity (r) to occupy short-lived, unpredictable habitats – forest clearings, newly exposed mud banks, surfaces exposed by land slides, etc. Such species succeed if they can discover the habitat quickly, reproduce rapidly and disperse readily in search of new habitats when the existing one becomes stabilized or its nutrients used up. On the other hand, "K strategists" or "stable species" characteristically occupy a longer-lived habitat, notably "climax" forest, and maintain a population level at or near the saturation level K. It is no longer advantageous for a species to have a high reproductive rate, r, rather selection is for genotypes which are long-lived, have a high competitive ability and once established are efficient in extracting the energy produced by the environment.

Such concepts were, of course, developed by zoologists with reference to animal populations, but are equally applicable to plant populations, with the singular problem that the individuals may be hard to identify in an organism with many active growth centers (meristems) and with the possibility of vegetative propogation. Extreme r- and K strategists are obviously opposite ends of a spectrum of possibilities, which in vascular plants may be represented at one extreme by ephemeral herbs with short life cycles and high reproductive output, while at the other extreme there are long-lived forest trees, reaching sexual maturity late and with limited production of large seeds. Clearly trees have different reproductive rates, although this is difficult to measure since they are so long-lived and little data are yet available. The figures quoted above for *Corypha elata* represent an apparently simple organism for which biomass data can be estimated. As we proceed with our descriptions of architectural models it is clear that we incorporate some information which is of value in assessing the reproductive capacity of a tree, since the relative number of vegetative versus reproductive (flower and inflorescence) meristems is often determined by features diagnostic for specific models. The information available is elemental and even quite crude; it needs the refinement of knowledge of flower number, seed number and size. Nevertheless we have felt free to comment on the likely relation of architecture to reproductive strategy where such discussion is appropriate, since the adaptive significance of a particular growth model in part is determined by methods of branching which establish the numbers of sexual meristems produced.

The reproductive characteristic of Holttum's model is the "big bang" effect (SCHAEFFER and GADGIL, 1975) similar to that of many weedy herbs. The same mechanism in a tree might suggest an efficient way of saturating a biotope and so escaping predators by making the interval between reproductive events very large, as suggested by JANZEN (1976, 1978). This would only work, however, at the population level if reproduction was completely synchronous (cf. bamboos, p. 142) or flowering individuals were widely scattered. Holttum's model in a tree may be favored either by a nonseasonal climate or by the succulent habit. It seems significant that the known species showing this model all exhibit continuous growth. Rhythmic growth in the vegetative state implies regular physiological changes in the apical meristem and any degree of developmental instability may be incompatible with the once-flowering state. However, branched trees can be monocarpic as the example of *Cerberiopsis candelabrum* (Apocynaceae) described by VEILLON (1971) in New Caledonia shows. A point of comparison between Holttum's model and Corner's model in relation to reproductive strategy is that many species of the latter are dioecious, but this is never found in the former[4]. *Corypha elata*, for example, is self-compatible (TOMLINSON and SODERHOLM, 1975) which seems as important in a long-lived woody r strategist as it is in an ephemeral weed (BAKER, 1959).

Taxonomic List of Examples (Holttum's Model)

MONOCOTYLEDONS

Agavaceae:
Many species of *Agave* L. and *Furcraea* Schult., Caribbean and C. America, GENTRY, 1972.
Bromeliaceae:
Puya raimondii Harms (Fig. 14D), Peruvian and Chilean Andes, KINZL, 1949 / *Puya* sp. indet., Ecuadorian Andes.
Musaceae:
Ensete gilletti (DeWild.) Cheesm., Cameroons / *Ensete ventricosum* (Welw.) Cheesm., Ethiopia, commonly cultivated.

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[4] One should qualify this statement since *Caryota* species may be functionally dioecious, a biological feature correlated with their long-life span as flowering individuals.

[H] herbs
[L] lianes
* Example cultivated in botanic gardens.

Palmae:
Arenga pinnata Merrill, Malaysia, Holttum, 1955 / *Caryota urens* L., Malaysia, *Corypha elata* Roxb.* (Fig. 14c), Indo-Malaya, Tomlinson and Soderholm, 1975 / *Corypha umbraculifera* L., "Talipot Palm", India, Ceylon / *Metroxylon vitiense* Benth. and Hook, Fiji, Tomlinson, 1971b / *Metroxylon salomonense* (Warb.) Beccari (Fig. 13), Solomon Islands / [L] *Plectocomia griffithii* Becc., Malaysia, Furtado, 1951 / *Raphia regalis* Becc., Fig. 14B, Congo.

DICOTYLEDONS

Araliaceae:
Harmsiopanax ingens Philipson, New Guinea, Philipson, 1973 / *Harmsiopanax* sp. New Guinea.
Boraginaceae:
Echium bourgaeanum Webb Canary Islands, Reisigl, 1964 / *Echium* sp.*, Canary Islands.
Compositae:
Argyroxiphium sandwicense DC., "Hawaiian silver sword", Maui, Hawaii, Carlquist, 1965 / *Phoenicoseris pinnata* (Bert. ex Decne.) Skottsb., Juan Fernandez Islands, Carlquist, 1965 / *Wilkesia gymnoxiphium* A. Gray, Kilauea, Hawaii.
Crassulaceae:
[H] *Aeonium nobile* (Praeger) Praeger, Canary Islands, Serebryakov and Serebryakova, 1972 / [H] *Aeonium tabulaeforme* Webb and Berth., Teneriffe, Canary Islands, Lems, 1960 / [H] *Aeonium urbicum* Webb and Berth., Canary Islands, Emberger and Chadefaud, 1960 / [H] *Kalanchöe gastonis-bonnieri* Hamet and Perrier (Biennial), Madagascar, Cremers, 1973.
Epacridaceae:
Dracophyllum verticillatum Labill., New Caledonia, Veillon, 1971.
Geraniaceae:
[H] *Geranium rubescens* Yeo, Madeira, Yeo, 1973.
Gesneriaceae:
[H] *Boea havilandi* Ridley, Malaysia, Burtt, 1964.
Lobeliaceae:
Lobelia deckenii Hemsl., Ethiopia, Cotton, 1944 / *Lobelia rhynchopetalum* Hemsl., Ethiopia, Hedberg, 1971.
Rutaceae:
Sohnreyia excelsa Krause (Fig. 14A), Manaus, Brazil, Krause, 1921 / *Spathelia brittonii* Wilson, Cuba, Marie-Victorin, 1948 / *Spathelia simplex* L., Cuba, Jamaica, Menninger, 1967.

Corner's Model

Definition. Vegetative growth of a single aerial meristem produces one unbranched axis, on which the inflorescences (or sporophylls in nonangiospermous plants) are lateral. Consequently the resulting monocaulous tree is not monocarpic and growth is not determinate.

The essential feature of this model is that sexuality does not arrest growth of the single axis. Reproductive branches vary considerably in their position in relation to the vegetative crown and cauliflory is common. This model differs from Holttum's model in the presence of an indefinitely functioning apical meristem during the reproductive phase. The axis is now pleonanthic, not hapaxanthic. It is named after E.J.H. Corner, former Professor of Botany at Cambridge University, acknowledging him as a source of inspiration for students of tropical trees (Corner, 1949.

Most single-stemmed palms correspond to Corner's model. However, a large taxonomic variety of tropical dicotyledonous trees which are monocaulous also conform precisely to this model, although they do not reach the height and age of many larger palms. Phyllotaxis is typically spiral, but distichy in *Oenocarpus distichus* Palmae – Arecoideae) is a striking exception (Fig. 17B).

Example. Carica papaya ("papaya" of Central America but widely cultivated in the tropics) serves to illustrate the model since it is widely familiar with its unbranched trunk, its crown of spirally arranged leaves and the congested persistent leaf scars on the older parts (Corner, 1949). Trees are dioecious, with inflorescences in the axils of current leaves (Badillo, 1971). Male trees have extended, often pendulous flowering branches (Fig. 16A) whereas the female tree has more or less sessile inflorescences or solitary flowers, the fruits ripening on the older part of the trunk below the leaves (H.O., 1970, p. 19). Growth of the axis is continuous, producing long-petioled palmatifid leaves, each of which subtends an inflorescence, once the reproductive phase is reached. Papaya is a soft-stemmed tree by virtue of its parenchymatous wood; however, individuals commonly exceed 6 m but always with a pronounced distal tapering of the trunk. Occasionally cultivated and wild species are branched but this represents reiteration (p. 269 and Figs. 73 to 75). It demonstrates the existence of dormant lateral meristems; vegetative branching within the model does not occur.

Other Examples

1. Tree Ferns. Some tree ferns (e.g., species in the genera *Dicksonia* and *Cyathea*) correspond to this model although it is important to recognize that the reproductive organ is a sporophyll, not a lateral axis (Fig. 15). Many tree ferns do branch (HALLÉ, 1966) and they may largely represent Tomlinson's model.

2. Cycads. Female trees in species of the genus *Cycas* (e.g., *C. circinalis, C. revoluta*; Asian tropics but widely cultivated) also represent Corner's model by virtue of their monopodial growth (Fig. 17C) and so contrast with sympodial (but still monocaulous) male trees which we have used to illustrate Chamberlain's model (Fig. 24A–C). *Cycas* shows rhythmic growth with the periodic production of successive whorls of scales, foliage leaves and megasporophylls (a, b, c in Fig. 17C). Vegetative propagation may occur by the production of bulbils on the trunk. Branching, which is common in cultivated specimens, indicates reiteration (p. 269). These examples are of interest in contrasting male and female individuals of the same species by including them as representatives of different models, since this provides extreme testimony of the divergence between architecture and taxonomy.

3. Monocotyledons. The single-stemmed dioecious palm, *Borassus aethiopum* (Palmae – Borassoideae) of tropical Africa represents the model precisely. In the younger sterile phase (Fig. 16B) leaf bases are usually persistent, and this is helpful in providing contrast to the adult reproductive phase (Fig. 16C) with its continuous production of lateral inflorescences, the trunk now being exposed by leaf-fall. In older trees the distal part of the trunk is typically inflated. Some indication of the taxonomic diversity of palms which conform to the model is provided in our subsequent list, but this is not intended to be complete as it would include several hundred species. Genera which are frequently, if not exclusively monocaulous, apart from *Borassus*, include *Copernicia, Elaeis, Howeia, Mauritia, Rhopalostylis, Roystonea,* and *Sabal* (MOORE, 1973; CORNER, 1966). The family Xanthorrhoeaceae (almost exclusively Australian) includes examples of Corner's model in the genera *Dasypogon, Kingia* (STAFF, personal communication).

4. Dicotyledons. Many families of dicotyledons include examples of Corner's model and we have illustrated a few of the more distinctive ones. Figure 16G shows *Hicksbeachia pinnatifolia* (Proteaceae, tropical parts of eastern Australia) which is cauliflorous. Another cauliflorous species is *Pithecellobium hansemanii* (Leguminosae – Mimosoideae, New Guinea) which is unusual for this family in its monocaulous habit (Fig. 16F), but which seems to be intermediate between

Fig. 15. Corner's model, tree ferns (*Cyathea* spp., Cyatheaceae) in the Tjibodas Garden, Java, Indonesia ▷

Corner's model and Troll's model (p. 242) which is otherwise typical of most legumes; specimens do occur which develop a relay axis. The tree reaches a height of 7 m without evidence of rhythmic growth, producing a series of bipinnate leaves each more than 120 cm long (HALLÉ, 1974). The trunk remains slender, its basal diameter not exceeding 5 cm and it bends distally. Another arborescent legume, *Archidendron beguinii* (Mimosoideae; Halmaheira Island, Indonesia), is described by DE WIT (1942) as unbranched and it may conform to Corner's model. This species is of further interest in that it retains a primitive condition in the flower with five to ten carpels.

Three smaller trees, none exceeding 5 m, but conforming to Corner's model, include *Tapeinosperma pachycaulum* (Myrsinaceae, Solomon Islands, Fig. 16E) described by STONE and WHITMORE (1970), *Guarea richardiana* (Meliaceae, French Guiana, Fig. 16D) and *Goethea strictiflora* (Malvaceae, Brazil, Fig. 16H). The last two are cauliflorous.

Variations. A number of minor architectural variations do not conflict with the uniformity of this model; the two most significant variants relate to the periodicity of growth and the position of inflorescences. The examples we have cited so far, except for *Cycas*, show no morphological evidence of rhythmic growth. However, other species reveal episodic events clearly. *Trichoscypha ferruginea* (Anacardiaceae, Central Africa) is a monocaulous and cauliflorous treelet to a height of 10 m. Figure 17D represents the apex of the trunk, with foliage leaf blades removed, and shows the series of alternately either reduced and scale-like or foliage leaves. Their scars on the older parts are readily contrasted. The bud in the resting condition is enclosed by a series of scales. Other examples of rhythmic growth in this model include *Allexis cauliflora*, *Chlamydocola chlamydantha* and *Clavija lancifolia*, the last two illustrated by H.O., 1970, pp. 19, 24, 25. All are from different families (Violaceae, Sterculiaceae and Theophrastaceae, respectively). Examples from New Guinea are *Barringtonia calyptrocalyx* (Lecythidaceae) and *Semecarpus magnificus* (Anacardiaceae) described by HALLÉ, (1974).

Temperate representatives of this model are uncommon but may be illustrated by species of *Berberis* (Berberidaceae).

Inflorescences are typically produced in the axils of leaves, but the time of their expansion varies. In stems with continuous

Fig. 16A–H. Corner's model. ▷

A *Carica papaya* L. (Caricaceae, central America; the paw-paw tree, commonly cultivated); a male tree.

B and *C* *Borassus aethiopum* (Mart.) Beccari (Palmae – Borassoideae, the Palmyra palm of west Africa – other *Borassus* species are identical). *B* The juvenile vegetative palm, still retaining its leaf bases; *C* the adult reproductive female with fruits, showing the typical inflated, bare trunk.

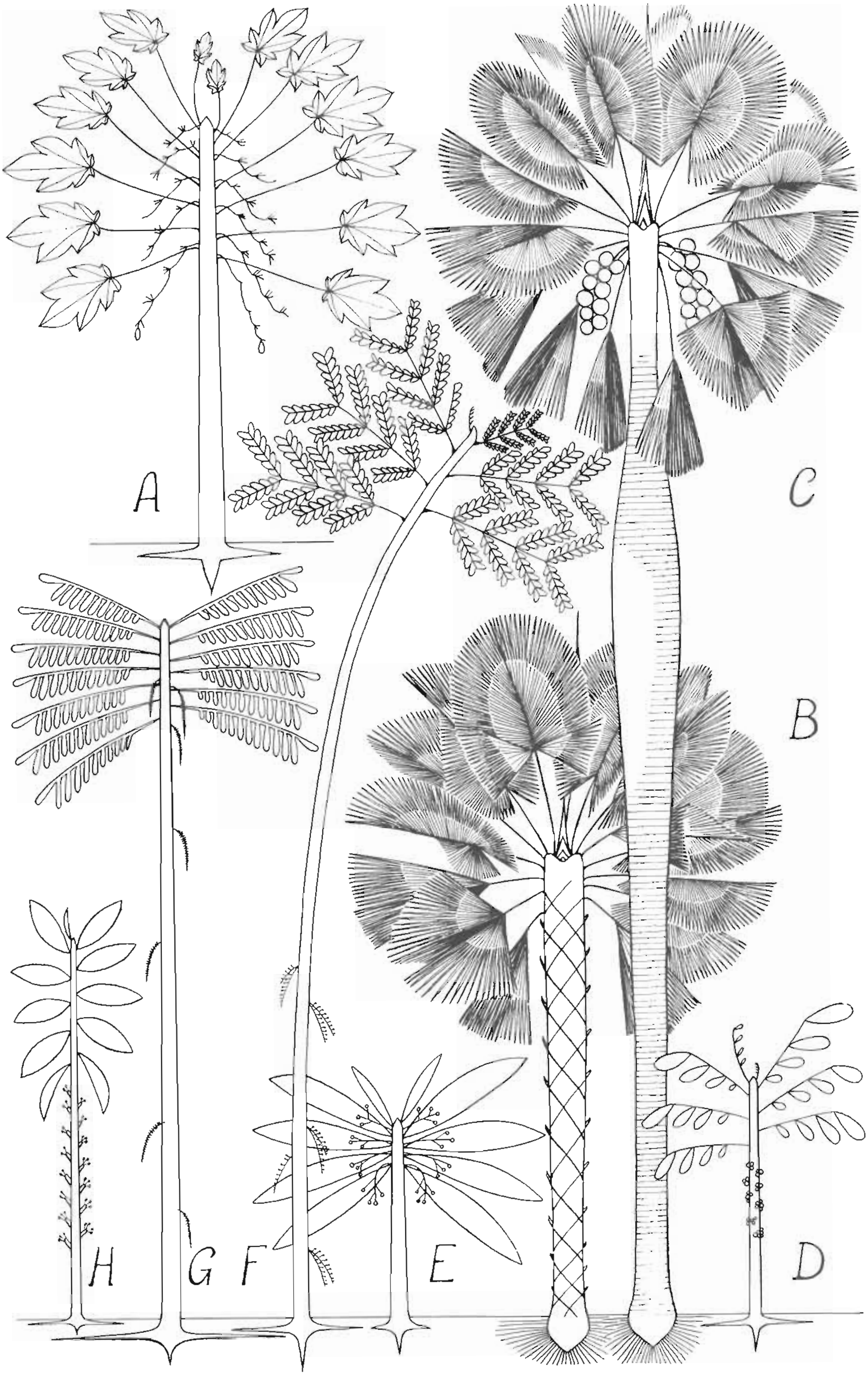
D *Guarea richardiana*. A. Juss. (Meliaceae, Approuague, French Guiana, *R.A.A. Oldeman 2393*). A monoaxial and cauliflorous treelet of the forest undergrowth, less than 2 m high.

E *Tapeinosperma pachycaulum* Stone and Whitmore (Myrsinaceae, Solomon Islands), from documentation provided by STONE and WHITMORE (1970).

F *Pithecellobium hansemanii* (F. Muell.) Mohl. (Leguminosae – Mimosoideae, New Guinea). A small monoaxial and cauliflorous tree of the rain-forest, 7–9 m high (F. HALLÉ, 1974).

G *Hicksbeachia pinnatifolia* F. Muell. (Proteaceae, Queensland and New South Wales, Australia; from a specimen cultivated in the Sydney Botanic Garden). A small tree, 7 m high.

H *Goethea strictiflora* Hook. (Malvaceae, Brazil; from a specimen cultivated in the Jean-Noël Maclet garden in Tahiti, French Polynesia). A cauliflorous treelet, less than 3 m high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growth, inflorescences appear and develop continuously, the most familiar example being the coconut. In many Arecoid palms the inflorescence does not expand until after its subtending leaf has fallen (e.g., *Roystonea* spp.) so that the inflorescence is conspicuous below the crown (Fig. 17B). In other palms inflorescences seem to be produced continuously, but their expansion is seasonal, as in *Sabal palmetto* in the southeastern United States, or in several *Copernicia* species. Otherwise, where a growth rhythm is established reproduction is correlated with this and perhaps *Cycas* provides the best example.

The dissociation in time and space of sexuality from vegetative growth is exemplified by cauliflory which seems quite common in this model, as in *Allexis cauliflora, Chlamydocola chlamydantha, Placodiscus bancoensis* and *Trichoscypha ferruginea. Chytranthus longiracemosus* shows the extreme of this in its long inflorescences at soil level (basiflory—see HALLÉ, N. and ASSI, 1962).

Phyllobotryon (=*Phyllobotryum*) *spathulatum* (Flacourtiaceae, Central Africa) shows another very unusual kind of floral specialization. This monocaulous treelet of the forest undergrowth, less than 7 m high, develops a crown of oblanceolate leaves (Fig. 17F), each leaf (Fig. 17G) more than 1 m long. Inflorescences are epiphyllous, i.e., morphologically adnate to the upper surface of the leaf. In their further development flowers may pierce the leaf surface and protrude adaxially.

Despite its distinctiveness, Corner's model shows relationships with other models, notably that of Tomlinson. This is shown by contrasted species of one genus, as in *Phoenix* where some represent Corner's model (e.g., *P. canariensis*), others Tomlinson's model (e.g., *P. reclinata*). In cultivated *Phoenix* palms hybridization and introgression between suckering and nonsuckering species may produce populations which vary in this respect. The transition between certain monoaxial dicotyledons to branched trees with reduced lateral branches which may then have a purely sexual function (i.e., a lateral inflorescence) is suggested in the Rubiaceae.

Fig. 17A G. Holttum's and Corner's models, variations and intermediates. >

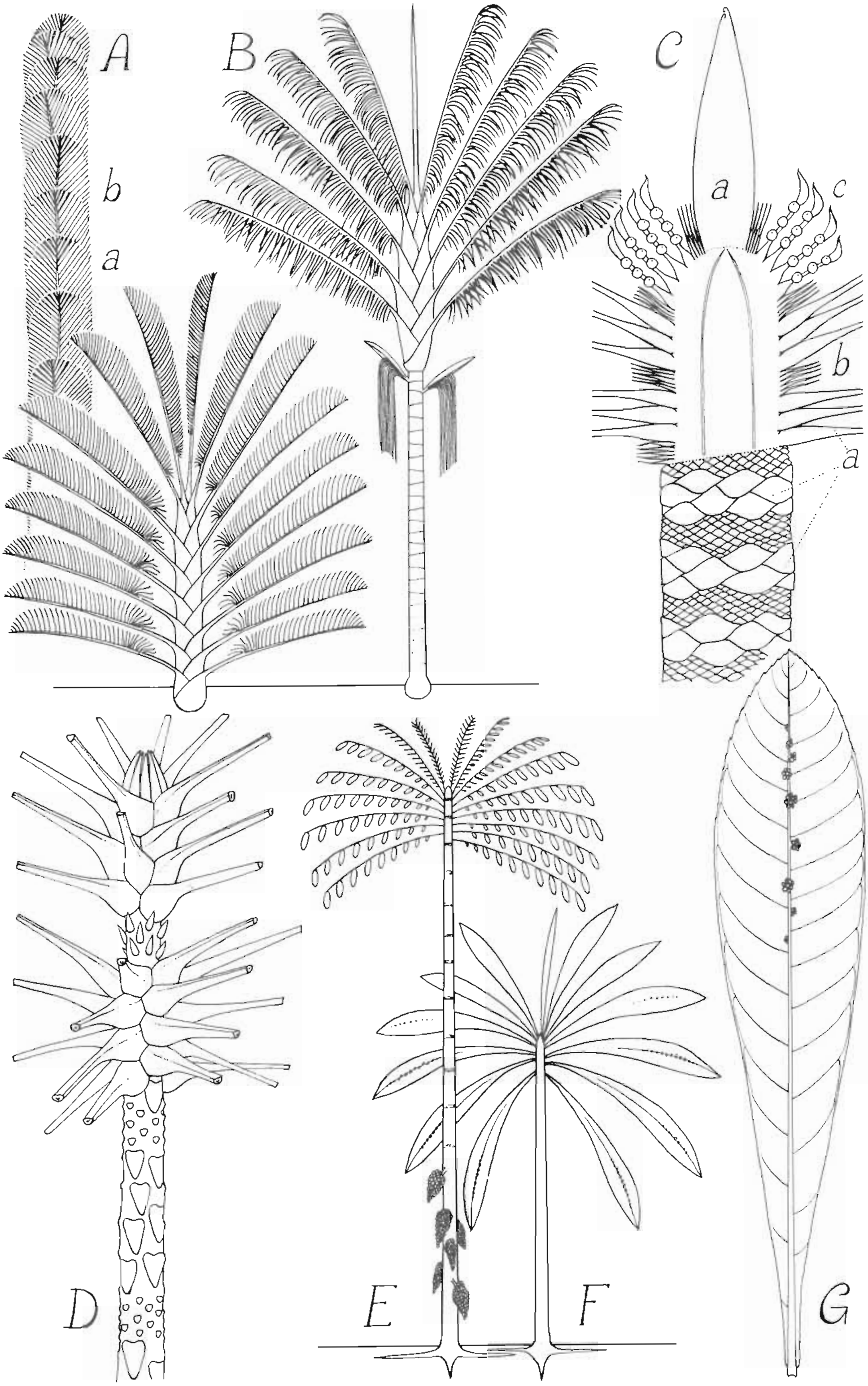
A *Wallichia disticha* T. Anders. (Palmae, Himalaya, from specimens cultivated in Miami, Florida, and in Bogor, Indonesia). Distinctive by virtue of its distichous phyllotaxis. *a* Front view of a young specimen; *b* lateral view. This palm is representative of the Caryotoideae, in which trees are hapaxanthic but with lateral inflorescences usually maturing in basipetal succession. This demonstrates an architecture intermediate between Holttum's and Corner's models.

B *Oenocarpus distichus* Mart. (Palmae, from the forest of Mosqueiro Island, Bélèm, Brazil). Again, this is a "distichous" palm; the inflorescences are infrafoliar and the tree belongs to Corner's model.

C *Cycas circinalis* L., female tree (Cycadaceae, southeast Asia, a sago-tree). Corner's model with rhythmic growth. *a* Foliage leaves, their primordia or their scars; *b* bud-scales or their scars; *c* megasporophylls or their scars. The trunk is a monopodium and should be contrasted with male trees, and probably all other cycads, which represent Chamberlain's model.

D and *E* *Trichoscypha ferruginea* Engl. (Anacardiaceae, from the Belinga forest, Gabon, *N. Hallé 2960*). *D* Details of apex with foliage leaves removed; rhythmic growth is indicated by successive series of foliage leaves and bud-scales. *E* Habit; a small monocaulous and cauliflorous tree of the rain-forest, up to 10 m high (N. and F. HALLÉ, 1965).

F and *G* *Phyllobotryon spathulatum* Muell.-Arg. (Flacourtiaceae, west equatorial Africa). *F* Habit; a monoaxial treelet of the forest undergrowth, less than 6 m high. *G* A single "flowering" leaf from above. The small inflorescences appear on the upper surface; the leaf may reach a length of 1 m (LETOUZEY et al., 1969)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There are close similarities between certain representatives of Petit's model in this family and related species which exhibit Corner's model. This is most notable in *Bertiera* (LEROY, 1974b).

Strategy of the Model. Physiognomically these trees, by virtue of their single trunk, can be confused with Holttum's model, but their indeterminate and usually extended life span produces trees with a potential *K* strategy with survival of individuals as efficient as survival of populations. Many of the plants we have described are undoubtedly short-lived; papaya mostly does not exceed an age of 15 years. On the other hand, many large palms are quite long-lived and may survive in excess of a century. A series of planted royal palms (*Roystonea regia*) which attained ages from 120 to 150 years in the "Place des Palmistes", Cayenne, French Guiana, is a historically documented example (Reverend Father BARBOTIN, 1972, personal communication). Size varies considerably in examples of Corner's model. Most dicotyledonous examples that we know do not exceed 10–15 m in height, whereas the *Roystonea* specimens we have just mentioned attained heights of 30 m in many cases. These differences relate to contrasted habitats in which such plants grow. Most of the dicotyledonous examples of Corner's model occur in the understorey of the tropical rain forest and here, of course, many single-stemmed palms also thrive. This environment is remarkably stable in its microclimate and it is in this kind of stable environment that *K* strategists survive, as, for example, BLONDEL (1975) has shown for birds. We must perhaps seek other explanations in those environments in which tall, single-stemmed palms are prominent, as in the palmyra palm (*Borassus*) savannas of the Old World, the *Mauritia flexuosa* swamps of Brazil and the Guianas, or the *Copernicia*-dotted pampas of South America. Equally the existence of Andean species of *Espeletia* which grow in a very rigorous climate requires a different explanation and vegetative aspects of strategy may predominate. SMITH (1974) showed in *Espeletia schultzii* Wedd., an acaulescent species of the páramo of the Venezuelan Andes, that strongly nyctinastic leaf movements are important in survival. At night the rosette leaves close around the apical bud, protecting it from freezing. Leaves retract and the rosette opens during the day.

Taxonomic List of Examples (Corner's Model)

PTERIDOPHYTES

Cyatheaceae:
**Alsophila australis* R.Br., Tasmania, Australia / *Cyathea camerooniana*, Trop. Africa, F. HALLÉ, 1966.
Dicksoniaceae:
Dicksonia sp., Melanesia, EMBERGER and CHADEFAUD, 1960.

GYMNOSPERMS

Cycadales:
Cycas circinalis L.♀ (Fig. 17C), Indo-Malaya/ *Cycas revoluta* Thunb.♀, Indo-Malaya/**Encephalartos laurentianus* De Wild., Trop. Africa. [Probably some *Macrozamia* spp. (Australia) belong to this model].

MONOCOTYLEDONS

Agavaceae:
Nolina recurvata Hemsl. Mexico.
Cyperaceae:
[H] *Hypolytrum heteromorphum* Nelmes, Ivory Coast, LOROUGNON, 1971 / [H] *Mapania baldwinii* Nelmes, Ivory Coast, LOROUGNON, 1971.
Palmae:
Areca catechu L., "betel-nut palm", E. Tropics / *Borassus aethiopium* Mart., "palmyra palm"

(Fig. 16B, C), Trop. Africa, in savannas / *Cocos nucifera* L., "coconut", pantropical in cultivation, sea-shores / *Elaeis guineensis* Jacq., "African oil palm", Trop. Africa, in secondary forest / *Mauritia flexuosa* Benth. and Hook., Trop. America / *Oenocarpus distichus* Mart. (Fig. 17B), Brazil / *Phytelephas macrocarpa* Ruiz and Pav., "ivory nut palm", Colombia, Ecuador / *Roystonea oleracea* O.F. Cook, "royal palm", Trop. America / *Sabal palmetto* Lodd. ex Schult., "cabbage palm", S.E. United States / *Socratea exorrhiza* Wendl., "stilt palm", Trop. America. (The full list is very long and includes the great majority of single-stemmed palms).

Pandanaceae:

Pandanus danckelmannianus K. Schum., Solomon Islands, STONE, 1972 / *Pandanus princeps* Stone, Madagascar, STONE, 1970.

Xanthorrhoeaceae:

+*Dasypogon bromeliifolius* R.Br., W. Australia / +*Kingia australis* R.Br., W. Australia.

DICOTYLEDONS

Anacardiaceae:

Semecarpus magnifica K. Schum., New Guinea, F. HALLÉ, 1974 / *Trichoscypha ferruginea* Engl. (Fig. 17D, E), C. Africa, N. and F. HALLÉ, 1965.

Araliaceae:

Brassaia palmata Decne. and Planch., Malaya, CORNER, 1952.

Berberidaceae:

**Berberis bealei* Fort., China.

Bignoniaceae:

**Colea lantziana* Baill., Madagascar / *Colea nana* Perr., Madagascar.

Byblidaceae:

[H] *Byblis liniflora* Salisb., Australia, EMBERGER and CHADEFAUD, 1960.

Caricaceae:

Carica papaya L. (Fig. 16A), papaya, Mexico, BADILLO, 1971 / (Other species of *Carica* have the same architecture).

Compositae:

Espeletia schultzii Wedd., Andes, SMITH, 1974 / *Espeletia spicata* Sch. Bip. ex Wedd., Andes, REISIGL, 1964.

Connaraceae:

Jollydora duparquetiana (Baillon) Pierre., C. Africa, CORNER, 1954.

Cunoniaceae:

+*Pancheria hirsuta* Vieill. New Caledonia.

Euphorbiaceae:

Agrostistachys borneensis Becc., Malaya, Borneo, CORNER, 1952 / *Agrostistachys sessilifolia* Pax and K. Hoffm., Malaya, CORNER, 1952 / *Cleidion* lasiphyllum* Pax and Hoffm., New Caledonia / *Euphorbia* ankarensis* Boiteau, Madagascar / *Euphorbia* bupleurifolia* Jacq., S. Africa / *Euphorbia* lophogona* Lam., Madagascar / *Euphorbia* meloformis* Ait., S. Africa / **Euphorbia moratii* Rauh, Madagascar / **Euphorbia symmetrica* White, Dyer and Sloane, S. Africa / *Pycnocoma angustifolia* Prain, W. Africa. F. HALLÉ, 1971.

Flacourtiaceae:

Phyllobotryon soyauxianum Baill., Trop. Africa, LETOUZEY et al., 1969 / *Phyllobotryon spathulatum* Muell-Arg. (Fig. 17F, G), Trop. Africa, LETOUZEY et al., 1969.

Geraniaceae:

[H] *Geranium canariense* Reut., Canary Isles, YEO, 1973.

Gesneriaceae:

[H] *Boea lanata* Ridl., Malaysia, BURTT, 1964.

Lecythidaceae:

**Barringonia calyptrocalyx* K. Schum., New Guinea, F. HALLÉ, 1974 / **Grias* sp., Brazil.

Leguminosae – Mimosoideae:

**Pithecellobium hansemanii* (F. Muell.) Mohlenbr. (Fig. 16F), New Guinea, F. HALLÉ, 1974.

Leguminosae – Papilionoideae:

Angylocalyx oligophyllus E.G. Baker, Gabon to Liberia. MANGENOT, 1957.

Lobeliaceae:

Brighamia rockii St. John, Hawaii, ST. JOHN, 1969 / *Cyanea giffardii* Rock, Hawaii, ROCK, 1919 / *Delissea undulata* Gaudich., Hawaii, ROCK, 1919.

Malvaceae:

**Goethea strictiflora* Hook. (Fig. 16H), Brazil.

Meliaceae:

**Dysoxylum urens* Valet., Batjan Islands / *Guarea richardiana* A. Juss., French Guiana.

Menispermaceae:

Penianthus sp., (N. Hallé 4056), Gabon.

Moraceae:

[H]**Dorstenia contrajerva* L., Trop. America / *Ficus theophrastoides* Seem., Solomon Islands, CORNER, 1967.

Myrsinaceae:

Oncostemon sp., Madagascar / *Rapanea grandifolia* S. Moore, New Caledonia / *Tapeinosperma cristobalense* Stone and Whit., Solomon Islands, STONE and WHITMORE, 1970 / *Tapeinosperma pachycaulum* Stone and Whit. (Fig. 16E), Solomon Islands, STONE and WHITMORE, 1970.

Myrtaceae:

Jambosa acris Panch. ex. Guill., New Caledonia.

Ochnaceae:

Campylospermum duparquetianum (Baill.) Van Tiegh., Trop. Africa, FARRON, 1968 / *Campylospermum sacleuxii* (Van Tiegh.) Farron, E. Africa, FARRON, 1968 / *Campylospermum subcordatum*

(Stapf) Farron, Trop. Africa, Farron, 1968 / *Campylospermum zenkeri* (Engl.) Farron, Trop. Africa, Farron, 1968.

Oxalidaceae:

[H] *Biophytum* sp., Ivory Coast.

Papaveraceae:

Bocconia sp., Colombia, Corner, 1949.

Proteaceae:

**Hicksbeachia pinnatifolia* F. Muell. (Fig. 16G), Queensland, N.S. Wales.

Rubiaceae:

Bertiera simplicicaulis N. Hallé, C. Africa, N. Hallé, 1964 / *Bikkia macrophylla* K. Schum. New Caledonia / *Captaincookia margaretae*, New Caledonia, N. Hallé, 1973 / *Coffea macrocarpa* A. Rich., Mauritius / *Gardenia conferta* Guill., New Caledonia / *Pentagonia gigantifolia* Ducke, Peru, Ducke, 1930; F. Hallé, 1967 / *Pseudomantalia macrophylla*, Madagascar, Leroy, 1973.

Sapindaceae:

Chytranthus longiracemosus Gilg. ex Radlk., Ivory Coast, N. Hallé and Assi, 1962 / *Chytranthus mangenotii* N. Hallé and Assi, Ivory Coast, N. Hallé and Assi, 1962 / *Chytranthus pilgerianus* (Gilg.) Pellegr., Gabon, N. and F. Hallé, 1965 / **Deinbollia* sp., Trop. Africa / *Placodiscus bancoensis* Aubr. and Pellegr., Ivory Coast / *Radlkofera calodendron* Gilg., Gabon, N. and F. Hallé, 1965.

Sapotaceae:

Delpydora gracilis A. Chev., E. Africa / *Delpydora macrophylla* Pierre, C. Africa.

Simaroubaceae:

Brucea antidysenterica Lam., Trop. Africa / *Eurycoma longifolia* Jack., Malaysia.

Sterculiaceae:

Chlamydocola chlamydantha (K. Schum.) Bod., Trop. Africa / *Cola buntingii* Bak. f., Liberia, Ivory Coast / *Cola caricaefolia* (G. Don) K. Schum., E. Africa / *Cola mahoundensis* Pellegr., Gabon, N. and F. Hallé, 1965 / **Herrania albiflora*, Surinam / *Ingonia digitata* (Mast.) Bod., Trop. Africa / **Theobroma mariae* K. Schum., Trop. America.

Theophrastaceae:

Clavija lancifolia Desf., Guianas / *Clavija longifolia* (Jacq.) Mez, Trop. America, Mez, 1903.

Verbenaceae:

Oxera coriacea Dubard, New Caledonia.

Violaceae:

Allexis cauliflora (Oliver) Pierre, C. Africa / *Neckia serrata* Korth., Sumatra, Boerlage and Koorders, 1901.

V. Polyaxial Trees

1. Vegetative Axes all Equivalent and Orthotropic

Tomlinson's Model

Definition. This architecture results from the repeated development of equivalent orthotropic modules in the form of basal branches which are initially restricted to the epicotyledonary region of the seedling axis (the first module), and the basal nodes in subsequent axes. Inflorescences may be terminal or lateral, growth of each module is either continuous or, less commonly, rhythmic.

In this model the development of each new axis as a branch from the base of a previous axis often permits each module to develop an independent root system and so to establish rapidly a physiological autonomy. In this way there can be a more complete quantitative equivalence between modules within the model than is usual for other models in which branching is aerial (cf. Leeuwenberg's model). Basal branching, it should be noted, is in no way unique to Tomlinson's model; one distinguishes the model by the precise delimitation of the basal zone of branching, i.e., the lateral meristems are restricted to the lower nodes of the seedling axis or a region at about the soil level in subsequent axes. Such branches are endogenously determined, they are developed regardless of the biotope of the plant. This precise delimitation of branch position distinguishes what otherwise might be regarded as basal reiteration of either Corner's or Holttum's model, which probably never occurs. By virtue of basal branching the initial internodes are horizontal, but whether this represents a form of plagiotropy remains to be established. This topic is discussed further when "mixed axes" are considered in detail (p. 232). The statements on the orientation of branch bases in orthotropic branch complexes (p. 51) are also relevant to the base of the modules in (Tomlinson's model.

This model shows the potential to establish an indefinite horizontal branch system at soil level without the physiological and mechanical restraints imposed on trees which add branch to branch in a vertical series. The frequency of this model in woody monocotyledons is undoubtedly correlated with their growth-limiting lack of a vascular cambium and hence lack of ability to produce secondary vascular tissues. These constraints have been discussed by others (e.g., SCHOUTE, 1903; HOLTTUM, 1955, 1961; TOMLINSON, 1964) and have been commented upon in earlier pages here (p. 68). The model is named after P.B. TOMLINSON (H.O., 1970; p. 27) in recognition of his work on architecture in arborescent monocotyledons, especially various Scitamineae (TOMLINSON, 1962) in which the model and its most significant biological variants are well expressed.

Example. The model is well represented in most "multiple-stemmed" or "clustering" palms and we exemplify it by *Euterpe oleracea* (Palmae – Arecoideae) widespread in forest and coastal swamps in tropical America (Fig. 19 D). Individual stems reach a height of 15 m with the inflorescences lateral, expanding after the subtending leaf has fallen and so appearing below the crownshaft, as in many Arecoid palms. The root system produces numerous slender, erect pneumatophores (OLDEMAN, 1969; DE GRANVILLE, 1974) as is common in other swamp-living palms. The bud is edible. Comparable palms from the other major tropical areas are *Phoenix reclinata* (Phoenicoideae, widespread in tropical Africa) and *Oncosperma tigillaria* (Arecoideae, tropical Asia). Both these further examples are characteristic of wet, even saline, swamps and one has the impression that multiple-stemmed palms are not as well adapted to dry situations as are single-stemmed palms, but no general rule has been established[5]. Tomlinson's model does not exclude the single-stemmed state if there is a sequence of branch production such that only one above-ground axis is extant at one time. This is the condition in *Raphia gigantea* illustrated in Figure 19A, with a new axis developing at the time of inflorescence of the hapaxanthic parent axis.

The model is shown by numerous species of palms, as in the genera *Areca, Bactris, Caryota, Chrysalidocarpus, Geonoma, Ptychosperma,* to name some of the commonly cultivated genera. The stature of multiple-stemmed palms is usually less than that of many single-stemmed palms, but the range is enormous, from *Geonoma stricta,* only 0.5–1 m high (WESSELS-BOER, 1968) to *Oncosperma filamentosa* over 30 m high (CORNER, 1966). Contrast between the size of single- and multiple-stemmed palms is best shown within genera which include examples of Tomlinson's and Corner's models (e.g., in *Caryota, C. mitis* up to 8 m high, with trunks 20 cm in diameter and *C. urens* up to 15 m high with trunks 30 cm in diameter.

Other Examples and Variations

1. Tree Ferns. This model is represented by certain tree ferns, notably *Cyathea manniana* (mountains of tropical Africa: HALLÉ, 1965, 1966; H.O., 1970, p. 30).

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[5] Dr. HENRY S. HORN (personal communication) has pointed out that this difference is explicable in terms of the calculated difference in amounts of root system needed by single- vs. multiple-stemmed palms. For two palms with separate root systems the total combined length of roots needed to exploit a given area is less by a factor of $\sqrt{2}$ (= 1.4) than the same two palms sharing a common root system of comparable total area, other things being equal.

Here stolons originate some distance up the trunk of the fern, enclosed by the fibrous mat of adventitious roots as they grow initially downwards into the soil. Subsequently their growth is horizontal, but the experiments of HALLÉ (1966) show that "plagiotropy" is induced by the foliage leaves since the stolons turn erect once these leaves are destroyed.

2. Dicotyledons. Tomlinson's model is rare in tropical arborescent dicotyledons, which seems a consequence of the close correlation between habit and anatomy, as we have mentioned. However, our inability to cite many dicotyledonous examples may simply reflect our ignorance of the subterranean parts of woody tropical plants.

Representatives, however, include *Lobelia giberroa* (Lobeliaceae, montane rainforest of Ethiopia, Fig. 18 and 19C). Axes are hapaxanthic, terminating in a slender, spike-like inflorescence (Fig. 18) but we remain uncertain about details of basal branching[6]. *Espeletia atropurpurea* (Compositae), which is also a plant of high altitudes, in Andean South America, seems also to conform to this model (ALAN P. SMITH, personal communication). Despite its apparent infrequency in dicotyledonous trees, this model is well represented by dicotyledonous herbs (e.g., *Euphorbia characias, Helleborus foetidus*).

3. Monocotyledons. A number of monocotyledonous families other than the palms include representatives of Tomlinson's model, and these lead to important variants around which one can build an understanding of the architecture of many monocotyledons.

First we should complete our description of palms. Erect axes of clustering palms bear either terminal (hapaxanthic) or lateral (pleonanthic) inflorescences, the latter condition much the most common. Hapaxanthic axes are represented in multiple-stemmed Caryotoideae, e.g., *Caryota mitis* (Malaysia, but widely cultivated) and species of *Raphia* and *Metroxylon* which should be compared with examples of Holttum's model exhibited by species in the same genera. As indicated by HOLTTUM (1955) a rational biological modification in this architecture is for successive modules to elaborate the initial horizontal phase of axis development, to produce a distinct scale-bearing rhizome or stolon[7], before it turns erect some distance from the parent shoot. This leads to the development of rhizomatous palms, most familiarly exemplified by *Rhapis excelsa* (Fig. 20D; Coryphoideae, eastern China but widely cultivated as a pot plant; TOMLINSON and ZIMMERMANN, 1966). In field-grown plants axes reach a height of 4 m, the individual rhizome segments extending as much as 2 m. Rhizomatous palms are not common, which is puzzling in view of the apparent advantages this spreading habit brings, but this may be because the habit is not successful in the absence of aerial branching, discussed later in McClure's model (p. 144). Another stoloniferous palm is exemplified by *Bactris coloniata* Bailey, a diminutive palm from Panama.

Branching in palms is normally basal, each axis retaining only a limited capacity

Fig. 18. Tomlinson's model, rare in arborescent ▷ dicotyledons, here represented by *Lobelia giberroa* Hemsl. (Lobeliaceae), Managasha Forest, Addis Ababa, Ethiopia. The erect stems sucker basally

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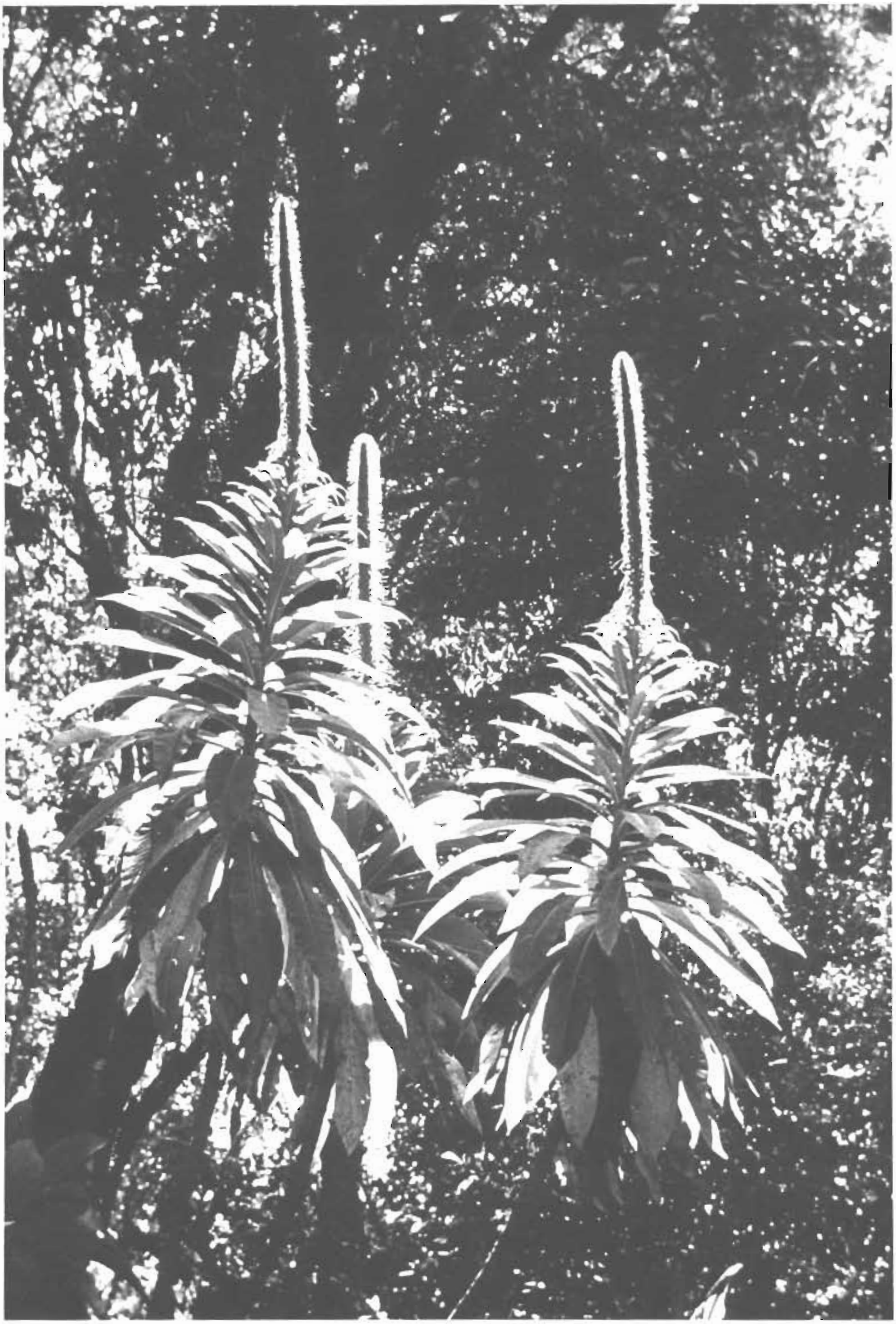
[6] It is not certain if basal suckering precedes or is a result of flowering in other *Lobelia* species which belong to this model, as is discussed by MABBERLEY (1974a).

[7] Rhizome and stolon may be regarded as interchangeable terms here since the distinction between them is a matter of definition and somewhat arbitrary.



to produce new suckers, e.g., in the seedling axis of *Rhapis* there are normally five lateral shoots, corresponding to the five orthostichies of the 2/5 phyllotaxis (TOMLINSON and ZIMMERMANN, 1966). Resting buds, such that the process can be repeated under an exogenous influence, are not characteristic of these shoots and this is the feature which distinguishes this architectural model; reiteration would not be endogenously determined.

Exceptionally, vegetative branches appear at high levels on the trunk, notably in individuals of the widely-distributed wild date palm (*Phoenix reclinata*). In cultivated dates (*P. dactylifera*) these aerial suckers produce roots and so provide material for clonal propagation, a possibility which also exists in some cultivars of the oil palm. A similar condition in *Chrysalidocarpus lutescens* has been examined by FISHER (1973), who showed that the lateral meristem has an unusual non-axillary position on the abaxial surface of the leaf base.

Within the Zingiberales (Scitamineae) the variations on Tomlinson's model are extensive and significant. In Strelitziaceae, *Ravenala madagascariensis* ("traveler's palm" of Madagascar, but widely cultivated) and species of *Strelitzia,* e.g., *S. nicolai* (Fig. 19B, southeast Asia) conform precisely to the model (FISHER, 1976). *Ravenala* is interesting in that there is periodicity in inflorescence production, suggesting rhythmic growth. Both examples have pleonanthic axes. An important variation is shown by *Phenakospermum guianense* (Guianas; the "baluru" of French Guiana). This occupies a variety of habitats, ranging from wet places, forest margins to quite dry situations. It produces woody trunks each with a somewhat bulbous base (Fig. 20A) and supporting a cluster of distichous, banana-like leaves, to a height of 5 m, the axis ultimately ending in a terminal inflorescence (hapaxanthy). Basal branching takes the form of slender stolons which in wetter sites themselves support root pneumatophores. After a period of horizontal growth these stolons become erect and establish a new module. The banana (cultivars of *Musa*) which is represented in the wild by upwards of 50 species (Asian tropics, SIMMONDS, 1962) corresponds to Tomlinson's model but with the erect axis represented largely by a massive fleshy corm and the "trunk" now an overwrapping series of spirally arranged leaf sheaths, forming a "pseudostem". Our illustration (Fig. 20C) is of *Musa maclayi* (New Guinea) distinguished by its erect inflorescence. Some species in New Guinea reach 15 m, e.g.,

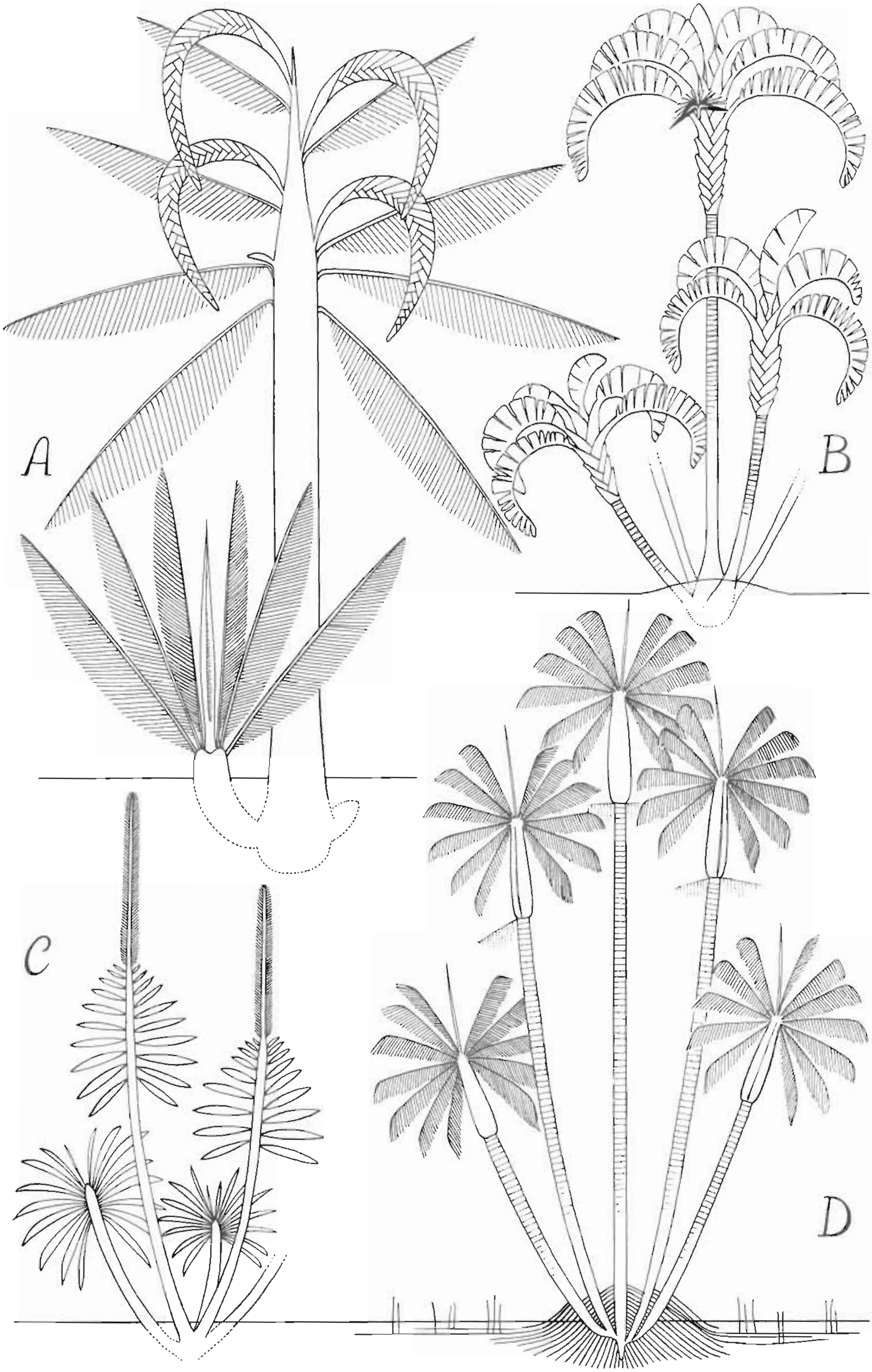
Fig. 19 A–D. Tomlinson's model. >

A *Raphia gigantea* A. Chev. (Palmae – Lepidocaryoideae, Central Africa). Individual axes are hapaxanthic, growing to a height of 10 m, and producing a series of long curved flowering branches in acropetal order from the axils of distal, little-modified foliage leaves (CORNER, 1966; slides). Basal renewal shoots are produced singly as the parent axis reaches the flowering stage, so that the palm only supports one mature axis at a time.

B *Strelitzia nicolai* Regel and Koch (Strelitziaceae, Southeast Africa; commonly cultivated in subtropical and mediterranean climates). Clusters of stems to a height of about 6 m, the axes pleonanthic with distichously arranged, banana-like leaves.

C *Lobelia giberroa* Hemsley (Lobeliaceae, montane rain forest of Ethiopia). A large plant, reaching more than 5 m in height. This architecture is infrequent among tropical arborescent dicotyledons.

D *Euterpe oleracea* Mart. (Palmae – Arecoideae, the "wassai" of Brazil, widespread in swampy forests in tropical America). A clustering palm, to 20 m high, now cultivated for its edible heart. Inflorescences are lateral, appearing below the crownshaft. The first-order horizontal roots bear erect branch roots as pneumatophores (OLDEMAN, 1969)


A
B
C
D

M. ingens (ARGENT, 1976). Interesting parallels with *Phenakospermum* are provided by other species of *Musa* (e.g., *M. itinerans*) which similarly have lateral stolon shoots. In both genera since a single erect shoot may produce several stolons the plant is not only clonally maintained, but multiplied. Further reduction of the aerial shoot (which may become annual) and elaboration of the underground system is evident in other Scitamineae (TOMLINSON, 1962). The architecture of Heliconiaceae and many Zingiberaceae corresponds to Tomlinson's model with the short-lived leafy aerial axis hapaxanthic and usually supported by a pseudostem, but the fleshy sympodial scale-bearing rhizome (comparable to the stolon of *Phenakospermum*) now constituting the perennial system. Some of these plants may be quite large, as in *Alpinia boia* (Fig. 20B; Zingiberaceae, Fiji) with aerial shoots to a height of 10 m, tall for a ginger but still only that of a low tree in tropical forests.

Sympodial rhizomes of identical architecture are common in many other monocotyledonous families, e.g., Bromeliaceae, Cannaceae, Costaceae, Liliaceae, Marantaceae, Orchidaceae. In Bromeliaceae and Orchidaceae the plants are often epiphytic. We have represented a rather generalized architecture found in many members of the subfamily Bromelioideae e.g., *Neoregelia pauciflora* (Fig. 20E; Bromeliaceae, tropical America). The rhizome systems of such plants usually demonstrate precisely regulated growth patterns which lend themselves to architectural analysis, undoubtedly a topic which has to be developed in future research (N. HALLÉ, 1967; BELL, 1974, 1976). One interesting strategy found in a few rhizomatous monocotyledons is the existence of dimorphism of aerial shoots, with distinct nonassimilating flowering axes contrasted with nonflowering leafy assimilating axes. *Zingiber officinale* (commercial ginger, Asian tropics) is a familiar example.

Strategy of the Model. In this model because of the essential equivalence and frequent later autonomy of each module the distinction between individual and population now becomes ambiguous – can we think of a population of axes rather than a clump of individuals? Also we are dealing with two fairly distinct types of strategy within the one model, relating to the clumping habit on the one hand and the stoloniferous habit on the other. They find their parallel in many

Fig. 20A–E. Tomlinson's model (further examples with transitions to herbs). ▷

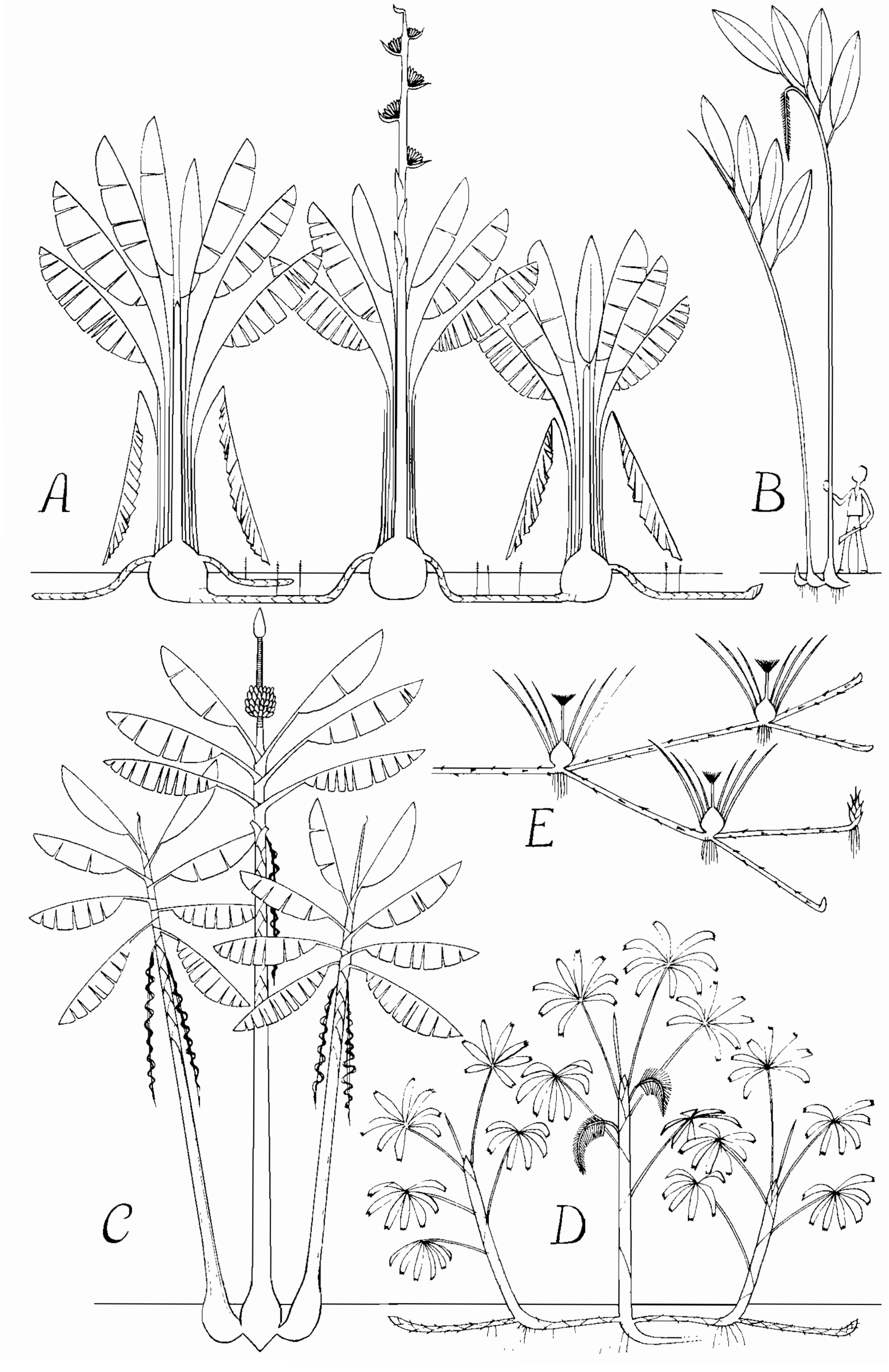
A *Phenakospermum guianense* (L.C. Rich.) Miq. (Strelitziaceae, Guianas and Brazil). The common "baluru" growing in swamp-forest and reaching a height of 12 m at flowering, with a terminal inflorescence. Axes extend sympodially by horizontal scale-bearing stolons (TOMLINSON, 1962) up to 3 m long. These shoots may develop erect roots which function as pneumatophores.

B *Alpinia boia* Seeman (Zingiberaceae, Savura Creek, Suva, Fiji). One of the largest gingers with the leafy shoots, up to 10 m high, arising from a massive underground rhizome. The erect vegetative axis is a pseudostem.

C *Musa maclayi* F. Muell. (Musaceae, New Guinea and Solomon Islands). A common wild banana of the forest understorey to a height of 10 m. Inflorescences are erect (synonym *M. erecta*). The vegetative axis again a pseudostem.

D *Rhapis excelsa* (Thunb.) Henry (Palmae – Coryphoideae, native to southwest China but commonly cultivated elsewhere). Erect axes to a height of 4 m proliferate by means of scale-bearing rhizomes (ZIMMERMANN and TOMLINSON, 1965; TOMLINSON and ZIMMERMANN, 1966).

E *Neoregelia pauciflora* L.B. Smith (Bromeliaceae – Bromelioideae, Brazil). A sympodial tank epiphytic herb, the leafy shoots spreading by basal scale-bearing stolons up to 20 cm long; the terminal inflorescences growing out of the tanks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herbaceous plants, notably the grasses and sedges which may be either tillering or stoloniferous. When conforming strictly to the definition of the model, species which illustrate it correspond to clustering, multiple-stemmed palms. When each axis is hapaxanthic, the population-centered strategy we have mentioned in describing Holttum's model is now reinforced by the addition of new "individuals" vegetatively. However, as we have already discussed, clumping of axes seems biologically inappropriate since numerous trunks growing close together compete for light, soil moisture and soil nutrients. A possible advantage in this strategy, as suggested by OLDEMAN (1969) in *Euterpe oleracea*, is that a closed nutrient circuit is built up with the decomposition of fallen leaves and dead axes providing humus for later generations of axes. In older clumps, however, there is undoubtedly slower growth and stunting of modules, especially those at the center of the clump. Another biological advantage of the clump habit may exist in the need for a long-lived center of dispersal for seeds. This is provided most effectively by species with pleonanthic axes, which are in the majority.

Stoloniferous species, on the contrary, are admirably adapted for vegetative spread and the exploitation of new habitats. Populations are likely to be built up clonally, but at the expense of sexual reproduction and genetic diversity. The study by BELL (1974) of *Medeola* (Trilliaceae) in New England may not seem relevant to a discussion of tropical trees but shows how a rhizomatous species may simultaneously exploit new areas of soil by extension of stolons while at the same time developing successive generations of shoots on one spot from a regularly produced proximal meristem; this plant "gets the best of both worlds". Vegetative mobility is an important ecological process and detailed examination of shoot organization in geophytes will undoubtedly reveal interesting patterns.

The stoloniferous habit would not seem well suited to the development of trees, since we have described it in terms of a trend towards herbs in the monocotyledons and commented on its infrequency in palms. McClure's model (p. 139), represented most spectacularly by the bamboos, must be considered in this respect; it is an example of a well-developed tree model with an extensive underground system. The trunk is largely nonassimilating and aerial branches produce the main photosynthetic area. This suggests that the unbranched trunks in Tomlinson's model are inadequate to supply assimilates to an extensive rhizome system (cf. p. 119). A parallel with stoloniferous plants may be sought, however, in dicotyledonous trees which produce root suckers. Ecologically this property may be very significant, as demonstrated by HORN (1975) in American beech (*Fagus grandifolia*).

A final comparison between branched and unbranched palms should be made with reference to *Euterpe*. *Euterpe oleracea*, which we have used to exemplify Tomlinson's model is typically found in the marshy forest along the coasts, along creeks and along rivers in northern South America, i.e., it is a plant of hydrologically stressed biotopes. In contrast, the single-stemmed *Euterpe globosa* Gaertn. [=*Prestoea montana* (Graham) Nicolson] conforms to Corner's model and has been shown to be a natural component of the Puerto Rican rain-forests by BANNISTER (1970), an environment which is hydrologically stable but which, like all rain forests, is stressed with regard to light. More thorough comparative ecological studies of single- and multiple-stemmed palms are desirable, in other genera and in other biotopes.

Taxonomic List of Examples (Tomlinson's Model)

PTERIDOPHYTES

Cyatheaceae:
Alsophila microdonta Desv., French Guiana / *Cyathea manniana* Hooker, Trop. Africa, F. Hallé, 1965, 1966.

MONOCOTYLEDONS

Bromeliaceae:
(Many bromeliads, both terrestrial and epiphytic, exhibit this model: the following examples represent those we have specifically studied) [H] *Aechmea lingulata* Baker, French Guiana / [H] *_Ananas comosus_ (L.) Merr., "pineapple", S. America / [H] *Araeococcus micranthus* Brogn., French Guiana / [H] *Guzmannia lingulata* (L.) Mez, French Guiana / [H] *_Neoregelia pauciflora_ L.B. Smith (Fig. 20E), Brazil.

Costaceae:
[H] *Costus dinklagei* K. Schum., Gabon, N. Hallé, 1967.

Cyperaceae:
(Many sedges conform to this model, only the following are listed) [H] *Cyperus alternifolius* L., Ivory Coast, Lorougnon, 1971 / [H] *Cyperus esculentus* L., Ivory Coast, Lorougnon, 1971 / [H] *Cyperus nudicaulis* Poir., Ivory Coast, Lorougnon, 1971 / [H] *Cyperus rotundus* L., Ivory Coast, Lorougnon, 1971 / [H] *Kyllingia erecta* Schum. and Thonn., Trop. Africa.

Gramineae:
(Many grasses could be also listed, only the following are cited) [H] *Cynodon dactylon* (L.) Pers., Pantropical / [H] *Hierochloa borealis* Roem. and Schult., Arctic, Serebryakova, 1971 / [H] *_Zea mays_ L., "corn", Trop. America.

Heliconiaceae:
[H] *Most _Heliconia_ spp., Trop. America.

Juncaceae:
Prionium serratum (L.f.) Drège, S. Africa, Hooker, 1868.

Musaceae:
(Probably all *Musa* spp., but especially) *_Musa_ cultivars "bananas" e.g., Gros Michel, "plantains" plantain subgroup, Malesia, Skutch, 1932 / *Musa maclayi* F. Muell. (Fig. 20C), New Guinea.

Palmae:
(Almost all multiple-stemmed palms conform to this model; the following species are merely representative) *Bactris gasipaes* HBK., Trop. America / [L] *_Calamus ciliaris_ Blume, Java / *Euterpe oleracea* Mart. (Fig. 19D), Trop. America, Oldeman, 1969 / *Hyphaene guineensis* Schum. et Thonn., Congo, Zaire / *Metroxylon sagu* Rottb., "sago palm", Malesia, Corner, 1966 / *Oncosperma tigillaria* Ridley, Malesia / *Phoenix dactylifera* L., "date palm", Middle East, N. Africa / *Phoenix reclinata* Jacq., "wild date palm", Trop. Africa / *Raphia gigantea* A. Chev. (Fig. 19A), E. Africa.

Strelitziaceae:
Phenakospermum guianense (L.F. Rich) Miq. (Fig. 20A), Guianas / *Ravenala madagascariensis* Sonn., Madagascar, Tomlinson, 1962 / *Strelitzia nicolai* Regel and Koch (Fig. 19B), S.E. Asia, Tomlinson, 1962; Fisher, 1976.

Zingiberaceae:
(Most members of the family, the following are simply representative) [H] *Aframomum polyanthum* (K. Schum.) K. Schum., Gabon, N. Hallé, 1967 / [H] *Alpinia boia* Seem. (Fig. 20B), Fiji.

DICOTYLEDONS

Acanthaceae:
[H] *Elytraria lyrata* Vahl., Trop. Africa, Ghana to Angola, Dokosi, 1971.

Compositae:
[H] *Carlina acanthifolia* All., Europe, Mediterranean, Meusel, 1970 / *_Dahlia imperialis_ Roezl., Mexico / *Wilkesia hobdyi* St. John., Kauai, Hawaii, St. John, 1971.

Crassulaceae:
[H] +*Kalanchoë fedtschenkoi* Perrier, Madagascar, Friedmann, 1975 / [H] +*Kalanchoë synsepala* Bak., Madagascar, Friedmann, 1975.

Euphorbiaceae:
[H] *Euphorbia characias* L., Mediterranean, Meusel, 1970 / *Euphorbia coelurescens* Haw., Cape Province, S. Africa, Cremers, 1976 / *Euphorbia decaryi* Guill., Madagascar, Cremers, 1976 / *Euphorbia millii* Desm. var *breoni* (Noiss.) Ursh. and Léandri, Madagascar, Cremers, 1976 / *Euphorbia orthoclada* Baker, Madagascar, Cremers, 1976 / +*Euphorbia stolonifera* Marloth, S. Africa.

Geraniaceae:
[H] *_Geranium anemonaefolium_ L'Hérit, Canary Islands, Yeo, 1973.

Gesneriaceae:
[H] *Boea* sp., Borneo, Burtt, 1964.

Lobeliaceae:
Dialypetalum sp., Madagascar / *Lobelia giberroa* Hemsley (Figs. 18, 19C), East Africa, Mabberley, 1974a

Melianthaceae:
*_Melianthus major_ L., S. Africa.

Piperaceae:
[H] *Pothomorphe peltata*, French Guiana.

Primulaceae:
[H] *Lysimachia punctata* L., Europe, Rauh, 1939a, b.

Ranunculaceae:
[H] *Helleborus foetidus* L., Europe, Jeannoda, 1977.

Schoute's Model

Definition. Growth is from meristems which produce orthotropic or plagiotropic trunks forking at regular but distant intervals by equal dichotomy, but otherwise producing no vegetative lateral branches. Inflorescences are always lateral.

This model is rare and most familiar in species of *Hyphaene* (Palmae – Borassoideae) which have obviously forked trunks (BECCARI, 1924). Recent evidence, however, which is discussed below, suggests that the model is more common than has been appreciated. The architecture superficially corresponds closely to Leeuwenberg's model but differs in the method of shoot bifurcation, since there is no terminal inflorescence to delimit modules, but a dichotomy of the shoot apex seemingly without cessation of its meristematic activity. There is an added tendency for basal suckering in some examples, which suggests an approach to Tomlinson's model. Nevertheless by this unique method of growth the model stands quite isolated.

Example. We have illustrated this model with *Hyphaene thebaica,* the Doum palm of tropical Africa, as a familiar example (Figs. 21, 22A). Populations of this species show a tendency for basal suckering (Fig. 22Aa) and in this respect *H. shatan* of Madagascar, which never suckers but forks regularly corresponds precisely to the model. Branching in *Hyphaene* was the subject of a classical study by the Dutch botanist J. C. SCHOUTE (1909), after whom the model is named. The tree has a distinctive appearance, with the trunk forking equally at regular but distant intervals, each bifurcation more or less at right angles to the previous ones so that bifurcation is three-dimensional (Fig. 22). Trees are dioecious and inflorescences are lateral as in all borassoid palms (MOORE, 1973). At each bifurcation the crown and trunk are progressively reduced in size in a way which tends to maintain mechanical stability and physiological efficiency.

Dichotomous Branching. The existence of true dichotomy[8] in this genus still remains to be established unequivocally by microscopic examination of the shoot apex, a difficult task in such a large plant with infrequent branching. Results obtained by dissection of 25 crowns of *Hyphaene thebaica* (H.O., 1970, p. 41) together with anatomical study of branching in *Nypa fruticans* by TOMLINSON (1971a), a palm with identical forking (Fig. 22C), has produced considerable circumstantial evidence in favor of dichotomy. This means that much of the controversy regarding the nature of branching in the Doum palm has now been settled. Schoute's observations, which were carried out on a single dried bifurcated specimen without leaves, lead him to suggest equal dichotomy at the level of a triangular scale-like leaf ("feuille angulaire" of EMBERGER and CHADEFAUD, 1960).

The following morphological features are diagnostic for this kind of branching in *Hyphaene* and *Nypa* (Fig. 22A, C):

1. Daughter shoots are in a plane perpendicular to the dorsiventral axis of the enclosing leaf. This is not an arrangement which can be accounted for by the simple modification of ordinary axillary branching. In some shoots, in fact, there may be an inflorescence in the axillary position of the enclosing leaf, i.e., the leaf immediately below the bifurcated shoot.
2. Daughter shoots consistently have mirror-image symmetry, the spiral of the parent axis being continuous into one axis, but reversed in the other (Fig. 22Ab).
3. There is no recognizable adaxial prophyll

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[8] If we can accept the existence of an equal division of an apical *meristem* as dichotomy. A comparison with axes which dichotomize by equal division of an apical *cell* is, of course, not appropriate.

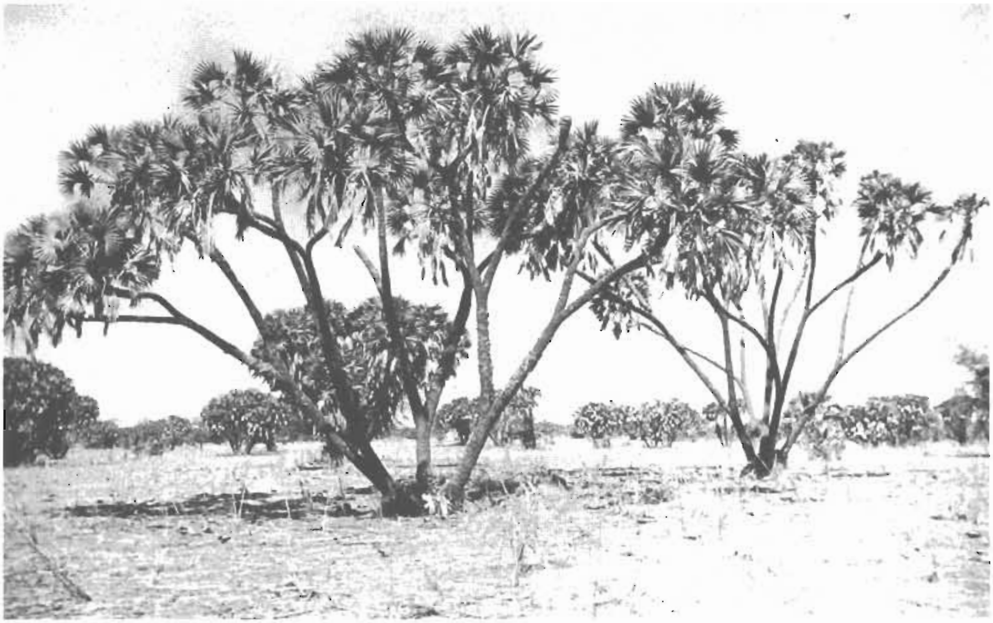


Fig. 21. Schoute's model, *Hyphaene thebaica* Mart. (Palmae – Borassoideae), Niamey, Niger

by which main axis can be distinguished from lateral axis, as is usual in monocotyledonous branching. The leaves immediately above the fork stand back-to-back and their leaf sheaths are correspondingly flattened (stippled leaves in Fig. 22Ac).

4. The triangular scale described by SCHOUTE does not exist but is an artifact of the specimen he examined. It probably represents the remains of the base of one or both "prophylls". It should be noted that prophyllar leaves may be partly fused, in monocotyledons with comparable "precocious" branching (FISHER, 1974, 1976).

5. The disposition of dichotomies in *Nypa* is revealed clearly by the unique leaf morphology. The massive rounded base of each foliage leaf develops a pronounced groove accomodating and enclosing the next youngest leaf. This seems related to the very extended plastochrone interval which distinguishes *Nypa* (TOMLINSON, 1971a). The enclosing leaf develops *two* equal grooves, each groove accommodating the first leaf of a branch (Fig. 22Cc). In *Nypa* the orientation of the enclosing leaf is such that the pair of new branches is always in a forward position, important for the regular spread of the plagiotropic shoot system. Grooves of the same kind do not develop in the enclosing leaves of *Hyphaene*, which conform developmentally to the pattern more typical of palms with a less massive leaf base and presumed shorter plastachron.

6. In *Nypa* again dissection and microscopic examination show that the two shoots resulting from dichotomy are always at identical stages in development. The youngest stages examined included branches in their second plastachron. Furthermore, there is no evidence of blind-ending vascular bundles below the fork, which otherwise would be expected if the apical meristem had aborted and been substituted, according to our knowledge of the development of the vascular system in monocotyledons embodied in the observations of ZIMMERMANN and TOMLINSON (1972).

From this it is reasonable to conclude that forking of these axes is a process of continuous growth, involving equal division of the apical meristem, and corresponds to the definition of terminal dichotomous branching given by BUGNON (1971). This may be contrasted with the bifurcation of the shoot system in *Tabernaemonta crassa* Benth. (Apocynaceae, Leeuwenberg's model) studied by PRÉVOST (1972). Here there is parenchymatization of the apical meristem and reconstitution of two new branches from axillary meristems and this is lateral branching according to the definition of BUGNON (1971). A similar type of branching seems to account for forked spines in *Carissa* (BRUNAUD, 1970). Schoute's model is not, however, in any way unique to monocotyledons since it was probably common in fossil trees (e.g., *Lepidodendron*, see p. 264) and has recently been demonstrated in two species of *Mammillaria* (Cactaceae; BOKE, 1976). Dichotomy occurs in the inflorescences of some *Asclepias* species (NOLAN, 1969). It has been suggested (TOMLINSON, 1971a) that the mechanism of vascular development in monocotyledons, in its distinction from that in dicotyledons (ZIMMERMANN and TOMLINSON, 1972) is favorable to dichotomous branching since axial bundles remain "uncommitted" in terms of linkage with a leaf. Certainly dichotomous branching, and other sorts of precocious branching in monocotyledons (FISHER, 1973, 1974) is more common than hitherto expected, so that *Hyphaene* is not unique in this respect. Apart from dichotomy in palms [*Hyphaene, Nypa, Vonitra, Chamaedorea cataractarum,* possibly *Allagoptera* (= *Diplothemium*)] (TOMLINSON, 1967) it is present in the rhizome of *Strelitzia reginae,* where the forks are not consistent mirror-images of each other (FISHER, 1976). The peculiar growth-limiting characteristics of most arborescent monocotyledons (absence of a cambium, lack of frequent axillary vegetative meristems) may promote this type of bifurcation. However, further discussion of this interesting problem takes us too far from the realm of architecture into developmental anatomy.

The close relation between Schoute's and Corner's models is demonstrated in *Hyphaene ventricosa* Kirk. This is normally unbranched (Corner's model) but one population described by LEWALLE (1968) had forked axes, corresponding to Schoute's model. It is important to distinguish these genetic events from the frequently remarked condition of forking palm stems which results from damage to crowns (DAVIS, 1969).

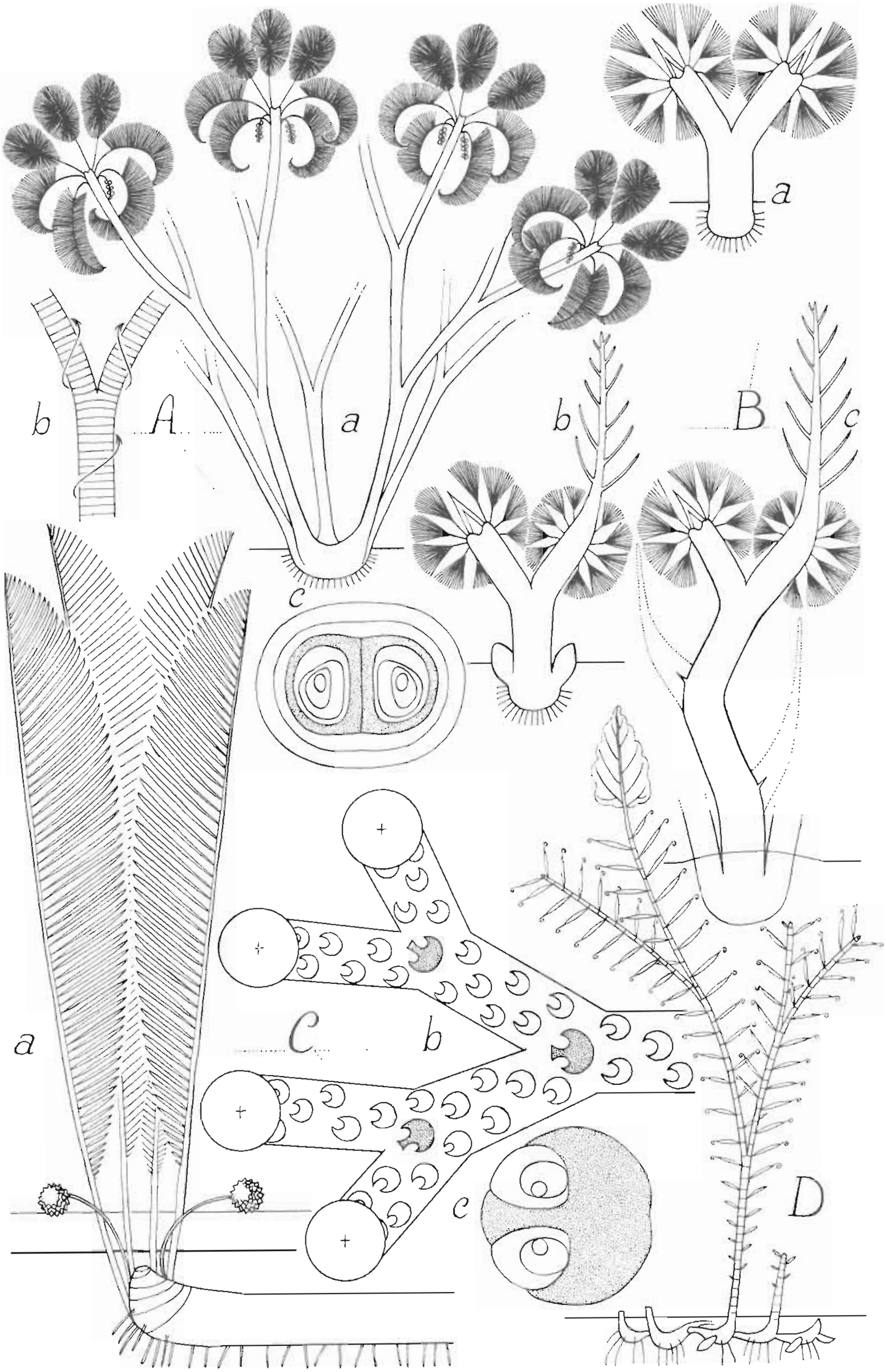
Fig. 22A–D. Schoute's model. >

A *Hyphaene thebaica* Mart. (Palmae – Borassoideae; the Doum palm of the African Sahel, Middle East and India). A savanna tree up to 20 m high, branching by equal dichotomy; *a* habit; *b* diagram of forking to show antidromous leaf spirals in axes above fork, i.e., with mirror-image symmetry; *c* diagrammatic transverse section of shoot immediately above a fork (after H.O., 1970, p. 42), showing mirror-image symmetry, "prophylls" of post-dichotomy axes stippled. Successive forkings are at right angles to each other.

B *Nannorrhops ritchiana* (Griffith) Aitchison (Palmae – Coryphoideae, northwest India and Afghanistan). *a* Forking is initiated equally, but one branch rapidly proceeds to inflorescence; *b* the other repeats the forking in a plane at right angles to the previous one, the axis develops *c* by this repeated forking (TOMLINSON and MOORE, 1968). *Nannorrhops* in some ways is intermediate between Schoute's and Koriba's models.

C *Nypa fruticans* van Wurmb. (Palmae – Nypoideae, the nypah palm of the Asiatic mangroves). *a* The massive creeping axis buried in mangrove mud, with erect leaves and axillary inflorescences; *b* seen from above diagrammatically with regular forking, the sheath of the enclosing leaf (*stippled*) with its two grooves always directed forwards and contrasted with normal leaves with one groove; *c* diagrammatic transverse section of bud at level of forking, enclosing leaf stippled, resulting shoots with mirror-image symmetry (TOMLINSON, 1971a).

D *Flagellaria indica* L. (Flagellariaceae, Old World tropics). Erect shoots arising from a creeping rhizome, supported by leaf tendrils, in many populations these aerial shoots bifurcating by equal dichotomy of the shoot apex before producing terminal inflorescences (TOMLINSON, 1970b). In some ways this is intermediate between Tomlinson's and Schoute's models


a
b
A
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Other Examples. Nypa fruticans (Fig. 22C), the common rhizomatous nypah palm of mangrove swamps in the Asian tropics, is considered in this account for comparative purposes, although it is scarcely a tree in the strict sense. Nevertheless, the stature is considerable since individual leaves reach a length of 7 m. *Nypa* represents precisely in its prostrate habit (Fig. 22Cb) the orthotropic shoot system of bifurcating species of *Hyphaene*. Seeds are viviparous, as in other mangrove species; they initiate a prostrate shoot system once the seedling becomes anchored. The rhizome of the adult is massive, with spirally arranged foliage leaves which become erect by unequal growth of the leaf base to provide characteristic emergent crowns (Fig. 22Ca). Inflorescences are axillary.

Variations of the Model. Nannorrhops ritchiana (Griffiths) Aitchison is a low-growing coryphoid palm of Afghanistan and northwest India. In cultivation, where it has been studied (TOMLINSON and MOORE, 1968), it develops vigorous erect shoots which include features of growth intermediate between the models of Schoute and Koriba. Erect axes bifurcate equally in a manner identical with that of *Hyphaene*, in so far as superficial observation reveals (Fig. 22B). The two trunks produced are initially identical but subsequently they diverge developmentally such that one becomes hapaxanthic ending in a massive terminal panicle up to 3 m high (Fig. 22Bb). The other trunk continues to grow vegetatively and repeats the forking at a higher level. Essentially each axis is an extended branch system with the persistent stubs of previous flowering modules marking old forks (Fig. 22Bc). Multiplication of aerial axes is a result of basal suckering, in the manner of Tomlinson's model.

Flagellaria indica L. (Flagellariaceae), a weedy monocotyledonous liane of the Asian tropics, also may include features of Schoute's model, as described by TOMLINSON (1970b). Aerial axes with distichously arranged leaves arise from a woody rhizome system comparable to that found in many monocotyledons (Fig. 22D). These erect shoots are scrambling and supported by leaf-tip tendrils. Normally the axes are unbranched, since leaves subtend no axillary vegetative meristems. Shoots are hapaxanthic, ending in a terminal panicle. In many populations, however, aerial axes bifurcate at regular but distant intervals which microscopic examination reveals as an equal dichotomy of the apical meristem (TOMLINSON and POSLUSZNY, 1977). Therefore, in the former condition (aerial axes unbranched) we have Tomlinson's model, in the latter condition (aerial axes bifurcated) we have features of Schoute's model. The continuum of architectural models is thus further displayed.

The greater precision in the definition and recognition of this model allows us to exclude two examples which were previously included (H.O., 1970, p. 42). *Connarus fasciculatus* (Connaraceae) is best regarded as an example of Corner's model but with unstable monopodial growth (OLDEMAN, 1974a). *Iodes liberica* (Icacinaceae) can be better considered as made up of short series of mixed axes, essentially a sympodium of tendril-terminated units.

Strategy of the Model. The architecture in Schoute's model can be interpreted as an elaboration of that in Corner's model, since effectively the number of axes is increased without axillary branching. This increases the number of lateral inflorescences that the plant can produce. Enhancement of the population's *r* strategy is achieved without loss in efficiency of the individual *K* strategy. The method is particularly efficient in a prostrate shoot system as demonstrated by *Nypa*.

Taxonomic List of Examples (Schoute's Model)

MONOCOTYLEDONS

Agavaceae:
+ *Yucca brevifolia* Engelm., S.W. United States.
Flagellariaceae:
[L] *Flagellaria indica* L. (Fig. 22D), Old World Tropics, TOMLINSON, 1970b; TOMLINSON and POSLUSZNY, 1977.
Palmae:
Allagoptera arenaria Kuntze, Brazil, TOMLINSON, 1967 / *Chamaedorea cataractarum* Mart., C. America, FISHER, 1973 / *Hyphaene thebaica* Mart. (Figs. 21, 22A), Trop. Africa, BECCARI, 1924; SCHOUTE, 1909 / *Hyphaene ventricosa* Kirk, C. Africa, LEWALLE, 1968 / *Nannorrhops ritchiana* (Griffith) Aitch. (Fig. 22B), N.W. India, TOMLINSON and MOORE, 1968 / *Nypa fruticans* van Wurmb. (Fig. 22C), Indo-Malaya, TOMLINSON, 1971a / *Vonitra utilis* Jumelle, Madagascar.
Strelitziaceae:
[H] *Strelitzia reginae* Banks, S. Africa, FISHER, 1976.

DICOTYLEDONS

Cactaceae:
[H] *Mammillaria parkinsonii* Ehrenberg, Mexico, BOKE, 1976 / [H] *Mammillaria perbella* Hildmann, Mexico, BOKE, 1976.

Chamberlain's Model

Definition. The architecture is modular and consists of a linear sympodium, i.e., the axis is apparently unbranched, physiognomically the tree is therefore monocaulous. Modules are all equivalent and usually orthotropic; each is hapaxanthic because of terminal flowering and produces a subsequent module from a meristem in the axil of one of the distal leaves.

There is in this model a constant repetition of a vegetative and reproductive stage, but in successive axes. This distal acrotonous branching is the major difference between Chamberlain's and Tomlinson's model, since in the latter the branches are restricted to the base of the plant. The model is named after C.J. CHAMBERLAIN, who had made a special study of the Cycads, which frequently conform to this model (e.g., *Dioon spinulosum* Dyer in CHAMBERLAIN, 1911). Superficially Chamberlain's model resembles Holttum's model but differs in the modular construction so that the tree is neither monocarpic nor hapaxanthic. Essentially Chamberlain's model is made by linear repetition of axes each of which represents the whole of Holttum's model; this is ecologically significant. A comparison which has more meaning in developmental terms is between this model and Leeuwenberg's model described subsequently.

Example. Male individuals of *Cycas circinalis* (Cycadaceae, Southeast Asia) illustrate the habit well. These should be contrasted with female individuals which exemplify Corner's model (p. 110). This species forms a savanna tree, reaching a height of 5 m in favorable circumstances (Figs. 23, 24A). In its strict habit, i.e., precisely corresponding to the model, it is monocaulous; the circumstances under which it branches, when it no longer conforms precisely to the model, are discussed below. There is a periodic (possibly seasonal) production of a terminal cone made up of closely overlapping microsporophylls (Fig. 24Bc). Cone development is preceded and succeeded by the production of several alternating whorls of foliage and scale leaves (Fig. 24Ba, b), the latter functioning as bud-scales during periods of rest. This periodicity should be contrasted with the female plant in which during every cycle of foliage and scale leaves there appear to be a whorl of megasporophylls (cf. Fig. 17C).

Dissection of the bud in the male reveals that the apparently unbranched tree is actually a sympodium, each terminal cone being substituted by a lateral bud

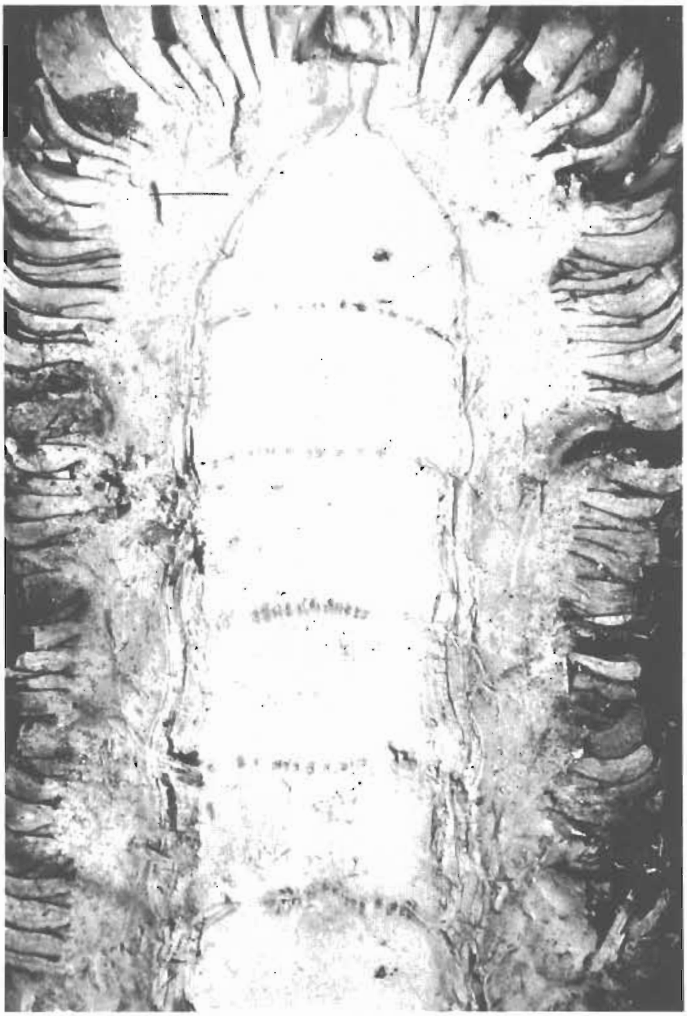


Fig. 23. Chamberlain's model, *Cycas circinalis* L., male tree (Cycadaceae) near Bulolo, New Guinea. Longitudinal section of trunk to show "cone-domes" which represent previous sites of a terminal cone in this sympodial trunk. The vascular system is continuous into the stalk of the detached male cone

which develops very early. The anatomical consequence of this is that the vascular system of the trunk retains a regular series of "cone-domes" (Figs. 23, 24B) which represent the persistent traces to each displaced cone as it becomes evicted by the succeeding module. This anatomical feature is the most convincing demonstration of modular construction (Fig. 24C) since the leaf scars are so congested that the cone scars and their morphological relationships are superficially obscured.

Examination of a large selection of cycads brought together in a Botanic Garden (as at Fairchild Tropical Garden, Miami, Florida), together with field observations, demonstrates in so far as is possible without detailed dissection that other genera of cycads with well-developed trunks conform to Chamberlain's model, i.e., larger species of *Ceratozamia*, *Dioon*, *Lepidozamia*, *Microcycas* and *Zamia*. When the stem is tall as in *Lepidozamia* and *Microcycas* the monocaulous habit is clear. Acaulescent cycads, like many species of *Zamia*, are probably the same since the sympodial habit was described for *Z. floridana* by GRACE SMITH (1907); however, the possibility of dichotomy in *Zamia* cannot be ruled out (see Schoute's model). *Bowenia* and *Stangeria* develop underground tuberous stems which are frequently branched, but no precise information is available. *Macrozamia* and *Encephalartos* have been excluded; they are usually monocaulous but there is little precise information about their architecture. *Encephalartos laurentianus* (Zaire) is certainly unbranched vegetatively, with lateral cones. Evidence that *Macrozamia* is similar may be provided by the frequent development of more than one cone at one time. However, GRACE SMITH (1907) showed that in *Zamia* several cones could arise in rapid succession by repeated sympodial branching, so the situation remains unresolved.

Other Examples

1. Monocotyledons. Chamberlain's model is well represented by certain monocaulous Araceae, although the trunk is always fleshy rather than woody. Examples include *Schizocasia lauterbachiana* (New Guinea), a forest treelet and species of *Dieffenbachia* (tropical America) some of which are cultivated as pot plants. The example of *Montrichardia arborescens* (Guianas) cited by H.O. (1970, p. 31) has to be reconsidered because although the aerial shoots certainly form a linear sympodium it is now known that they arise from a branched underground system. This also occurs in *Dieffenbachia sanguina*. Araceae are restricted in stature because they are not woody and most plants are lianescent as root climbers. Sympodial development is characteristic of the family but not universal, as demonstrated by ENGLER (1877); often the modules are very reduced and stereotyped. *Philodendron selloum* (tropical America), like many other species of *Philodendron*, shows this specialization well (Fig. 24F–H). This is a treelet, usually with reclining trunks and thick aerial roots. Its sympodial construction is not obvious without dissection. Each module (or sympodial unit) consists of very few parts, a scale-like prophyll, a single foliage leaf and a pair of inflorescences. The succeeding module arises in a morphologically lateral position in the axil of the previous prophyll. The whole system is condensed because internodes do not elongate. Leaves abscise cleanly and their scars form a regular series on the surface of the trunk (Fig. 24Gf) with the base of the inflorescence evident (Fig. 24Gi). Prophylls appear as scale-like structures in the crown, their scars are not obvious and the establishment of their relationship to other parts requires careful dissection. The modular construction of the axis is exactly the same as that of *Cycas* (cf. Fig. 24C, H). *Monstera*, of the same family, has essentially the same construction but plants are epiphytic root climbers. Specialized juvenile stages form an important aspect of the biology of the genus (MADISON, 1977).

Some scandent members of the Cyclanthaceae which are epiphytic root climbers also conform to this model as in *Evodianthus funifer*. This has terminal inflorescences but forms linear sympodia. Such plants, like *Monstera*, have a characteristic ability to migrate from lower to higher levels of the forest canopy (OLDEMAN, 1974a) since the older stem parts die back as the growing parts progress upwards. Contact with the soil is made by means of long "feeding roots" which contrast with the short "anchoring roots".

Other more obviously tree-like monocotyledons which show this habit include members of the Agavaceae, like *Cordyline indivisa* (New Zealand), from temperate submontane forest (Fig. 24D). This is monocaulous in contrast to other *Cordyline* species and it seems significant that the leaves are the largest in the genus (TOMLINSON and FISHER, 1971). *Dracaena umbraculifera* (Java) is comparable. In the Xanthorrhoeaceae, *Xanthorrhoea australis* and *X. resinosa* conform to this model. Here the leaves are linear and a special biological adaptation is seen in the development of reaction fibers which aid in crown expansion (STAFF, 1974).

2. Dicotyledons. Several small dicotyledonous trees of the forest undergrowth express this model straightforwardly. *Talisia mollis* (Sapindaceae, French Guiana) reaches a height of 15 m which may represent a maximum for this model. Each module is relatively long (up to 1 m), with ten or more internodes, until it produces a terminal inflorescence, which collapses after fruiting to leave a conspicuous stub (Fig. 24E). This stub persists as a pronounced articulation during the formation of several subsequent modules and these characteristic "bayonet-junctions" reveal the sympodial construction of the trunk. *Potalia amara* (Loganiaceae, Guiana) which occupies a similar habitat is architecturally identical (see H.O., 1970, p. 33). The spacing of leaf scars on the trunk is not uniform and suggests rhythmic or intermittent growth. Another example is *Jatropha multifida* (Euphorbiaceae), a native of tropical America but commonly cultivated (H.O., 1970, p. 28).

Other species cited in the list of examples below are mostly small trees. An exception is provided by *Oroxylon indicum* (Bignoniaceae), native to Malaysia but cultivated for its strange aspect ("midnight horror"; CORNER, 1952). It retains its monocaulous habit only when juvenile, but this state may be retained to a height of 10–15 m beyond which it becomes branched. How can this species be considered to represent Chamberlain's model? This leads to a discussion of reiteration (p. 269) in this model.

Variation and Regeneration. Two species described in an earlier publication [as variants of Schoute's model (H.O., 1970, p. 43)], i.e., *Connarus fasciculatus* (Connaraceae) and *Iodes liberica* (Icacinaceae), are now best considered as variants of Chamberlain's model, since Schoute's model can be defined more precisely (p. 132). The first is a small tree of the Guianese forest, the second an African liane. A linear sympodium is formed in both species not as a result of flowering but because the apical meristem either

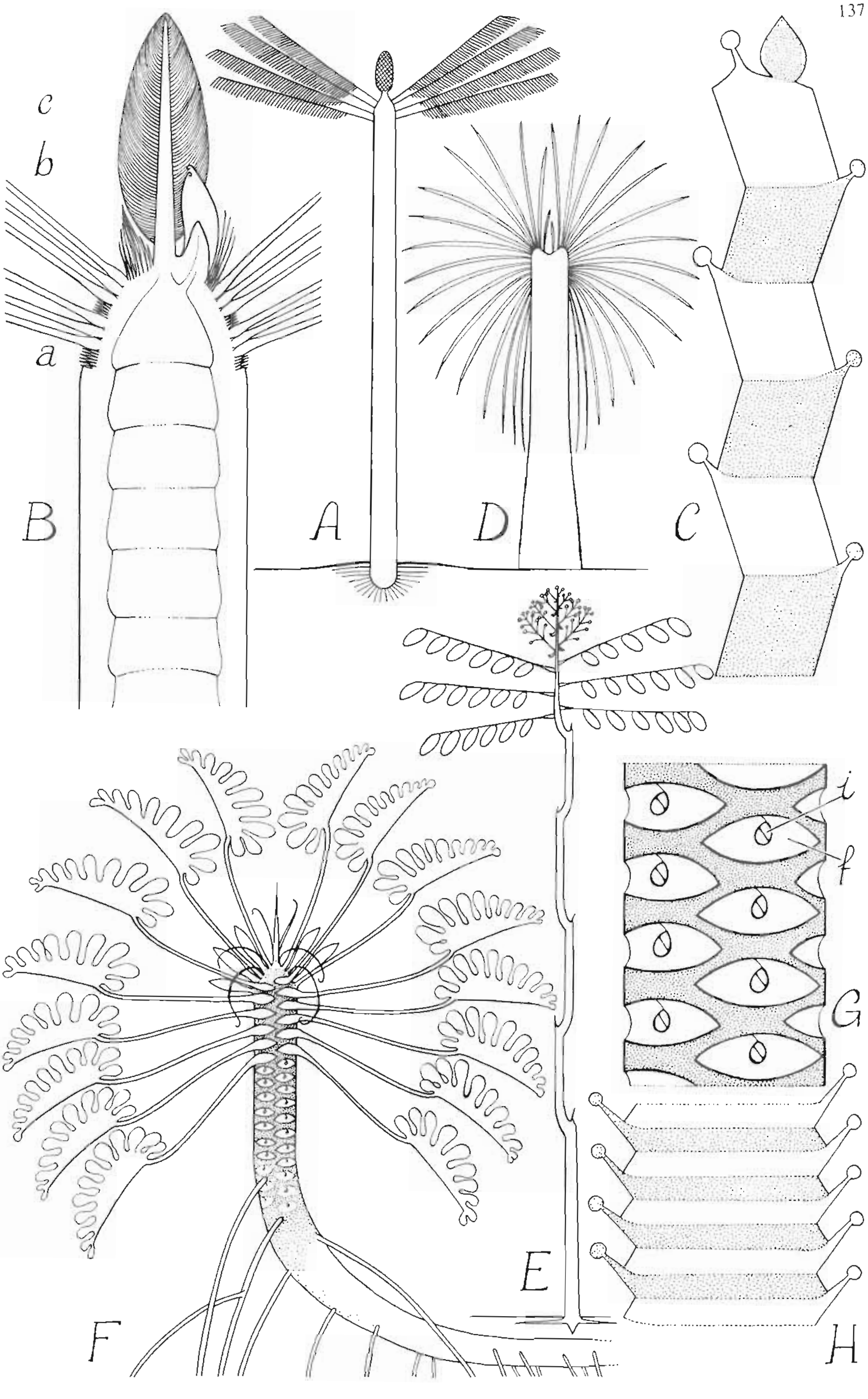
Fig. 24A–H. Chamberlain's model. ▷

A–C *Cycas circinalis* L., male tree (Cycadaceae, southeast Asia, the sago-tree). *A* Habit, a small monocaulous savanna tree reaching a height of 5 m. *B* Longitudinal section of the trunk showing terminal cone and sympodial growth which is indicated internally by the series of "cone-domes" (Fig. 23); *a* foliage leaves; *b* bud-scales; *c* microsporophylls (see CHAMBERLAIN, 1911). *C* Diagram of the sympodially constructed trunk composed of a series of modules.

D *Cordyline indivisa* Steud. (Agavaceae, New Zealand). A sympodial, monocaulous tree to a height of 5 m (TOMLINSON and FISHER, 1971).

E *Talisia mollis* Kth. ex Camb. (Sapindaceae, Camopi River, French Guiana, *Oldeman and Sastre 111*). A small rain-forest tree with a sympodial trunk, observed to a height of 6 m.

F–H *Philodendron selloum* C. Koch (Araceae, tropical America, commonly cultivated). *F* Habit, trunk erect to a height of 3 m, monocaulous but in fact a highly organized and condensed sympodium with each foliage leaf enclosing a terminal inflorescence, the modules each originating from the axillary meristem of the scale-like prophyll which begins each new unit. *G* External aspect of the trunk, *f* foliage leaf; *i* terminal inflorescence. *H* Axis construction represented diagrammatically in one plane, to show succession of modules; prophyll not illustrated (see RITTERBUSCH, 1971)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aborts (as in *Connarus*) or is transformed into a tendril (in *Iodes* as described by Cremers, 1974). *Connarus* is unusual in combining this monocaulous sympodium with cauliflory and hence Oldeman (1974a) considers it close to Corner's model. The inflorescence in *Iodes* is lateral, from the axil of a leaf just below the tendril. Readers familiar with any of the examples cited above, especially the species of *Cycas*, will perhaps be puzzled to find them cited as examples of monocaulous trees, when specimens in cultivation (but rarely in the wild) are commonly branched. This applies to many of the dicotyledonous examples (e.g., *Clerodendron*, *Jatropha*, *Oroxylon*). The paradox arises because the branching observed is not a character of the model, i.e., it is not *endogenously* determined, but represents a multiplication of axes indicative of changes occurring in the *biotope*. In cultivation, for example, *Cycas* is usually well fertilized and trunks become damaged during weeding or lawn mowing. This stimulates the formation of adventitious buds, usually on the lower portions of the trunk, which can generate further axes. This process is discussed in more detail under the section dealing with reiteration (p. 269). It illustrates how it may be difficult to establish the architecture of a model without carefully controlled growth conditions.

Forms intermediate between Chamberlain's model and Leeuwenberg's model, described later, may be recognized in view of a more or less strong tendency for essentially monocaulous species to multiply the number of relay axes. Arborescent Bignoniaceae like *Jacaranda* and *Spathodea*, as well as *Oroxylon* itself illustrate this intermediate condition. The architectural continuum is readily appreciated at this point.

Strategy of the Model. This model, in many of its examples, simply repeats the strategies we have discussed for Corner's model, since flowering is a recurrent process. The parallel is most apt in those species which produce several inflorescences more or less simultaneously, as in some Araceae and Cyclanthaceae. However, there is a peculiar dependence of vegetative growth on flowering, since each new module is initiated as a response to flowering. Effectively this permits a degree of environmentally modifiable flexibility between the extremes of Holttum's model and Corner's model. It is equally clear that examples of Chamberlain's model which are less specialized biologically (i.e., in nonarchitectural terms) occupy the rain-forest understorey, while biologically more specialized ones, and notably the climbers, exploit other ecological niches within the rain-forest.

Taxonomic List of Examples (Chamberlain's Model)

GYMNOSPERMS

Cycadales (many cycads exhibit this model, the following are representative):
Ceratozamia sp., Mexico / *Cycas circinalis* L.♂ (Figs. 23, 24A–C), Malesia / *Cycas revoluta* Thunb.♂, Malesia / *Dioon edule* Lindl., Mexico, Chamberlain, 1911 / *Dioon spinulosum* Dyer, Mexico, Chamberlain, 1911 / [H] *Zamia floridana* A.D.C., Florida, Bahamas, Grace Smith, 1907.

MONOCOTYLEDONS

Agavaceae:
Cordyline indivisa Steud. (Fig. 24D), New Zealand, Tomlinson and Fisher, 1971 / *Dasylirion longissimum* Lem., Mexico / *Dracaena umbraculifera* Jacq., Java, Graf, 1974.
Araceae:
[H] *Arum maculatum* L., Europe, Walton, 1964 / [H] *Dieffenbachia picta* Schott. Trop. America. Meusel, 1951 / [L] *Philodendron selloum* C. Koch

(Fig. 24F–H), Trop. America / [H] *Schizocasia lauterbachiana* Engl., New Guinea.

Cyperaceae:

[H] *Eriospora pilosa* Bench., W. Africa, BONARDI, 1966.

Xanthorrboeaceae:

Xanthorrhoea media R.Br., Australia, GILL and INGWERSEN, 1976.

DICOTYLEDONS

Apocynaceae:

**Pachypodium decaryi* L., Madagascar.

Araliaceae:

Eremopanax angustata Baill., New Caledonia, VEILLON, 1976 / *Gastonia* sp., Madagascar / *Meryta balansae* Baill., Madagascar, New Caledonia, VEILLON, 1976.

Berberidaceae:

**Nandina domestica* Thunb., Japan.

Bignoniaceae:

Oroxylum indicum Vent. Malaysia, CORNER, 1952.

Capparidaceae:

Euadenia eminens Hook. f., Trop. Africa.

Crassulaceae:

[H] +*Kalanchoë rhombopilosa* Mann. and Boit., Madagascar.

Droseraceae:

[H] *Drosera indica* L., Old World Tropics [H] *Drosera intermedia* Hayne., Europe, FAVARD, 1969 / [H] *Drosera madagascariensis* D.C., Trop. Africa, JEANNODA, 1977 / [H] *Drosera rotundifolia* L., Europe, FAVARD, 1969.

Euphorbiaceae:

Euphorbia hypericifolia L., Madagascar, CREMERS, 1976 / **Jatropha multifida* L., Trop. America (commonly cultivated).

Gesneriaceae:

[H] *Boea elegans* Ridl., Malaysia, BURTT, 1964.

Leeaceae:

Leea guineensis G. Don, Trop. Africa.

Loganiaceae:

Potalia amara Aublet, French Guiana.

Malvaceae:

[H] *Pavonia* cf. *flavispina* Miq., (Oldeman and Sastre 132), French Guiana.

Meliaceae:

Cedrela aff. *barbata* C.DC., French Guiana.

Meliantbaceae:

Bersama yangambiensis Toussaint, Trop. Africa.

Polygalaceae:

Polygala venenosa Juss. ex. Poir., Java.

Quiinaceae:

Quiina oiapoquensis Pires, French Guiana.

Sapindaceae:

**Otophora spectabilis* Blume, Java / *Talisia mollis* Kth. ex Camb. (Fig. 24E), French Guiana / *Talisia* aff. *elephantipes* Sandw., French Guiana.

Simaroubaceae:

Picrolemma cf. *pseudocoffea* Ducke, (Oldeman 2166), French Guiana.

Verbenaceae:

**Clerodendron japonicum* (Thunb.) Sweet, Indonesia.

McClure's Model

Definition. The architecture consists of differentiated axes of two kinds: first, "sigmoid" trunk axes which are essentially mixed, originate by basal branching and bear, second, plagiotropic leafy branches; both kinds show determinate growth due to a high degree of preformation.

This model has been established to accomodate a very distinct type of tree, represented most familiarly by the bamboos, but occurring in a number of other groups. Our present account is only tentative since the number and diversity of observed species remains for the moment small. However, naming this model serves to draw attention to a structurally isolated group of plants.

Probably the most essential feature of this model is that all the aerial parts are *vegetatively* determinate in their growth, with a clear differentiation between trunk and branch. It is useful, therefore, to think of each trunk plus series of dependent branches (which is a kind of supermodule) as a very large determinate organ, something like a very elaborate compound leaf (cf. the leaf of *Raphia regalis* mentioned on p.104).

The bamboos (Gramineae – Bambusoideae) are a large characteristic group conforming to McClure's model in their majority (Fig. 25). Their dominance among the known examples makes it difficult but necessary to avoid a taxonomic orientation in defining this model. Its existence in other monocotyledons is now recognized, however, and its rarity in dicotyledons may only reflect our ignorance of the underground branching of plants with little secondary thickening and of dicotyledons in general.

The model is appropriately named after F.A. McClure in recognition of his definitive contributions to our knowledge of the bamboos (McClure, 1966).

Example. The common bamboo, *Bambusa arundinacea* (Asian tropics, but widely cultivated) illustrates this model (Fig. 26C–E). In its juvenile stages there is an extended period of establishment growth (p. 68) which lasts four or five years, during which time the adult dimension of both aerial and underground parts is built up by the production of progressively thicker erect axes, which are progressively more specialized. Each erect axis arises by basal branching from a parent axis; the lateral axis in its overall dimensions (total height, basal diameter) eventually exceeds those of the parent axis (cf. Fig. 26D). At maturity the erect axes reach a height of 25 m, with a basal trunk diameter of 30 cm. Specialization of the erect axis is such that foliage leaves are virtually restricted to the plagiotropic branch system which develops at each node, the trunk itself is nonassimilating.

The description of the erect axis of *Bambusa arundinacea* is difficult because of our still incomplete understanding of orthotropy and plagiotropy (p. 48). This axis seems closely comparable with the inherently plagiotropic mixed axes displayed in Troll's model. However, its orientation changes twice, once at the base from horizontal to erect and once distally from erect to all but horizontal; the result is a "sigmoid" overall shape. The directional change at the base can perhaps be compared with the "getaway" segment of axes in an orthotropic branch complex (Fig. 12A). Hence it remains uncertain whether the basal part of the module in McClure's model is truly plagiotropic. It will be described here by the term "prostrated", coined by Jean-Noda (1977), which does not necessarily imply a stable, endogenous, differentiation of the axis itself. The distal horizontal segment of the sigmoid axes conforms much better to the definitions of plagiotropy as given earlier (p. 54, Fig. 12).

The basitonic, very regular branching pattern unites the basal prostrated portions of the successive main axes into the rhizome system whose characteristics have been described by different authors (e.g., Takenouchi, 1931; Arber, 1934; McClure, 1966). Individual rhizome segments bear a distichous series of scale leaves with the plane of distichy horizontal. Adventitious roots form more or less regular concentric series distal to each node. Proximal internodes are narrow but they increase, in a distal direction, to the diameter of the erect trunk (Fig. 26E). Distal internodes include a lateral series of massive buds, of which two usually develop as renewal shoots.

Differentiation of the terminal bud as an erect shoot involves a good deal of underground preformation, with most, if not all of the nodes established prior to any marked stem elongation. Once this stage of preformation is completed extension of the shoot is rapid and dramatic, with initial rates of up to 1 m a day being easily measured. Growth is determinate,

Fig. 25. McClure's model, *Dendrocalamus giganteus* (Gramineae – Bambusoideae), Papeari Botanic Garden, Tahiti, French Polynesia. Trunk axes, bearing distichously arranged scale leaves developing basally from the rhizome system ▷

even though the total height achieved usually exceeds 20 m. The axis is gradually tapering, and bears scale leaves almost throughout (i.e., is a nonassimilating trunk) but the distal, narrowest nodes support foliage leaves. This distal part is essentially plagiotropic.

Each node of the trunk in *Bambusa* develops a determinate, plagiotropic branch or branch system to which other foliage leaves are largely confined. A branch system develops from a bud complex in the axil of the scale leaf usually with several branch orders inserted close together. The length of these determinate branches varies along the trunk, the lower ones being reduced and usually spinous.

Bambusa arundinacea is like many bamboos in its gregarious flowering (JANZEN, 1976). A single clone will remain sterile for up to 20 years before it flowers, in the company of other clumps arising from a contemporary genetic source, whether this be seed or cutting. Flowering involves the development of terminal panicles on most ultimate branch units. After seed development is complete, the clone dies. We were able to witness this gregarious flowering recently in South Florida during the summers of 1973–1974. Most clumps were an estimated 20 years old, but flowered within 6–12 months.

Determinate growth and a tapering trunk seem to be features of bamboos, but they are less pronounced in other monocotyledons which illustrate this model.

Variations and Other Examples. In bamboos MCCLURE (1966) made a distinction between *pachymorph* and *leptomorph* species based on the difference between species with thick congested underground shoot systems and species with slender elongated axes. In the first group aerial culms are crowded (Fig. 26), in the second group they are dispersed. This essentially parallels the difference between tufted and rhizomatous grasses. Leptomorph rhizomes also tend towards monopodial branching.

1. Other Monocotyledons. McClure's model is repeated in a number of monocotyledons from unrelated families; there is a strong tendency towards the scandent habit in the few examples known. Three examples may be described briefly.

Ripogonum scandens (Smilacaceae, New Zealand) is a high-climbing liane of evergreen temperate forest (SIMPSON and PHILIPSON, 1969; MACMILLAN, 1972; TOMLINSON and ESLER, 1973). In the adult form the twining, orthotropic aerial shoots bear scale leaves, with foliage leaves (except for distal nodes) restricted to lateral branches which may themselves be branched again. Lateral branches arise in the axils of scale leaves. Leaf arrangement is distichous in juvenile shoots but becomes opposite in adult shoots and is unusual in that the pairs of leaves are all in one plane. Flowers are borne in

Fig. 26A–E. McClure's model. ▷

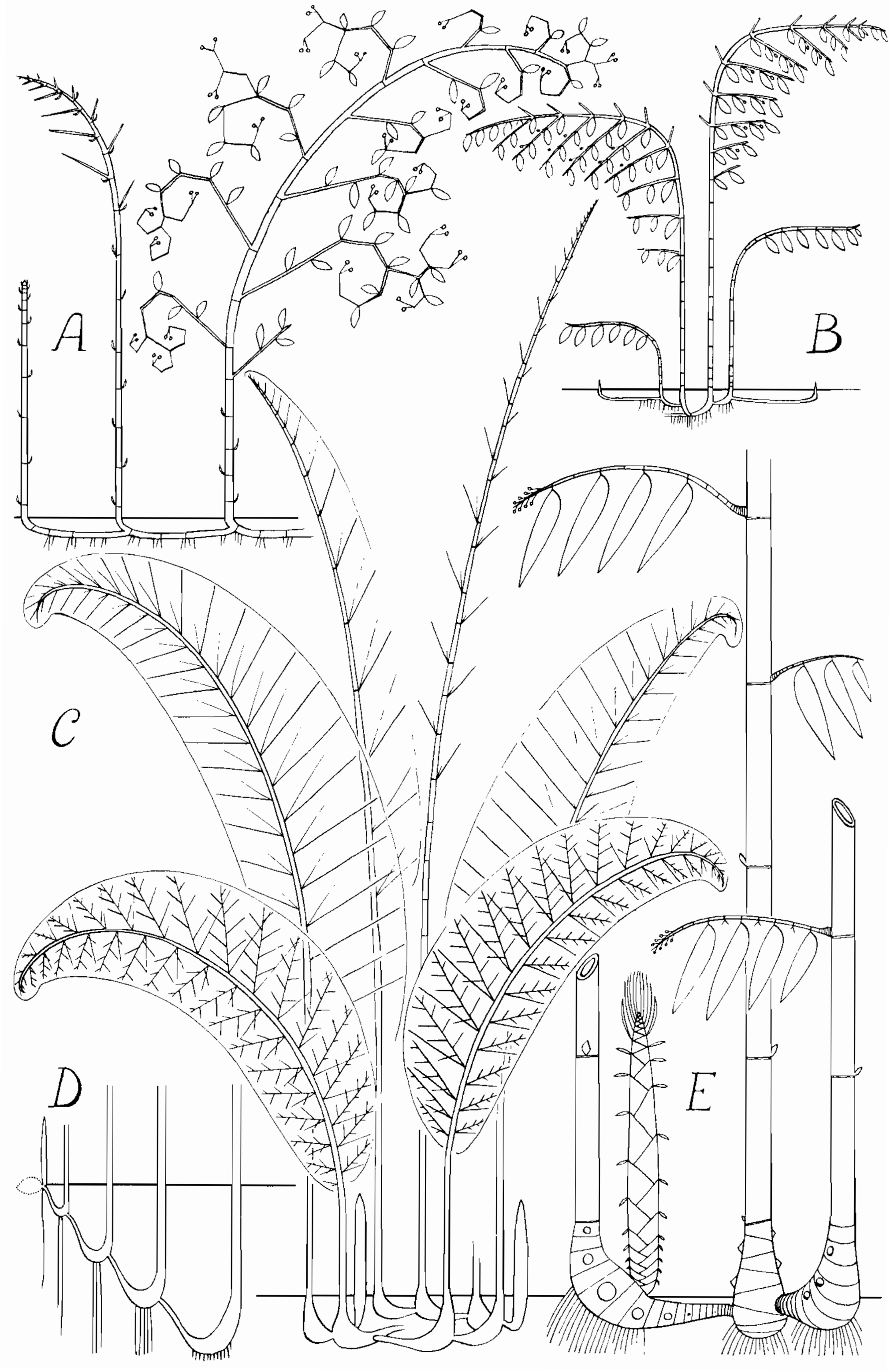
A *Hypselodelphis violacea* (K. Schum.) Milne-Redhead (Marantaceae, tropical West Africa). An appreciably woody erect plant exceeding 5 m in height (TOMLINSON, 1961).

B *Polygonum cuspidatum* Sieb. and Z. (Polygonaceae, temperate regions of the Far East, introduced in Europe and North America). A very common weedy plant, up to 2 m high.

C *Bambusa arundinacea* Retzius (Graminae–Bambusoideae, the common bamboo, from tropical Asia but widely cultivated). An arborescent member of the grass family, more than 25 m high.

D *Dendrocalamus strictus* (Roxburgh) Nees (Graminae–Bambusoideae, tropical Asia). The juvenile stage shows each erect axis arising by basal branching from a parent axis (MCCLURE, 1966). One example of establishment growth (p. 68).

E *Bambusa vulgaris* Schrader ex Wendland (Graminae–Bambusoideae, known only in cultivation). A part of a clump showing the basal branching and apical flowering (MCCLURE, 1966)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terminal panicles on the leafy shoots. The aerial shoots arise from a regularly branched sympodial rhizome system which typically develops two renewal buds per segment. The juvenile phase (TOMLINSON and ESLER, 1973) shows establishment growth of the kind which involves progressive branch enlargement; only the first few erect axes produced during the early ontogeny of the individual support foliage leaves directly.

Hypselodelphis violacea (Marantaceae, tropical West Africa; Fig. 26A) as described by TOMLINSON (1961) conforms to McClure's model. Individuals are quite woody with the erect shoots reaching a height of 5 m or more, scrambling and supported by surrounding vegetation via reflexed aerial plagiotropic branches of the second and third order.

Tapeinocheilos hollrungii (Costaceae, Queensland and New Guinea) also exemplifies this model. Axes here are fleshy rather than woody, but still reach a height of 4–5 m. Branching of orthotropic aerial shoots is diffuse rather than continuous, and distal nodes support foliage leaves rather than scale leaves. Spicate inflorescences may be terminal on the orthotropic shoots but there is some tendency towards shoot dimorphism and the production of specialized, wholly flowering erect shoots. *Tapeinocheilos* is closely allied, both taxonomically and architecturally, to many *Costus* species which conform to Tomlinson's model. *Tapeinocheilos pungens* Miq. is a specialization of this habit since the erect axes do not branch until after they have flowered, when they become top-heavy, fall and root. Other examples of this model are found in the families Philesiaceae, Liliaceae, and possibly Stenomeridaceae, and Dioscoreaceae in which the plants are usually herbaceous and tend to be climbers. *Asparagus* species (Liliaceae) probably represent the most familiar examples.

2. *Dicotyledons.* McClure's model, as far as we know, is almost restricted to the monocotyledons, which might suggest that it is a particular specialization of plants lacking secondary vascular tissues. *Polygonum cuspidatum* (Polygonaceae, Himalayas, but common as a weed in Europe and North America) is here offered as an example of the model (Fig. 26B). The annual orthotropic aerial shoots arise from a perennial rhizome system. They have rapid determinate growth, ending in a plagiotropic segment. First-order plagiotropic shoots subtended by the leaves are themselves leafy and produce lateral flower spikes. Other dicotyledonous examples are likely to come to light when the underground parts of species which otherwise recall Troll's model are examined more carefully. Basal branching which is part of the model and not reiteration would be an essential criterion.

Strategy of the Model. We have commented in our discussion of Tomlinson's model on the apparent inability of unbranched woody aerial vegetative stems to be supported by a subterranean branch system, for which there seems no rational explanation. McClure's model achieves this stage in an incisive and "imaginative" way. The complex and long-lived nature of the vegetative body so constructed indicates a *K* strategist; although examples of this model are all denizens of disturbed sites in the tropics, their occupation of such biotopes is thorough and not at all ephemeral. Many bamboos are indeed aggressive and persistent weeds. The monocarpic habit implicit in their gregarious flowering – which may, again, not be as general in the model as it is in bamboos – transforms such plants in to highly specialized *r* strategists. JANZEN (1976) has interpreted their reproductive biology as an extreme method of avoiding seed predators. In large dicotyledonous forest trees with prolific reiteration a long developmental phase serving a *K* strategy is followed by profuse flowering in the completely expanded crown (p. 277); such transitions from *K* to *r* strategy are distinctive of trees and in this sense McClure's model certainly belongs to the tree-models.

However, it is clear from the studies of NUMATA et al. (1974) that views of the reproductive cycle of bamboos can be oversimplified. These authors showed that flowering of *Phyllostachys bambusoides* is preceded by the appearance of short slender culms which can regenerate a new colony of tall shoots. The species is therefore not monocarpic. This illustrates how important a detailed knowledge of vegetative morphology is in interpreting reproductive biology of plants.

Taxonomic List of Examples (McClure's Model)

MONOCOTYLEDONS

Costaceae:
[H] **Tapeinocheilos hollrungii* Schum., Trop. Australasia / [H] **Tapeinocheilos pungens* Miq., New Guinea.
Gramineae – Bambusoideae:
(Most bamboos represent this model, only the following cultivated species are cited as examples) / *Bambusa arundinacea* Retzium (Fig. 26C), Trop. Asia / *Bambusa vulgaris* Schrad. ex Wendl. (Fig. 26E), Known only in cultivation / *Dendrocalamus strictus* (Roxb.) Nees (Fig. 26D), Trop. Asia.
Liliaceae:
[H] *Asparagus officinalis* L., "asparagus", cultivated.
Marantaceae:
[H] *Hypselodelphis violacea* (K. Schum.) Milne-Redhead (Fig. 26A), W. Africa.
Philesiaceae:
[L] *Geitonoplesium cymosum* A. Cunn., Australia, Pacific Islands.
Smilacaceae:
[L] *Ripogonum scandens* Forst., New Zealand.

DICOTYLEDONS

Polygonaceae:
[H] *Polygonum cuspidatum* Sieb. and Z. (Fig. 26B), Himalayas.

2. Vegetative Axes Differentiated into Trunk and Branch

a) Axes Orthotropic and Plagiotropic

Leeuwenberg's Model

Definition. The model consists of equivalent orthotropic modules, each of which is determinated in its growth by virtue of the ultimate production of a terminal inflorescence[9]. Branching is three-dimensional to produce the several equivalent modules and is correlated with flowering, except in a few examples with branched sterile juvenile axes.

This model is comparable to Chamberlain's model but with the very important elaboration in the production of more than one relay axis below the inflorescence which terminates the seedling axis. All relay axes are equivalent and subsequently repeat the construction of the parent axis. The tree is now obviously branched and extends three-dimensionally. A feature which is quite characteristic of this model is the decrease in length and primary width of successive modules, i.e., they are qualitatively but necessarily not quantitatively equal. This is discussed later in relation to trunk formation in several examples.

As we have already mentioned intermediate forms between Chamberlain's model exist. For example, *Jacaranda copaia*

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[9] *Acalypha grandis* Benth. (Euphorbiaceae, Celebes) has a terminal female inflorescence but *lateral male* inflorescences on each module.

(Bignoniaceae, tropical America) forms a linear sympodial trunk early in its life, exactly as in Chamberlain's model, until an appreciable age when it may be 10–15 m high, after which it produces more than one relay axis and now conforms to Leeuwenberg's model (cf. Figs. 27, 28). This transition from one model to another which occurs within a single individual is also represented by *Euphorbia dendroides* (Euphorbiaceae) and *Oroxylon indicum* (Bignoniaceae) which are also monocaulous when young.

The close similarity between Chamberlain's and Leeuwenberg's models is further demonstrated by the frequent existence of examples of both in different species of a single genus, cf. in the monocotyledons: *Cordyline indivisa* and *C. australis* (Agavaceae), *Dracaena umbraculifera* and *D. draco* (Agavaceae), *Xanthorrhoea australis* and *X. preissii* (Xanthorrhoeaceae); in the dicotyledons: *Jatropha multifida* and *J. gossypifolia* (Euphorbiaceae), *Psychotria* sp. and *Psychotria nervosa* (Rubiaceae), *Espeletia* sp. and *Espeletia humbertii* (Compositae).

The model is named after A.J.M. LEEUWENBERG who described its architecture well in his revision of the African genus *Anthocleista* (Loganiaceae, LEEUWENBERG, 1961; see also the account of *A. procera* in H.O., 1970, pp. 34–36).

Example. For illustrative purposes we have selected *Messersmidia* (*Tournefortia*) *argentea* (Boraginaceae) which is common on sea shores of islands and atolls in the Pacific. It forms a small tree (Fig. 29B) usually less than 10 m high and is readily recognized by its silvery leaves. Figure 29C shows the early stages of development with the first module (epicotyledonary axis) having produced a terminal inflorescence (a pair of scorpioid cymes) and then being replaced by two (or more) lateral branches immediately below the inflorescence. This process is repeated with the branches spreading upwards in three dimensions to produce an adult tree with a hemispherical outline.

A feature of this architecture shown by all the other species illustrated in Figure 29 is the progressive shortening and narrowing of successive modules with the epicotyledonary module much the longest and with the largest leaves. Progressive diminution of module length and primary diameter is correlated with a proportionate diminution in leaf size. This affords a nice example, within a single individual, of "Corner's rule" discussed earlier (p.81).

Other Examples

1. Dicotyledons. Tree species of the genus *Senecio* (Compositae, East Africa) illustrate the model well. The alpine forms are here represented by *Senecio keniodendron* (Fig. 29E) which is endemic to the montane grasslands of Mount Kenya and Mount Aberdare, between 3500 and 5000 m (HEDBERG, 1964). Individuals have few branches and only reach a height of 5 m, the stout trunks being clothed by the persistent remains of leaves. The massive terminal inflorescence is striking. By contrast *Senecio johnstonii* subsp. *johnstonii* (Fig. 29D), endemic to Mount Meru, between 3000 and 3500 m, and analyzed architecturally by MABBERLEY (1973), is a forest-dwelling species, somewhat more branched and to a height of 10 m. This species illustrates the progressive decrease in length of modules well. In the Andes identical architectures are shown in the genus *Espeletia,* notably *E. humbertii.*

Taller, lowland representatives of Leeuwenberg's model may be seen in the Araliaceae. Possibly the largest araliad known

Fig. 27. Leeuwenberg's model, *Aloë* sp. (Liliaceae), Tsimbazaza Botanic Garden, Madagascar ▷

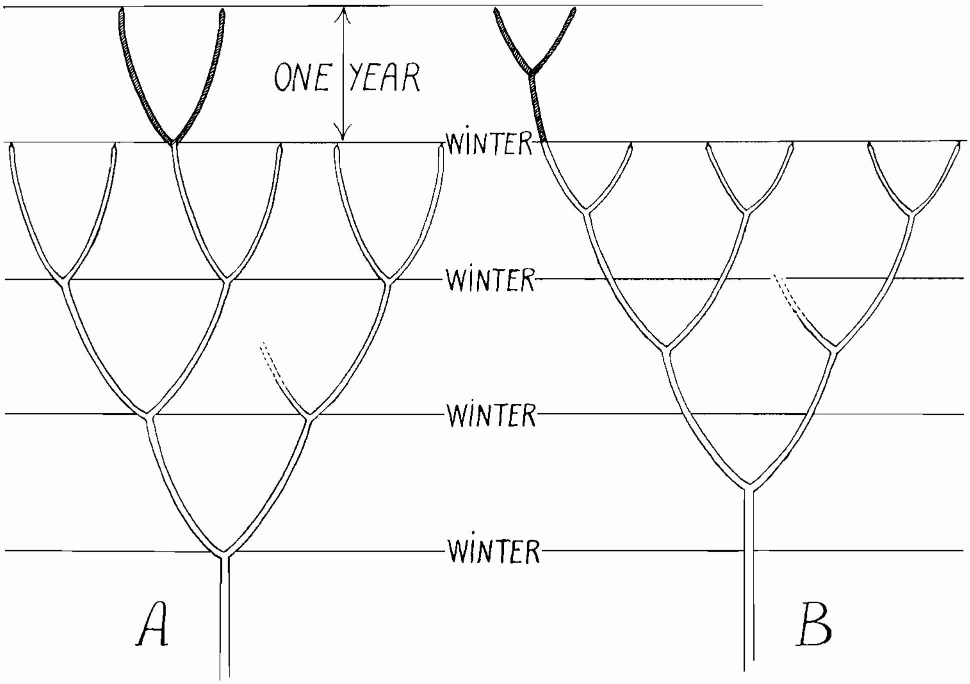

Fig. 28A and B. Leeuwenberg's model.

A In a tree with meristems determinate at end of season, e.g., *Rhus*, renewal shoots produced by prolepsis.

B Branching in middle of growing season by syllepsis, as in *Cornus stolonifera*. In the tropics similar responses may be initiated by dry seasons, or may be determined by endogenous rhythms

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Fig. 29A–H. Leeuwenberg's model.

A *Gastonia spectabilis* (Harms) Philipson (Araliaceae, New Guinea and Solomon Islands). Up to 40 m high and possibly the largest member of the Araliaceae known, with inflorescences in forks of the branch system, but well below the leaves (Philipson, 1970a).

B and *C* *Messersmidia* (syn. *Tournefortia*) *argentea* (L.) I.M. Johnst. (Boraginaceae, in coral and around atolls in the Pacific Ocean). *B* Habit, a small tree usually less than 10 m high; *C* young plant, 1 m high with cymose inflorescences in the distal forks, lower forks represent levels where earlier flowering took place.

D *Senecio johnstonii* Oliver ssp. *johnstonii* Mabberley (Compositae, East Africa). A forest-living *Senecio*, endemic to Mount Meru, Kenya, between 3,000 and 3,500 m. (After Mabberley, 1973).

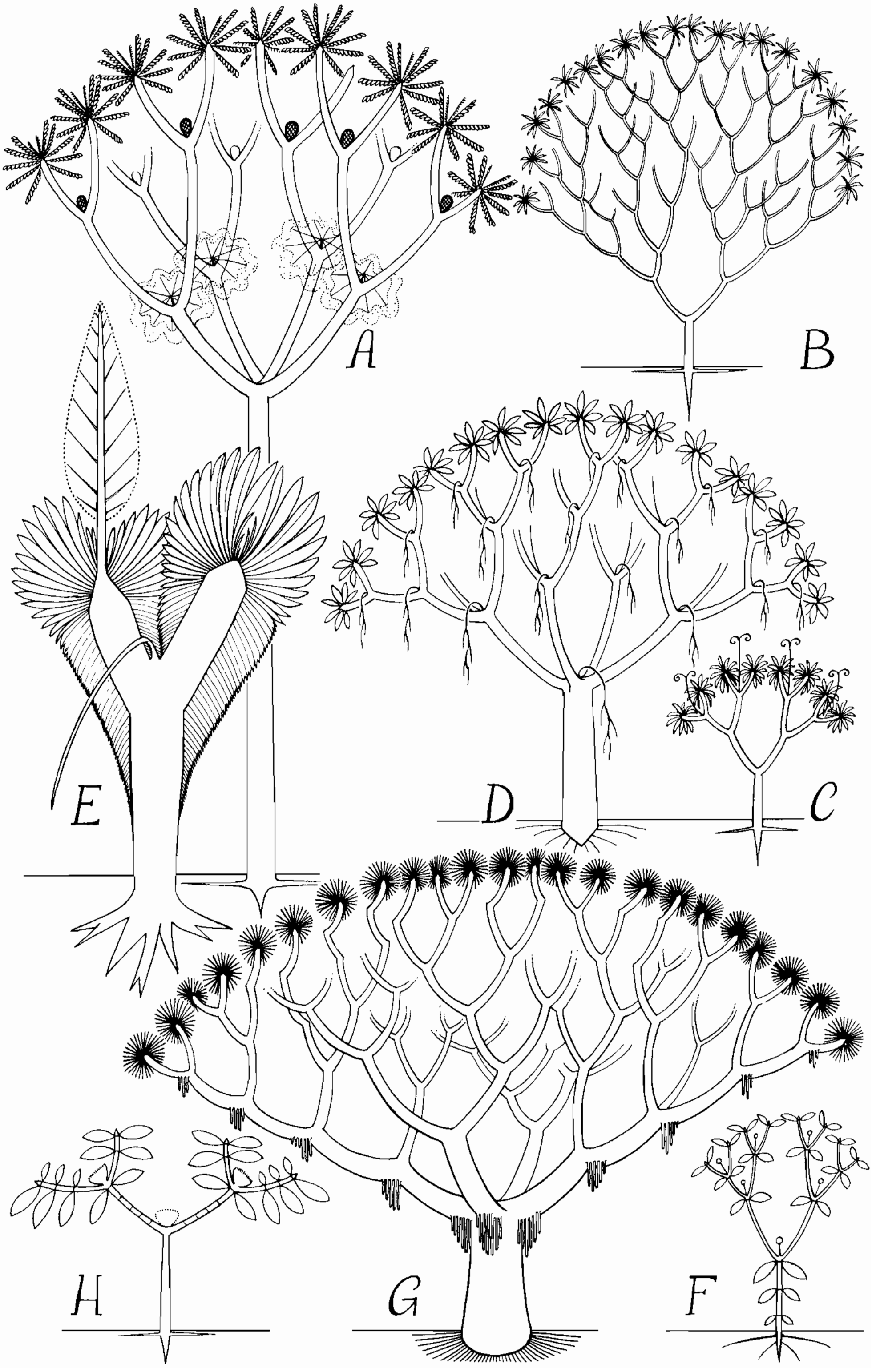
▷

E *Senecio keniodendron* R.E. and T.C.E.Fr. (Compositae, East Africa). A small sparsely branched tree, up to 5 m high, endemic to the "alpine" grasslands of Mount Kenya and Mount Aberdares between 3,500 and 4,500 m (Hedberg, 1964).

F *Acanthospermum hispidum* D.C. (Compositae, tropical Africa). In this small ruderal herb, each module after the first bears only two leaves, otherwise the architecture remains the same as in trees of this model.

G *Dracaena draco* L. (Agavaceae, Macronesia but widely cultivated). A tall specimen 15 m high seen in the Botanic Gardens, Sydney; roots arising from the base of the thicker modules.

H *Cephaëlis tomentosa* (Aubl.) Vahl (Rubiaceae, Brazil and Guianas). A common treelet of the forest undergrowth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(PHILIPSON, 1970a) is *Gastonia* (=*Peekeliopanax*) *spectabilis* (New Guinea and the Solomon Islands, Fig. 29A), since it may reach a height of 40 m, with a basal diameter of 2 m; this height being achieved largely by an extended epicotyledonary axis. *Gastonia* is distinctive because the expansion of inflorescences is much delayed. They are initiated in the manner characteristic of the model, i.e., terminally on the ultimate modules, but they remain inhibited as massive buds, covered by bud scales, in the branch forks. Unfolding is so delayed that expanded inflorescences appear well below the foliage of current shoots and this may have significance in pollination biology. Leeuwenberg's model is found in other araliaceous trees in genera like *Cussonia*, *Oreopanax*, and *Schefflera*, all with large leaves and massive twigs, but none reaches quite the stature of *Gastonia*.

Two other species of contrasted stature and habitat complete our illustrations of dicotyledonous examples of this model. *Cephaëlis tomentosa* (Rubiaceae) is a common treelet of forest undergrowth in the Guianas (Fig. 29H), with spreading branches. Inflorescences are congested panicles situated in the distal forks and these give the plant its generic name. To demonstrate the existence of this model in herbs we have also illustrated *Acanthospermum hispidum* (Compositae), a weed native to tropical Africa (Fig. 29F). Each module in this species, beyond the epicotyledonary axis, bears only one pair of opposite leaves (i.e., the prophylls). This diminutive herb is architecturally identical with the trees we have described. Other herbs in genera like *Croton*, *Euphorbia* (Euphorbiaceae) and *Oldenlandia* (Rubiaceae) are comparable.

Dicotyledonous families which are particularly rich in examples of this model, apart from Araliaceae, include Apocynaceae (PRÉVOST, 1967) where the plants are usually quite low, as well as Euphorbiaceae. Two important euphorbiaceous genera which show this model are *Manihot* (*M. esculenta* "cassava", *M. glaziovii*, "ceara-rubber") and the castor-bean plant, *Ricinus communis*, which is widespread as a weed tree in the tropics, growing to a height of 7 m. It may be cultivated as an ornamental herb at higher latitudes. Most tropical representatives of this model are evergreen, but deciduous species are represented in the tropics by the African *Voacanga africana* (Apocynaceae) and the Brazilian *Schizolobium excelsum* (Leguminosae – Caesalpinioideae). In these examples there is complete synchronization of successive events like defoliation, flowering, refoliation and fruiting in the outermost series of modules. This is comparable to the situation in temperate examples of this model, represented by species of *Rhus* ("sumac", Anacardiaceae) and *Cornus* (Cornaceae) in which each module is the produce of one season's growth. One can determine the age of each tree quite accurately by the number of branch forks or stem articulations. In *Rhus* branching occurs at the beginning of the season, in *Cornus* in the middle of the season (Fig. 28).

2. *Monocotyledons*. *Dracaena draco* (Agavaceae) the "dragon tree" of the Canary Islands (Fig. 29G) is representative of this model. This species is commonly cultivated and reaches a considerable size, but in girth of trunk, not height, in a relatively short period (e.g., SYMON, 1974). The putative longevity of these plants is undoubtedly a result of considerable exaggeration (TOMLINSON and ZIMMERMANN, 1969). The specimen illustrated (Fig. 29G) was unusual in that adventitious roots had developed at the base of the lower modules (see discussion of *Schefflera* later, p. 153). Most species in the Agavaceae represent the model well, e.g., *Beaucarnea*, *Cordyline*, *Dasylirion*

and *Yucca*, as in the familiar Joshua tree, *Yucca filamentosa* and cabbage tree, *Cordyline australis*. Other examples include species of *Aloë* (Fig. 27) (e.g., *A. dichotoma*, Liliaceae) and *Xanthorrhoea* (e.g., *X. preissii*, Xanthorrhoeaceae). All these examples are notable for the presence of a secondary vascular cambium (TOMLINSON and ZIMMERMANN, 1969) which provides the mechanical stability needed by these branched monocotyledons.

Variations. Complexity in the seemingly simple morphogenetic pattern of Leeuwenberg's model should not be underestimated. This model lacks a central meristem capable of assuming the role of "organizing apex" (cf. BANCILHON, 1965; ROUX, 1968) comparable to that of the leader shoot of many branched trees, or the apical meristem of unbranched trees. Conformity to the model generally decreases after three or four series of relay modules have been produced, and this is understandable if one considers the number of interacting meristems then present. Measurements on *Rhus typhina*, kindly supplied by Dr. J. WHITE, which have been used to make Figure 30, clearly illustrate this competition between meristems such that the actual number of growing shoots rapidly falls below the theoretical number as a result of abortion and abscission of both young and old meristems. Differences in vigor between modules become more significant, the more numerous are the modules. Experimental research on the physiology of examples of this model should shed light on physiological correlations between numerous meristems with equivalent rôles, comparable in some respects to the "apical complexes" described by CHAMPAGNAT (1965).

The absence of a differentiated trunk would appear to restrict the size which plants showing this architecture might attain and indeed this is true for many examples (e.g., *Manihot*, *Rhus*, *Ricinus* and most Apocynaceae). However, other trees may reach a considerable height, as in *Gastonia* and comparable Araliaceae. *Cordyline australis* may reach 20 m (TOMLINSON and FISHER, 1971). In trees which conform precisely to the model this height is achieved mainly by the development of a protracted, sterile juvenile phase so that the first module is very long. In *Schizolobium excelsum* for example the epicotyledonary axis may become 15 m high before it flowers and branches. One might contrast this with many Apocynaceae with the first module scarcely 20 cm long. Growth in height may otherwise be provided by individually long modules as in many Araliaceae, or by their growth close to the vertical, as in *Cordyline*.

A striking variation within Leeuwenberg's model is in the method of branching found in the earlier modules. We have characterized the model by branching below terminal inflorescences, which would suggest that branching does not precede flowering, i.e., the onset of reproductive maturity. In most instances this is correct (e.g., in *Cordyline*, *Dracaena*, *Anthocleista*, *Manihot*, *Ricinus*, *Schizolobium*) where the epicotyledonary axis is sexual, although the inflorescence it produces may abort. Less commonly the first modules are sterile, but branching still occurs; there follows a series of aborted and finally functional inflorescences in successive branch orders. *Tabernaemontana crassa* (Apocynaceae) provides an example. Growth of the first modules is arrested by parenchymatization of the apex, a process studied in detail by PRÉVOST (1972). This involves the maturation of an "intermediate zone" of parenchyma cells in the shoot apex, essentially dividing it equally into two portions; the two newly constituted meristems, which are axillary to the distal pair of foliage leaves,

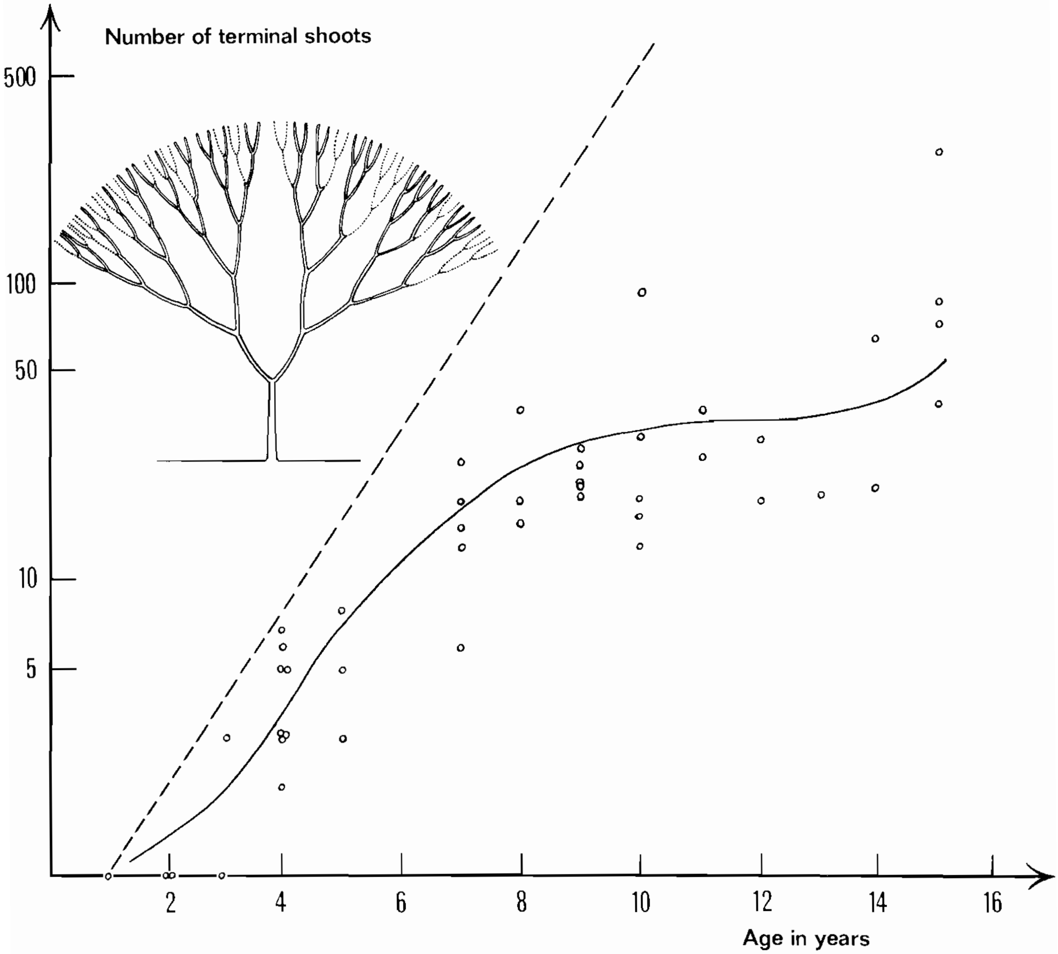


Fig. 30. Rhus typhina (Leeuwenberg's model). Theoretical versus actual number of shoots on trees of various ages. Abcissa, age of trees determined from morphology or annual rings; ordinate, total number of living terminal shoots in the corresponding trees. Each circle in the graph represents a single tree. The dotted lines represent the theoretical total number of shoots if each module gave rise to only two further relay axes each year, leading to the regular geometrical progression shown. Commonly more than two relay axes are, in fact, formed, but the actual numbers show that the branching pattern falls well below the theoretical maxima. (From data supplied by Dr. JAMES WHITE, with his permission)

initiate the next pair of modules. This process is repeated several times during the first two or three years in the life of the plant, producing several generations of sterile modules. Subsequently axes flower terminally in the manner normal for the model, but still with the occasional interpolation of sterile modules according to an as yet undetermined periodicity. In *Tabernaemontana* the stimulus for this parenchymatization is not known, though it appears to be wholly endogenous and one assumes that the sterile modules had aborted the terminal meristem as if they had flowered. Similar branching occurs in other apocynaceous shrubs, the commonly cultivated frangipani (*Plumeria alba*) providing a good example.

In this respect one can contrast temperate species of *Rhus* (e.g., *R. copallina, R. typhina*) which pass through a similar sterile but branched juvenile stage where growth of modules is limited by photoperiod, i.e., exogenously. This was established by NITSCH (1959) who showed that under an appropriate short-day regime (corresponding to late summer in North America) the shoot apex aborts and abscises. In adult trees the same stimulus is responsible for flowering and, by analogy, the process of apical abortion in *Rhus* can be regarded as an incomplete expression of terminal flowering. Similar considerations probably apply in tropical species, as the work of PRÉVOST (1972) on *Tabernaemontana* and MÉDARD (1973) on *Manihot esculenta* indicates, since the timing of flowering and branching is coincident. The question of causes needs more precise analysis and is a subject ripe for experimental study. At the histological level we do not know if branching precedes or follows the onset of reproduction, i.e. which is cause and which is effect.

Strategy of the Model. Leeuwenberg's model is less common in rain-forest species than in species of secondary vegetation and disturbed sites both in the tropics (e.g., *Anthocleista, Psychotria, Ricinus, Schefflera, Solanum*) and in temperate regions (e.g., *Rhus*), i.e., in biotopes fairly rich in climatic diversity but poor in competing species. The distribution suggests an adaptation towards an *r* strategy, centered upon biotope saturation by means of rapidly established populations, rather than individual specialization and long life span. This strategy is emphasized in *Rhus* by frequent proliferation via root suckers. However, this model is still to be contrasted with that of Holttum since flowering and fruiting are spread over extended periods, making the tree less susceptible to temporarily unfavorable circumstances. Montane vegetation in the tropics includes a good representation of Leeuwenberg's model, as our examples show. *Schefflera attenuata* (= *Didymopanax attenuatum*) (Araliaceae) is interesting in this respect. This species grows in hollows at an altitude of about 1000 m in Martinique and Guadeloupe (French Antilles). It has a very short epicotyledonary module and since distal relay axes are often pendulous the spreading crown comes to rest on the ground, where adventitious roots may be formed. This habit recalls that of small alpine herbs generally described as "cushion-plants" (Polster- or Kissenpflanzen; RAUH, 1950). Adventitious rooting generally gives an axis a certain autonomy since it may become independent of the main root system. Such autonomy exists in certain reiterated complexes (p. 282). The boundary here between growth of the model and reiteration is not sharp, a general phenomenon to be discussed later.

Taxonomic List of Examples (Leeuwenberg's Model)

MONOCOTYLEDONS

Agavaceae:
Cordyline australis (Forst. f.) Endl., "cabbage tree", New Zealand. TOMLINSON and FISHER, 1971. (Most other *Cordyline* spp. also represent this model). *Dracaena draco* L., "dragon tree" (Fig. 29G), Canary Islands, SYMON, 1974 / *Dracaena fragrans* (L.) Ker-Gawl., Trop. Africa, ZIMMERMANN and TOMLINSON, 1969, 1970 / **Nolina beldingi* Brandegee, Baja, California / *Yucca aloifolia* L., W. Indies, C. America, TOMLINSON and ZIMMERMANN, 1969.

Liliaceae (Fig. 27):
Aloë dichotoma L.f., S. Africa, Schoute, 1918 / *Aloë eminens* Reynolds and Bally, Somalia, Reynolds, 1966 / *Aloë suzannae* R. Decary, Madagascar, Reynolds, 1966.

Pandanaceae:
Pandanus androcephalanthos Martelli, Madagascar, Guillaumet, 1973 / *Pandanus centrifugalis* St. John, Madagascar, Guillaumet, 1973 / *Pandanus mammillaris* Martelli and Pichi-Serm., Madagascar, Guillaumet, 1973 / *Pandanus platyphyllus* Martelli, Madagascar, Guillaumet, 1973 / *Pandanus rollotii* Martelli, Madagascar, Guillaumet, 1973 / *Sararanga sinuosa* Hemsl., New Guinea, Solomon Islands, Zimmermann et al., 1974; Stone, 1961.

DICOTYLEDONS

Amaranthaceae:
[H]**Achyranthes aspera* Duss, Guadeloupe.

Anacardiaceae:
(Many species of *Rhus*, the following are representative) (cf. Fig. 28A). *Rhus copallina* L., E.N. America / *Rhus coriaria*, L., Mediterranean.

Apocynaceae:
**Alstonia filipes* Schlechter ex Guill., New Caledonia / **Alstonia sericea* Blume., Malesia / *Crioceras dipladeniiflorus* (Stapf) K. Schum., Congo / [L] *Landolphia dulcis* (R. Br. ex Sabine) Pichon. (Fig. 69B), Ivory Coast, Cremers, 1974 / *Nerium oleander* L., "oleander", widely cultivated, Asia Minor / *Pachypodium brevicaule* Bak., Madagascar, Koechlin, 1969 / *Pachypodium rosulatum* Bak., Madagascar, Koechlin, 1969 / *Paravallaris microphylla* Pitard, S.E. Asia, Prévost, 1967 / *Plumeria rubra* L., "frangipani", widely cultivated, C. America / +*Rauvolfia* cf. *macrophylla* Stapf, Gabon / *Rauvolfia obscura* K. Schum., Trop. America / *Rauvolfia vomitoria* Afzel., Ivory Coast, Prévost, 1967 / *Tabernaemontana crassa* Benth., Trop. Africa, Prévost, 1967 / *Tabernaemontana iboga* Baill., C. America / *Tabernaemontana undulata* Vahl, French Guiana / *Voacanga africana* Stapf, Trop. Africa / *Voacanga thouarsis* Roem. and Schult., Trop. Africa.

Araliaceae:
Cussonia bancoensis Aubr. and Pellegr. (Fig. 5A), E. Africa / *Cussonia barteri* Seem., E. Africa / *Gastonia spectabilis* (Harms) Philipson (Fig. 29A), New Guinea, Philipson, 1970a / *Gastonia* sp., (F. Hallé 2346), Madagascar / **Oreopanax nymphifolius* Decne. and Planch. ex Nicholson, Mexico / *Polyscias fulva* (Hiern.) Harms, Congo / *Schefflera attenuata* (Sw.) Frodin, Martinique, Oldeman, 1968 / *Schefflera morototoni* (Aubl.) Frodin, Trop. America, Hladik, 1970 / *Schefflera paraënsis* Huber, Brazil.

Bignoniaceae:
Phyllarthron madagascariensis K. Schum., Madagascar.

Boraginaceae:
Messersmidia argentea (L.) I.M. Johnst. (Fig. 29B, C), Pacific Islands.

Cactaceae:
**Pereskia bleo* D.C., Trop. America.

Campanulaceae:
[H] *Sphenoclea zeylanica* Gaertn., Zaire.

Caprifoliaceae:
Memecylanthus balansae Baill., New Caledonia, Veillon, 1976.

Compositae:
[H] *Acanthospermum hispidum* DC. (Fig. 29F), Zaire / [H] *Asteriscus pygmaeus* (DC.) Coss. and Durieu, Mediterranean, Meusel, 1957 / [H] *Carlina racemosa* Gilib., Europe, Meusel, 1970 / [H] *Odontospermum aquaticum* Sch. Bip., Mediterranean, Meusel, 1957, 1970 / [H]+*Pectis ciliaris* L., Martinique / [H] *Psiadia altissima* Benth. et Hook., Madagascar / *Senecio canaliculatus* Boj. ex DC., Madagascar / *Senecio johnstonii* Oliver (Fig. 29D), Kenya, Mabberley, 1973 / *Senecio keniodendron* R.E.Fr. and Th. Fr. (Fig. 29E), Kenya, Mabberley, 1973 / *Senecio leucadendron* (Forst. f.) Hemsley, St. Helena, Mabberley, 1975 / [H] *Spilanthes acmella* Murr., Congo / [H] *Synedrella nodiflora* Gaertn., Pantropical weed / *Vernonia appendiculata* Less., Madagascar.

Cornaceae:
**Aucuba japonica* Thunb., Korea, Japan / *Cornus capitata* Wall-Asia / **Cornus stolonifera* Michx. (cf. Fig. 28B), N. America.

Crassulaceae:
[H] +*Kalanchoë streptantha* Bak., Madagascar.

Dipsacaceae:
[H] *Scabiosa prolifera* L., Mediterranean, Meusel, 1970.

Epacridaceae:
Dracophyllum involucratum Brongn. and Gris, New Caledonia, Veillon, 1976 / *Dracophyllum ramosum* Panch. ex Brongn. and Gris., New Caledonia, Veillon, 1976.

Ericaceae:
[H] *Erica tetralix* L., Europe, Temple, 1975 / *Rhododendron aurigeranum* Sleum., Malesia, Temple, 1975 / *Rhododendron maximum* L., N. America / *Pieris floribunda* (Pursh) Benth. and Hook., E.N. America, Lems, 1962.

Euphorbiaceae:
[H] *Croton hirtus* L'Hérit., Zaire / +*Euphorbia aphylla* Brouss., Canary Islands / *Euphorbia dendroides* L., Mediterranean, Meusel, 1970 / *Euphorbia emirnensis* Bak., Madagascar, Cremers, 1976 / *Euphorbia intisy* Drake, Madagascar, Cre-

MERS, 1976 / +*Euphorbia kraussiana* Bernh., S. Africa / **Euphorbia leucocephala* Lotsy, Trop. America / **Euphorbia mellifera* Ait., Canary Islands / +*Euphorbia obtusifolia* Poir. ssp. *regis-jubae*, Canary Islands / **Euphorbia stricta* Boiss., Persia / *Jatropha curcas* L., Trop. America, MÉDARD, 1973 / *Jatropha gossypiifolia* L., Trop. America / *Manihot esculenta* Crantz, "cassava", Trop. America / *Manihot glaziovii* Muell.-Arg., "ceara rubber", Trop. America / *Ricinus communis* L., "castor-oil plant", pantropical, in cultivation.

Guttiferae:
Montrouziera sphaeroides Planch., New Caledonia, VEILLON, 1976 / *Montrouziera verticillata* Planch., New Caledonia, VEILLON, 1976.

Labiatae:
[H] +*Ocimum micranthum* Willd., Martinique / *Perriereastrum oreophilum* Guill., Madagascar.

Lecythidaceae:
Barringtonia edulis Seem., New Guinea, F. HALLÉ, 1974.

Leguminosae – Caesalpinioideae:
**Schizolobium excelsum* Vog., Brazil, commonly cultivated.

Leguminosae – Papilionoideae:
Laburnum anagyroides Medic., Europe.

Loganiaceae:
Anthocleista djalonensis A. Chev., W. Africa, LEEUWENBERG, 1961 / *Anthocleista liebrechtsiana* De Wild. and Dur., C. Africa, LEEUWENBERG, 1961 / *Anthocleista nobilis* G. Don, W. Africa, LEEUWENBERG, 1961 / *Anthocleista procera* Lepf., W. Africa, LEEUWENBERG, 1961 / *Anthocleista vogelii* Planch., Trop. Africa, LEEUWENBERG, 1961 / [H] *Spigelia anthelmia* L., Congo.

Loranthaceae:
Viscum album L., Europe, LEGAY, 1971.

Melastomaceae:
Amphorocalyx albus Jum. and Per., Madagascar / *Bellucia cacatin* (Aufl.) Sagot, French Guiana / *Macrocentrum* sp., French Guiana, OLDEMAN, 1968 / *Miconia plukenetii* Naud., French Guiana.

Myrsinaceae:
Tapeinosperma psaladense Mez, New Caledonia, VEILLON, 1976.

Nyctaginaceae:
Pisonia grandis R.Br., Marquesas.

Ochnaceae:
Schuurmansia heningsii K. Schum., New Guinea, F. HALLÉ, 1974.

Phytolaccaceae:
[H] *Phytolacca decandra* L., N. America, introduced in Europe / [H] *Rivina* sp., (F. Hallé 1882), Kisantu, Zaire.

Pittosporaceae:
Pittosporum pronyense Guill., New Caledonia, VEILLON, 1976.

Polygalaceae:
[H] *Polygala peplis* H. Bn. var *boinensis* H. Perrier, Madagascar.

Proteaceae:
Banksia dentata L. f., New Guinea / +*Protea madiensis* Engl., Trop. Africa.

Rhamnaceae:
**Phylica ericoides* L., S. Africa.

Rubiaceae:
Cephaëlis tomentosa Vahl (Fig. 29H), Guianas / *Psychotria bracteata* DC., French Guiana / *Psychotria nervosa* Sw., W. Indies / *Psychotria sulzneri* Sm., W. Indies.

Rutaceae:
Dictyoloma sp., (F. Hallé 2354), Brazil / [H] *Monnieria trifolia* L., French Guiana.

Sapindaceae:
Pseudima frutescens Radlk., Guianas / *Toulicia guianensis* Aubl., French Guiana / *Tina striata* Radlk., Madagascar.

Simaroubaceae:
+*Quassia africana* (Baill.) Baill., Gabon.

Solanaceae:
[H] *Capsicum frutescens* L., "bird chillies", Trop. America, common in cultivation / *Cyphomandra abutiloides* Grisch., Peru / *Solanum atropurpureum* Schrank, Brazil / *Solanum aviculare* Forst., Australasia / *Solanum bahamense* L., W. Indies / *Solanum erianthum* D. Don, Pantropical.

Thymeleaceae:
[H] *Gnidia bakeri* Gilg., Madagascar.

Tiliaceae:
Entelea arborescens R. Br., New Zealand / [H] *Triumfetta cordifolia* A. Rich, Trop. America.

Verbenaceae:
[H] *Stachytarpheta urticifolia* Sim., Pantropical as a weed, JEANNODA, 1977.

Koriba's Model

Definition. The architecture is modular, each axis orthotropic and branching three-dimensionally to produce a series of initially equivalent modules but subsequently one of these becomes erect and dominant, functioning as a relay axis which constitutes one unit of a sympodially formed trunk, the other modules remaining as branches. Inflorescences are terminal, branching is correlated with flowering or in young sterile stages with abortion of the apex.

In its initial growth this architecture is identical to that of trees in Leeuwenberg's model but is subsequently distinguished by late specialization of modules formed as a tier of relay axes. One of these becomes more vigorous and stands vertical, overtopping the others. This dominant module forms a trunk unit and repeats the branching at a higher level, whereas the overtopped axes, which also repeat the pattern of growth, remain subordinated as the first elements of an orthotropic branch complex. We have commented on the restriction that the architecture in Leeuwenberg's model imposes on the development of tall trees, except by the production of very long modules. This deficiency is overcome in Koriba's model and one finds many large forest trees which conform to this model. The close similarity between Leeuwenberg's and Koriba's models is shown by the frequency of both of them in some families, notably Apocynaceae and Euphorbiaceae.

The model is dedicated to Professor KWAN KORIBA, interim director of the Botanic Gardens, Singapore, during World War II. His study of tropical trees is informative and his description of *Sapium discolor* (Euphorbiaceae, KORIBA, 1958, p. 19) was the first which recognized this mode of growth.

Example. The model is here illustrated by *Himatanthus articulatus* (Apocynaceae), common as a treelet to a height of about 12 m in secondary vegetation in the Guianas (Fig. 31 A–D). Modules are orthotropic and in the adult state hapaxanthic, producing a rather inconspicuous, essentially paniculate inflorescence with few branches, the axis narrowing abruptly at the level of flowering. Younger modules are sterile, growth being terminated by abortion of the apex. Each module has spirally arranged leaves (phyllotaxis 5/13), each of which subtends a dormant bud enclosed by a pocket in the leaf base itself filled with resinous material. Leaves on the unbranched seedling axes (Fig. 31 A) are oblanceolate and about 40 cm long; on subsequent axes they are appreciably shorter, in keeping with Corner's rule. At the level of apical abortion a tier of five to seven branches is developed (Fig. 31 B), each branch originating by syllepsis from the axil of a distal leaf. The branches are all identical. Subsequently one vigorous branch becomes prominent (Fig. 31 C) by its erect orientation and it overtops the other branches, which remain as a tier of less vigorous shoots, although they repeat the parental construction but on a limited scale. The erect vigorous shoot forms the next relay axis of the trunk;

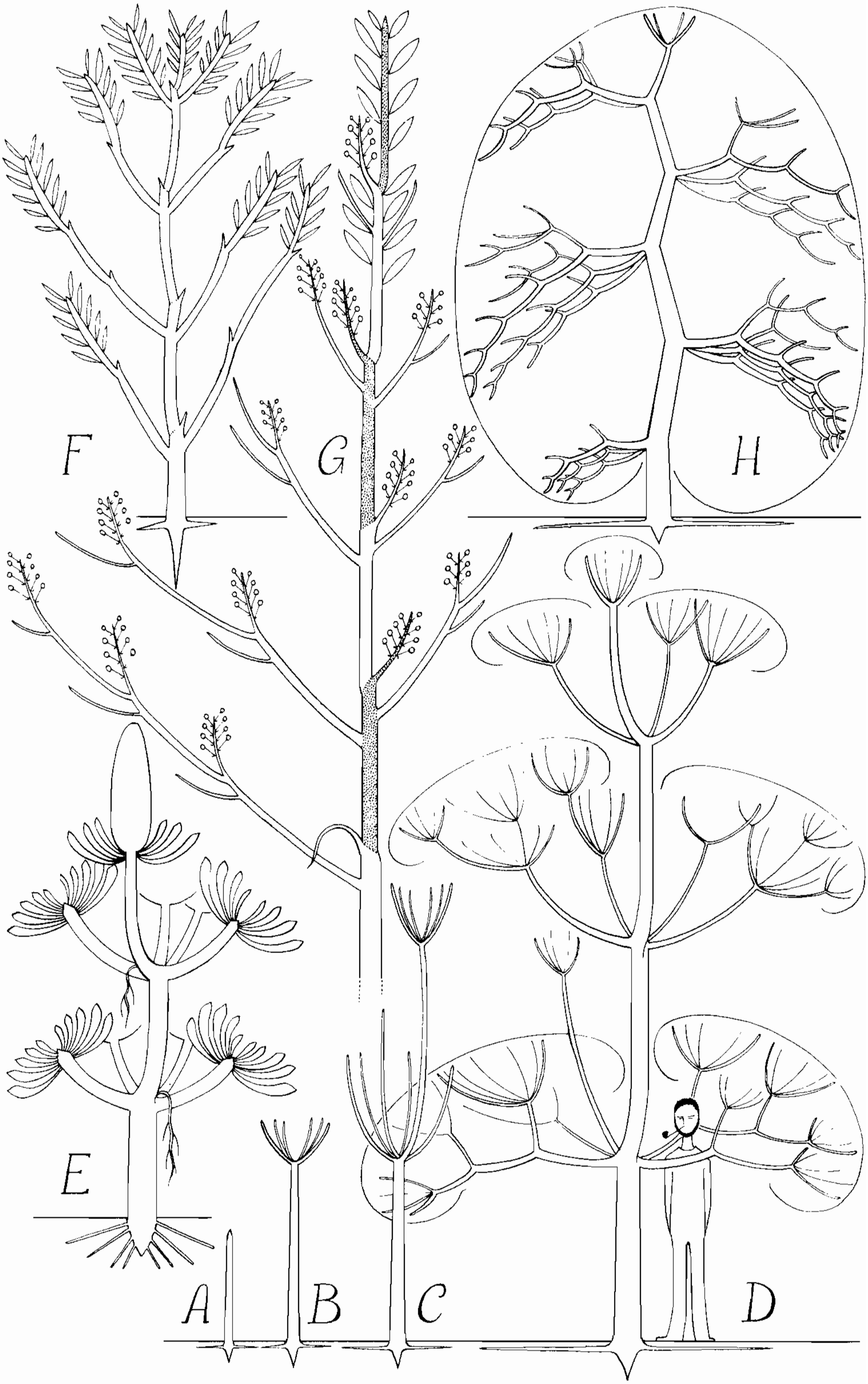
Fig. 31 A–H. Koriba's model. ▷

A–D Himatanthus articulatus (Vahl) Woods. (Apocynaceae, French Guiana, *R.A.A. Oldeman 1880*). Four stages in the growth of the tree, with the adult reaching a height of 12 m.
A Unbranched sapling; *B* equal branching below aborted apical meristem; *C* establishment of dominance of one branch as axis of next module; *D* adult tree with sympodial trunk and tiers of branches.

E Senecio erici-rosenii R.F. and T.C.E. Fr. (Compositae, East Africa). A tree *Senecio*, endemic to the Virungas mountains and Ruwenzori between 2600 m and 4000 m (MABBERLEY, 1973).

F and *G Suriana maritima* L. (Simaroubaceae, Moorea, Society Islands, Polynesia, but pantropical). *F* Young specimen, 30 cm high, still vegetative; *G* adult flowering specimen, a small tree 6 m high, growing on surelevated coral reefs. Each module is less than 5 cm long and bears three further modules, the upper one alone growing erect.

H Ochrosia coccinea Miq. (Apocynaceae, New Guinea, from the Botanic Garden of Bogor, Indonesia). A small tree, 5 m high, each trunk module is 50 cm long


F
G
H
E
A
B
C
D

this process is repeated at successive levels (Fig. 31 D), but in association with flowering, in subsequent modules.

Other Examples. The illustrations in Figure 31 E–H represent further examples of small trees which conform to Koriba's model. The genus *Senecio* (Compositae) includes an example in *S. erici-rosenii* (Fig. 31 E), endemic to certain parts of the East African mountains at altitudes between 2600 and 4000 m (MABBERLEY, 1973). As in other tree *Senecios* the axes are stout and little-branched; the inflorescences are particularly conspicuous. In a very different ecotype the model is exemplified by *Suriana maritima* (Simaroubaceae – or Surianaceae), a common coastal shrub of sand-dunes and atolls in the tropics, scarcely exceeding 4 m in the tallest specimens, but dense-crowned and spreading. Figure 32 F illustrates the construction of the plant, which has two to three relay axes at each level of branching. Figure 31 G is a diagram of a flowering specimen with the individual trunk units distinguished by hatching. These are very short, scarcely exceeding 5 cm. Branching is by syllepsis and each inflorescence of conspicuous yellow flowers appears to be leaf-opposed. Histological details of branch construction still need to be worked out.

Ochrosia coccinea (Apocynaceae, New Guinea) represents this model in the forest (Fig. 31 H). It grows to a height of about 5 m, with each trunk module about 50 cm long.

As an example of a large tree conforming to the model we cite *Hura crepitans* ("sand-box tree", Euphorbiaceae) of tropical America, but often cultivated. In the Guianese rain-forest specimens may be more than 50 m high with a basal trunk diameter up to 3 m. The tree may be recognized by its cordate glandular leaves and prominent stem spines; the latex is poisonous. The plant grown from seed in 1972 in the greenhouses at Harvard Forest and cut down when it had exceeded the space available for it, illustrates the sequence of events in development of the model and provided information about the mechanism of secondary erection of axes. This seedling reached a height of 1 m in ten months whereupon it flowered, producing three equal branches, two of which flowered again within six months, at which time the future trunk module was evident by its more erect position. After two more years it had produced five orders of branches, with the trunk axes now clearly defined. Cut down at the age of $3^1/_2$ years its basal diameter was 11.5 cm, the total height 3 m. Events at the lowest level of branching which are summarized in Table 8 and illustrated in Figure 32 show the way in which the trunk differentiates.

Figure 32 A shows the characteristic method of bifurcation, with three sylleptic branches arising below a terminal inflorescence, whose scar is still visible. Figure 32 B shows the lowest branch tier, which originated exactly as in the previous figure, but in which one branch has become erected as the next unit of the trunk. This is the tier referred to in Table 8. Erection of this trunk axis is the result of pronounced development of tension wood on the upper side of the branch (Fig. 32 C) compared with its limited development on the lower side (Fig. 32 D).

Variations. There is variation in the number of axes which are developed at each level of branching. It is fixed at three in *Combretodendron* and *Ochroma,* but four in *Alstonia macrophylla,* two to six in *Cochlospermum vitifolium,* five to seven in *Himatanthus* and *Octolobus heteromerus.* Only one of these becomes the trunk axis. There is also considerable variation in the level at which the axes become reproductive, even though this may be preceded by branching, a situation com-

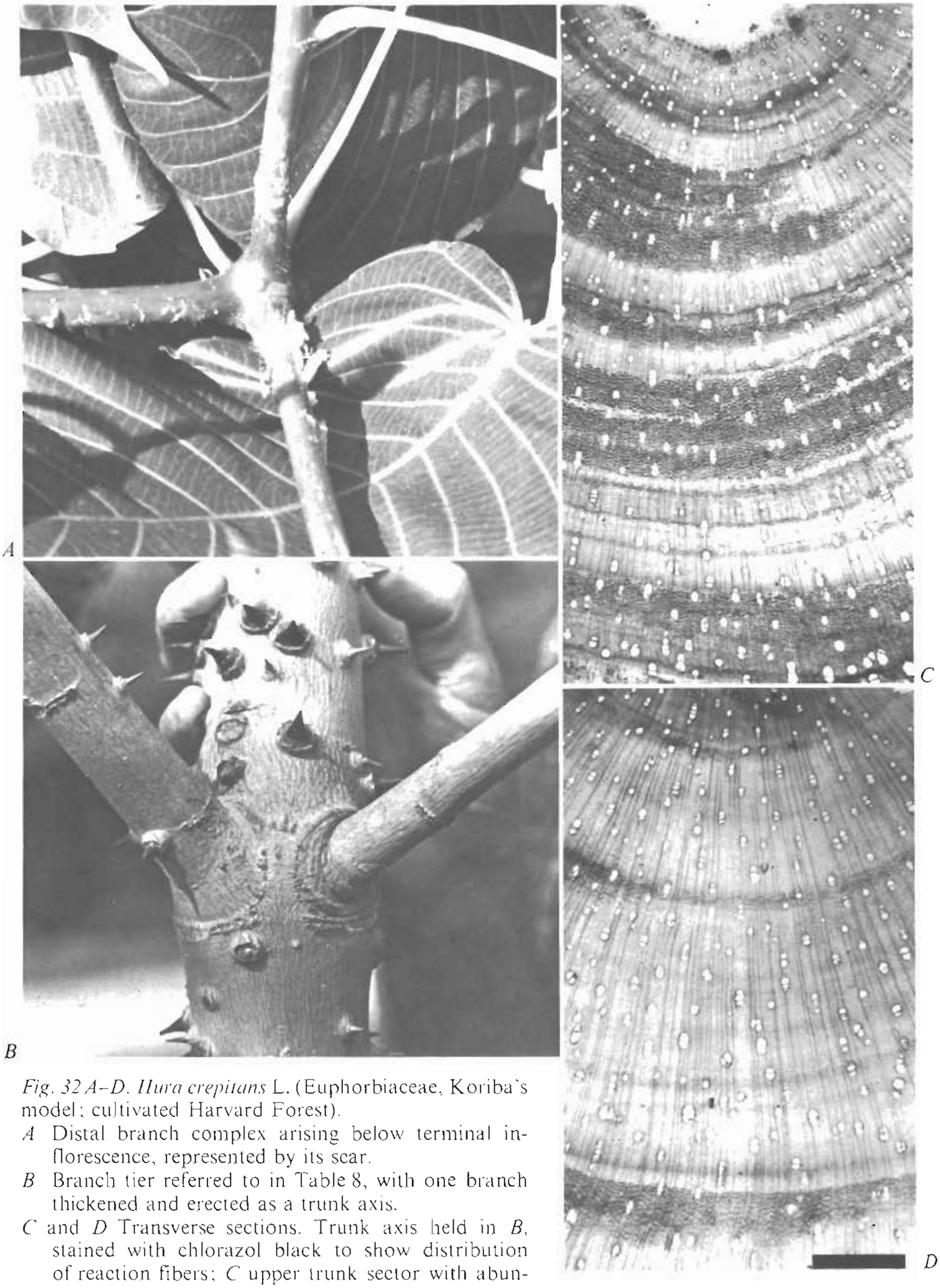


Fig. 32 A–D. Hura crepitans L. (Euphorbiaceae, Koriba's model; cultivated Harvard Forest).

- *A* Distal branch complex arising below terminal inflorescence, represented by its scar.
- *B* Branch tier referred to in Table 8, with one branch thickened and erected as a trunk axis.
- *C* and *D* Transverse sections. Trunk axis held in *B*, stained with chlorazol black to show distribution of reaction fibers; *C* upper trunk sector with abundant reaction wood; *D* lower trunk section with little reaction wood. Scale in *D* = 2 mm

Table 8. Hura crepitans. Changes in dimensions at lowest level of branching (seedlings germinated 24.II.72)

	III/73		VIII/75	
Branch number	Branch diameter (mm)	Branch angle (to vertical)	Branch diameter (mm)	Branch angle (to vertical)
1	15	70°	22	40°
2	15	70°	55	25°
3	15	70°	17	70°

parable to that in Leeuwenberg's model. In several species the epicotyledonary axis itself is sexual, producing a terminal inflorescence as in *Hura*; *Ochroma* is similar except that the flowers commonly abort or may be reduced to one. Early modules may otherwise branch in association with necrosis of the terminal bud, as in *Lophira alata* and *Suriana*. In other species the apex aborts abruptly by parenchymatization as in the species of *Combretodendron, Alstonia,* and *Himatanthus* listed below.

The secondary changes in branch orientation which are an important feature of this model and lead to the development of a vertical trunk, deserve detailed study. It is evident that reorientation involves development of tension wood (Fig. 32). The difference in orientation between closely inserted modules implies a finely regulated hormonal balance.

Strategy of the Model. The array of biotopes occupied by examples of this model does not permit much generalization about their strategy. Smaller species like *Himatanthus articulatus, Croton* spp., *Cochlospermum vitifolium* occupy secondary vegetation and riverbanks in tropical America.

Suriana maritima and *Daphnopsis caribaea,* distinguished by the smallness of their modules and pronounced sylleptic development of their sympodia, which leads to almost continuous flowering, are pioneer species in open or disturbed habitats with a population-orientated ecological strategy.

However, species which are more evidently individual-centered ecologically are represented by the examples common in rain-forest, especially those large trees with a long life span we have commented upon. Smaller species of the forest understorey have been mentioned (e.g., *Ochrosia*) while at an intermediate stature we have *Aparisthmium cordatum* (Euphorbiaceae, Guianas) reaching a height of 25 m, developing buttresses when "adult" and reiterating. The model is not unknown in temperate trees; *Ailanthus altissima* and *Catalpa bignonioides,* which are commonly cultivated, provide good examples.

Taxonomic List of Examples (Koriba's Model)

DICOTYLEDONS

Apocynaceae:
Alstonia macrophylla Wall., Malaysia, Prévost, 1967 / **Cerbera manghas* L., Malaysia / *Himatanthus articulatus* (Vahl) Woods. (Fig. 31 A–D), French Guiana / *Himatanthus bracteatus* (DC.) Woods., Guianas / *Malouetia tamaquarina* (Aubl.) DC., French Guiana, Oldeman, 1972 / *Ochrosia balansae* (Guill.) Baill., New Caledonia, Veillon, 1976 / **Ochrosia coccinea* Miq. (Fig. 31 H), New Caledonia.

Bignoniaceae:
Catalpa bignonioides Walt., N. America, cultivated in Europe / *Catalpa punctata* Griseb., Bahamas, Cuba / **Tabebuia donnel-smithii* J.N. Rose, C. America.

Bombacaceae:
Ochroma lagopus Swartz, "balsa", Trop. America.

Cochlospermaceae:
**Cochlospermum vitifolium* (Willd.) Spreng., Trop. America.

Compositae:
Senecio erici-rosenii R.F. and T.C.E.Fr. (Fig. 31 E), E. Africa. MABBERLEY, 1973.
Didiereaceae:
+*Alluaudia comosa* Drake, Madagascar.
Euphorbiaceae:
**Acalypha grandis* Benth., Celebes / *Aparisthmium cordatum* Baill., French Guiana / *Euphorbia plagiantha* Drake, Madagascar, CREMERS, 1976 / *Grossera vignei* Hoyle, W. Africa, F. HALLÉ, 1971 / **Homalanthus populneus* Pax, Trop. Asia / *Hura crepitans* L. (Fig. 32), "sand-box tree", Trop. America / +*Mareya brevipes* Pax, Gabon / *Sapium discolor* Muell.-Arg., S. China to Malaysia, KORIBA, 1958.
Lecythidaceae:
Combretodendron africanum (Welw.) Exell., Trop. Africa.
Monimiaceae:
Kibara sp., Bulolo, New Guinea.
Ochnaceae:
Lophira alata Banks ex Gaertn. f., Trop. Africa.
Phytolaccaceae:
**Phytolacca dioica* L., S. America.
Rubiaceae:
Cephaëlis sp., Congo.
Sapindaceae:
+*Dodonea madagascariensis* Radlk., Madagascar.
Simaroubaceae:
Ailanthus altissima (Mill.) Swingle, "tree of heaven", Japan / *Suriana maritima* L. (Fig. 31 F, G), Pantropical.
Sterculiaceae:
Octolobus cf. *heteromerus* K. Schum., (N. Hallé 405), Gabon.
Thymeleaceae:
Daphnopsis caribaea Griseb., Martinique.
Winteraceae:
Zygogynum sp., New Caledonia. VEILLON, 1976.

Prévost's Model

Definition. The architecture is modular, with trees developing two distinct types of modules forming respectively trunk and branch which are clearly distinguishable from their inception. Both are essentially orthotropic with spirally arranged leaves, but branch modules originate by syllepsis in a restricted subapical region of the trunk module. Successive trunk modules are proleptic and subdistal, i.e., below the branch tier. Branches are plagiotropic by substitution. Determinate growth of modules is by hapaxanthy, but the inflorescence, especially on trunk modules, is often vestigial or aborted.

This model was described in some detail in an earlier publication (H.O., 1970, pp. 49–57), since which time little new information has been added. The model resembles that of Koriba, but is readily distinguished by the presence of two kinds of modules, differentiated from the moment of their initiation and precisely located in the architecture. A close resemblance is also seen to Nozeran's model, in which plagiotropy of branches is, however, inherent, with distichous phyllotaxis. There is also an approach to Mangenot's model in some species.

The model is named after MARIE-FRANÇOISE PRÉVOST (O.R.S.T.O.M., Ivory Coast) who has provided detailed descriptions of architecture in African Apocynaceae, some of which exhibit this model (PRÉVOST, 1967).

Example. The model is exemplified by many species of *Cordia* (Ehretiaceae – or Boraginaceae) of the American tropics (see Fig. 33), and we have selected *Cordia nodosa* (Fig. 34 Ba), a small tree to a height of 10 m, common in the undergrowth of the Guianese forest, to illustrate it in detail. The specific name refers to the swollen articulations which delimit each plagiotropic module and which are characteristically ant-inhabited. Leaves are spirally arranged throughout, but those on the branch modules are in pseudowhorls of three or four, dorsiventrality being expressed by the small leaves on the upper side of the branch. Each trunk module arises proleptically from the axil of a subdistal leaf on the previous trunk module. This grows to a height of about


A

B

◁ *Fig. 33A and B.* Prévost's model.

A *Cordia tetrandra* Aubl. (Ehretiaceae), Comté River, French Guiana. Only the uppermost tier persists, the joints in the trunk which mark the limits of sympodial units are very clear.

B *Cordia exaltata* Aubl. (Ehretiaceae), Saint Laurent, French Guiana. Distal tier of branches from above, with the aborted apex of the last trunk module (center)

50 cm before its apex is transformed into a cymose inflorescence, which may be vestigial. This trunk articulation is not swollen and never becomes ant-inhabited. On each vigorous trunk module there is a gradual increase in leaf size, with the distal series largest and forming a pseudowhorl (usually of three). The sympodial trunk is made up of a linear series of such modules (Fig. 34Ba). A branch tier is formed immediately below the differentiated apex of the trunk module by (usually three) branches, each of which originates by syllepsis in the axil of a distal trunk leaf. These branches are plagiotropic by substitution, with pronounced dorsiventrality. Each bears an initial pseudowhorl of three leaves and an ultimate pseudowhorl of four leaves below the terminal inflorescence (Fig. 34Bb). The end of the module is swollen and hollow, the cavity becoming occupied by ants which apparently gain entry by a hole in the axil of the large, lower leaf of the pseudowhorl, which never develops an axillary bud (Fig. 34Bc). The missing bud may, in fact, be represented by the invagination by which the joint becomes hollow. The cavity is lined by an epidermis covered by the same kind of stiff hairs which form the indumentum of the leaf blade and stem.

Branching of the plagiotropic system is continued by further modules, repeating the parent structure; these branches originate in pairs by syllepsis, each from the axil of a lateral leaf of the terminal pseudowhorl of the previous module. This pattern is illustrated in surface view in Figure 34Bb which shows the whole of one pair of modules and part of both the previous and subsequent modules. This pattern is quite regular, leading to the formation of a tier of regularly forked branches, as illustrated in Figure 34Bd. There is some variation in the position and degree of development of inflorescences on the plagiotropic shoots. A second inflorescence may develop late, apparently from a meristem originating in the axil of a scale-leaf representing a fifth leaf of the terminal pseudowhorl. Branches associated with the first pseudowhorl of leaves have been seen and have developed inflorescences.

The frequency of this model in *Cordia* is shown by two other illustrations of different species (Fig. 33A, B).

Other Examples and Variations. In the Old World tropics the apocynaceous genus *Alstonia* (Africa to Australia) forms a parallel series of species which are identical architecturally with *Cordia*, but more often produce tall trees. *Alstonia boonei* (tropical Africa) described by PRÉVOST (1967) and illustrated in detail by H.O. (1970, pp. 50–53) forms a tree 40 m high, with a basal trunk diameter of 2 m. *Alstonia scholaris* of Malaya, as described by CORNER (1952) is even larger. In such large trees it is difficult to envisage so massive a trunk formed by sympodial growth, but secondary wood formation obscures the original articulations on the trunk which are at first so evident (see H.O., 1970, p. 53).

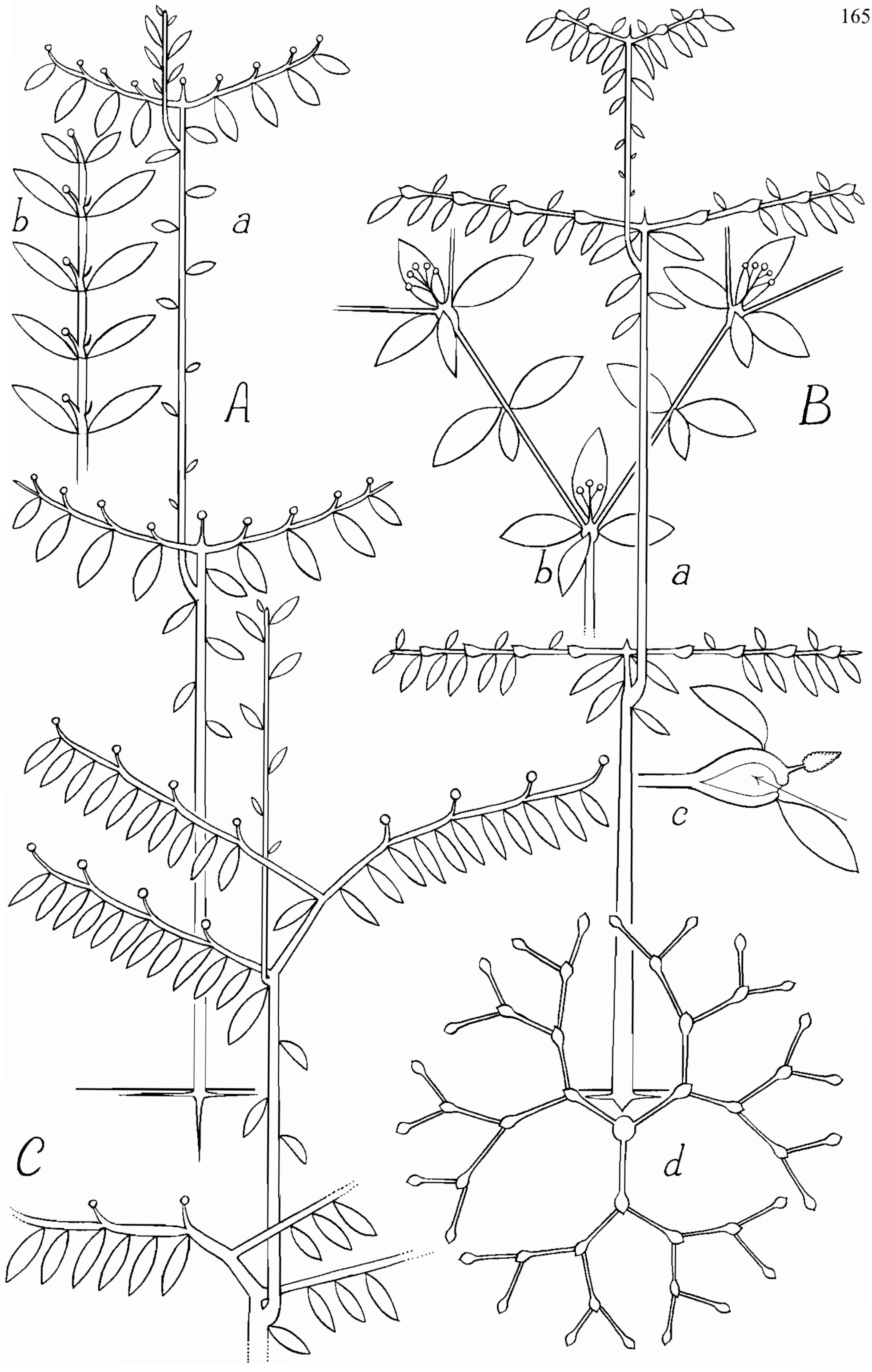
In other examples of this model, the branch modules may be so specialized that their fundamentally orthotropic character is completely lost. This is known in *Excoecaria bicolor* (Euphorbiaceae, Malaysia). The sympodial trunk structure is shown in Figure 34Aa, with the very evident transition in leaf size along each trunk module. Plagiotropic branch modules are specialized such that each module includes only three leaves (Fig. 34Ab); the first two leaves are normal assimilating foliage leaves, the last leaf below the terminal inflorescence is a scale leaf, subtending the next module. These branches form linear sympodia. An African example of this model, provided by *Lasianthera africana* (Icacinaceae), a small rain-forest tree, is of interest because each trunk module has a distal tendency to become plagiotropic before flowering (Fig. 34C). Here the trunk module contributes appreciably to the uppermost branch of each associated tier. This condition is carried further in the species of *Piper* (Piperaceae) from the Guianese rain-forest described by H.O. (1970, p. 55).

Fig. 34A–C. Prévost's model. ▷

A *Excoecaria bicolor* Hassak (Euphorbiaceae, Malaysia; from the Botanic Garden Frère Gillet, at Kisantu, Zaïre, *F. Hallé 1880*). *a* Sympodial structure of the trunk which bears spirally-arranged leaves; *b* sympodial structure of the plagiotropic branch, seen from above, showing apical inflorescences.

B *Cordia nodosa* Lam. (Ehretiaceae – or Boraginaceae, French Guiana, *R.A.A. Oldeman 2128*). A small tree, less than 10 m high, of the forest undergrowth; *a* general architecture; *b* two branch modules, seen from above, showing apical inflorescences. Each branch module is about 60 cm long and regularly bears seven foliage leaves, a pseudowhorl of three followed by a pseudowhorl of four; *c* the ant nest at the apex of the branch module, just below the apical inflorescence; *d* one entire whorl of branches seen from above.

C *Lasianthera africana* P. Beauv. (Icacinaceae, Equatorial Africa). A small rain-forest tree; each module of the trunk bends at the top and becomes plagiotropic before its meristem becomes a terminal inflorescence


b
a
A
B
b
a
c
C
d

Here the last two internodes of each trunk module form the first two internodes of one of the associated branch modules. The next relay axis originates from the second node under the (flowering) apex of the previous trunk module. Consequently, the sympodial nature of the trunk is almost obscured. This tendency to change towards distal plagiotropy takes us towards Mangenot's model and mixed axes in general.

Funtumia elastica (Apocynaceae, tropical Africa) is unusual in that the trunk module originates from the same leaf axil as one of the branch modules (H.O., 1970, pp. 57–58). The same occurs in *Citronella.*

A final example will show the close relation between Leeuwenberg's and Prévost's models. *Cordia abyssinica* (East Africa) exemplifies the former in its orthotropic three-dimensional branching below terminal inflorescences. Late development of orthotropic axes occurs below the level of this forking, but these shoots are always feeble and contribute little to the architecture – they may even be regarded as examples of reiteration. However, they occupy the precise position of the trunk module in *C. nodosa* and other species. *Cordia abyssinica* in this respect has a place in the architectural continuum intermediate between two models (H.O., 1970, their Fig. 30).

From these examples we can see that the uniformity of the model is somewhat lost because modules do not always terminate in a developed inflorescence, plagiotropy is often very pronounced in branch modules and orthotropy is not always strictly maintained in trunk modules.

Strategy of the Model. Most known examples of this model are forest species, ranging from tall trees as in species of *Alstonia* and *Cordia,* to treelets like *Lasianthera* and *Thomandersia.* The very specialized growth pattern in this limited biotope, typical of Prévost's model, lends to it a pronounced aptitude for a *K* strategy, with high probability of individual survival. Its method of flowering such that seeds in small quantities are periodically released each time a series of branch modules has flowered, maintains a steady supply of individuals, but is scarcely appropriate for biotope saturation (as in *r* strategy). However, examples from open habitats, e.g., *Euphorbia pulcherrima,* the commonly cultivated "poinsettia", are known.

Taxonomic List of Examples (Prévost's Model)

Acanthaceae:
Thomandersia anachoreta Heine, Ivory Coast, Sell, 1969 / *Thomandersia butayei* De Wild., C. Africa / *Thomandersia congolana* De Wild. and Dur., C. Africa.

Apocynaceae:
Alstonia angustiloba Miq., Malaysia, Corner, 1952 / *Alstonia boonei* De Wild., Trop. Africa, Prévost, 1967 / *Alstonia constricta* Muell., Australia, Prévost, 1967) / *Alstonia scholaris* (L.) R.Br., Malaysia, Corner, 1952 / *Alstonia spathulata* Bl., Malaysia, Corner, 1952 / *Carissa edulis* Vahl, Egypt, commonly cultivated / *Funtumia elastica* (Preuss.) Stapf. (Fig. 38A), Trop. Africa / **Mascarenhasia arborescens* DC., Madagascar / **Rouppelina boivini* H.Br., Madagascar.

Ehretiaceae (or Boraginaceae):
**Cordia abyssinica* R.Br., Ethiopia / *Cordia* cf. *collococca* L., Martinique/*Cordia exaltata* Aubl. (Fig. 33B), French Guiana / *Cordia laevifrons* Johnst., French Guiana / *Cordia* cf. *nervosa* Lam., Guianas / *Cordia tetrandra* Aubl. (Fig. 33A), Guianas.

Euphorbiaceae:
**Euphorbia pulcherrima* Auct., "poinsettia", Trop. America / **Excoecaria bicolor* Hassak (Fig. 34A), Malaysia.

Icacinaceae:
Lasianthera africana P. Beauv. (Fig. 34C), C. Africa.

Fagerlind's Model

Definition. The architecture is determined by a monopodial, orthotropic and episodically growing trunk which produces tiers of modular branches, each branch sympodial and plagiotropic by apposition, with spiral or decussate (not distichous) phyllotaxis. Branch modules are usually hapaxanthic. This is the first example among the models we have so far described of a tree with differentiated axes which is monopodial in the growth of its trunk (Fig. 35D). This provides the most distinctive feature in comparison with previously described models. The situation is summarized diagrammatically in Figure 35.

The model is dedicated appropriately to Folke Fagerlind who has contributed to its understanding in his study of the genus *Randia* (FAGERLIND, 1943).

Example. Fagraea crenulata (Loganiaceae, Malaysia) is a moderate-sized tree (to a height of 20 m, Figs. 36A and 37) which illustrates the architecture well. A young tree is shown in Figure 36 B at the time the terminal bud of the epicotyledonary axis has reached its initial resting phase. During this first phase of growth, it has produced its first tier of branches. This is continued in subsequent increments so that a regular series of branch tiers is developed, each tier apparently reflecting one cycle of rhythmic growth. Branching is consistently monopodial. Leaf arrangement on both trunk

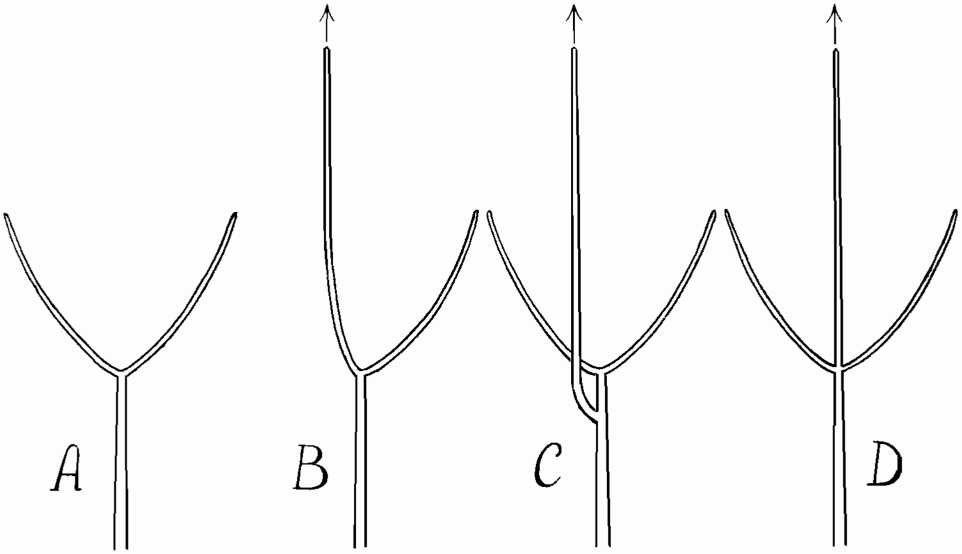


Fig. 35 A D. Different methods of height growth in tropical trees. Diagram to show contrasted trunk formation in four models.

A Leeuwenberg's model (sympodial, modular); trunk formed by first module.

B Koriba's model (sympodial, modular); trunk formed by secondary erection of one module.

C Prévost's model (sympodial, twice modular); trunk formed by successive trunk modules each with determinate growth, whereas branch modules are distinct.

D Fagerlind's model (monopodial, nonmodular); trunk a monopodium, with indefinite growth of the trunk meristem and branch is spiral but leaf length on the trunk is almost twice that on the branches, emphasizing their degree of differentiation. Spines are developed on the lower part of the trunk and the lower side of the branches.

Plagiotropy of the branch tiers is established early by apposition growth which also results in the multiplication of branches by forking below the evicted parent axis. Ultimately, however, each branch module is determinate by flowering, although, as suggested in Figure 36A, the sequence of flowering does not necessarily reflect the age of the module.

Other Examples. There is a considerable range in the extent to which other examples develop distinct tiers. *Hymenosporum flavum* (Pittosporaceae, Australia), is a slender tree reaching a height of 10 m which shows the pagoda habit well (Fig. 36C) and the branching in these tiers is very regular. By contrast in *Magnolia grandiflora* (Magnoliaceae, eastern North America), a small commonly cultivated tree to a height of 8 m, the tiers are obscured since they are little separated one from another and branches are oblique rather than horizontal. Its architecture is represented by Figure 36D although it is not obvious to a casual observer that this species has exactly the same architecture as the very well-structured *Hymenosporum*. In *Magnolia* the branch modules are, of course, terminated by a single large flower, rather than an inflorescence.

Variations. In the above examples the apical meristem clearly persists through one period of dormancy to the next and growth is strictly monopodial. This is not necessarily so in *Conohoria* (= Rinorea) *riana* (Violaceae) and several other species of the same genus in which an axis is developed which may be described as an "unstable monopodium" (OLDEMAN, 1974a).

Conohoria riana is a small tree of the Guianese forest undergrowth, scarcely reaching 5 m and distinguished by the pronounced articulations on the trunk which mark the insertion of each branch tier (Fig. 36Ea). Each joint marks a pseudowhorl of large leaves which is formed immediately below a woody plate of tissue. Usually three or four sylleptic branches, each from the axil of one of the large leaves, form the branch tier (Fig. 36Eb) below the plate, but a number of other resting buds are developed on top of the plate (Fig. 38C). The period of dormancy is long, but one of these buds may form the next trunk segment. It is, therefore, not easy to establish if it is the original terminal meristem which continues growth; strict monopodial development is not maintained, and the tendency to form a sympodial trunk in this

Fig. 36A–E. Fagerlind's model. ▷

A and *B* *Fagraea crenulata* Maingay ex C.B. Cl. (Loganiaceae, Malaysia). *A* Habit; a tree 20 m high with thorns on the trunk and lower side of branches, leaves on the trunk are larger than those on the plagiotropic, sympodial branches; *B* young specimen, less than 1 m high; the first tier of branches is already developed.

C *Hymenosporum flavum* F. Muell. (Pittosporaceae, Australia). A slender tree with a very pronounced "pagoda habit" (CORNER, 1952).

D *Magnolia grandiflora* L. (Magnoliaceae, North America). In this small tree, 5–10 m high, the upward inclination of the tiers, together with dense branching, conceals the "pagoda-habit", but otherwise the architecture is exactly the same as in *Hymenosporum*.

E *Conohoria riana* (Aubl.) Oldeman (Violaceae, Iracoubo, French Guiana, *R.A.A. Oldeman 2195*). A treelet of the rain-forest undergrowth 2–3 m high; *a* general architecture, the *arrow* indicates the level of possible sympodial branching (Fig. 38C) in this unstable monopodium; *b* a single tier of plagiotropic flowering branches, seen from above

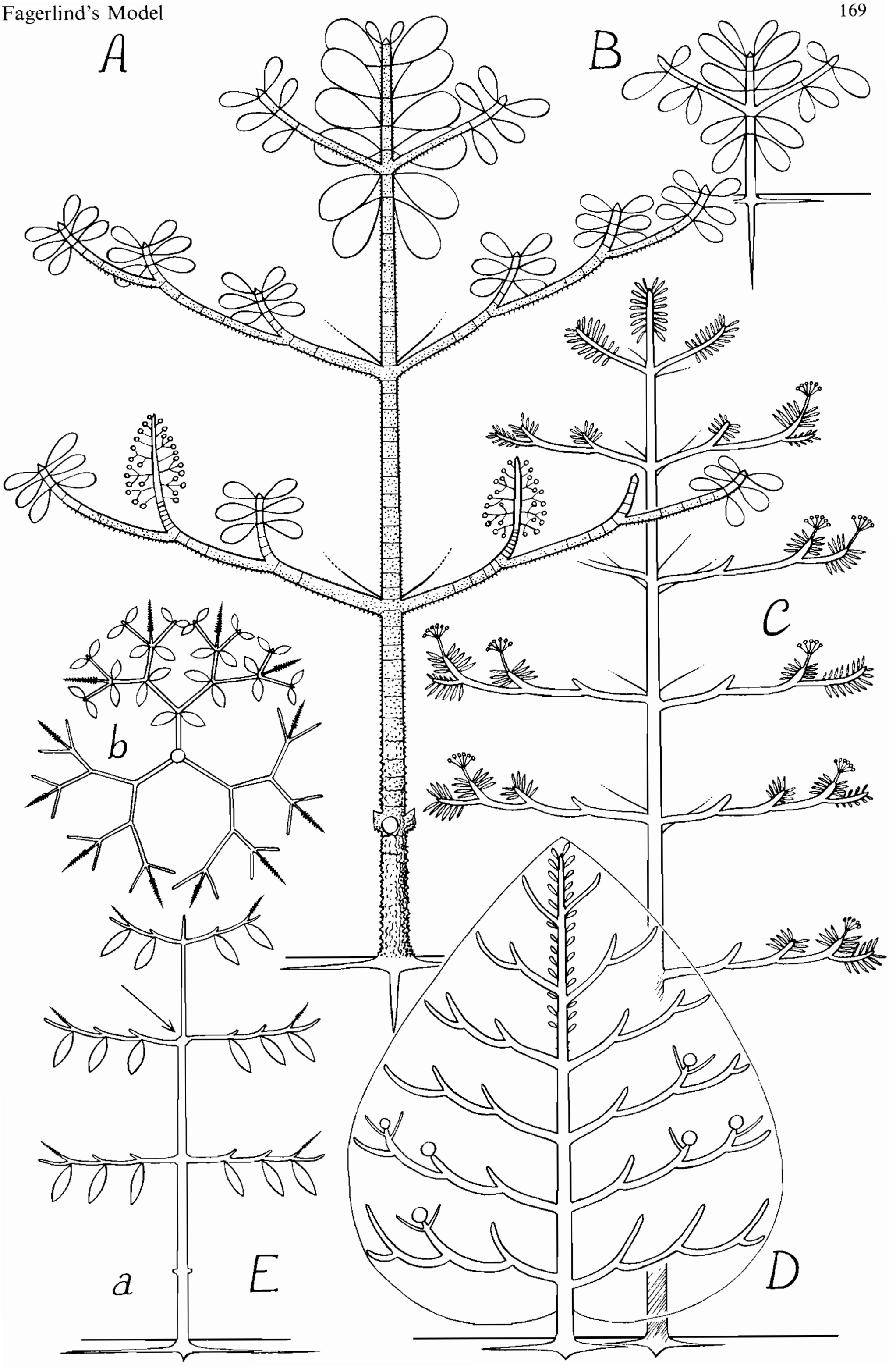

A
B
C
b
a
E
D

Fig. 37. Fagerlind's model, *Fagraea crenulata* Clarke (Loganiaceae), Campus of the University, Kuala Lumpur, Malaysia, a precise example of the "pagoda-habit"

species invites comparison with Prévost's, Koriba's, and Nozeran's models (Fig. 38). This species also indicates a degree of specialization of the branch modules, since each consists of one long internode which separates a basal pair of prophyll scales from a distal pair of foliage leaves (the phyllotaxis appears to be decussate).

Variation in the number of leaves developed by each branch module is considerable in this model. In *Duroia, Fagraea,* and *Hymenosporum* the modules are long, leaves are numerous but inconstant in number. In *Rothmannia longiflora,* modules are only 10 cm long and bear three foliage leaves; two leaves is the usual number of *Conohoria,* but in *Quararibea guianensis* there is only one (H.O., 1970, p. 60). This variability is correlated somewhat with flower number, in *Quararibea* there is only a single terminal and rather conspicuous flower, biologically quite different from that of *Magnolia.* Otherwise the inflorescence is spicate, as in *Byrsonima* or *Conohoria,* but conspicuously capitulate in *Duroia.*

Lack of regularity in the branching pattern may provide the opportunity for the older parts of the branch to undergo several successive flowerings. This is shown in *Eriobotrya japonica* ("loquat", Rosaceae), native to Japan but commonly cultivated in the tropics and subtropics. After a module flowers, it may produce one or more short orthotropic modules which flower in turn, and so on.

A clearly expressed example of this architecture is seen in *Cornus alternifolius* (Cornaceae, eastern North America, Fig. 39A), which is unusual for the genus, as its name implies, in its spiral (not decussate) phyllotaxis. The rhythmic growth

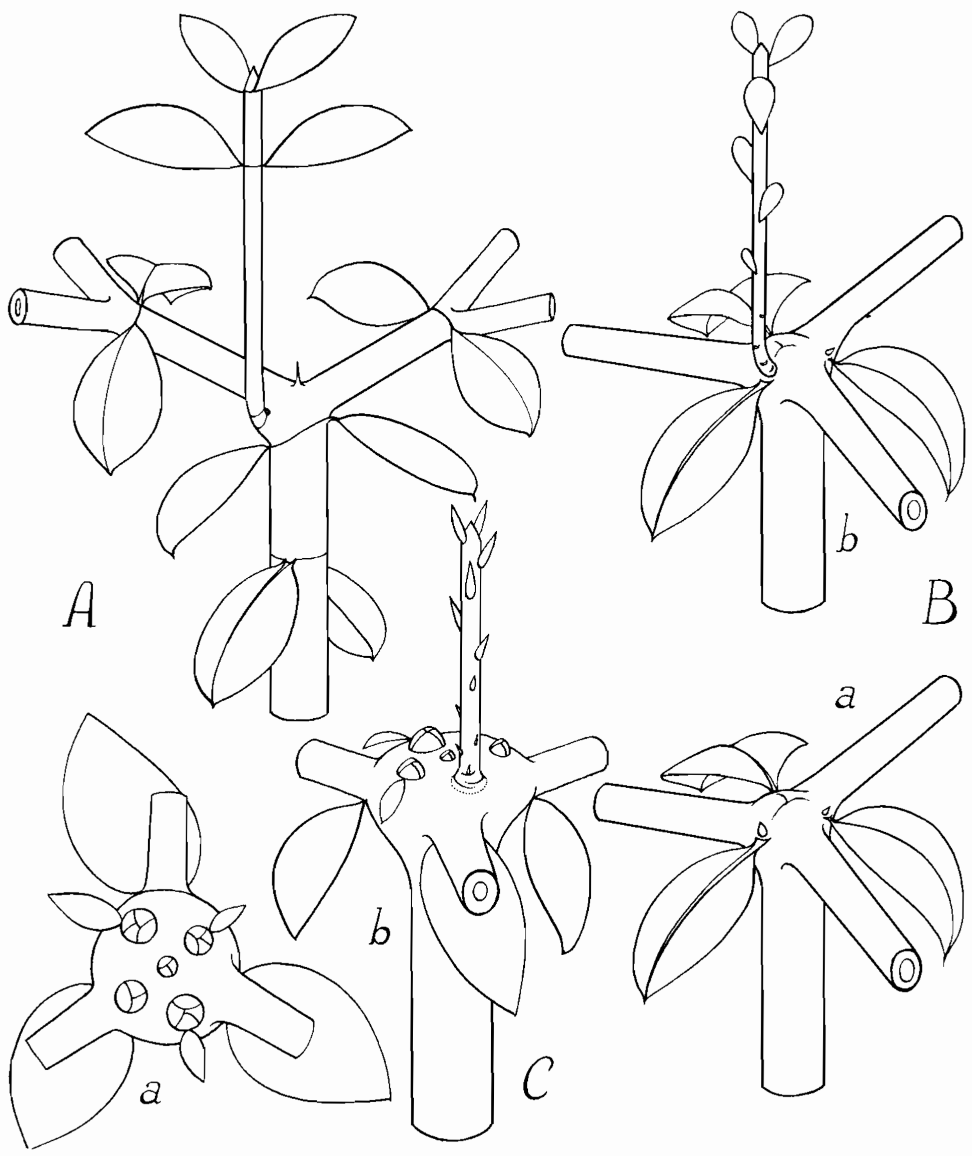


Fig. 38A–C. Methods of height growth in Prévost's, Nozeran's and Fagerlind's models.

- *A* *Funtumia elastica* (Apocynaceae – Prévost's model). Orthotropic trunk axis originating by prolepsis within same leaf axil as a sylleptic branch.
- *B* *Citronella suaveolens* (Icacinaceae – Nozeran's model). *a* Trunk module at resting stage with tier of plagiotropic sylleptic branches; *b* development of new orthotropic module, by prolepsis. In this species the axillary bud complex is horizontal.
- *C* *Conohoria* (Rinorea) *riana* (Violaceae – Fagerlind's model). *a* End of trunk axis from above, with resting buds subtended by reduced leaves; *b* side view with orthotropic module developing. This is an unstable monopodium because the previous terminal meristem may or may not survive or provide the renewal shoot

Fig. 39 A and B. Fagerlind's model, *Cornus alternifolius* L. (Cornaceae, eastern North America). *A* Small tree 4 m high in the forest understorey, showing the very pronounced branch tiers and sympodial branching of the trunk, which is an unstable monopodium, at the level of the last "adult" tier. *B* Detail of the terminal shoot showing development of a distal tier of branches by syllepsis. This shoot complex, which includes at least two orders of branches, is the result of the activity of the leader meristem during a single growing season

in the trunk of this small deciduous tree (to a height of 7 m) is obvious, with conspicuous bud-scale scars delimiting each seasonal (annual) growth increment, but the monopodium is unstable (Fig. 39A). A tier of branches is developed sylleptically, towards the end of the growing season, an unusual condition for a north temperate tree (Fig. 39B). Sympodial development by apposition is evident in plagiotropic branches, with up to four branch orders being established by syllepsis within a single growing season. Evicted terminal buds do not become sexual immediately but may grow for several seasons before they flower, and there is some tendency for continued development of an axis by substitution growth even after it has flowered. Growth in height is determined by the trunk, but this does not necessarily extend annually so that low, flat-topped trees are common, contrasting strikingly with most other temperate trees.

In Fagerlind's model the position of the tier of branches in relation to the level of development of the resting bud is variable. Usually branch development immediately precedes the onset of dormancy in the terminal meristem (*Conohoria*, *Hymenosporum, Cornus, Quararibea*) but branching may be independent of the resting phase (or at least removed from it), as in *Fagraea*; in *Magnolia* branching is proleptic and succeeds the resting phase, as is usual in temperate trees.

Strategy of the Model. No trees belonging to Fagerlind's model, in so far as we understand it, are very large, the limit of 20 m being approached by *Fagraea, Duroia* and *Tovomita*. Trees of this architecture seem restricted to the understorey of the forest, and they are designed to produce small numbers of seeds at frequent intervals, the frequency of flowering being related to the length of the module. It is interesting to speculate on the limiting influence that inflorescence position may have on the size of a tree by comparing Fagerlind's model (no large trees) with Aubréville's model which differs architecturally in its lateral flowers and which includes many very large trees.

Taxonomic List of Examples (Fagerlind's Model)

Anacardiaceae:
Pentaspadon sp., Malaysia.
Bombacaceae:
Quararibea guianensis Aubl., French Guiana / *Quararibea turbinata* Poir. in Lam., French Guiana.
Cornaceae:
Cornus alternifolius L.f., E.N. America.
Ehretiaceae (or Boraginaceae):
Cordia alliodora (R. and P.) Cham., Brazil.
Guttiferae:
Tovomita plumierii Griseb., Martinique.
Loganiaceae:
Fagraea crenulata Maingay ex C.B. Clarke (Figs. 36A, B, 37), Malaysia.
Magnoliaceae:
Magnolia grandiflora L. (Fig. 36D), E.N. America.
Malpighiaceae:
Byrsonima cf. *verbascifolia* (L.) Rich., Guianas.
Melastomaceae:
Miconia sp., (Oldeman 2288), Guianas.
Pittosporaceae:
**Hymenosporum flavum* Muell. (Fig. 36C), Australia.
Proteaceae:
**Banksia littoralis* R.Br., Australia.
Rhamnaceae:
Paliurus sp., Ethiopia.
Rosaceae:
**Eriobotrya japonica* Lindl., "loquat", Japan.
Rubiaceae:
Duroia aquatica (Aubl.) Brem., French Guiana / *Euclinia longiflora* Salisb., W. Africa / *Genipa americana* L., Brazil / *Ixora* sp., New Hebrides, VEILLON, 1976 / *Randia fitzalani* F. Muell., Asian Tropics, FAGERLIND, 1943 / *Rothmannia longiflora* Salisb., W. Africa.
Violaceae:
Conohoria flavescens Aubl., French Guiana / *Conohoria riana* (Aubl.) Oldeman (Figs. 36E, 38C), French Guiana.

Petit's Model

Definition. The architecture of the tree is determined by the continuous growth of a monopodial, orthotropic trunk axis which produces, either continuously or in a diffuse manner, plagiotropic branches with spiral or decussate phyllotaxis. Branches are modular, plagiotropic by substitution, each module being hapaxanthic.

The method of growth of the branch tiers in Petit's model is identical with that in Fagerlind's model, but the two models are contrasted in the growth of their trunks, continuous in the former, rhythmic in the latter. In many examples this continuous growth, once branch initiation has begun, results in continuous branching, i.e., a branch at every node on the trunk. Otherwise branching is irregular but without the production of distinct tiers, i.e., without an endogenous rhythm.

The model is named after E. PETIT, who has contributed to our understanding of the architecture of such trees in his study of African Rubiaceae belonging to the tribe Gardenieae (PETIT, 1964). Many of the trees which conform to this model are small and there is a high degree of reduction in the organization of their branch modules, as earlier descriptions indicate. However, we have also included a large, less specialized example in our later description of a species of *Sclerolobium*, recently observed in French Guiana.

Example. The model is illustrated initially by *Gossypium hirsutum* (Malvaceae, tropical America) widely cultivated as one of the commercial cottons. It forms, at most, a treelet scarcely 3 m high and, as we shall see, it is very precisely organized. The architecture is represented by Figure 40B. Leaves on the trunk are spirally arranged with a phyllotaxis of 2/5 and each subtends a branch which has a strict sympodial plagiotropy, represented schematically in Figure 40Db. Each branch module includes only two leaves and ends in a solitary terminal flower. The first leaf is reduced to a scale and may be regarded as one of a pair of prophylls of which the second is a foliage leaf separated by the long internode which forms the axis of the module. This foliage leaf is inserted just below the terminal flower and subtends the next module. A number of latent meristems are produced on this shoot system and their developmental potential was shown to be limited by the pruning experiments of ATTIMS (1969). The results are complex but they show that meristems at progressively higher levels have an inherent potential to complete partially the architecture of the tree, according to the model, but not to reiterate it completely (viz. OLDEMAN, 1974a, p. 40). It is this high degree of organization in cotton which facilitates the preparation of "composite plant diagrams" (MUNRO and FARBROTHER, 1969).

Other Examples and Variations. A number of other treelets represent this model and show equally the specialization of the plagiotropic system. *Leptaulus daphnoides* (Icacinaceae, of west tropical Africa) shown in Figure 40A is a small tree up to 8 m high, with continuous branching of its trunk. The modules which make up the plagiotropic branch system are reduced in the extreme, including but one foliage leaf below the terminal inflorescence, this leaf subtending the next module and so on (Fig. 40Dc). But for the leaf-opposed position of the inflorescence such a branch could easily be mistaken for a regular monopodium.

Morinda citrifolia (Rubiaceae, the "nono" of Polynesia, but with a pantropical distribution at least in cultivation) is represented in Figure 40C. This species is familiar to travellers in the tropics because of its edible infructescences, which are essentially fleshy capitula. The plagiotropic branch modules are three-leaved

Fig. 40A–E. Petit's model. ▷

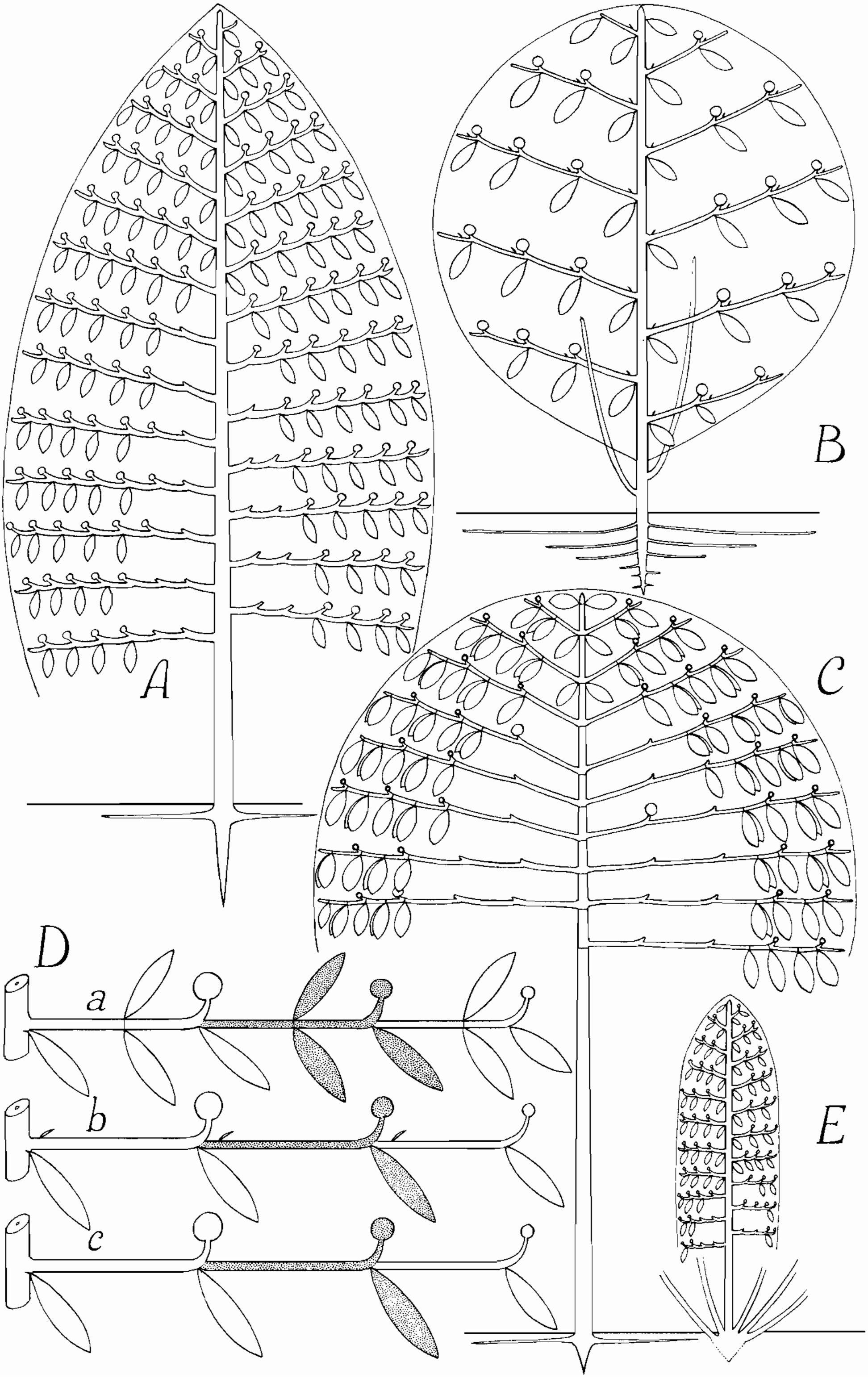
A *Leptaulus daphnoides* Benth. (Icacinaceae, west tropical Africa). A small rain-forest tree, up to 8 m high.

B *Gossypium hirsutum* L. (Malvaceae, dry regions of tropical America, familiar as one variety of cotton and pantropical in cultivation). A bush to 2 m high (ATTIMS, 1969).

C *Morinda citrifolia* Hunter (Rubiaceae, Hiva Oa Island, Marquesas, French Polynesia, *F. Hallé 2142*). The "nono" of Polynesia. A small tree in coastal vegetation, to 5 m high.

D A diagrammatic comparison between the plagiotropic flowering branches of the preceding species (not to the same scale). *a Morinda citrifolia*, in which each branch module bears three foliage leaves; *b Gossypium hirsutum* with two leaves, of which the first is a prophyll scale, the second a foliage leaf; *c Leptaulus daphnoides* with a single foliage leaf distally on each module.

E *Waltheria indica* L. (Sterculiaceae, a pantropical weed). A woody herb, to 1 m high, common in disturbed dry areas


A
B
C
D
a
b
c
E

and consist of a pair of foliage leaves followed by a single leaf (which subtends the next module) opposed to the inflorescence (Fig. 40 Da). The trend towards herbs is indicated further by our illustration (Fig. 40 E) of *Waltheria indica* (Sterculiaceae, a widely distributed tropical weed). The branch module is again represented by a single leaf and internode. Basal branching, which seems to be reiteration, is common and often obscures the architecture.

Large trees may conform to Petit's model, as is indicated by *Sclerolobium* sp. nov. (Leguminosae – Caesalpinioideae), a recently discovered tree of the Guianese forest (Saül, Fr. Guiana) which reaches a height of 40 m. All parts of the plant are big and leaves are spirally arranged throughout. Individual paripinnate leaves are 2 m long and even the stipules, up to 6 cm long, are compound (Fig. 4). The leaves give the impression of growing by an apical meristem because the parts are unfolded periodically, each pair of leaflets expanding completely before the next pair starts to unfold. However, this is preformation and not epigenesis because all leaflet primordia are initiated simultaneously (ROUX, personal communication). The tree has an extended unbranched juvenile phase and may reach a height of 10 m before discontinuous and irregular branching starts. Plagiotropic branch modules are massive; each bears several dozen leaves. Substitution of the distal part of each module is pronounced, but details are lacking since the tree has not been observed in the flowering state. The tree is most characteristic of steep hillsides where large populations of young, suppressed trees may occur.

Strategy of the Model. Trees which conform to this model occupy a wide variety of habits, ranging from the lowest to the higher levels of rain-forest, but also in savanna, even in quite dry places. The main biological feature in this model is the strong tendency towards specialization of the plagiotropic system, mainly indicated by reduction in the number of parts in each module. As suggested here (Fig. 40 D) and also in H.O., 1970, p. 63, the number of leaves per module is fixed and small, e.g., four (but the last pair very unequal) in *Rothmannia hispida*, three in *Schumanniophyton problematicum* and *Morinda citrifolia*, three but one reduced in *Atractogyne bracteata*; three but one a scale leaf in *Tetrorchidium oppositifolium*, two but one a scale leaf in *Tetrorchidium didymostemon* and *Gossypium hirsutum*, and finally only one foliage leaf per module in *Leptaulus daphnoides*. These represent some of the most stereotyped kinds of branch organization in the woody angiosperms; they largely belong to small trees. In combination with the continuous growth of the trunk, they represent a method of producing a steady supply of diaspores.

Taxonomic List of Examples (Petit's Model)

MONOCOTYLEDONS

Pandanaceae:
[L] *Freycinetia marquisensis* F.B.H. Brown, Marquesas.

DICOTYLEDONS

Annonaceae:
Fusaea longifolia Aubl., Brazil, FRIES, 1959.
Euphorbiaceae:
Tetrorchidium didymostemon (Baill.) Pax, Trop. Africa, ROUX, 1968; F. HALLÉ, 1971 / *Tetrorchidium oppositifolium* Pax, W. Africa.
Icacinaceae:
Gomphandra cf. *quadrifida* (Bl.) Sleum., (F. Hallé 2000), Malaysia / *Leptaulus bangouensis* Koechlin, Congo / **Leptaulus daphnoides* Benth. (Fig. 40 A, Dc), Trop. Africa.

Leguminosae – Caesalpinioideae:
Sclerolobium sp., (Oldeman s.n. Cay), Guianas / *Tachigalia bracteolata* Dwyer, Guianas / *Tachigalia* cf. *multijuga* Benth., (Oldeman 2196), Guianas / *Tachigalia paniculata* Aubl., Brazil.

Malvaceae:
Gossypium anomalum Wawra and Peyr, Trop. Africa, Attims, 1969 / *Gossypium arboreum* L., Asia / *Gossypium australe* Muell., N. Australia / *Gossypium barbadense* L., Trop. America / *Gossypium herbaceum* L., Asia / *Gossypium hirsutum* L. (Fig. 40B, Db), Trop. America / *Gossypium raimondii* Ulbrich, Peru / *Gossypium somalense* (Gürke) Hutch. E. Africa / *Gossypium thurberi* Todaro, Arizona.

Piperaceae:
**Piper aduncum* L., Trop. America, F. Hallé, 1974 / *Piper* sp., (Oldeman 2503). French Guiana.

Rubiaceae:
Aidia micrantha (K. Schum.) White, Trop. Africa, Petit, 1964 / *Amaralia* sp., Trop. Africa Petit, 1964 / [L] *Atractogyne bracteata* (Wernh.) Hutch. and Dalz. (Fig. 69C), Trop. Africa, F. Hallé, 1967 / [L] *Atractogyne gabonii* Pierre, C. Africa, Petit, 1964 / *Bertiera orthopetala* (Hiern) N. Hallé, C. Africa, N. Hallé, 1964 / *Bertiera racemosa* (G. Don.) K. Schum., Trop. Africa, F. Hallé, 1967 / *Chimarrhis cymosa* Jacq., W. Indies / *Leptactina arnoldiana* De Wild., Congo / *Massularia acuminata* (Benth.) Bullock, Trop. Africa, F. Hallé, 1967 / *Morinda citrifolia* Hunter (Fig. 40C, Da), Pantropical, commonly cultivated / *Morinda lucida* Benth., W. Africa / *Rothmannia hispida* (K. Schum.) Fagerlind, Trop. Africa, F. Hallé, 1967 / *Schumanniophyton hirsutum* (Hiern) Good, C. Africa, Petit, 1964 / *Schumanniophyton magnificum* (K. Schum.) Harms, C. Africa, F. Hallé, 1967 / *Schumanniophyton problematicum* (A. Chev.) Aubr., W. Africa.

Sterculiaceae:
Abroma augusta L. f., New Guinea, F. Hallé, 1974 / [L] *Byttneria* sp., Brazil / [H] *Waltheria indica* L. (Fig. 40E), Pantropical weed.

Nozeran's Model

Definition. The architecture is modular and determined by an orthotropic, sympodial trunk, each unit of the sympodium bearing a distal tier of plagiotropic branches, with plagiotropy always established by leaf arrangement which contrasts with that on the trunk. Growth of both trunk and branch axes may be rhythmic or not. Branches themselves are either monopodial or sympodial. Flowering may be either on trunk or branch but does not influence the model.

This is an uncommon but distinctive model (Figs. 41 and 42) and since it is exemplified by cocoa (*Theobroma cacao*, Sterculiaceae, Central America) it has been well described by agronomists (e.g., Cook, 1911, 1916; Brooks and Guard, 1952; Urquhart, 1955). There are also numerous studies on growth of cocoa (e.g., Humphries and McKee, 1944; Greenwood and Posnette, 1950; Greathouse and Laetsch, 1969, 1973; Greathouse et al., 1971). The model is named after René Nozeran, whose students have investigated the organization of the aerial and underground parts of cocoa (Charrier, 1969; Dyanat-Nejad, 1971; Dyanat-Nejad and Neville, 1972; Vogel, 1975).

Nozeran's and Prévost's models resemble each other since both have a sympodial trunk and tiered branches. In the latter the branches are plagiotropic by apposition, however, whereas in the former plagiotropy is an inherent character of the axes themselves (see Fig. 12). This is readily observed in nature, because the leaves, which are grouped in dense spirals on the erect extremities of the branch modules in Prévost's model, differ conspicuously in their arrangement on the branch axes in Nozeran's model, where they are evenly spaced out and most often distichous. Experimentally the difference is also clear; for example, in *Alstonia boonei* (Prévost's model) the plagiotropy of the branch modules is lost once they are independently propagated or separated from the trunk; in *Theobroma cacao* plagiotropy largely persists in an independently propagated branch (H.O., 1970,

p. 90) and completely so in *Theobroma speciosum* (Fig. 42E; OLDEMAN, 1974a).

Example. Geissospermum sericeum (Apocynaceae, Guianas), a large rain-forest tree up to 40 m high, with a basal diameter of little more than 1 m illustrates the model well, with a number of additional features of biological interest. Figure 42Aa shows a sapling at a height of about 4 m at which stage the architecture of the model may be shown quite precisely. The sapling includes a distinct trunk made up of a series of modules, each successive module indicated on the older trunk by a slight articulation, but on the younger trunk by a more obvious "bayonet-junction". The trunk unit of the sympodium is orthotropic and with spirally arranged leaves. After a vigorous period of growth the apex of each module produces a tier of usually three plagiotropic branches, whereupon its apex aborts by parenchymatization. Each branch develops by syllepsis from the axil of a distal leaf on the trunk, and shows dorsiventral symmetry expressed by its distichous phyllotaxis and branching in one plane. This branching also involves abortion of the apex, but the cause is unknown. The result is a very regular branch tier, with the length and diameter of modules progressively reduced distally (Fig. 42Ab). At a later stage in the development of the tree, when it has become quite tall, flowers develop terminally on the peripheral parts of the tiers. These "flowering modules" may be very short in the biggest trees, as has been illustrated for this species in Flora Brasiliensis (MARTIUS et al., 1840–1906). The relay axis (renewal shoot) which raises the total height of the tree and constructs the next tier develops below the previous tier, by prolepsis from a dormant bud on the main trunk. The correlation between syllepsis, plagiotropy and distichous phyllotaxis on the one hand and between prolepsis, orthotropy and spiral phyllotaxis on the other, is consistent in this species, as in *Theobroma*.

A distinctive feature of older trees is the fluted trunk which seems to be associated with reiteration. *Minquartia guianensis* (Olacaceae, French Guiana), another rain-forest tree is noteworthy in this respect, it also has a fluted trunk and also conforms to Nozeran's model (Fig. 80).

Other Examples. Mabea piriri (Euphorbiaceae, Guianas) is a small latex-producing rain-forest tree reaching a height of 10 m, and illustrates this model in an unusual way. The seedling is plagiotropic as described by OLDEMAN (1968) and the first orthotropic trunk module is produced basally, from the axil of a leaf just above the cotyledons (Fig. 42Ba). The distal part of the seedling axis is lost, so that by the time the tree reaches a height of 5 m the architecture is that of the model. In *Mabea taquari* (illustrated in OLDEMAN, 1974a) this phenomenon is not limited to the seedling but recurs from time to time in the older modules where a sympodial series of plagiotropic axes may take the place of an orthotropic trunk unit, suggesting an approach to Troll's model.

Further small examples of Nozeran's model include *Gonocaryum littorale* (Icacinaceae, Indonesia and New Guinea). Here the inflorescences arise from the leafless parts of the branches (Fig. 42C). *Citronella suaveolens* in the same family and from the same region is identical in its architecture (HALLÉ, 1974). The Icacinaceae (250 species) is architecturally very rich since it is presently known to include no less than seven models.

In the Sterculiaceae, apart from *Theobroma*, a second genus *Tribroma* illustrates Nozeran's model. *Tribroma bicolor* ("patashte" from Mexico to Brazil) is a much larger tree than cocoa, but shows the same architectural features (Fig. 42D). It is, however, not cauliflorous

Fig. 41 A and B. Nozeran's model, *Anthostema aubryanum* Baill. (Euphorbiaceae), Adiopodoumé, Ivory Coast.
A Distal branch tier developed in association with abortion of shoot apex of trunk axis.
B Old branch tier and two units of the sympodial trunk axis. Note effects of secondary thickening

and the flowers are lateral on branch modules. Branching in patashte has been studied by Cook (1916).

Variation. We have emphasized that flowering is not architecturally significant in Nozeran's model and it is, therefore, not surprising to find that the expressed range in inflorescence is considerable, varying from terminal through lateral to ramiflory and finally cauliflory. In *Mabea* inflorescences are terminal on long branches with distichous leaves; in the related *Dichostemma glaucescens* (Euphorbiaceae), a small tree of Central Africa, the inflorescences are similar, but dorsiventrality of the vegetative part of the branch is expressed by secondary rearrangement of spirally arranged leaves (cf. Fig. 12E, F). In other examples, flowers are otherwise axillary on the plagiotropic branches, e.g., in *Tribroma*. In *Geissospermum* they only appear when the tree is quite tall, as we have mentioned. An approach to the cauliflorous situation of *Theobroma* is suggested by *Gonocarpus* with its ramiflorous condition. The step from flowers lateral on a trunk versus terminal on a branch may not be such a big one because in a specimen of *Theobroma speciosum* cultivated in Cayenne flowers once were developed terminally on a branch complex, specifically on a first axis of the second tier. In *Theobroma cacao* flowering generally begins in the third year and is initially diffuse on both trunk and branches, but always on the older parts (Lent, 1966).

Rhythmic Growth in Nozeran's Model. The existence of trees with such markedly differentiated trunk and branch axes has attracted the attention of several investigators concerned with the relative periodicity of growth in the two. This was described in detail earlier (p. 36).

Strategy of the Model. The range of stature in plants which conform to Nozeran's model is not large; no herbaceous representatives have yet been recognized. This seems to be because plants of this model are almost entirely forest species. We have indicated this for *Geissospermum* and *Minquartia* (up to 40 m); *Theobroma speciosum*, the "cupuaçu" of northern Brazil, as well as *Tribroma*, are smaller trees. Another group includes trees of the forest undergrowth, exemplified by cocoa, which is cultivated under shade and which Cook (1911) has stressed is architecturally adapted to growth beneath a forest canopy. Other examples include the several Euphorbiaceae we list below from tropical Africa and America: they are substituted in Asia by Icacinaceae. *Gonocaryum littorale* is a forest species; despite its specific name it is not coastal.

Fig. 42A–E. Nozeran's model. ▷

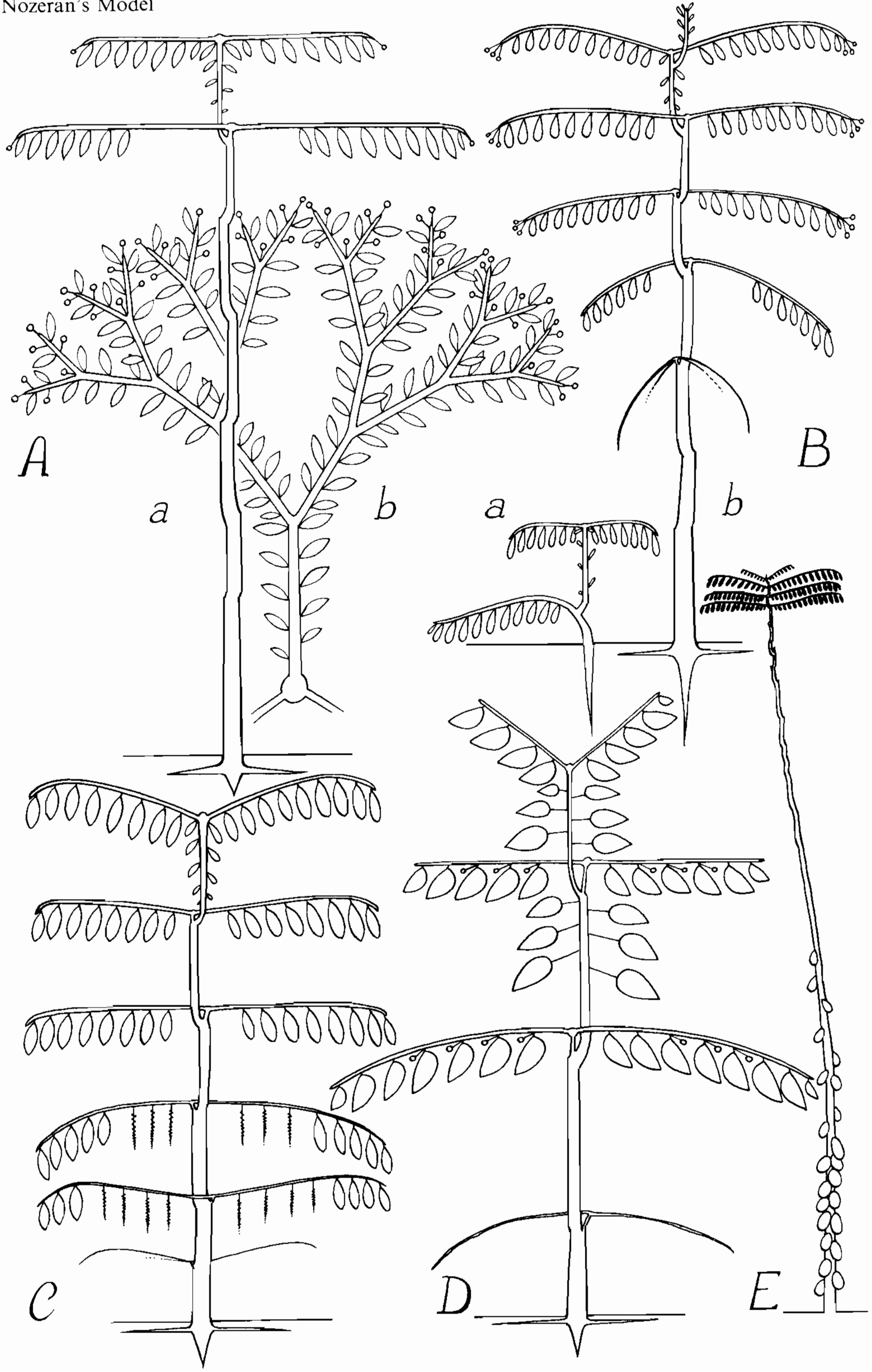
A *Geissospermum sericeum* (Sagot) Benth. (Apocynaceae, French Guiana, *R.A.A. Oldeman 2647*). A large tree of the South American rain-forest, to 40 m high. *a* General architecture of a sapling, 4 m high; *b* part of one plagiotropic tier showing the sympodial structure of the branch and the terminal inflorescences, sometimes leaf-opposed.

B *Mabea piriri* Aubl. (Euphorbiaceae, French Guiana, *R.A.A. Oldeman 999*). A small tree of the rain-forest, to 10 m high; *a* the seedling, with the axis peculiarly at first plagiotropic, later producing an orthotropic lateral axis (Oldeman, 1968); *b* general architecture of a young tree, 5 m high.

C *Gonocaryum littorale* (Bl.) Sleumer (Icacinaceae, Indonesia and New Guinea). A small tree, to 10 m high, with pendulous inflorescences borne on the leafless parts of the branches.

D *Tribroma bicolor* (Humb. and Bonpl.) Cook (Sterculiaceae, from Mexico to Brazil, the "patashte"). A much larger tree than the related *Theobroma cacao*, and not cauliflorous; branching habit studied by Cook (1916).

E *Theobroma speciosum* Spreng. (Sterculiaceae, Guianas and Brazil). A tree of the rain forest, physiognomically monocaulous.


A
a
b
B
a
b
C
D
E

From this distribution of examples in stable biotopes and the variation in inflorescence position, a *K* strategy is suggested, but we have too few examples to make a convincing argument. It should be noted, however, that if few species are known to conform to this model, those which do are at least in South America represented by important populations in the forest. This indicates a noteworthy ecological success.

Taxonomic List of Examples (Nozeran's Model)

Apocynaceae:
Geissospermum sericeum (Sagot) Benth. (Fig. 42A), French Guiana.
Euphorbiaceae:
Anthostema aubryanum Baill. (Fig. 41), Trop. Africa, Roux, 1968; F. Hallé, 1971 / *Anthostema senegalensis* Juss., W. Africa / *Dichostemma glaucescens* Pierre, C. Africa / *Mabea caudata* Pax and Hoffm., French Guiana / *Mabea piriri* Aubl. (Fig. 42B), French Guiana, Oldeman, 1968 / *Mabea taquari* Aubl. var. *angustifolia* Muell.-Arg. (Fig. 69D), Guianas.
Icacinaceae:
**Citronella suaveolens* (Bl.) Howard, New Guinea, F. Hallé, 1974 / **Gonocaryum littorale* (Bl.) Sleumer (Fig. 42C), Trop. Asia.
Olacaceae:
Minquartia guianensis Aubl., French Guiana.
Sterculiaceae:
Theobroma cacao L. "cocoa", Trop. S. America, Ljashenko, 1967; Greathouse and Laetsch, 1969 / *Theobroma speciosum* Spreng. (Fig. 42E), French Guiana / *Tribroma bicolor* (Humb. and Bonpl.) Cook (Fig. 42D), "patashte", Trop. America, Cook, 1916.

Aubréville's Model

Definition. The architecture is determined by a monopodial trunk with rhythmic growth and spiral or decussate phyllotaxis, bearing whorled branch tiers with similar phyllotaxis. Branches grow rhythmically but are modular, each branch plagiotropic by apposition. Since inflorescences are lateral the modules grow indefinitely.

The model is named after André Aubréville since he drew attention to it as being particularly common in the Sapotaceae (Aubréville, 1964).

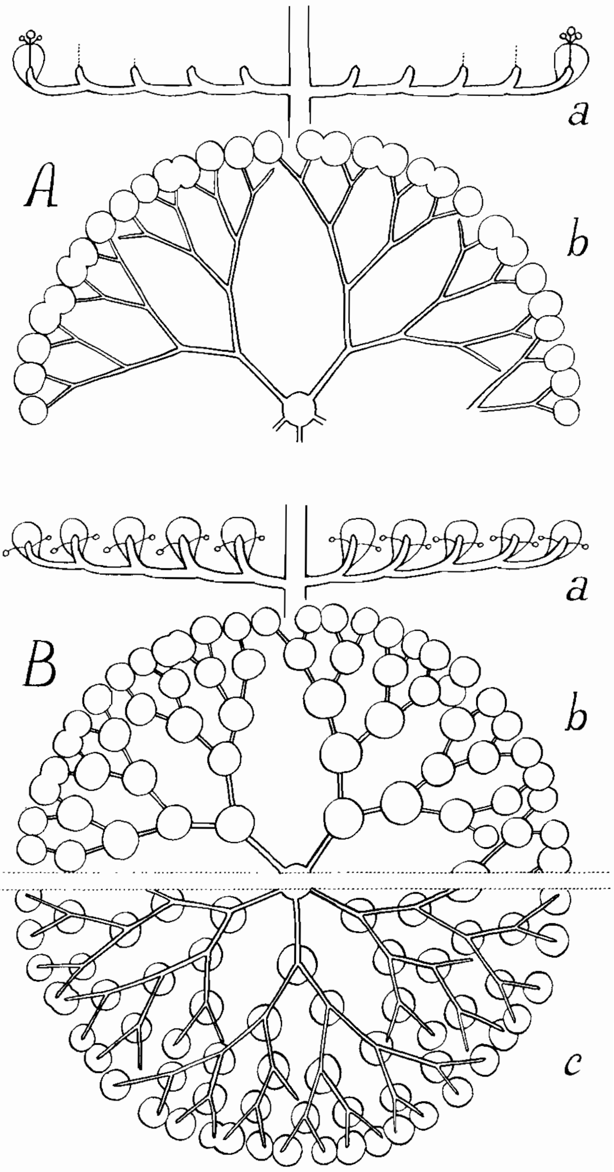
Aubréville's model differs from Fagerlind's model simply in the growth of the branch modules, which are indeterminate since they do not produce a terminal inflorescence (cf. Fig. 43A, B). However, because the plagiotropic branches are sympodial by apposition growth, these terminal meristems are evicted periodically by a lateral sylleptic branch, become erect, and effectively function as short shoots since internodes remain unelongated (Fig. 44). These erect short shoots grow rhythmically like the monopodial main trunk, as is often evident in the distribution of leaf scars. The biological aspect of this seemingly trifling growth feature is very important since each branch tier consists of a series of leafy rosettes distributed throughout the complex and not restricted more or less to the periphery.

The physiognomy of most trees which conform to this model is very distinct and has attracted the attention of numerous authors; recent and less recent descriptions are supplied by Mildbraed (1922), Massart (1923), Allen (1956), Aubréville (1959), Taylor (1960), Voorhoeve (1965), Schnell (1970). More or less precise descriptions of branch patterns are given by several authors (e.g., Corner,

Fig. 43A and B. Diagrammatic comparison between a tier of branches in two models.

A Fagerlind's model, tier in side view *a*, and from above *b*. Newly initiated leafy rosettes are restricted to the periphery of the tier because each meristem is determinate via terminal flowering.

B Aubréville's model, tier in side view *a*, from above *b*, and from below *c*. The meristems are indeterminate, since flowering is lateral, and each continues to produce a leafy rosette so that the photosynthetic surface is more extensive



1952; RACIBORSKI, 1901; TROLL, 1937–1943; KORIBA, 1958; DAMPTEY and LONGMAN, 1965; LJASHENKO, 1967). Perhaps the earliest description is that of RUMPHIUS (1741–1755) while LINNAEUS (1759) was aware of it since it was the distinctive feature he emphasized in naming the genus *Terminalia*. What is surprising, despite these numerous reports, is that there has been little experimental work on this aspect of tree growth, nor any appreciation of the fact that this kind of plagiotropy is very strict and not to be confused with superficially comparable phenomena in the periphery of orthotropic branch complexes (see Fig. 12A, B) which are to be found in other models (e.g., Attims' and Rauh's).

A lucid impression of this plagiotropic branching system is given by CORNER (1952):

> "A tier can be likened to a dense mat of foliage composed of rosettes of leaves set closely together at the same level on the upturned ends of slow-growing twigs, which are produced in a particular order to fill the spaces that repeatedly arise at the outgrowing edge of the mat."

This refers to *Terminalia catappa* in which the architecture is so clearly expressed that it is the "type" of all "pagoda trees", as CORNER called this physiognomy, and which is indicated by the frequent reference to this arrangement as "*Terminalia*-branching". The precise analysis by FISHER (1978) is the first which establishes quantitative aspects of this type of branching and should provide the necessary background for experimental studies.

Examples. The genus *Terminalia* is a large, widely distributed and commercially important one since it includes several tall forest timber trees (*T. amazonia, T. ivorensis, T. superba*), all representing Aubréville's model. Species of the same model which are smaller trees occur in other habitats e.g., the familiar sea-shore *T. catappa. Terminalia superba,* one of the largest trees of the African rain-forest, commonly reaching a height of 45 m (Fig. 45A) and *T. amazonia* (Fig. 45B) reaching heights of 55 m in the Amazon basin, both exemplify this architecture well. The seedling axis is orthotropic and grows rhythmically, each flush separated by a series of close set leaf scars. Eventually a pattern of monopodial branching is initiated, intimately related to this rhythm. Phyllotaxis is spiral and a series of four to eight sylleptic shoots from the axis of the uppermost congested leaves of each flush produces a pseudowhorled branch tier. Consequently branches are developed towards the end of a cycle of extension. Separation of the successive branch tiers is achieved by the long internodes which occur in the early stages of each trunk axis flush. Behavior of individual branches of each tier is complex and not necessarily coincident with the growth flushes of the trunk axis. The branch complex is from the start a complex of short modules, 40–50 cm long. Each consists of a basal "hypopodium" or first internode which is more or less horizontal in orientation. Distally the spiral of leaves is produced with progressively shorter internodes and at the same time the orientation of the apical meristem becomes erect. By syllepsis, one or two lateral branches develop from the axils of leaves (usually the third and fifth) on the lower side of the shoot, at the level where the axis is bent upward. These branches in turn produce an initial long hypopodium and the process is repeated. Since the reorientated terminal meristem continues its rhythmic growth with short internodes and lateral inflorescences, the result is a long-lived erect short shoot. New rosettes are added as the tier expands laterally (Fig. 44) and the result is the flat branch complex which characterizes this model. Since the uppermost tier will branch repeatedly while the trunk axis remains dormant, trees are characteristically flat-topped, here and there with individuals throwing up the next segment of the trunk as the leader undergoes extension.

A feature of *Terminalia* species well shown in young trees, as in Figure 45B, is the progressive downward bending of the individual branches as they age.

FISHER (1978) in a detailed investigation of *Terminalia catappa* has provided precise quantitative documentation of

Fig. 44. Aubréville's model, *Terminalia* cf. *amazonia* Exell (Combretaceae), Bélèm, Para, Brazil, part of plagiotropic branch complex from below to show spacing of leaf rosettes

growth features. His results are derived from an examination of growth of shoot populations over a period of one year, on plants grown in South Florida and include information about phenology together with periodicity, orientation and position of branches in relation to rates of shoot extension. Of particular value are the analyses of branch length and angles of bifurcation in plagiotropic complexes, because these provide the first data which can be related to efficiency of leaf distribution, an important lead for future ecological investigation.

Other Examples. The Sapotaceae provide many examples among large forest trees. We have illustrated *Manilkara bidentata* ("balata") (Fig. 45C), a large tree of the Guyanese and Brazilian rain-forest. Reorientation of lower branch complexes is well shown in early stages of development when the architecture is precisely expressed. Other forest giants of the New World tropics include *Nispero achras,* the tallest tree of the Yucatán, and in the Amazonian hylaea there is *Manilkara huberi.*

An Old World example would be *Baillonella toxisperma,* the largest and most imposing tree of the central African rainforest. Other sapotaceous African trees of comparable size exist in the genera *Autranella* and *Tieghemella.* Therefore within this one family there is plenty of evidence to demonstrate the ecological success of this model.

However, the range of species from which examples of this model can be selected is very large and we include some details of several trees from a variety of habitats. First is *Bruguiera sexangula* (Rhizophoraceae, mangroves of tropical

Asia). The viviparous seedling produces an axis which results in a regularly branched tree reaching a height of 30 m; phyllotaxis is bijugate. The tree develops tiers of branches about 40 cm apart, as a result of rhythmic growth of the terminal bud (Fig. 46 A). In the resting phase this bud is enveloped by the stipules of the youngest pair of exposed leaves, as is characteristic of all rhizophoraceous mangroves; no bud-scales are produced. During subsequent shoot extension a tier of two to four branches is produced by syllepsis. Growth of the plagiotropic branch modules is rhythmic and sympodial by apposition, the evicted terminal short shoot produces lateral flowers. *Bruguiera* betrays its habitat in its basal stilt roots and its pneumatophores which develop by the periodic upward arching of plagiotropic roots close to the surface of the substrate.

Euphorbia is a genus rich in architectural models and one species which exemplifies Aubréville's model provides ecological contrast to *Bruguiera. Euphorbia decaryana* (Euphorbiaceae, southern Madagascar) is a low shrub, to 4 m high which grows in semi-desert environments and is deciduous. The branch tiers are very pronounced (Fig. 46 Ba), spreading and bifurcating in a regular manner (Fig. 46 Bb). A feature of this plant is the tuberous root system, an obvious adaptation to its environment.

Dendrocnide microstigma (Urticaceae, Indonesia) further illustrates this model (Fig. 46 C). This is a dioecious tree to 10 m high of forest margins, armed with stinging hairs, and somewhat weedy (Chew, 1969). The rhythmic growth of the trunk and regular plagiotropic branches bearing pendulous spikes of inconspicuous flowers are distinctive. A final example is provided by *Scaevola plumieri* (Goodeniaceae), a low shrub, scarcely 2 m high and common in the vegetation close to tropical beaches. Its architecture is shown in Figure 46 D, but this is somewhat obscured in nature by the spreading lowermost branch tiers which commonly take root. This provides a mechanism within the model for vegetative propagation of the plant.

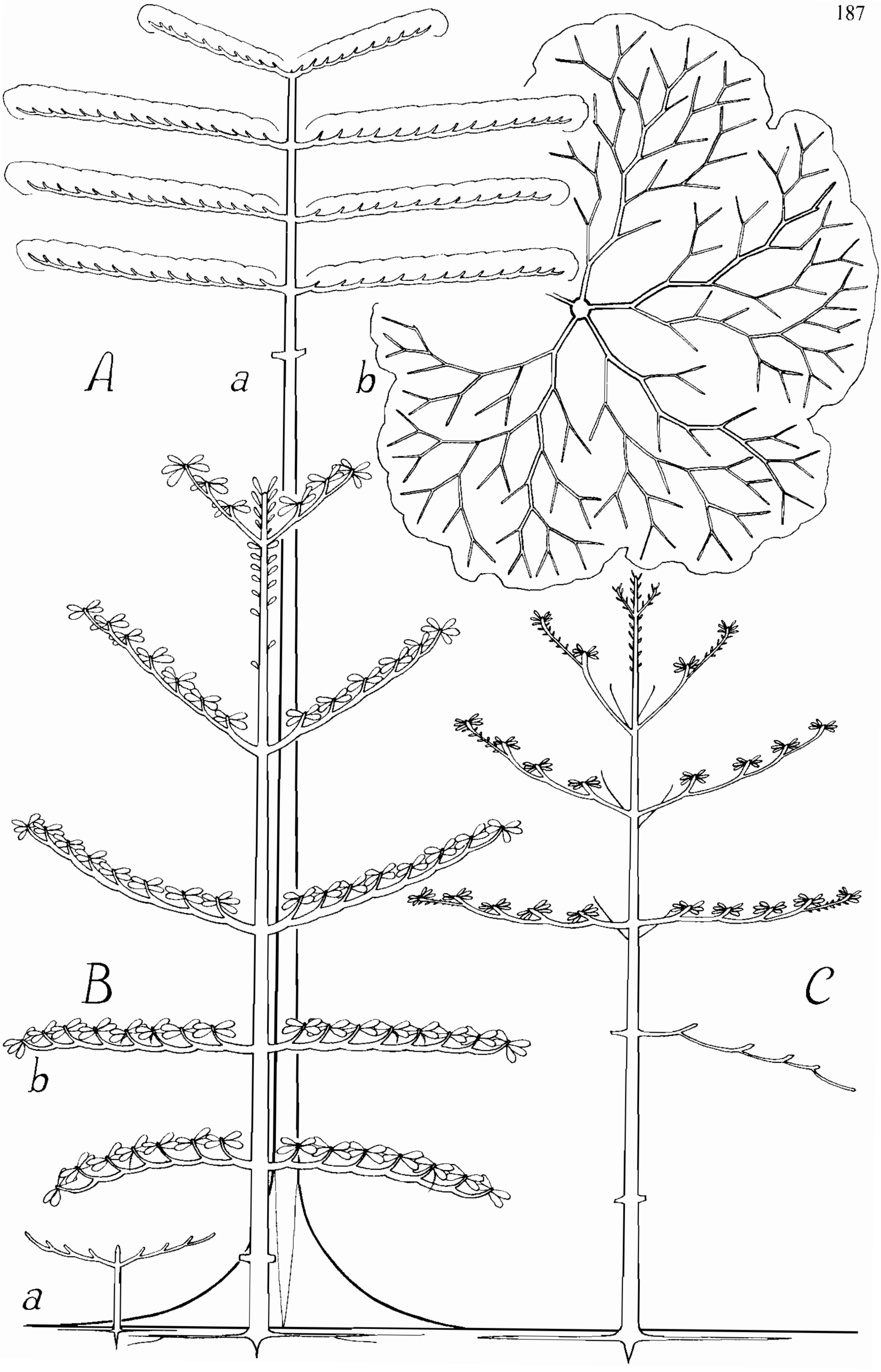
Strategy of the Model. The range of types thus described is large, but variation is entirely quantitative, and Aubréville's model is remarkably homogeneous in its expression. The rhythm of the episodic meristematic activity may be long or short, giving rise to long or short trunk segments between branch tiers; the angle the branches ultimately make with the trunk is not necessarily 90°, i.e., they may be ascending or somewhat pendulous; the phyllotaxis, leaf density and position of prophylls on the branch modules is not the same in all species. This variation is not architecturally important and such trees provide one of the better and more discrete examples of a model. One perhaps need look no further than the distribution of leaves on this type of tree to account for its success. The point is best made by comparing one of its branch tiers

Fig. 45 A–C. Aubréville's model. ▷

A *Terminalia superba* Engl. and Diels. (Combretaceae, tropical Africa). The "fraké", or "limba", one of the largest trees of the African rain-forest, reaching a height of 45 m. *a* General architecture of a young tree, 20 m high; *b* a plagiotropic tier, seen from above, to show the Terminalia-branching (Corner, 1952).

B *Terminalia amazonia* Exell (Combretaceae, Brazil and Guianas, *R.A.A. Oldeman 3190*). One of the largest trees of the Amazonian basin, reaching a height of 55 m. *a* The first branching; *b* general architecture of a young tree, 15 m high.

C *Manilkara bidentata* (D.C.) Chev. (Sapotaceae, Brazil and Guianas). The "balata", a large tree of the American rain forest, used as a source of gum


A
a
b
B
b
a
C

with the very similarly organized branch tier in an example of Fagerlind's model (Fig. 43A, B). Sympodial growth in the latter is by substitution and in the former by apposition. If one views such a tier from above, one sees that in Fagerlind's model (Fig. 43A) old branches are progressively defoliated since their apical meristems are determinate by development of a terminal inflorescence (Fig. 43Aa). Leaves are restricted to the youngest, current branch modules at the margin of the plagiotropic tier (Fig. 43Ab). But in Aubréville's model (Fig. 43B) all the branch modules are leafy, potentially even the oldest, by virtue of their indeterminate growth and lateral inflorescences (Fig. 43Ba). The photosynthetic area is much more extensive (Fig. 43Bb, c). It surely seems significant that Aubréville's model includes large forest trees, whereas Fagerlind's model does not. This larger capacity for assimilation also seems a mechanism apt as a compromise between *K* and *r* strategies. When the tree is young the photosynthetic apparatus can be very closely fitted to the low light intensity of the forest undergrowth and the disposition of the leaf rosettes in tiers is seen as a mechanism to avoid mutual shading. Therefore, survival of individuals is promoted. When the tree is old there is a large number of modules with a flowering potential so that the biotope is well inundated with diaspores. This mechanism is largely independent of whether the tree reiterates or not. Such plants so regularly conform to their model that there exists the symmetry which has drawn them to the attention of so many botanists.

This successful architecture is undoubtedly the result of precise organizational control of apical meristems, and this is evident in the experimental work which has been carried out on the morphogenesis of this tree (e.g., that of ATTIMS, cited in H.O., 1970, pp. 67–68, on *Terminalia catappa*; and of DAMPTEY and LONGMAN, 1965, on *T. ivorensis*). Plagiotropy of the branch is induced in its first module by the activity of the apical meristem of the orthotropic trunk. If this apex is removed it is replaced by the apex of one of the youngest branch tiers below, which immediately becomes orthotropic. If the orthotropic trunk is cut off at a much lower level, there is no proleptic substitution by a dormant meristem on the trunk, rather there is dedifferentiation of the apical meristem of the plagiotropic branch module nearest the cut. This shows that the slow growth of the evicted meristem (the terminal short shoot) is also dependent on the growth of the orthotropic axis. Finally it can be shown, at least in *Terminalia catappa*, that each segment of the plagiotropic branch system determines the plagiotropic orientation of younger segments, since a branch segment propagated

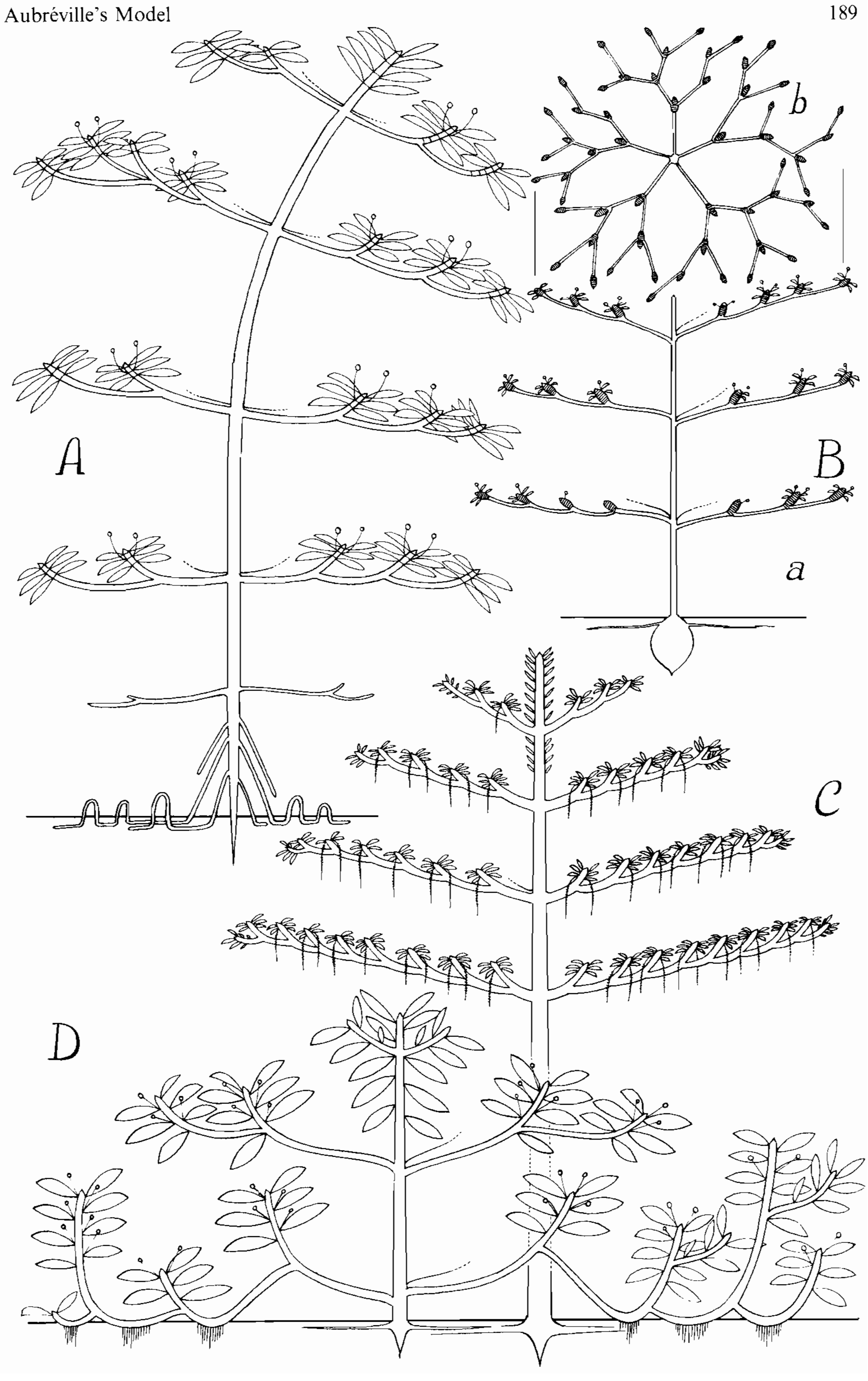
Fig. 46 A–D. Aubréville's model (further examples). ▷

A *Bruguiera sexangula* (Lour.) Poir. (Rhizophoraceae, tropical Asia). A large tree of the Asiatic mangroves, to 30 m high, with basal stilt roots and pneumatophores; the shoot apex may become inclined as if the tree were top-heavy.

B *Euphorbia decaryana* (L.) Croizat (Euphorbiaceae, Madagascar). A deciduous shrub 4 m high, growing in dry areas, roots are tuberous (RAUH, 1967). *a* General architecture; *b* a tier of plagiotropic branches seen from above.

C *Dendrocnide microstigma* (Gaud. ex Wedd.) Chew (Urticaceae, Indonesia). Dioecious tree to 10 m high, with very conspicuous *Terminalia*-branching (CHEW, 1969).

D *Scaevola plumieri* Vahl (Goodeniaceae, from Moorea, Society Islands, Polynesia). A shrub to 2 m high, growing on sandy beaches. The figure illustrates how the lower tiers in the *Terminalia*-branching system can become rooted and provide an efficient mechanism for vegetative propagation


b
A
B
a
C
D

by marcotting will immediately dedifferentiate and become orthotropic. The precision of these various levels of control is indicated by the rapidity of changes, once the normal growth pattern is disturbed.

In summary, we can recognize four types of vegetative meristems in *Terminalia catappa*:

1. Apical meristem of the trunk, growth vertical, rhythmic and rapid in the active phase; long-lived.
2. Apical meristem of a young plagiotropic branch module, growth horizontal for a brief period.
3. Apical meristem of an old plagiotropic branch module, growth vertical, rhythmic and always slow in the active phase; long-lived.
4. Apical meristems in the latent condition, i.e., reserve buds on trunk and branch; sometimes long-lived.

The experiments described above suggest that reserve buds are not readily brought into action; rather the model "readjusts" very rapidly to environmental disturbance.

Taxonomic List of Examples (Aubréville's Model)

Anacardiaceae:
Campnosperma brevipetiolata Volk., New Guinea, F. Hallé, 1974.

Bombacaceae:
Bombax valetonii Hochr., Java, Corner, 1952 / *Pachira aquatica* Aubl., Trop. S. America / *Pachira insignis* Savigny, Trop. America.

Combretaceae:
Terminalia amazonia Exell (Figs. 44, 45B), Trop. S. America, Oldeman, 1974a / **Terminalia archipelagi* M. Coode, Bismark Archipelago / *Terminalia bellerica* Roxb., Malaysia, Corner, 1952 / *Terminalia calamansanay* Rolfe, Philippines / *Terminalia catappa* L., Trop. Asia, Corner, 1952 / *Terminalia ivorensis* A. Chev., Trop. Africa, Damptey and Longman, 1965 / *Terminalia mantaly* H. Perr., Madagascar / *Terminalia pamea* (Aubl.) Sagot, Trop. S. America / *Terminalia superba* Engl. and Diels (Fig. 45A), Trop. Africa.

Elaeocarpaceae:
Elaeocarpus littoralis Teysm. and Binn., Malaysia, Corner, 1952 / *Elaeocarpus pedunculatus* Wall., Malaysia, Corner, 1952 / *Elaeocarpus pseudopaniculatus* Corner, Malaysia, Corner, 1952 / *Elaeocarpus rugosus* Roxb., Malaysia, Corner, 1952 / *Sloanea massonii* Sw., Martinique / *Sloanea* cf. *sinemariensis* Aubl., (Oldeman 2135), Guianas.

Euphorbiaceae:
Endospermum malaccense (Benth.) ex Muell.-Arg., Malaysia, Corner, 1952 / *Euphorbia decaryana* (L.) Croizat (Fig. 46B), Madagascar / **Euphorbia hedyotoides* N.E.Br., Madagascar / *Euphorbia* sp., (Cremers 2398), Madagascar, Cremers, 1976 / *Macaranga populifolia* Muell., Malaysia, Corner, 1952 / *Richeria grandis* Vahl, Guadeloupe.

Flacourtiaceae:
Pangium edule Reinw., Malaysia, Corner, 1952.

Goodeniaceae:
**Scaevola sericea* Vahl, New Guinea / *Scaevola plumieri* Vahl (Fig. 46D), almost Pantropical.

Lauraceae:
Beilschmiedia mannii (Meisn.) Benth. and Hook., Trop. Africa / *Ocotea rodiaei* Mez, Guianas / *Sassafras officinale* Nees, E. United States.

Loganiaceae:
Fagraea fragrans Roxb., China.

Malpighiaceae:
Byrsonima spicata Rich., Martinique.

Moraceae:
Pourouma minor R.Ben., Guiana.

Myrsinaceae:
cf. *Cybianthus* sp., (F. Hallé 2299), French Guiana.

Rhizophoraceae:
Bruguiera sexangula (Lour.) Poir. (Fig. 46A), Trop. Asia.

Rubiaceae:
+*Adina microcephala* Hiern, Madagascar / *Guettarda speciosa* L., Polynesian littoral.

Sapotaceae:
Autranella congolensis (De Wild.) A. Chev., Trop. Africa, Aubréville, 1964 / *Baillonella toxisperma* Pierre, C. Africa, Aubréville, 1964 / *Butyrospermum parkii* (G. Don.) Kotschy, "shea butter tree", W. Africa, Aubréville, 1964 / *Chrysophyllum taïense* Aubr. and Pellegr., W. Africa / *Englerophytum hallei* Aubr. and Pellegr., C. Africa, Aubréville, 1964 / *Manilkara bahamensis* (Baker) Lamet Meesis., W. Indies / *Manilkara bidentata* (DC.) Chev. (Fig. 45C), Trop. S. America / **Manilkara huberi* (Ducke) A. Chev., Brazil / *Manilkara lacera* (Bak.) Dubard, Trop. Africa / +*Manilkara mo-*

chisia (Bak.) Geist., Zambia / *Manilkara zapota* (L.) van Royen, "sapotilla", Trop. America / **Mimusops huberi* Ducke, Brazil / *Neolemmoniera ogouensis* (Pierre) Heine, Trop. Africa, Aubréville, 1964 / *Nispero achras* (Mill.) Aubr., C. America, Aubréville, 1964 / *Omphalocarpum elatum* Miers, Trop. Africa / **Palaquium gutta* (Hook.) Baill., Malaysia / *Synsepalum dulcificum* (Schum. and Thonn.) Daniell, "miracle fruit", Trop. Africa, Aubréville, 1964 / *Tieghemella heckelii* Pierre ex A. Chev., Trop. Africa / *Zeyherella mayombense* (Greves) Aubr. and Pellegr., C. Africa, Aubréville, 1964.

Sarauiaceae:

Sarauia sp., New Guinea.

Sterculiaceae:

**Firmiana fulgens* K. Schum., Malaysia, Corner, 1952 / **Sterculia foetida* L., Malaysia / *Sterculia tragacantha* Lindl., Trop. Africa.

Ternstroemiaceae:

Archytaea vahlii Choisy, Malaysia, Corner, 1952 / *Ternstroemia merrilliana* Kobuski, New Guinea.

Urticaceae:

Dendrocnide longifolia (Hemsl.) Chew, New Guinea / *Dendrocnide microstigma* (Gaud. ex Wedd.) Chew (Fig. 46C), Indonesia, Chew, 1969.

Massart's Model

Definition. The architecture is determined by an orthotropic, monopodial trunk with rhythmic growth and which consequently produces regular tiers of branches at levels established by the growth of the trunk meristem. Branches are plagiotropic either by leaf arrangement or symmetry, but never by apposition. The position of flowers is not significant in the definition of the model.

This model is named after Jean Massart, who saw and described the architecture in a specimen of *Virola surinamensis* cultivated in the Botanical Gardens, Rio de Janeiro (Massart, 1923). The model differs from that of Rauh in the plagiotropy of the branches and this often imparts a symmetry in the tree which renders it striking, not only to the botanical traveller in the tropics, but also in familiar temperate gymnospermous genera like *Abies, Araucaria, Agathis* (Figs. 47 and 48). The best example of this symmetry is undoubtedly *Araucaria heterophylla* (syn. *A. excelsa*, "Norfolk Island pine", Araucariaceae), but the model can exist without marked symmetry. In some examples, symmetry can be promoted by self-pruning, a process studied in some detail by Licitis-Lindbergs (1956) in *Agathis australis*. The distinctive physiognomy of *Araucaria* in New Caledonia and the reasons for it have been studied by Veillon (1976, 1978). Growth expression in examples of this model is accordingly very diverse and often distinctive; we have illustrated some of its variety.

Example. Duabanga sonneratioides (Sonneratiaceae, Malaysia) provides a good illustration of the model (Fig. 49A). The trunk with spirally arranged leaves produces a close series of branches as a result of its rhythmic growth. The branches are plagiotropic, with opposite leaves, and become pendulous with age. Growth units of the trunk are delimited clearly by variation in the shape and dimensions of the leaves as is shown by the detailed illustration of the apex (Fig. 49Ab). The level at which the terminal bud has undergone a period of rest is indicated by a series of scale leaves. As the meristem regains its activity there is a gradual increase in leaf size with the tier of three to five branches developing always at a specific level on this morphogenetic unit, in the axils of the largest leaves (Fig. 49Ab). Each branch develops by syllepsis. Subsequently, leaf size decreases abruptly as the apical meristem enters its next period of rest. Plagiotropy of the sylleptic branches is pronounced, leaves are opposite and consistently larger than those on the trunk; however, the periodicity of branch growth is not understood. Branching of these axes in turn is infrequent; it may or may not be the result of the terminal inflorescences which eventually develop.

Other Examples and Variations

1. Gymnosperms. Most of the species illustrated in Figures 48 and 49 are either treelets or represent stages in the development of tall trees. An exception is seen in Figure 50 Ab, which represents *Araucaria columnaris* (Araucariaceae, New Caledonia) at a height of 60 m. Throughout its life this tree conforms very precisely to the model (Fig. 47). A young tree, 15 m high (Fig. 50 Aa), shows the regularity of the architecture well. At this age there has been no self-pruning. Later there is considerable self-pruning, but also some replacement of primary branches by adventitious branches along the trunk in a quite regular manner, leading to the formation of a secondary crown. The process can be repeated so that a series of "nesting crowns" is produced (VEILLON, 1976, 1978).

Sexuality in *Araucaria* is closely linked with architecture, since female cones occur on second-order branches, male cones on third-order and replacement branches. This means that upper and distal parts are exclusively female. Plagiotropy in *Araucaria* generally is very strict, as shown by the classic experiments of VOCHTING (1904) on *A. heterophylla.* Massart's model is expressed with a similar precision in a number of temperate conifers ("Christmas trees") like species of *Abies, Picea* and to a lesser extent in *Taxus* and *Cephalotaxus* (NOZERAN and BOMPAR, 1965). In *Agathis australis* the symmetry is readily lost because branches lose their plagiotropy relatively easily.

2. Dicotyledons. Massart's model is important in illustrating the morphological diversity which can be accommodated within the physiological expression of plagiotropy, and indeed many examples approach other models, notably that of Rauh. The diversity includes foliar dimorphism, leaf arrangement, flower position, type of branching (either monopodial or sympodial), growth expression (rhythmic or continuous) and variation in the length of the units of growth.

Rhythmic growth of the branches, for example, is shown in *Litsea sebifera* (Lauraceae, Malaysia). This is a tall forest tree and Figure 49 B illustrates a young specimen, but already about 20 m high. Rhythmic growth of the branches is indicated by the conspicuous, regular fluctuation in leaf size along each branch. Zones of rest are indicated where scale leaves are developed. Flowers develop on the older parts in sites corresponding to zones originally supporting foliage leaves; here also occasional vegetative branches are developed. *Shorea ovalis* (Dipterocarpaceae, Malaysia; Fig. 50 Ca) shows this rhythmic branching most strikingly in the regular production of second-order branches (Fig. 50 Cb). These illustrations represent a tree before flowering, 7 m high, producing three to five first-order branches per tier. The frequency of rhythmic growth in first-order branches in examples of Massart's model is illustrated further by the diversity of families in which it has been seen, e.g., Myristicaceae (*Virola, Pycnanthus*; see H.O., 1970 and OLDEMAN, 1974a), Ebenaceae (*Diospyros*), Apocynaceae (*Aspidosperma* and *Lacmellea*), and Bombacaceae (*Ceiba*).

In contrast we may note other examples, which resemble *Duabanga,* with continuous growth of their branches. Figure 49 E shows a reiterated stump sprout in *Myristica subalulata* (Myristicaceae,

Fig. 47. Massart's model, *Araucaria columnaris* ▷ (Forst.) Hook (Araucariaceae) native to New Caledonia, here cultivated in Kenya, the symmetry very precise since the tree conforms strictly to the model

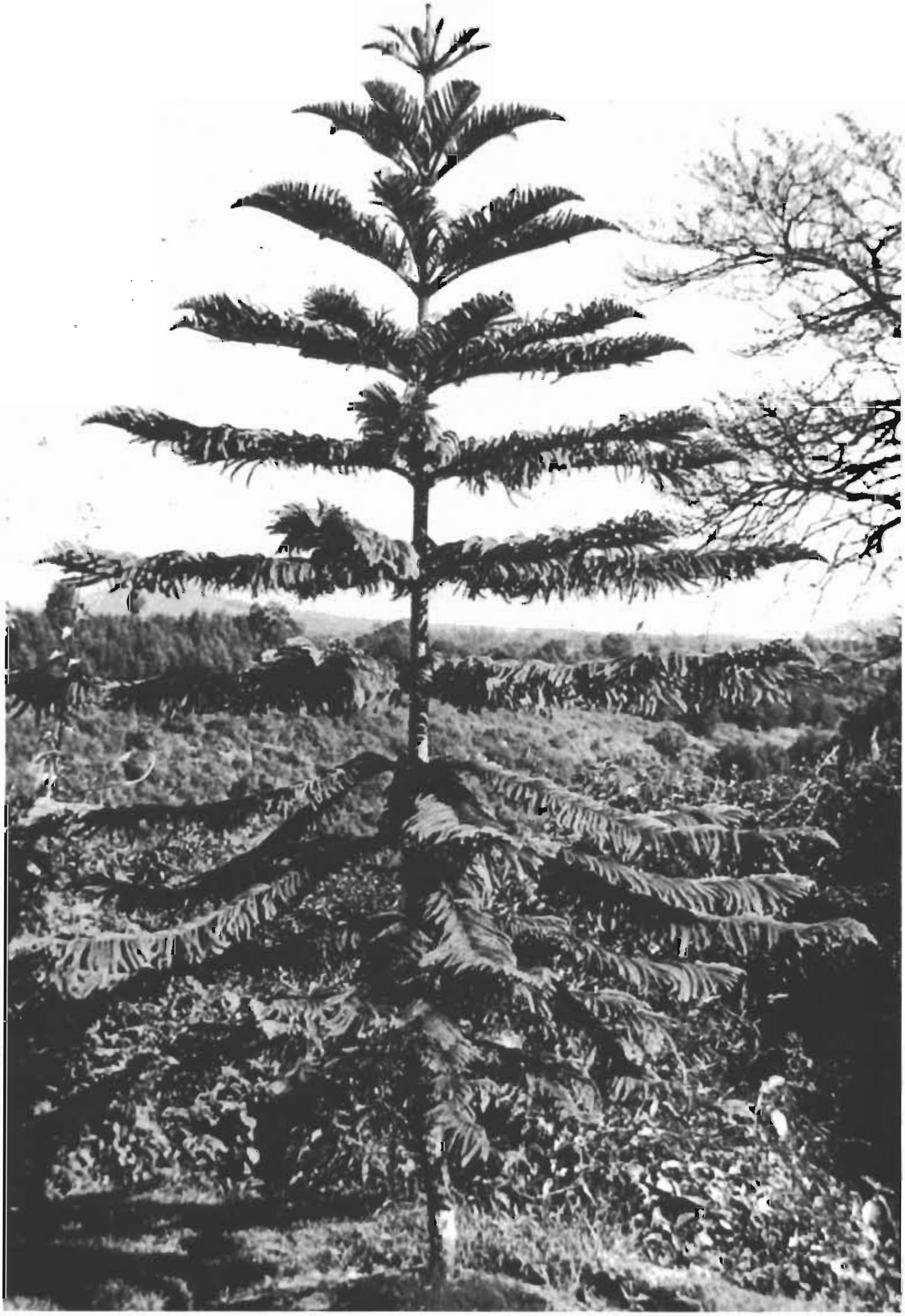


Fig. 48. Massart's model, *Diospyros sericea* A.DC. (Ebenaceae). Saut Maripa, Oyapock River, French Guiana. The tiered plagiotropic branches are clearly seen as branches with distichous leaves. A flush of growth initiated by the trunk meristem has just begun, this orthotropic shoot has spiral phyllotaxis

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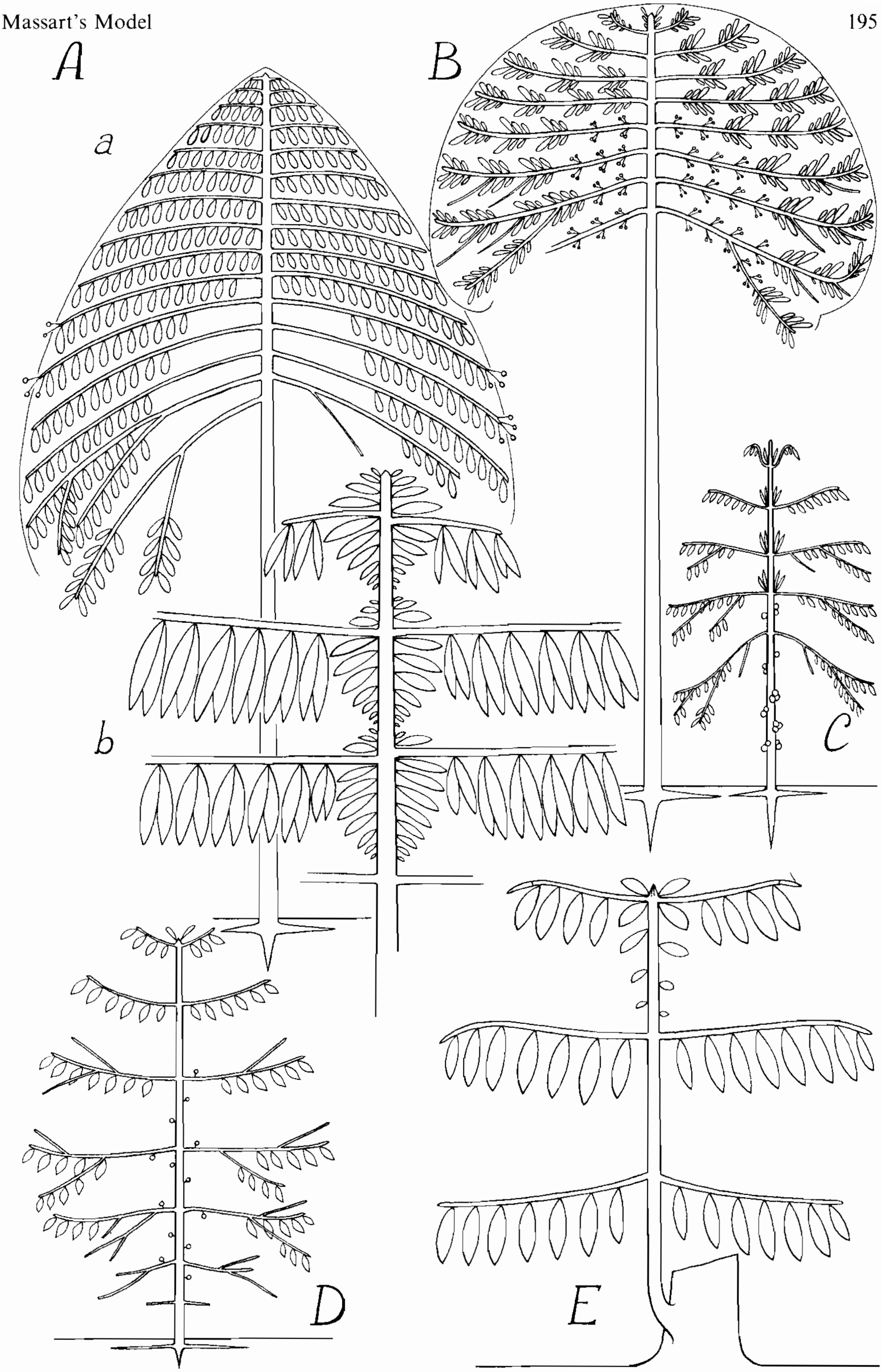
Fig. 49A–E. Massart's model. ▷

- *A* *Duabanga sonneratioides* Buch. Ham. (Sonneratiaceae, Fraser's Hill, Malaysia, *F. Hallé 2017 and 2018*). *a* General architecture of a young tree, 20 m high, with regular tiers including 3 to 5 branches per tier; *b* the top of the same tree; the leaves are alternate on the trunk, but opposite and much larger on the plagiotropic branches.
- *B* *Litsea sebifera* Bl. (Lauraceae, Malaysia, from the Botanic Gardens, Bogor, Indonesia). The general architecture of a young tree, 20 m high; the growth of the branches is clearly rhythmic.
- *C* *Napoleona leonensis* Hutch. and Dalz. (Lecythidaceae, Mvahdi Road, Gabon, *N. Hallé 3436*). A cauliflorous treelet, 2 m high, occurring in forest undergrowth.
- *D* *Diospyros matherana* (Mart.) A.C. Smith (Ebenaceae, Saül, French Guiana, *R.A.A. Oldeman 1973*). A cauliflorous treelet of the rain-forest undergrowth, up to 9 m high.
- *E* *Myristica subalulata* Miq. (Myristicaceae, New Guinea). A young reiteration shoot, 6 m high, arising from the stump of a large tree. The trunk and branches are hollow and inhabited by ants


A
a
b
B
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E

New Guinea). This is 6 m high and has produced three tiers of branches all with continuous growth. The trunk and branches in this tree are hollow and ant-inhabited.

Plagiotropy of branches is inherent in the definition of the model, and the diversity of growth expression is large, as further examples show. In the most distinctive examples leaf arrangement on the branches is distichous in comparison with the spiral arrangement on the trunk. Examples are found in species of *Aspidosperma, Virola, Pycnanthus* and some species of *Diospyros* cited below (e.g., Fig. 49D). The condition is illustrated in small trees of the undergrowth of African forest. *Napoleona leonensis* (Lecythidaceae, West Africa) is a treelet scarcely 2 m high occurring in forest undergrowth (Fig. 49C). Except on the seedling axes the spirally arranged leaves on the trunk are small and are lost early, so that the branches with their distichous leaves support the foliage. Flowering is essentially cauliflorous, but on the base of the branches as well as the trunk. In *Desplatsia chrysochlamys* (Tiliaceae, Fig. 50B) the tree may reach a height of 10 m and shows remarkable leaf dimorphism, with smaller, spirally arranged leaves on the trunk and larger distichously arranged leaves, each leaf obviously asymmetric, on the branches. Flowering here is axillary on the lower branches. This foliar dimorphism also characterizes *Theobroma grandiflorum, Pycnanthus dinklagei* and other species. In other examples the leaves on the branches are spirally arranged (less often decussate) but become displaced into a horizontal plane by a more or less precocious torsion of the internode which is most obvious in species with decussate leaves. *Qualea* cf. *rosea* (Vochysiaceae) shows this well, as do several species of *Eugenia* (Myrtaceae) in the West Indies and *Craterispermum* (Rubiaceae, tropical Africa). *Anisophyllea corneri* (Rhizophoraceae, Malaysia) express this dorsiventrality by unequal leaf size on upper and lower sides of the branch (Fig. 50D). Primary leaf arrangement in this species is spiral on trunk and branch, but only obvious on the trunk. On the branch the leaf arrangement recalls *Selaginella,* with a double series of scales on the upper surface and a double series of large leaves placed laterally (Fig. 11). The illustration (Fig. 50D) shows a seedling 40 cm high which has developed two tiers. Here the leaves on the trunk are scale-like and scarcely larger than those on the upper surface of the branch.

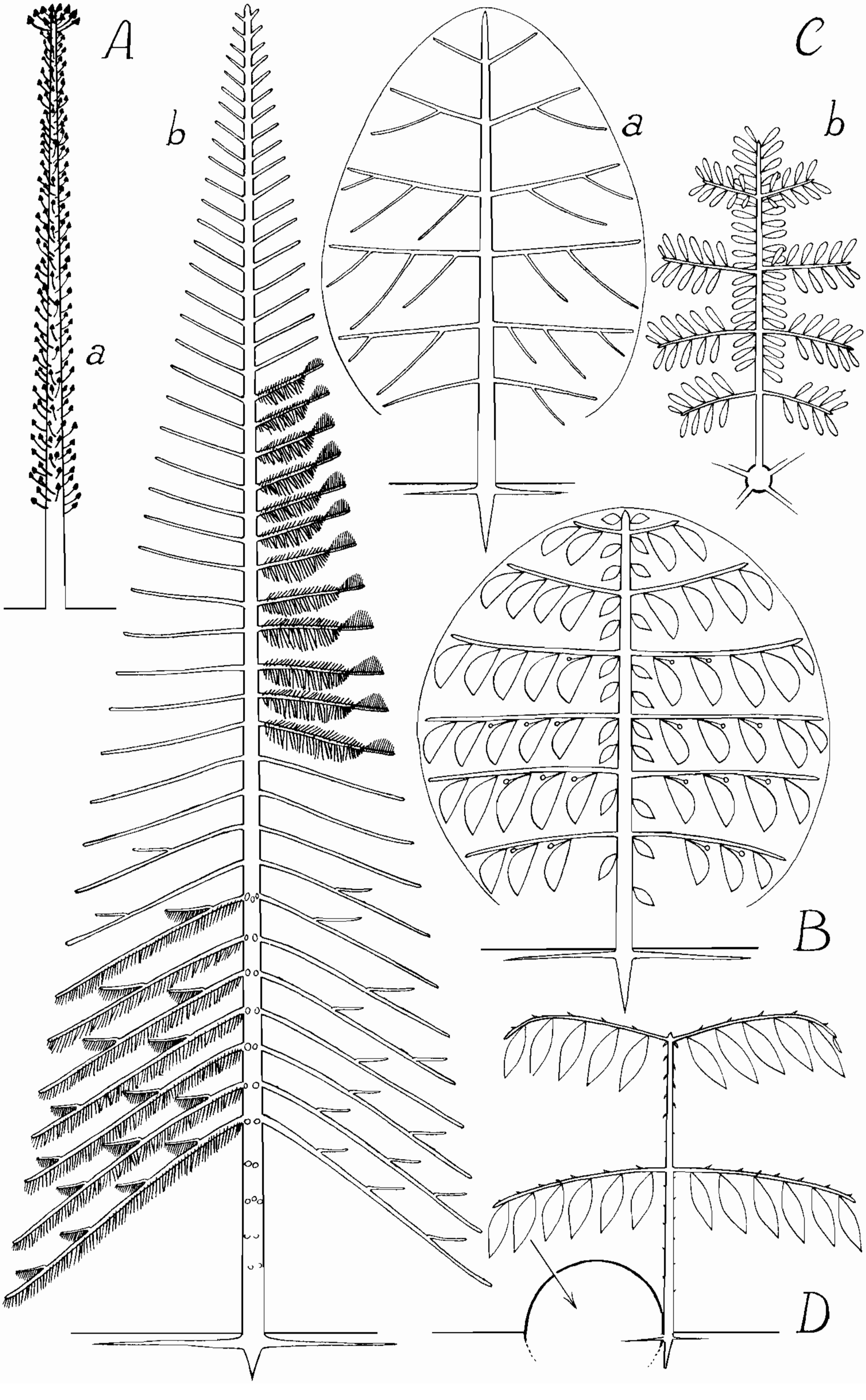
Fig. 50A–D. Massart's model (further examples). ▷

A *Araucaria columnaris* (Forst.) Hook. (Araucariaceae, New Caledonia, from a specimen cultivated in Tjibodas, Java). *a* Young tree, 15 m high, before any self-pruning of branches; *b* schematic outline of the mature tree, up to 60 m high; by self-pruning of the first-order branches, together with adventitious branching from the trunk itself, the tree gets its characteristic columnar appearance (SARLIN, 1954).

B *Desplatsia chrysochlamys* Mild. and Burret (Tiliaceae, tropical West Africa). A small tree of the rain-forest undergrowth, usually less than 10 m high. The leaves on the branches are strongly asymmetrical and larger than those on the trunk.

C *Shorea ovalis* Bl. (Dipterocarpaceae, Malaysia). *a* General architecture of a young vegetative tree, 7 m high, each tier includes 3–5 branches; *b* single first-order plagiotropic branch, seen from above showing that second-order branching is also rhythmic.

D *Anisophyllea corneri* Ding Hou (Rhizophoraceae, Malaysia, from a specimen cultivated in Bogor, Indonesia, *J. Dransfield 2396*). A seedling, 40 cm high, with two branch tiers (*arrow* indicates the seed). The main axis and the upper side of each branch bear scale leaves, from which anisophylly the generic name is derived


A
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b
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D

In some American Lauraceae (e.g., *Ocotea guianensis* and *O. splendens* illustrated by H.O., 1970, p. 99) plagiotropy is determined relatively late in the development of the branch, younger parts are initially upright, the horizontal position being achieved secondarily. However, plagiotropy, once established, remains fixed with differences between dorsal, ventral and lateral leaves (Fig. 12 D, E). A similar type of dorsiventrality is expressed by *Cordia* species, e.g., *C.* cf. *goeldiana, C. alliodora.* In *Ceiba pentandra* plagiotropy is least well expressed morphologically (Fig. 12C), since it results merely from the torsion of the petioles, but is strongly imposed physiologically. *Ceiba* is, nevertheless, a good example of Massart's model, the regular tiers of horizontal branches are familiar to every tropical botanist. *Taxus* and *Sequoia* species provide temperate, gymnospermous examples of the same phenomenon.

Nevertheless, these examples of less distinct branch plagiotropy illustrate how close is the approach to Rauh's model. We mention the example of *Rhamnus frangula* (Rhamnaceae, Massart's model) with a tendency towards orthotropy in its branches and *Malus pumila* (Rosaceae, Rauh's model) with a tendency towards plagiotropy of its branches.

Branching of the plagiotropic system is usually monopodial, but in some species, e.g., *Diospyros hoyleana* and *Napoleona leonensis,* it is sympodial. In the latter species, for example, the meristem of the plagiotropic branch is short-lived and aborts at the end of each period of growth.

From our comments it is clear that the position of flowers is quite variable, inflorescences on branches may be terminal (e.g., *Ceiba, Randia*) or lateral (e.g., *Lacmellea* and other Apocynaceae). Ramiflory is shown in *Pycnanthus,* with flowers on the older parts of the first-order plagiotropic branches, while in *Napoleona* (Fig. 49C) we have seen the transition to cauliflory. In *Iryanthera hostmannii* and female individuals of *Diospyros matherana* the branches are sterile and inflorescences are restricted to the trunk.

Length of the morphogenetic units of the trunk determines largely whether the tiers are distinct or not. In *Ceiba pentandra,* for example, the tiers are separated by over 1 m of trunk, but in many smaller trees the interval is only 10–30 cm and tiers are obscured to superficial observation (e.g., in species of *Martretia, Craterispermum, Pentadesma, Platonia, Myristica*). *Pycnanthus dinklagei* (Myristicaceae, West Africa) represents the other extreme since it is a liane, with the orthotropic trunk units slender and supple in their primary stage of growth (p. 252).

Strategy of the Model. Massart's model is mainly represented by forest trees, with a range in stature which includes all levels of the canopy. Large trees are represented by *Araucaria, Shorea* (and probably many other Dipterocarpaceae), *Qualea, Couratari, Litsea,* and *Ceiba.* Moderate-sized trees are represented by *Pycnanthus, Virola,* and *Anisophyllea.* Smaller, understorey trees include species of *Diospyros, Napoleona* and *Myristica.* The specialized plagiotropic organization of the branches confers a high individual survival potential (*K* strategy) in the lower storeys of the forest since light interception is efficient. These advantages are comparable to those in Aubréville's model. The success of this model in the tropical rainforest is to a limited extent repeated in temperate forests since it is represented by understorey trees like *Abies, Cephalotaxus* and *Taxus* amongst gymnosperms and *Ilex* amongst dicotyledons.

The special adaptability of the model in extreme environments is shown by *Abies balsamea* ("balsam fir") at timberline in eastern North America. This forms the characteristic "Krummholz" of mountain tops, a vegetation which results from the early loss of all orthotropic shoots by wind pruning. Plagiotropy is fixed and the branches continue to spread horizontally close to the ground, an ideal growth habit in such a biotope. Selection of genotypes undoubtedly is important in this adaptation, since it would increase the efficiency of a tree form which still allows a considerable amount of adjustment of the architecture.

Taxonomic List of Examples (Massart's Model)

GYMNOSPERMS

Araucariaceae:
**Agathis lanceolata* Warb., New Caledonia / * *Agathis moorei* Mast., S. Pacific / *Agathis ovata* Warb., New Caledonia, VEILLON, 1976 / *Araucaria columnaris* (Forst.) Hook. (Figs. 47, 50A), New Caledonia, VEILLON, 1976 / *Araucaria heterophylla* (Salisb.) Franco [= *A. excelsa* (Lamb.) R.Br.], "Norfolk Island pine", Norfolk Island.

Cephalotaxaceae:
**Cephalotaxus drupacea* Sieb. and Zucc., Japan / * *Cephalotaxus fortunei* Sieb. ex. Zucc., Japan, BOMPAR, 1974.

Pinaceae:
Abies alba Mill., Europe, DEBAZAC, 1966 / *Abies balsamea* (L.) Mill., "balsam fir", N. America / *Abies pectinata* DC., Europe, DEBAZAC, 1966.

Taxodiaceae:
Taxus baccata L., "yew", Europe, N. Africa / *Sequoia sempervirens* (D. Don) Endl., "redwood", W. N. America.

DICOTYLEDONS

Apocynaceae:
Aspidosperma megalocarpon Muell.-Arg., French Guiana / *Aspidosperma* sp., (Oldeman T-142), Guianas / *Lacmellea aculeata* (Ducke) Monach., French Guiana.

Alangiaceae:
Alangium bussyanum Harms, New Caledonia, VEILLON, 1976 / **Alangium chinense* (Lour.) Harms, Indonesia.

Aquifoliaceae:
Ilex aquifolium L., "holly", Europe / **Ilex cornuta* Lindl., E. China.

Bombacaceae:
**Ceiba pentandra* Gaertn., "kapok", Pantropical / **Chorisia speciosa* St. Hil., S. America / *Rhodognaphalon lukayense.* De Wild. and Dur.) Robyns, Trop. Africa.

Datiscaceae:
Octomeles sumatrana Miq., New Guinea, F. HALLÉ, 1974.

Dipterocarpaceae:
**Dipterocarpus costulatus* v. Sloot., Malaysia / * *Dipterocarpus trinervis* Bl., Indonesia / * *Shorea ovalis* Bl. (Fig. 50C), Malaysia.

Ebenaceae:
(Many species of *Diospyros*, the following are representative.) *Diospyros canaliculata* De Wild., W. Africa / *Diospyros conocarpa* Gürke and K. Schum., Congo / *Diospyros dichroa* Sandw., Trop. S. America / **Diospyros discolor* Willd., Philippines / *Diospyros heudelotii* Hiern, W. Africa / *Diospyros hoyleana* F. White, Congo / *Diospyros macrocarpa* Hiern, New Caledonia / *Diospyros matherana* (Mart.) A.C. Smith (Fig. 49D), Guianas / *Diospyros physocalicina* Gürke, Trop. Africa / *Diospyros* cf. *pseudoxylopia* Mildbr., (Oldeman 2165), French Guiana / *Diospyros sanzaminika* A. Chev., W. Africa / *Diospyros sericea* A.DC. (Fig. 48), Guianas / *Diospyros xanthochlamys* Gürke, Ivory Coast.

Euphorbiaceae:
Aporusa sp., (F. Hallé 1950), New Guinea / **Euphorbia bubalina* Boiss., S. Africa / +*Euphorbia wakefieldii* Haw., E. Africa / *Martretia quadricornis* Beille, Trop. Africa / *Sapium aucuparium* Jacq., Antilles.

Guttiferae:
**Platonia insignis* Mart., Trop. America.

Lauraceae:
**Litsea sebifera* Bl. (Fig. 49B), Malaysia / *Ocotea guianensis* Aubl., (Fig. 12D) Guianas / *Ocotea splendens* (Meissn.) Mez, (Fig. 12E) French Guiana.

Lecythidaceae:
Couratari cf. *stellata* A.C. Smith, French Guiana / *Napoleona leonensis* Hutch. and Dalz. (Fig. 49C), Trop. Africa / *Napoleona vogelii* Hook. and Planch., W. Africa.

Loganiaceae:
[L] **Strychnos horsfieldiana* Miq., Indonesia / [L] *Strychnos* sp., (F. Hallé, 1798), Congo.

Myristicaceae:
Coelocaryon oxycarpum Stapf, Trop. Africa / **Horsfieldia globularia* Warb., Java / *Iryanthera hostmanii* (Benth.) Warb., French Guiana / **Myristica fatua* Houtt., Moluccas / *Myristica fragrans*

Houtt., "nutmeg", Moluccas / *Myristica subalulata* Miq. (Fig. 49E), New Guinea / *Pycnanthus angolensis* (Welw.) Warb., Trop. Africa, F. HALLÉ, 1971 / [L] *Pycnanthus dinklagei* Warb. (Fig. 69E), Ivory Coast, CREMERS, 1973 / *Staudtia gabonensis* Warb., C. Africa / **Virola melinonii* (R. Ben.) A.C. Smith, Guianas / *Virola surinamensis* (Rol.) Warb., Trop. S. America, MASSART, 1923.

Myrsinaceae:
**Ardisia crenata* Sims., Japan, frequently cultivated / **Ardisia polycephala* Wall., Burma, cultivated.

Myrtaceae:
**Eugenia confusa* DC., West Indies.

Olacaceae:
Heisteria coccinea Jacq., Martinique.

Rhamnaceae:
Rhamnus frangula L., Europe.

Rhizophoraceae:
Anisophyllea corneri Ding Hou. (Fig. 50D), Malaysia / *Anisophyllea disticha* Baill., Malaysia, KORIBA, 1958 / *Anisophyllea* sp., (F. Hallé 1534 and 1499), C. Africa / **Carallia* cf. *urophylloides*, Malaysia / *Gynotroches axillaris* Bl., Malaysia.

Rubiaceae:
Craterispermum caudatum Hutch., Trop. Africa / *Randia ruiziana* DC., French Guiana

Sonneratiaceae:
Duabanga sonneratioides Buch. Ham., (Fig. 49A), Malaysia.

Sterculiaceae:
Theobroma grandiflora (Wild. ex Spreng.) Schum., Trop. America / *Theobroma microcarpa* Mart., Trop. America.

Tiliaceae:
Desplatsia chrysochlamys Mild. and Burret, (Fig. 50B), West Africa

Vochysiaceae:
Qualea cf. *rosea* Aubl., Trop. S. America.

Roux's Model

Definition. The architecture is determined by a monopodial orthotropic trunk meristem which shows continuous growth; branches are plagiotropic (but never by apposition) and inserted continuously (rarely diffusely). Leaf arrangement is spiral on the trunk but in contrast is most often distichous on the branches. Flowering is variable, but mainly lateral on the branches and does not influence the architecture.

The model is named after JACQUES ROUX in recognition of his contribution to our understanding of plagiotropy as a consequence of his investigation of the pantropical genus *Phyllanthus* (Euphorbiaceae; ROUX, 1968). The significance of plagiotropy in the architecture of tropical trees will have become evident in our description of models with differentiated branches.

The model is very close to Massart's model, from which it differs in the continuous, not rhythmic, growth and branching of the trunk. Similarities with Petit's model are also evident, the distinction between the two models being the nature of the plagiotropic branches. The most familiar example of this model is coffee (i.e., some species of *Coffea,* Rubiaceae, Fig. 51) which has been investigated and described by several workers (e.g., DE MARCHAND, 1864; COOK, 1911; MASSART, 1923; ARNDT, 1929; VAROSSIEAU, 1940; CARVALHO et al., 1950; MOENS, 1963; LEROY, 1973). Knowledge of its architecture is used in its cultivation (see below).

Example. Here we exemplify the model by *Shorea pinanga* (Dipterocarpaceae, Borneo), a large tree up to 30 m high (Fig. 52A). Growth of the trunk is continuous and produces a continuous series of plagiotropic branches which become pendulous with age. Flowering is either terminal or lateral on the branches which themselves also grow continually but branch infrequently.

Other Examples. The continuous growth, which so often results in continuous branching and which defines the model, is often most obvious in sucker sprouts because of their vigorous growth. Two further examples illustrate this; Figure 52B shows *Adinandra dumosa*

Fig. 51. Roux's model, *Coffea arabica* L. (Rubiaceae), Entebbe, Uganda. Flowering of plagiotropic branches produced continuously by nonflowering trunk axis

(Theaceae, Indonesia) as a stump sprout 4 m high and Figure 52D shows *Casearia papuana* (Flacourtiaceae, New Guinea) at a somewhat earlier stage. In the latter example there is pronounced dimorphism between leaves on trunk and branch, a condition which brings us close to Cook's model, next to be described.

The examples all refer to sizeable trees, but Figure 52E shows the same model in *Heisteria trillesiana* (Olacaceae, Congo), which scarcely reaches 10 m in height.

So far we have dealt with species with lateral flowers (sometimes terminal in *Shorea pinanga*) and it seems significant that these are restricted to the branches, as further evidence for the differentiation between trunk and branch. However, in *Gonzalagunia dicocca* (Rubiaceae, Guianas, Fig. 52C), a common shrub of the secondary forest, scarcely 4 m high, branching of the plagiotropic system is correlated with terminal flowering. Figure 52Ca shows the architecture of the plant with continuous trunk growth resulting in a pair of branches at each node. Pendulous inflorescences are terminal on the branches resulting in sympodial growth by substitution, as is best shown in the plan of a branch pair in Figure 52Cb. This example is clearly transitional to Petit's model.

Branching of the trunk is much less frequently diffuse, as shown in Figure 52F, which represents *Tachia guianensis* (Gentianaceae, Guianas). This reaches a height of 4 m, with decussate phyllotaxis. The orthotropic axis produces one, two or no branches at each node but no distinct tiers resulting from rhythmic growth can be distinguished as in Massart's model. Flowers on the plagiotropic branches are all lateral in the axils of leaves, orientated to occupy one plane (Figs. 3A, B and 52F).

The existence of plagiotropy in Roux's model is of significance in coffee in relation to its cultivation and has provoked experimental work. *Coffea arabica* ("Arabian coffee") is a small tree and scarcely reaches 8 m if grown without pruning, whereas *Coffea liberica* ("Liberian coffee") may grow to 20 m. Both heights are still inconvenient for easy harvesting and in cultivation the trunk is usually decapitated. This stimulates further growth of orthotropic shoots, always from latent meristems on the existing trunk, which in turn may be decapitated. Thus a tree of modest dimensions is obtained and in addition growth of new and existing plagiotropic branches is promoted. CARVALHO et al. (1950) have shown that plagiotropy in *C. arabica* is irreversible; if branches are propagated by cutting, a plagiotropic coffee plant can be produced although this is difficult.

Variations. Much of the variation in Roux's model relates to the growth and construction of the plagiotropic shoots and parallels the range found in Massart's model. The subject has been dealt with fairly fully in H.O.,1970, pp. 108–110, and only a brief summary is included here.

In most examples the branches are monopodial, but with the inflorescence either lateral or terminal. In *Vismia augusta* (Guttiferae) branches are sympodial but not modular with a succession of segments, each with a terminal inflorescence. This example is not included in Petit's model because the axes of the sympodium lack the stereotyped character of modules; nevertheless, a tendency towards Petit's model is clear. Branches themselves exhibit different levels of plagiotropy in different species. In one group of species the apical meristem of the branch preserves a radial symmetry like that of the trunk, but with secondary reorientation often associated with some degree of anisophylly. Examples include species of *Notobuxus, Coffea, Octoknema, Cassipourea,* and *Symphonia.* MASSART (1923) has described in some detail these different mechanisms whereby dorsiventrality is achieved.

In a second group of species the plagiotropy of the branch is underlain by a distichous primary leaf arrangement which differs from the radial arrangement in the trunk (spiral or decussate). Examples are to be found in the genera *Coula, Heisteria, Pachypodanthium, Bertholletia, Microdesmis,* and *Goupia.*

This differentiation between orthotropic and plagiotropic axes is particularly well shown by species in the pantropical genus *Trema* (Ulmaceae) in which, however, there is a tendency for a sponta-

Fig. 52A–F. Roux's model. ▷

A *Shorea pinanga* Scheff. (Dipterocarpaceae, Kalimantan, from the Botanic Garden at Bogor, Indonesia). A large tree, up to 25 m high, with long pendulous plagiotropic branches.

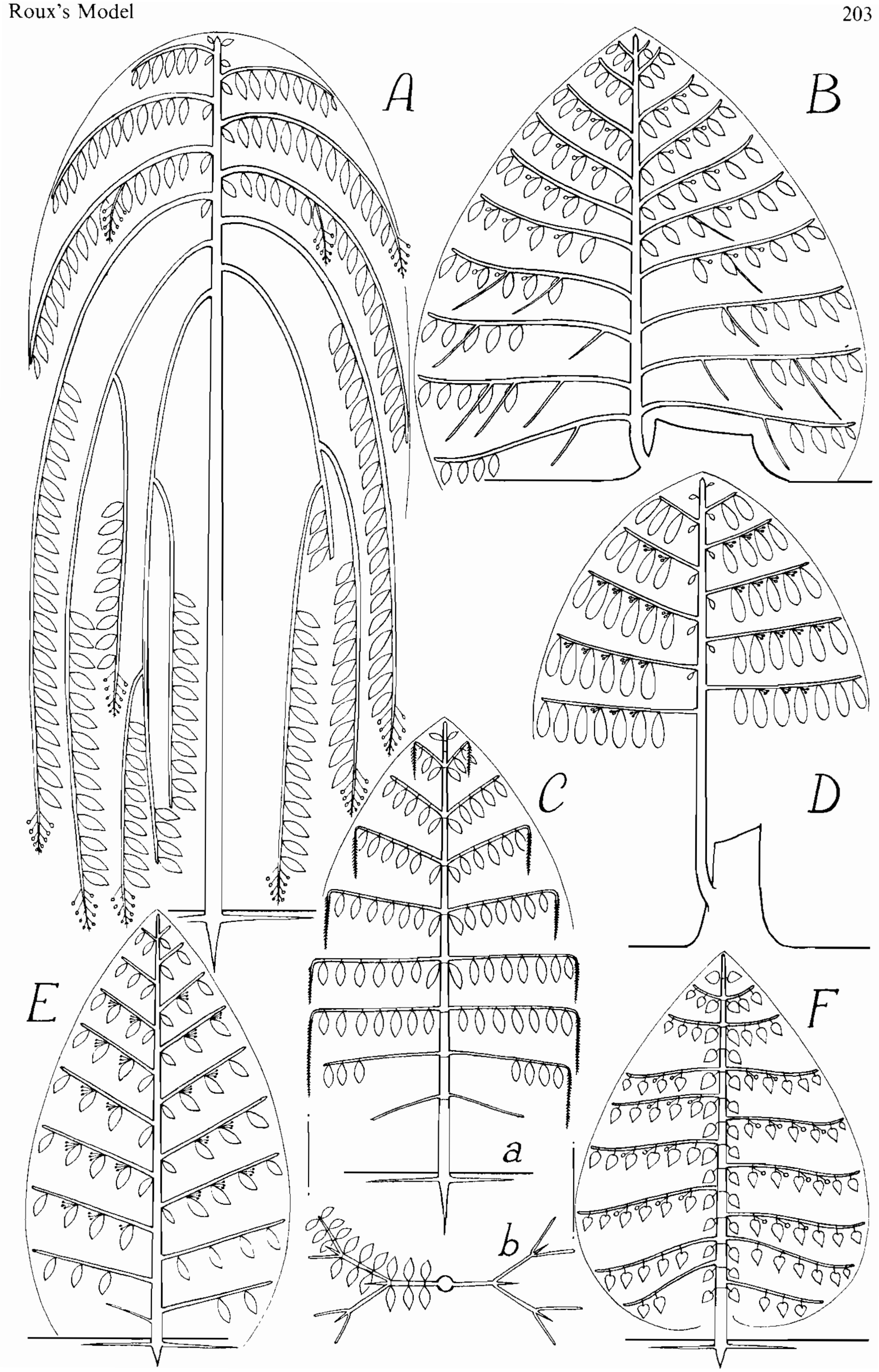
B *Adinandra dumosa* Jacq. (Theaceae, Sumatra, from the Botanic Garden at Bogor, Indonesia). A young reiteration shoot, 4 m high, arising from the stump of a large broken tree.

C *Gonzalagunia dicocca* Ch. and Sch. (Rubiaceae, secondary forest near Saül, French Guiana, *F. Hallé 2297*). *a* General architecture of the shrub, 4 m high; *b* a pair of plagiotropic branches, showing the terminal flowering and the sympodial growth.

D *Casearia papuana* Sleum. (Flacourtiaceae, New Guinea). A stump sprout, 2 m high; leaves on the trunk are very small.

E *Heisteria trillesiana* Pierre (Olacaceae, river bank at Foulakari, Congo, *F. Hallé 1466*). A small tree, up to 10 m high.

F *Tachia guianensis* Aubl. (Gentianaceae, Iracoubo, French Guiana, *R.A.A. Oldeman 2182*). A shrub, 3 m high, with axillary inflorescences on plagiotropic branches; diffuse branching


A
B
C
D
E
F
a
b

neous reversion to the orthotropic condition in the distal parts of longer branches, which suggest that the change might be conditioned by the distance between two active meristems, a feature we have noted in *T. orientalis* (Old World tropics) as well as *T. micrantha* (New World tropics).

Differences between the leaves borne on trunk and branch may also occur. In *Coffea arabica,* for example, there is no such difference. In other genera, the leaves on the trunk are symmetrical, while those on the branches are more or less asymmetrical about the midribs, a difference most obvious at the leaf base. *Celtis integrifolia* (Ulmaceae) shows this well. In a final group of species leaves on the trunk are smaller than those on the branch (e.g., species of *Notobuxus, Goupia, Microdesmis,* and *Phyllanthus*). This differentiation is carried further in Cook's model.

Strategy of the Model. Giant forest trees are rare in this model and where an example does exceptionally occur, as in *Goupia glabra,* the exception seems to be made possible here by the series of supernumerary buds which permits proliferation of axes. This species is still very vulnerable to shade (SCHULZ, 1960). Examples of Roux's model seem particularly common in the understorey of the forest, a situation to which the pronounced plagiotropy of the branches adapts because of a presumed greater efficiency of light interception. However, a number of species which conform to this model are characteristically weedy species of open, disturbed sites. Species of *Trema* and *Phyllanthus* provide examples. These have lateral flowers and continuous branching, suggesting that the model is well suited to an *r* strategy in rapidly growing species with small disseminules.

The common denominator of the distinct biotopes where Roux's model is to be found is clearly the constancy of the climate, be it the macroclimate of open sites or the microclimate of the lower forest storeys. The continuous character of both vegetative growth and reproduction are in keeping with such environmental conditions; it might serve either a *K* or an *r* strategy according to the biotic features of the biotope, i.e., the nature of competitors and predators.

Taxonomic List of Examples (Roux's Model)

GYMNOSPERMS

Gnetaceae:
Gnetum gnemon L., Trop. Asia, H.O. 1970.

DICOTYLEDONS

Alangiaceae:
**Alangium salvifolium* Wanger., India.
Annonaceae:
Cananga odorata Hook. f. and Thomas, "ylang-ylang", Malaysia, VEILLON, 1976 / *Cardiopetalum surinamense* Fries, French Guiana / *Duguetia* cf. *obovata* Fries, (Oldeman 2762), French Guiana / *Guatteria* cf. *ouregou* (Aubl.) Dun., (Oldeman 2512), French Guiana / *Pachypodanthium staudtii* Engl. and Diels, Trop. Africa / **Polyalthia lateriflora* (Bl.) King, Indonesia / **Polyalthia longifolia* Benth. and Hook., Malaysia / *Xylopia aethiopica* (Dunal) A. Rich. / *Xylopia discreta* Spr. and Hutch., French Guiana, OLDEMAN, 1974.
Apocynaceae:
**Alyxia ruscifolia* R.Br., Australia.
Bombacaceae:
**Durio zibethinus* Murray, "durian", Malaysia.
Buxaceae:
Notobuxus acuminata (Gilg.) Hutch., Trop. Africa, ROUX, 1964–1965.
Capparidaceae:
Capparis decidua (Forsk) Edgew., Chad / *Capparis tomentosa* Lam., Cameroons.
Celastraceae:
[L] *Celastrus crenatus* Forst., Marquesas / *Goupia glabra* Aubl., French Guiana.
Davidiaceae:
**Davidia involucrata* Wanger., China.

Dichapetalaceae:
Dichapetalum angolense Chod., Ivory Coast / [L] *Dichapetalum* sp., Trop. Africa, Breteler, 1973.

Dipterocarpaceae:
+*Dipterocarpus zeylanicus* Thw., Sri Lanka / **Dryobalanops aromatica* Gaertn., Malaysia / **Dryobalanops lanceolata* Burch., Kalimantan / **Hopea odorata* Roxb., Trop. Asia / **Shorea foxworthii* Sym., Malaysia / **Shorea pinanga* Scheff. (Fig. 52A), Kalimantan.

Escalloniaceae:
Kaliphora madagascariensis Hook., Madagascar.

Euphorbiaceae:
Drypetes aylmeri Hutch. and Dalz., W. Africa / *Drypetes chevalieri* Beille, W. Africa / **Galearia filiformis* Boerl., Sumatra / *Glochidion* sp., (F. Hallé 1973), New Guinea / *Microdesmis puberula* Hook. ex Planch., W. Africa, Roux, 1968; F. Hallé, 1971 / *Phyllanthus discoïdeus* (Baill.) Muell.-Arg., Trop. Africa / *Phyllanthus koghiensis* Guill., New Caledonia, Veillon, 1976.

Flacourtiaceae:
Casearia bracteifera Sagot, French Guiana / **Casearia papuana* Sleum. (Fig. 52D), New Guinea / *Casearia* sp., (F. Hallé 1449), Congo / *Homalium molle* Stapf, W. Africa / *Hydnocarpus anthelminticus* Pierre, Vietnam, Mendes, 1950 / *Ryania speciosa* Vahl, Guianas.

Gentianaceae:
Tachia guianensis Aubl. (Fig. 52F), French Guiana.

Guttiferae:
Symphonia globulifera L.f., French Guiana, Oldeman, 1974 / *Vismia augusta* Miq., Guianas.

Hippocrateaceae:
[L] *Cuervea macrophylla* (Vahl) Wilczek ex N. Hallé, Trop. Africa, Cremers, 1973 / *Salacia* cf. *pronyensis* Guill., New Caledonia, Veillon, 1976.

Icacinaceae:
Medusanthera laxiflora (Miers) Howard, New Guinea, F. Hallé, 1974.

Lauraceae:
[L] *Cassytha filiformis* L., Zaire / *Cryptocarya* sp., New Caledonia, Veillon, 1976.

Lecythidaceae:
Bertholletia excelsa Humb. and Bonpl., "brazil-nut", Brazil.

Leguminosae:
Sesbania sp., (F. Hallé 1762), Congo.

Linaceae:
Aneulophus africanus Benth., Congo.

Loganiaceae:
**Fagraea racemosa* Jack, Australia, New Guinea.

Magnoliaceae:
Elmerillia papuana Dandy, New Guinea / **Michelia velutina* Bl., Java.

Monimiaceae:
**Siparuna guianensis* Aubl., Guianas.

Moraceae:
Antiaris welwitschii Engl., Trop. Africa / **Artocarpus sepikana* Diels, New Guinea / *Chlorophora regia* Chev., "iroko", Trop. Africa / *Perebea guianensis* Aubl., Guianas.

Ochnaceae:
**Ochna kirkii* Oliver, Trop. Africa / *Ouratea affinis* Engl., Ivory Coast.

Octocnemaceae:
Octocnema borealis Hutch. and Dalz., Trop. Africa.

Olacaceae:
Coula edulis Baill., Trop. Africa / *Heisteria trillesiana* Pierre (Fig. 52E), Congo / *Strombosia glaucescens* Engl., Trop. Africa.

Polygonaceae:
Coccoloba latifolia Lam., French Guiana.

Rhamnaceae:
Alphitonia excelsa Reiss., Marquesas / *Alphitonia* cf. *incana* (Roxb.) Teys., New Guinea / *Colubrina asiatica* Brongn., Marquesas / *Lasiodiscus mildbraedii* Engl., Congo / *Maesopsis eminii* Engl., Trop. Africa / *Paliurus australis* Gaertn., Europe, Roux, 1968.

Rhizophoraceae:
Cassipourea barteri (Hook. f.) N.E.Br., Ivory Coast / *Cassipourea nialatou* Aubr. and Pellegr., Ivory Coast.

Rubiaceae:
Bertiera racemosa (G. Don.) K. Schum., Trop. Africa, F. Hallé, 1967; Leroy, 1974b / *Chapeliera muelleri* K. Schum., Madagascar / *Coffea arabica* L. (Fig. 51), "Arabian coffee", Ethiopia / *Coffea liberica* Bull. ex Hiern, "Liberian coffee", W. Africa / *Colletoecema dewevrei* (De Wild.) Petit, Congo / *Gaertnera* sp., (F. Hallé 2010), Malaysia / *Gonzalagunia dicocca* Ch. and Sch. (Fig. 52C), French Guiana / *Monosalpinx guillaumetii* N. Hallé, Ivory Coast, N. Hallé, 1968 / *Pauridiantha hirtella* (Benth.) Bremek., Trop. Africa / *Tricalysia gossweilerii* S. Moore, Gabon, F. and N. Hallé, 1965 / *Urophyllum* sp. (F. Hallé 1996), Java.

Sapotaceae:
Chrysophyllum subnudum Bak., Trop. Africa.

Scrophulariaceae:
Halleria tetragona Bak., Madagascar.

Solanaceae:
Cestrum latifolium Lam. var *tenuiflorum*, French Guiana.

Styracaceae:
**Styrax benzoin* Dryand., Malaysia.

Theaceae:
**Adinandra dumosa* Jacq. (Fig. 52B), Sumatra.

Tiliaceae:
Grewia, sp., (F. Hallé 2343), Madagascar / **Guazuma ulmifolia* Lam., Trop. America.

Ulmaceae:
Celtis integrifolia Lam., W. Africa / *Trema cannabina* Lour., New Guinea / *Trema floridana* Britton, W. Indies, TOMLINSON and GILL, 1973; TOMLINSON, 1978 / *Trema micrantha* Bl., Trop. America / *Trema orientalis* (L.) Bl., Trop. Africa.

Cook's Model

Definition. The architecture is the result of continuous growth of a monopodial trunk with spiral or decussate phyllotaxis on which branches are produced continuously; branches are phyllomorphic and inflorescence position does not influence the architecture.

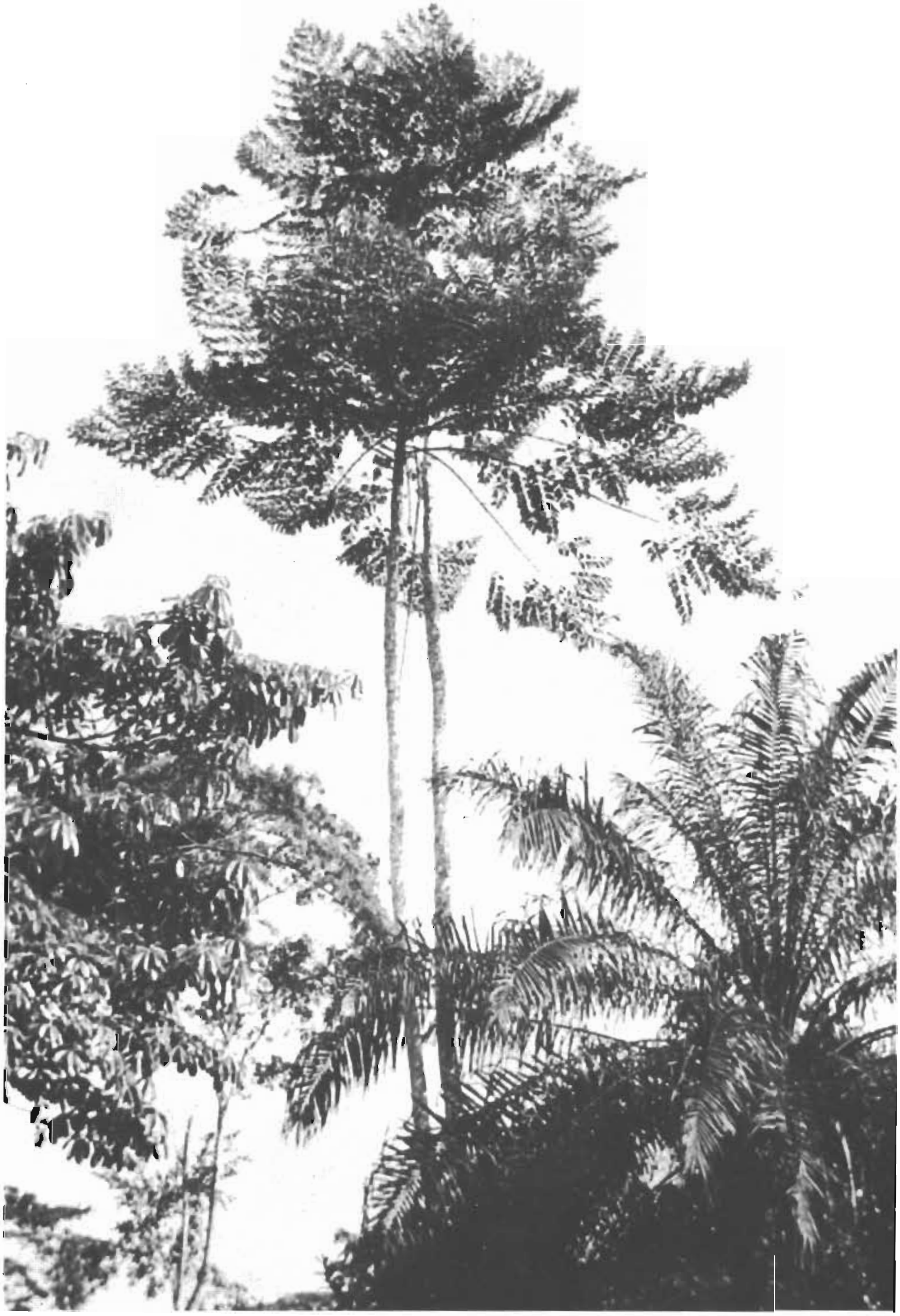
This model (Fig. 53) differs from the preceding one in the existence of phyllomorphic branches (as defined by HALLÉ, 1967, from a term coined by CORNER, 1949), i.e., axes which are morphologically recognizable as branches, but which are equivalent to compound leaves as functional units (Fig. 54). This topic has been discussed in the earlier section which described the continuum of branch types (Fig. 12) and only the outline is repeated here.

The model is dedicated to O.F. COOK, the agronomist, who in his detailed study of the Central American rubber tree (*Castilla elastica,* Moraceae) described the architecture and biology of the tree in drawing attention to the phenomenon of branch dimorphism in tropical trees (COOK, 1903, 1911).

Examples. The appearance of *Castilla elastica* is familiar to the traveller in the American tropics since it is often cultivated and is very striking. It forms a large tree, to 20 m high with numerous slender, spreading branches (Fig. 54A) which stand out almost at right angles to the trunk. Growth is continuous, the trunk axis producing spirally arranged small leaves, each of which subtends a sylleptic branch, which is plagiotropic with a distichous series of pendulous, shortly petiolate leaves. Flowers are restricted to the older parts of the branches, developing as clusters at nodes from which the leaves have fallen. Growth of the orthotropic axis is rapid, so that a height of 5 m may be achieved in 18 months (COOK, 1903). The branches have a limited life span (they are described as temporary by COOK) and though they may reach a length of 4 m, their basal diameter rarely exceeds 2.5 cm. Eventually they abscise to leave a conspicuous sunken scar. COOK (1911) also recognized "permanent branches" in his description, distinguished by their more erect posture. longer life span and origin in an extra-axillary position, but at the base of a "temporary branch". We can now recognize these as reiterated trunks which initiate new models. They develop by prolepsis, either from dormant meristems or possibly adventitiously. COOK (1911) noted that only the orthotropic ("vegetative") branches could be used to propagate the tree, the flowering branches would not take root.

Schumanniophyton magnificum (Rubiaceae, Central Africa) described by HALLÉ (1962) illustrates Cook's model in a striking way (Fig. 54B). The phyllomorphic branch which rarely exceeds 1 m is here reduced to three leaves ($1^1/_2$ pairs) and terminates in an inflorescence (Fig. 54Bb). In *Barteria fistulosa* (Passifloraceae, Central Africa) the phyllomorphic branches are subtended by minute leaves (Fig. 54Ca); each branch is somewhat over a meter long, with distichous

Fig. 53. Cook's model, *Canthium glabrifolium* ▷ Hiern (Rubiaceae), West Africa, with a determinate plagiotropic branch complex at each node on the trunk axis



leaves (Fig. 54Cb). The proximal part of the axis is smaller and ant-inhabited, the ants gaining access via holes on the upper surface of the branch. JANZEN (1972) has shown in Nigeria that *Pachysima* ants which make these nests have a protective function for *Barteria*.

As a final example, also from Central Africa, we have illustrated *Glossocalyx longicuspis* (Monimiaceae). Branching is initiated in seedlings about 20 cm tall (Fig. 54Da) and is continuous and sylleptic. The base of each phyllomorphic branch is swollen; upon abscission of the branch, which occurs after a relatively short time, a prominent branch scar is left (Fig. 54Db).

Variations. We can mostly present information which establishes the distinctiveness of Cook's model if we indicate some of the biological pecularities of its examples.

In many of the species listed below, notably in the genera *Barteria, Cicca, Glochidion, Panda, Ryania,* but especially *Phyllanthus* (ROUX, 1968) the orthotropic axis lacks assimilating leaves, except in the juvenile state before branching begins. In all these examples the transition from assimilating to scale leaves on the trunk coincides more or less exactly with the onset of branching so that branches are only subtended by scale leaves. These scales are often quite ephemeral so that the axillary position of the branch is indicated by a scale-leaf scar or a scar plus stipule scars. We may then speak of a "nonassimilating" trunk, with assimilation assured only by the phyllomorphic branches. The leaf-like character of the phyllomorphic branches is emphasized by their determinate growth, dorsiventrality and limited branching. In *Panda oleosa, Castilla elastica,* and *Schumanniophyton magnificum* we have observed that the apical meristem of the branch produces no axillary meristems; in *Phyllanthus muellerianus* ROUX (1968) indicated that the axils of the leaves on the branches were generally empty.

In some examples propagation of the phyllomorphic branch by either cuttings or marcottage is impossible, as we have mentioned for *Castilla elastica* after COOK (1903, 1911) and has been demonstrated in *Schumanniophyton magnificum* by HALLÉ (1967). In herbaceous species of *Phyllanthus* the experiments of ROUX (1968) showed variation from one species to another. In *P. niruroides* branch propagation was possible, with the indefinite prolongation of plagiotropy. In *P. urinaria,* by contrast, the functional duration of the meristem is fixed and branches cannot be propagated. This inability to propagate may in part be related to the feeble development of secondary vascular tissue or even its total absence.

In some species, notably *Castilla elastica, Glossocalyx longicuspis, Phyllanthus*

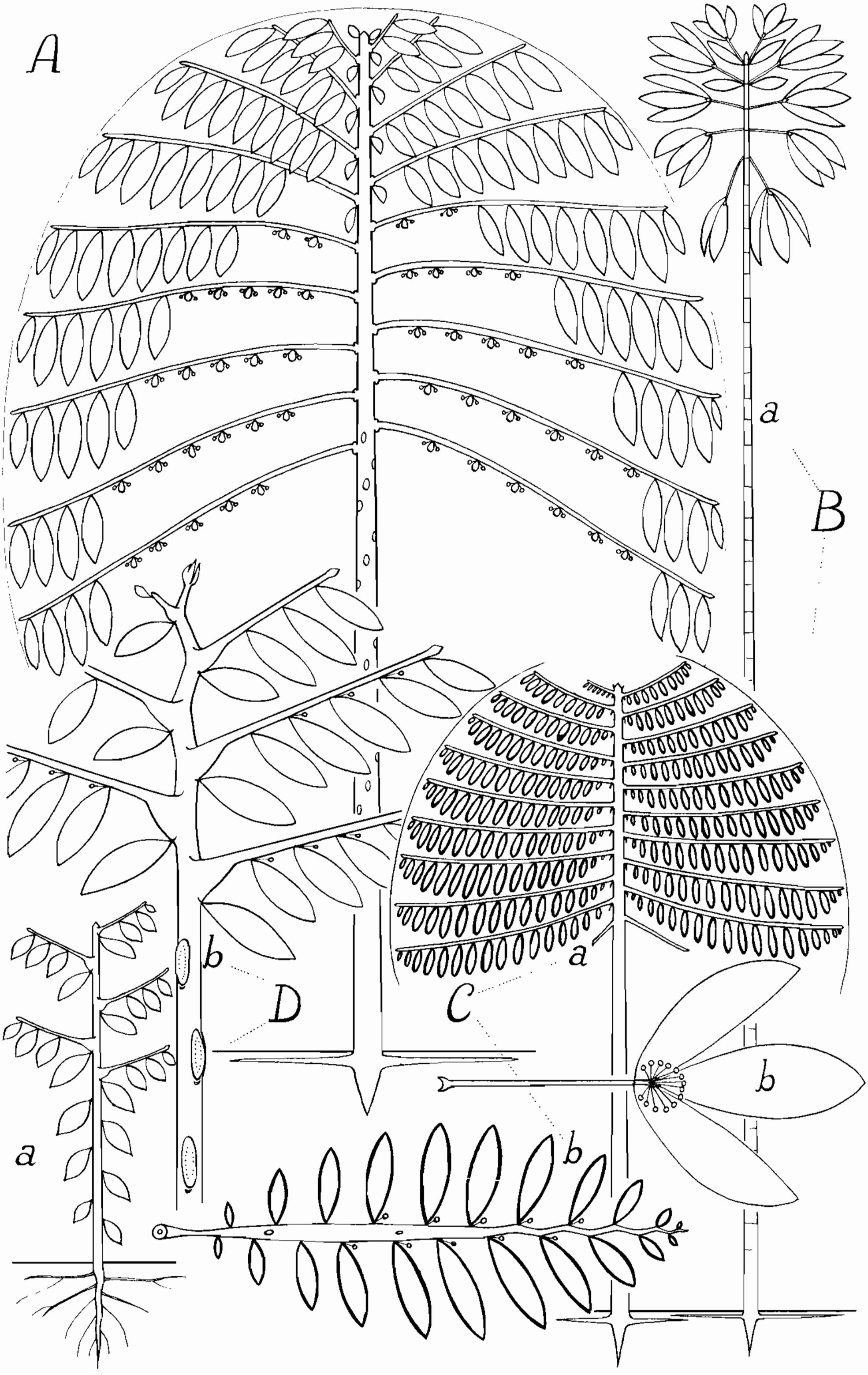
Fig. 54 A–D. Cook's model. ▷

A *Castilla elastica* Cervantes (Moraceae, the Central American rubber tree). A large tree, up to 20 m high, with phyllomorphic branches up to 4 m long (COOK, 1903).

B *Schumanniophyton magnificum* (K. Schum.) Harms (Rubiaceae, equatorial West Africa). *a* General architecture of this slender tree, 15 m high; *b* a phyllomorphic branch, 1 m long, with its apical inflorescence (HALLÉ, 1967).

C *Barteria fistulosa* Masters (Passifloraceae, equatorial West Africa). A small tree of the secondary forest, up to 10 m high. *a* General architecture, leaves on the trunk are small; *b* the phyllomorphic branch, 130 cm long, seen from above, showing the holes of the ant's nests.

D *Glossocalyx longicuspis* Benth. (Monimiaceae, Abanga, Gabon, *N. Hallé 2182*). A treelet of the primary forest undergrowth, up to 12 m high. *a* A young plant 30 cm high, showing the first branching; *b* the top of a full-grown tree, showing self-pruning (N. and F. HALLÉ, 1965)


A
a
B
b
D
a
C
b
b
a

mimosoides, *Ryania speciosa* var. *bicolor*, *Schumanniophyton magnificum* the branches are deciduous, with a definite abscission layer developing at the insertion just as in a leaf. Branch scars, however, are often elongated in contrast to most leaf scars. In *Castilla* the scars are deeply sunken.

In at least two examples, *Panda oleosa* and *Phyllanthus muellerianus*, a further step in the direction of a leaf is taken by the branches because they are sterile, sexuality being restricted to specialized axes which originate from supernumerary serial buds, above the branch. Superficially there appears to be an "inflorescence" in the axil of a "compound leaf".

In contrast to the leaf-like character of branches it is appropriate at this point to consider those aspects of the morphology of compound leaves in tropical plants wherein they resemble branches. In *Aporrhiza talboti* (Sapindaceae), for example, the leaflets are inserted spirally on the rachis so that dorsiventrality is obscured (EMBERGER and CHADEFAUD, 1960). In several species of *Aglaia*, *Guarea*, and *Chisocheton* (Meliaceae) the leaves have an indeterminate growth as a result of activity of an apical bud which produces new leaflets over a period of several years, during which time the older leaflets are lost. These leaves may reach a length of 6 m (SINIA, 1938). Figure 55 provides an example of this branch-like leaf. In *Sclerolobium* sp. we have commented on a superficially similar process with periodic expansion of leaflet pairs, but not involving epigenesis (p. 21, 176). We should also mention the situation in *Chisocheton spicatum* (Meliaceae) described by CORNER (1964) in which the apical bud of leaf and parent axis are synchronous in their activity.

In *Guarea rhopalocarpa* (Meliaceae) the rachis has a functional cambium, which may develop growth rings (SKUTCH, 1946). Of interest in this respect are the experiments of WEIDLICH (1974) who showed that it was possible by grafting to stimulate cambial activity in petioles of *Acer*, where it normally does not occur. *Carapa procera* (Meliaceae) retains a branch-like feature in the failure of the leaves to develop a basal abscission zone. The rachis becomes embedded in the trunk after the leaflets have fallen.

The existence of epiphyllous inflorescences draws attention to the biological adaptability of leaves, as in species of *Phyllobotryum* (Flacourtiaceae). HARMS (1917) has described a member of the family Meliaceae in which there are flowers on the leaf rachis. The situation in *Tapura guianensis* (Dichapetalaceae), which conforms to Cook's model, is particularly complex. Here the inflorescences are situated at the distal end of the petiole so that we have a branch-like character on a leaf which is itself part of a leaf-like branch! An interesting parallel between leaf and branch is shown in species of *Phyllanthus* in which sleep movement of leaves is carried out, analogous to the sleep movement of compound leaves.

In conclusion, it can be stated that the fundamental morphological rule distinguishing leaf and branch, i.e., that the branch is always subtended by a leaf, no matter how small, is never broken in woody dicotyledons. This is not true, of course, in many of the lower vascular plants (BIERHORST, 1971).

Fig. 55 A–C. Guarea sp. (Meliaceae, Rauh's model) as an example of a compound leaf with incompletely determinate growth, Upper Yaroupi River, French Guiana. ▷

- *A* Crown of orthotropic shoot with older leaves still incompletely extended.
- *B* Leaf apex from above showing incompletely expanded leaflet primordia.
- *C* Leaf apex from front, with unexpanded leaflets which form a kind of terminal "bud"


A
B
C

Strategy of the Model. With the progressive specialization of the branches in examples of Cook's model, we arrive at trees which biologically are "unbranched" and monoaxial as indicated by N. and F. Hallé (1965). This suggests that we are essentially dealing with trees as in Corner's model, with large compound leaves, and remarks about the reproductive strategy of the latter are applicable to the former (p. 116). The comparison is most apt in those plants with "axillary" inflorescences on the main trunk (*Panda oleosa, Phyllanthus muellerianus*). The similarity is best recognized when it is appreciated that the size relationships expressed in Corner's law here apply to phyllomorphic branch, not actual leaf. Thus when the trunk supports only minute scale leaves, the internodes are still short, in correlation with the length of the branch. The otherwise apparent exception is overruled by thinking of the plant as a monocaulous tree with large, compound leaves. The correlation between trunk and branch size corresponds exactly to Corner's rule, as Cook (1903) showed in *Castilla*. When the orthotropic trunk becomes branched in the process we now recognize as reiteration, the bigger the reiterated axis, the bigger are the phyllomorphic branches it bears.

Tree species which conform to this model are characteristic of the understorey of tropical rain-forest, almost without exception. They are relatively few, but serve to show the strongly adaptive nature of this habit of growth, since two structurally quite different types of tree (Cook's and Corner's models) coincide very precisely in general appearance. It is evident, however, that the same model successfully exists in short-lived, weedy herbs, notably in *Phyllanthus*. Here a high reproductive capacity is maintained when the phyllomorphic branches are themselves branched again, with each leaf subtending a flower. It seems likely that much of the biomass of these plants is devoted to seed production. However, the final remarks on strategy, climate and biological competition in Roux's model certainly apply strongly also to plants displaying Cook's model.

Taxonomic List of Examples (Cook's Model)

Annonaceae:
Drepananthus sp., Malaysia, Corner, 1949.
Dichapetalaceae:
Tapura guianensis Aubl., Guianas.
Euphorbiaceae:
Cicca acida Merr., Malaysia, Corner, 1952 / *Glochidion laevigatum* Hook. f., Malaysia, Corner, 1952 / *Phyllanthus mimosoides* Sw., Guadeloupe, Roux, 1968; Bancilhon, 1971 / [L] *Phyllanthus muellerianus* (O. Ktze.) Exell (Fig. 69G), W. Africa, Roux, 1968 / [H] *Phyllanthus urinaria* L., almost Pantropical, Roux, 1968; Bancilhon, 1971.
Flacourtiaceae:
Homalium sp., Ivory Coast / *Ryania speciosa* Vahl var. *bicolor* D.C., Guianas. *Smeathmannia pubescens* Soland. W. Africa.
Monimiaceae:
Glossocalyx longicuspis Benth. (Fig. 54D), Gabon, N. and F. Hallé, 1965.
Moraceae:
Castilla elastica Cerb. (Fig. 54A), C. America, Cook, 1903, 1911 / *Castilla ulei* Warb., Brazil.
Pandaceae:
Panda oleosa Pierre, Trop. Africa.
Passifloraceae:
Androsiphonia adenostegia Stapf, Ivory Coast / *Barteria fistulosa* Masters (Fig. 54C), C. Africa
Rhamnaceae:
[L] *Ventilago africana* Exell, Ivory Coast, Cremers, 1973 / *Zizyphus papuanus* Lauterb., New Guinea.
Rubiaceae:
Canthium glabriflorum Hiern (Fig. 53), Trop. Africa / *Pauridiantha callicarpoides* (Hiern) Bremek., Gabon, N. and F. Hallé, 1965 / *Pouchetia africana* A. Rich., Equatorial Africa N. and F. Hallé, 1965 / *Schumanniophyton magnificum* (K. Schum.) Harms (Fig. 54B), Equatorial Africa, F. Hallé, 1967 / **Zuccarinia macrophylla* Bl., Sumatra.

b) Axes all Orthotropic

Scarrone's Model

Definition. The architecture is determined by an orthotropic rhythmically active terminal meristem which produces an indeterminate trunk bearing tiers of branches, each branch-complex orthotropic and sympodially branched as a result of terminal flowering.

This model is readily compared with Leeuwenberg's model since branch complexes in the two are virtually identical with peripheral "plagiotropoid" phenomena increasingly pronounced in Scarrone's model (Figs. 12A, 56 and 57). However, there is now a well developed monopodial trunk which produces the branches. The similarity between these models is indicated by their existence in related genera and species, notably in *Pandanus* and certain Ericaceae. The model is named after Francis Scarrone, since the mango (*Mangifera indica*) which he has investigated in great detail provides an example of its architecture (Scarrone, 1964, 1965, 1966).

Example. We turn to the monocotyledons to illustrate this model first, since it is known for a number of species of *Pandanus* (Pandanaceae) as a result of the investigations by Guillaumet (1973). *Pandanus vandamii,* endemic to Madagascar, is illustrated (Fig. 57A). The epicotyledonary axis produces an erect, monopodial trunk which by rhythmic growth gives rise to regularly spaced tiers of branches, the branches usually in threes. Each branch develops sympodially with branching below a terminal inflorescence, the first unit usually longer than subsequent ones. Because of their stereotyped nature, these units can be regarded as hapaxanthic modules, each one comparable

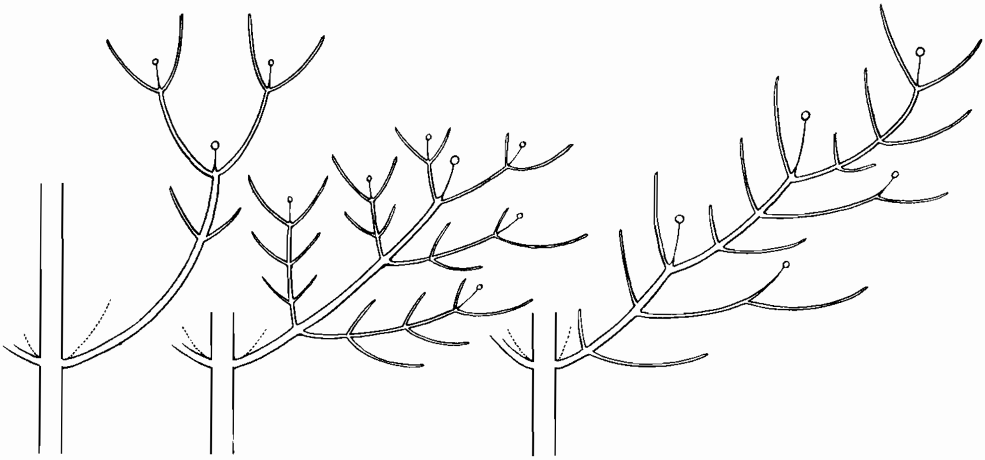


Fig. 56. Scarrone's model, three branch complexes with differing disposition of lateral branches to show increasing asymmetry of the orthotropic complex and increasing complexity of its elements, from left to right. The left-hand complex is essentially as in Leeuwenberg's model. On large complex branches, e.g., lower on the trunk of old mango trees, the peripheral elements are simpler than the initial, proximal ones (see Fig. 12*A*). The elements which are representative for branch architecture in a species have to be observed on the youngest branches just under the trunk apex

to the units which collectively make up the entire tree in Leeuwenberg's model. Substitution growth in *Pandanus* below the terminal inflorescence is distinctive because it occurs without the unifying activity of secondary tissues, so that branch development is precocious, as described by several authors (e.g., TOMLINSON, 1970a), but earliest and most precisely by SCHOUTE (1906). The length of the individual branch complexes varies considerably in *P. vandamii* so that trees may have either rounded or elongated crowns and the tiers may or may not be distinct, as illustrated by GUILLAUMET (1973). GUILLAUMET has described other Madagascan species in this model which vary in the life-span of individual branch complexes and show differences between branch complexes at different heights in the model, but this variation does not obscure the basic architecture.

Other Examples and Variations. In dicotyledons Scarrone's model permits the development of large trees of which the dense-crowned mango, reaching a height of 25 m, is a familiar example whose architecture has been described by H.O., 1970, p. 73. This stature, at least in mango, is probably a consequence of the rhythmic growth of the branches, which may initially branch monopodially before eventually flowering terminally (H.O., 1970, p. 72). Mango is of interest because there is a disassociation between flowering and vegetative growth (SCARRONE, 1969). Terminal inflorescences occur at one time of the year (e.g., in the dry winter in Florida), vegetative growth is much later (e.g., in early summer in Florida).

Gardenia imperialis (Rubiaceae, tropical Africa), a tree of swampy savannas reaching a height of 20 m, illustrates this model and shows another important variation (Fig. 57B). The branch tiers are very diffuse and in their early development show a repetition of the monopodial growth of the parent trunk before sympodial branching by substitution begins. Other trees of this model do this quite commonly, e.g., species of *Mangifera*, *Spondias* (Anacardiaceae), and *Triplaris surinamensis* (Polygonaceae). Amongst small plants which conform precisely to this model is *Bidens* sp. (Compositae) a shrub less than 2 m high (Fig. 57C), recorded in montane grassland in the Marquesas (GILLETT, 1973).

Two stages in the development of a small apocynaceous plant only 2 m high, *Cerberiopsis comptonii*, are shown in Figure 57Da, b. This treelet is endemic to New Caledonia (VEILLON, 1971) and is a characteristic element of scrubby vegetation on serpentine soils. The assymmetry of the spreading branch system is well shown, with the trunk remaining short. In this species a limit to the height of the tree seems to be imposed by the slow growth of the trunk. This is carried further in *Fagara rhoifolia* (Rutaceae, French Guiana), as illustrated by H.O. (1970, p. 74), in which the monopodial trunk is of limited growth, the apex eventually aborting, and further growth in height of

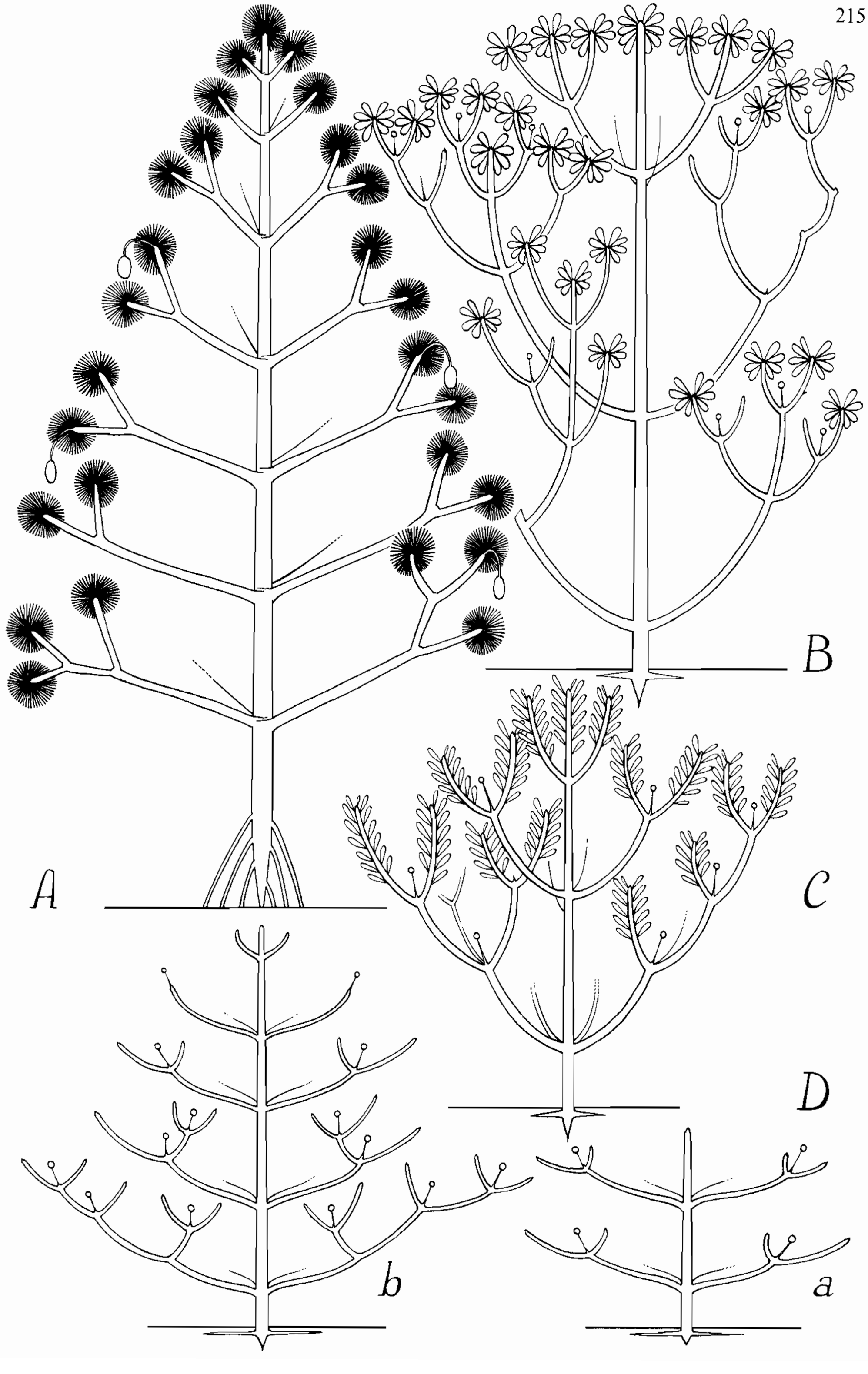
Fig. 57A–D. Scarrone's model. ▷

A *Pandanus vandamii* Martelli and Pichi-Sermolli (Pandanaceae, endemic to Madagascar, *Guillaumet 2175*). This habit represents the most frequent architecture of the genus *Pandanus* (GUILLAUMET, 1973).

B *Gardenia imperialis* K. Schum. (Rubiaceae, tropical West Africa). A tree of swampy savanna, up to 20 m high.

C *Bidens* sp. (Compositae, Hiva-Oa Island, Marquesas, French Polynesia, *F. Hallé 2186*). A shrub less than 2 m high, in montane grassland (GILLETT, 1973).

D *Cerberiopsis comptonii* Guill. (Apocynaceae, endemic to New Caledonia). A treelet up to 2 m high in scrub on serpentine soils. *a* Juvenile stage, but already in flower; *b* adult stage (VEILLON, 1971)


A
B
C
D
b
a

the tree is due to the branches, much as in Koriba's model. This architecture then represents an intermediate between the models of Scarrone, Leeuwenberg and Koriba (Fig. 56, middle).

These examples, and others, show that Scarrone's model occupies a central place among several others. We have commented on the elementary difference which distinguishes it from Leeuwenberg's model, while *Fagara rhoifolia* essentially conforms to Scarrone's model only when it is young, but may be referred to Koriba's model when it is old and loses its monopodial trunk. *Thevetia peruviana* (Apocynaceae) and several species of *Cussonia* (Araliaceae) are similar. The tendency for the branches initially to be orthotropic and repeat the monopodial pattern of the parent trunk, if carried on indefinitely, would lead us to Rauh's model, shortly to be described. Finally Stone's model, next to be described, differs only in that the trunk has continuous growth. The architectural continuum seems more uniform in and around this group of models than elsewhere.

Strategy of the Model. Remarks concerning the strategy of Leeuwenberg's model (p. 153) seem relevant at this point, because Scarrone's model is more advanced in the independence between branching and flowering in the early stages of growth which the monopodial trunk provides. Although the number of examples of this model is not large, and their precise ecotope is only exceptionally known, it still can be stated that a remarkable proportion out of those observed in French Guiana live in old pioneer forest (*Fagara*) or secondary post-pioneer forest (*Carapa, Anacardium, Spondias*; *Schizolobium* and *Triplaris* in Ecuador). Hence it would seem that as a working hypothesis the "improvement" in the *K* strategy, which is the result of the monopodial trunk and the complexity of the orthotropic branches, corresponds to an aptitude to live in certain not yet completely "mature" forest environments.

Taxonomic List of Examples (Scarrone's Model)

MONOCOTYLEDONS

Pandanaceae:
Pandanus bakeri Warb., Madagascar, STONE, 1970; GUILLAUMET, 1973 / *Pandanus bilamellatus* Martelli, Madagascar, GUILLAUMET, 1973 / *Pandanus candelabrum* P. Beauv., Trop. Africa / *Pandanus guillaumetii* B.C. Stone, Madagascar, GUILLAUMET, 1973 / *Pandanus punctulatus* Martelli, Madagascar, GUILLAUMET, 1973 / *Pandanus vandamii* Martelli and Pichi-Serm. (Fig. 57A), Madagascar, GUILLAUMET, 1973 / *Pandanus* sp., New Hebrides, VEILLON, 1976.

DICOTYLEDONS

Anacardiaceae:
**Anacardium occidentale* L., "cashew", Trop. America / **Mangifera indica* L., "mango", Trop. Asia, widely cultivated, SCARRONE, 1969 / **Spondias mombin* L., "mombin", Trop. America / *Rhus taratana* (Baker) Perrier, Madagascar.

Apocynaceae:
Cerberiopsis candelabrum Vieill., New Caledonia, VEILLON, 1971 / *Cerberiopsis comptonii* Guill. (Fig. 57D), New Caledonia, VEILLON, 1971 / +*Craspidosperma verticillata* (Bojer) Vandrik, Madagascar / *Macoubea guianensis* Aubl., Trop. America / **Thevetia peruviana* K. Schum., Trop. America, commonly cultivated.

Bignoniaceae:
Jacaranda mimosaefolia, "jacaranda", Venezuela.

Boraginaceae:
**Echium acanthocarpum* Svent., Teneriffe.

Chloranthaceae:
Ascarina solmsiana Schlechter, New Caledonia, VEILLON, 1976.

Compositae:
[H] *Bidens* sp. (Fig. 57C), (F. Hallé 2186), Marquesas, GILLETT, 1973 / [H] *Carlina salicifolia,* Mediterranean, MEUSEL, 1970.

Crassulaceae:
[H] *Aeonium decorum* Webb, Canary Islands, SEREBRYAKOV and SEREBRYAKOV, 1972.

Cruciferae:
[H]* *Cheiranthus cheirii* L., "wall-flower", N. Temp.
Dilleniaceae:
**Dillenia indica* L., Trop. Asia.
Dipsacaceae:
[H] *Scabiosa cretica* L., Mediterranean, MEUSEL, 1970.
Ericaceae:
Arbutus unedo L., "strawberry tree", Mediterranean, MEUSEL, 1970 / *Rhododendron ferrugineum* L., Europe, TEMPLE, 1975 / *Rhododendron hirsutum* L., C. Europe, TEMPLE, 1975 / *Rhododendron lochae* F. Muell., Australia, TEMPLE, 1975 / *Rhododendron mucronulatum* Turcz., Temp. Asia, TEMPLE, 1975.
Hippocastanaceae:
**Aesculus hippocastanum* L., "horse-chestnut", Temp. Asia / *Aesculus pavia* L., "red buckeye", N. America, CHAMPAGNAT, 1947.
Leguminosae – Caesalpinioideae:
Cassia siamea L., Siam, widely cultivated / *Peltophorum ferrugineum* Benth., Trop. Asia / *Schizolobium* sp., Amazon Basin.
Loganiaceae:
**Anthocleista amplexicaulis* Baker, Madagascar / *Anthocleista* sp., Madagascar / **Crateriphytum moluccanum* Scheff., Indonesia.
Malvaceae:
Hibiscus tiliaceus L., "mahoe", Pantropical.
Melastomaceae:
Tococa guianensis Aubl., Trop. S. America, OLDEMAN, 1974a.
Meliaceae:
Carapa guianensis Aubl., Trop. S. America, OLDEMAN, 1974a.
Polygalaceae:
[H]**Polygala myrtifolia* L., S. Africa.
Rubiaceae:
**Gardenia imperialis* K. Schum. (Fig. 57B), Trop. Africa.
Rutaceae:
Fagara pentandra Aubl., Guianas / *Fagara rhoifolia* (Lam.) Engl., Guianas / **Flindersia pubescens* F.M. Bailey, Queensland.
Simaroubaceae:
**Simarouba amara* Aubl., Trop. America / *Simarouba glauca* DC., "paradise tree", W. Indies.
Tiliaceae:
Cephalonema polyandrum K. Schum., Gabon.

Stone's Model

Definition. The architecture results from the continuous growth of the meristem of the orthotropic trunk, which produces orthotropic branches either continuously or diffusely. Further branches develop sympodially below terminal inflorescences, and the trunk may flower terminally.

In the earlier account of tree architecture (H.O., 1970, p. 78) three "theoretical models" were recognized since they seemed likely to exist on the basis of the frequent associations of several different criteria used in the definition of models. One of these (Theoretical model III) has since been recognized and named by GUILLAUMET (1973). Since it occurs in several species of *Pandanus* it is appropriate to name it after BENJAMIN C. STONE, whose studies on Pandanaceae are wellknown. The closeness of Stone's model to those of Scarrone and Rauh is evident.

JEANNODA (1977) found that in herbs with this architecture the main axis often flowers terminally, and suggested not to exclude such species from Stone's model. GUILLAUMET (1973) described the same phenomenon in *Pandanus*.

Examples. 1. Monocotyledons. Pandanus pulcher (Pandanaceae), endemic to Madagascar and growing in deep swamps, represents the model in striking fashion (Fig. 58). This species forms a tree 18 to 20 m tall and its spectacular obelisk shape was noted by DU PETIT-THOUARS (1808), but was illustrated only recently by STONE (1970), who described the habit as "coniferoid" because of its resemblance to certain *Araucarias*. The architecture of the tree was described in detail by GUILLAUMET (1973). The monopodial trunk produces a very regular series of branches, apparently one at every node, and arranged in the spiral tristichy

Fig. 58. Stone's model, *Pandanus pulcher* Martelli (Pandanaceae), Tampoketsy, Ankazobe, Madagascar. Note the contrast in size between leaves on trunk and branch axes, in conformity with Corner's rules

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Fig. 59 A–D. Stone's model. ▷

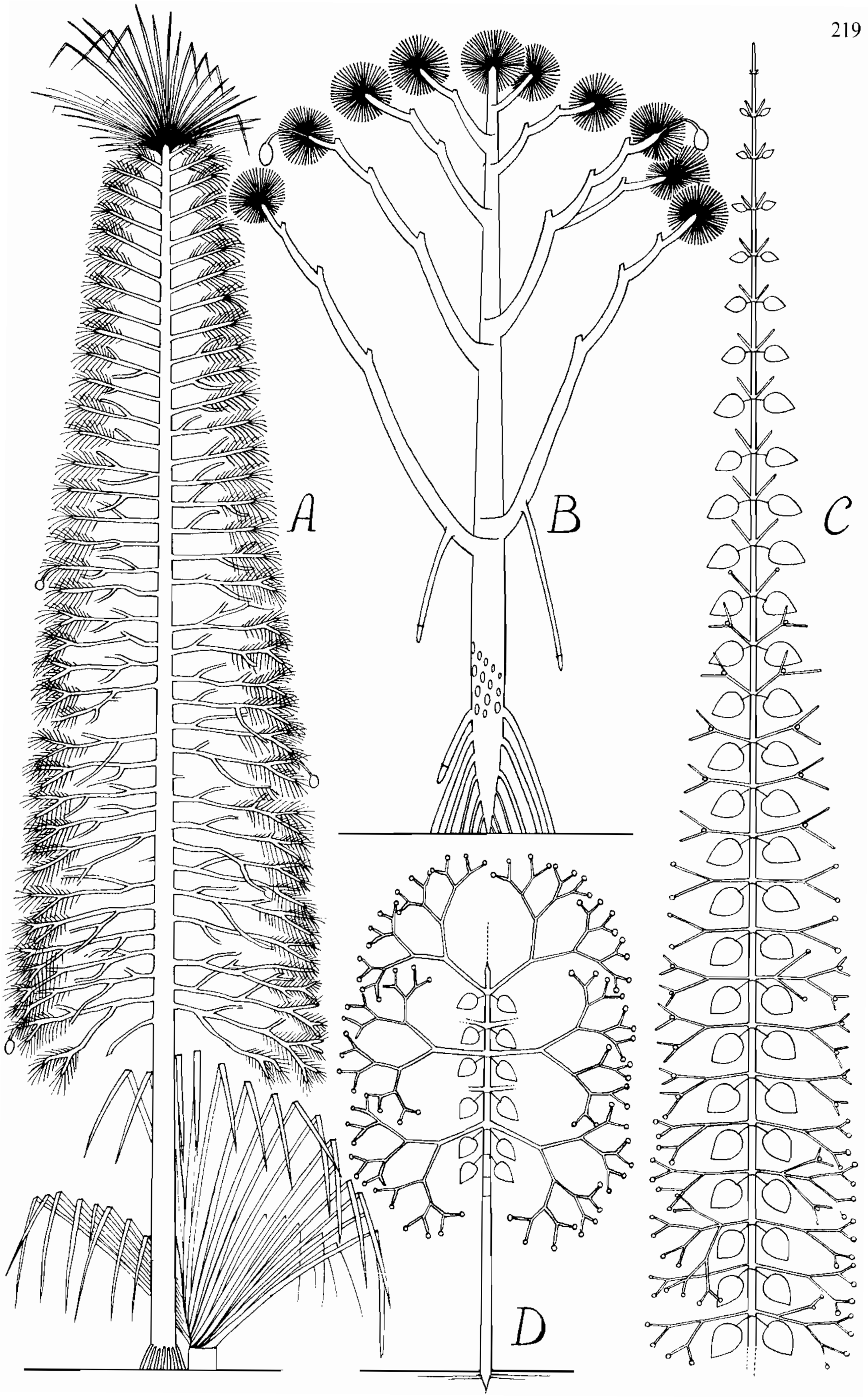
A *Pandanus* aff. *pulcher* Martelli (Pandanaceae, in forest swamps near Perinet, Madagascar, *F. Hallé 2345*). A tree up to 20 m high, with the characteristic appearance of an obelisk (DU PETIT-THOUARS, 1808). Leaves borne on the trunk are up to 4 m long, while those on the branches are about 50 cm long (STONE, 1970; GUILLAUMET, 1973).

B *Pandanus tectorius* Solander (Pandanaceae, Ua-Huka Island, Marquesas, Polynesia, *F. Hallé 2029*). A very common tree of the Pacific islands, up to 20 m high, remarkable for its stilt roots.

C *Mikania cordata* (Burm. f.) B.L. Robinson (Compositae, pantropical). A weedy vine of the secondary forest vegetation, common throughout the tropics.

D *Sigesbeckia orientalis* L. (Compositae, pantropical). A herbaceous weed, 1 m high. Example of the model with late terminally flowering trunk.

Note: In *C* and *D* the leaves on the flowering branches are not represented


A
B
C
D

characteristic of *Pandanus* (Fig. 59A). There is a pronounced leaf dimorphism such that leaves on the trunk, up to 4 m long, are about 20 times as long as the leaves on the branches, which do not exceed 15 cm (cf. basal and distal trunk leaves with branch leaves in Fig. 59A). The "coniferoid" physiognomy is a consequence of the very limited growth of the older branches, which persist for a very long time but do not flower until they are quite old. Consequently fruits only appear low down in the crown (STONE, 1970). There seems also to be some differentiation of branches at different levels on the trunk, such that basal branches produce branches of higher orders most readily. It must be remembered in examining such a tree that all parts of the plant are primary and produced by terminal meristems, as in all *Pandanus* species there is no secondary growth.

In other species of *Pandanus* which conform to this model (GUILLAUMET, 1973), the length of the branches is not unlimited and this leads to a tree with a very different shape, often with few, rather irregular branches, as in *P. imirniensis*. *Pandanus* species with diffuse branching which conform to this model are frequent, as indicated by GUILLAUMET for several species native to Madagascar. From other regions we have illustrated *P. tectorius*, widely distributed in coastal regions in the South Pacific Islands (Fig. 59B). Diffuse branching is reflected in the wide and irregular spacing between successive branches or groups of branches. Individual branches are obliquely erect and form almost a linear sympodium.

2. Dicotyledons. To find examples of this architecture in dicotyledons is difficult and the two we illustrate are not trees. First, we have *Sigesbeckia orientalis* (Compositae), a pantropical weed, here illustrated from specimens growing to a height of 1 m, collected in the Marquesas Islands. Branches are diffuse but fairly regular in their distribution (Fig. 59D, leaves not shown on the branches). Second, we have *Mikania cordata* (Compositae) which is common in many parts of the tropics as a weedy vine in secondary vegetation. In Figure 59 C the plant is illustrated very diagrammatically, without leaves on the branches which, in fact, may be quite long. Branching is here continuous.

Strategy of the Model. This architectural model is evidently uncommon, as witness the time it took to recognize it. It surely is significant that it occurs in *Pandanus*, an unusual tree genus because it is often branched and yet lacks secondary thickening growth by means of a vascular cambium. Stone's model is recognized chiefly (at least so far) in *Pandanus* species endemic to Madagascar, which is a known refugium for relictual forms and in dicotyledons is known (again so far) only in specialized examples. From this we may conclude that its relative success in arborescent monocotyledons has been superseded in dicotyledons (with secondary growth) by such a model as that of Attims which is similar to Stone's model but shows lateral inflorescences. A free vegetative terminal meristem and secondary growth permit unlimited branch extension, which seems to account for the greater efficiency of Attims' model. However, it appears to be rhythmic growth and branching which are necessary for ecological success, such as Rauh's model, which occupies a predominant position among forest trees.

Taxonomic List of Examples (Stone's Model)

MONOCOTYLEDONS

Pandanaceae:
Pandanus imirniensis Martelli, Madagascar, GUILLAUMET, 1973 / *Pandanus pulcher* Martelli (Figs. 58, 59A), Madagascar, STONE, 1970; GUILLAUMET, 1973 / *Pandanus tectorius* Soland. (Fig. 59B), Polynesia.

DICOTYLEDONS

Campanulaceae:
[H] *Sphenoclea zeylanica* Gaertn., Zaire.
Compositae:
[H] *Ageratum conyzoides* L., Pantropical weed / [L] *Mikania cordata* (Burm.) Rob. (Fig. 59C), almost Pantropical, a weedy vine / [H] *Sigesbeckia orientalis* L. (Fig. 59D), Marquesas, a weed.
Melastomaceae:
Leandra solenifera Cogn., French Guiana.

Rauh's Model

Definition. Architecture is determined by a monopodial trunk which grows rhythmically and so develops tiers of branches, the branches themselves morphogenetically identical with the trunk. Flowers are always lateral and without effect on the growth of the shoot system.

This model is one of the most frequent among seed plants and can be recognized in other vascular plants, as the example of a fern described below demonstrates (Fig. 60). The model itself produces a rather unspecialized shoot system which is inherently very adaptable because all meristems are equivalent and rhythmic. It is very common among trees of high latitudes (e.g., *Acer, Fraxinus, Pinus, Quercus*), so much so as to be almost a "type", but it is equally common in the tropics. It is named appropriately after Professor W. RAUH whose description of temperate trees illustrates their architectural features precisely (RAUH, 1939a). Our list of examples is very long, but equally incomplete. In addition to many familiar trees of temperate forest in Europe and North America there are many examples in common and commericially important tropical trees, e.g., rubber (*Hevea*); timber trees like *Swietenia, Khaya, Triplochiton*; fruit trees like *Artocarpus, Persea, Mammea*; weed-trees like *Cecropia, Macaranga, Musanga* and ornamentals like *Couroupita, Cassia. Hevea* and *Musanga* have been described in detail by H.O., 1970, pp. 79–83.

Example. To illustrate the model we have selected one of the tallest trees of the African rain-forest, the sipo (*Entandrophragma utile,* Meliaceae) a commercially valuable timber tree reaching a height of 50 m (Fig. 61A). Rhythmic growth of the monopodial trunk leads to the development of distinct tiers of branches, these initially repeat the construction of the parent axis but a degree of "escape asymmetry" (Fig. 12A) is imposed and this becomes predominantly characteristic in the distal part of the branch system. The developing leaves, as seen from below, extend as terminal rosettes (Fig. 61Ab). Flowers are axillary and expand in lateral panicles from the axils of the last leaves pertaining to the rosette, at a time when the terminal bud is in its resting condition (Fig. 61Ac). Periodicity of growth is seasonal, but details are lacking.

Other Examples
1. Dicotyledons. Sipo is a tall forest tree, our further illustrations show a little of the range in size and ecological diversity of the other examples. *Macaranga aleuritoides* (Euphorbiaceae) is the Asian counterpart of the African *Musanga* and the

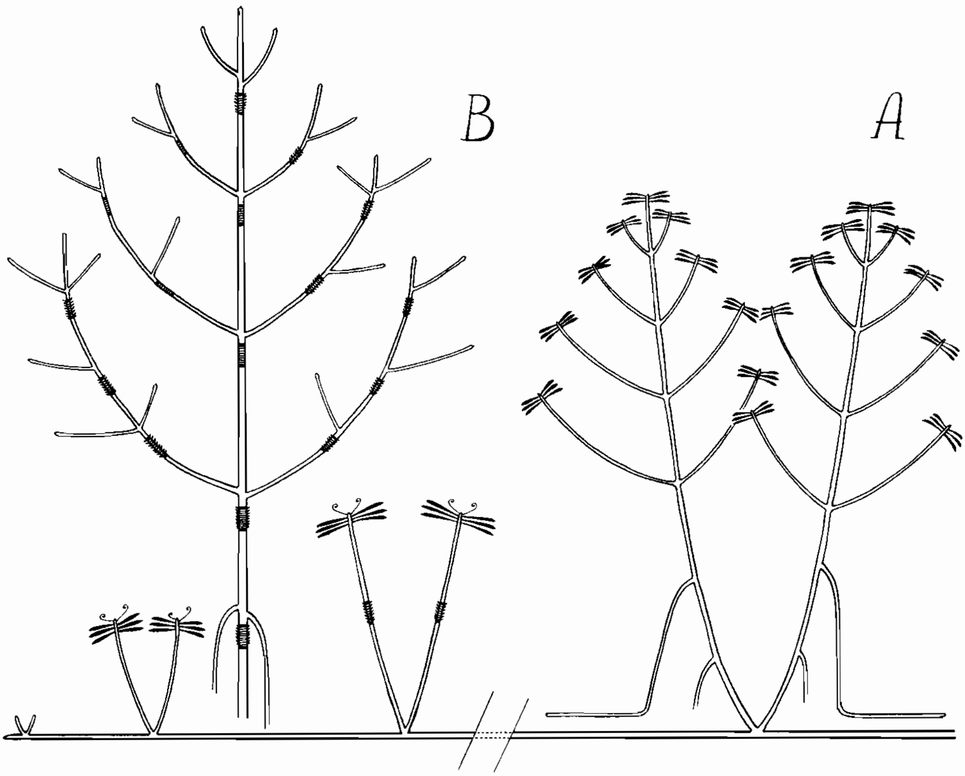


Fig. 60A and B. Oleandra pistillaris, an example of Rauh's model in a herbaceous fern.
A Horizontal shoot system from the side.
B Old erect shoot, essentially repeating the branching pattern of the horizontal shoot system

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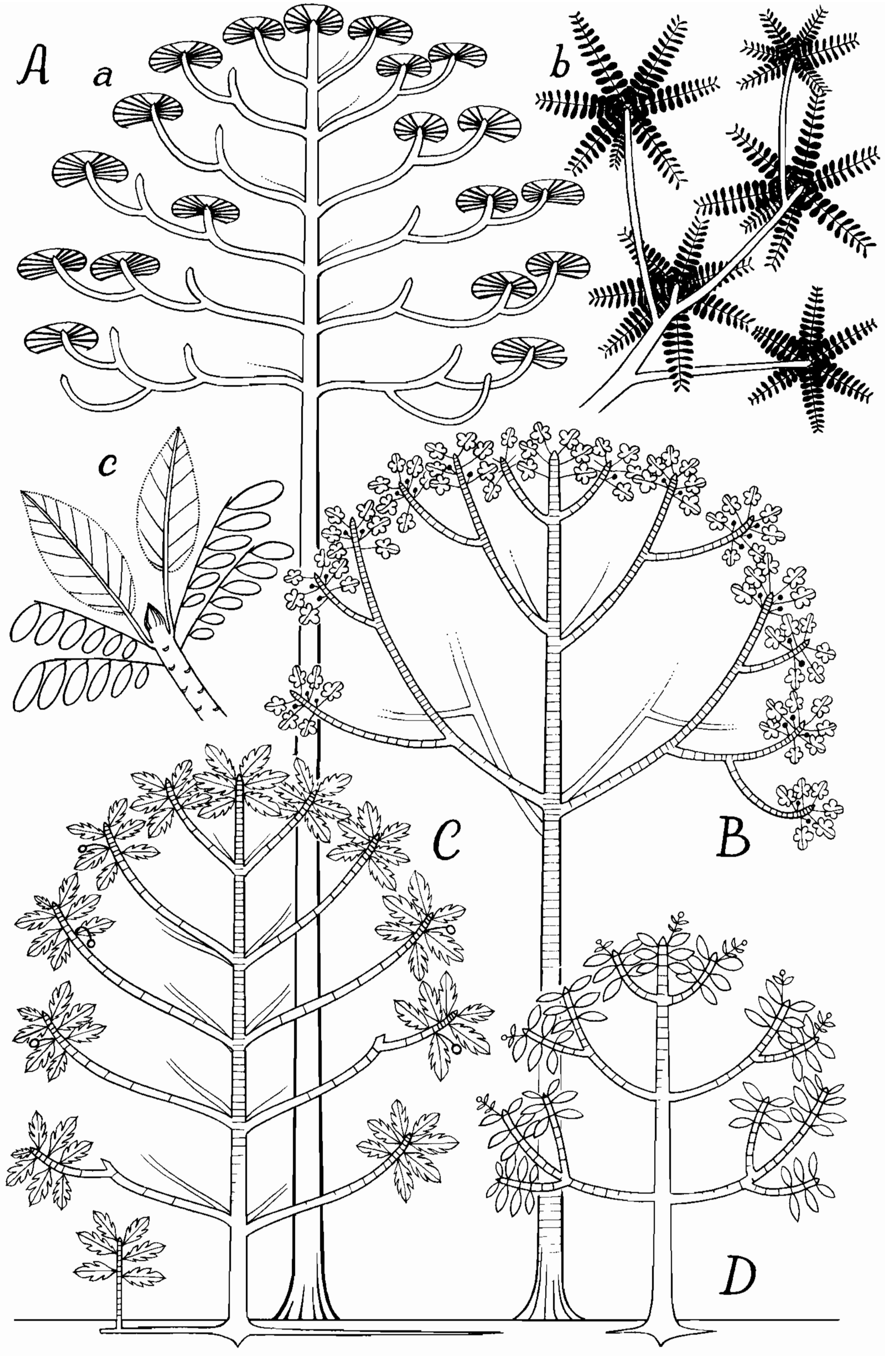
Fig. 61A–D. Rauh's model.
A *Entandrophragma utile* (Dawe) Sprague (Meliaceae, tropical Africa, the "sipo"). *a* General architecture; the sipo is one of the tallest trees of the African rain-forest, reaching a height of 50 m; *b* typical disposition of the newly expanded leaves, seen from below (as described by AUBRÉVILLE, 1959, p. 168); *c* axillary flowering, near the apical resting bud.
B *Macaranga aleuritoides* F. von Muell. (Euphorbiaceae, New Guinea). This common roadside weed-tree, up to 15 m high, resembles the African *Musanga* and the American *Cecropia* (both Moraceae).
C *Artocarpus incisa* Thunb. (Moraceae, Indo-Pacific Islands, the "mayore" or bread-fruit tree). This small tree, 10 m high, is now cultivated for its edible fruits throughout the tropics; the best varieties are parthenocarpic and propagate by root suckers.
D *Kalanchoë beharensis* Drake (Crassulaceae, endemic to southern Madagascar). A treelet, less than 5 m high, growing in thorny scrub

▷


A
a
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C
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D

American *Cecropia* (Moraceae) in its general appearance and its weedy tendencies, as well as its architecture (Fig. 61 B). This tree is common on the road-side in New Guinea, growing to a height of 15 m, but it never forms extensive secondary vegetation. *Artocarpus incisa* ("bread-fruit", Moraceae) of the Indo-Pacific islands is widely cultivated in the tropics and also illustrates this model (Fig. 61 C). The best varieties are parthenocarpic and clonally propagated by root suckers which reiterate the model completely. It forms a tree to a height of 30 m and its natural habitat is probably the Pacific rain-forest. An example from dry areas is provided by *Kalanchoë beharensis* (Crassulaceae) a treelet less than 5 m high (Fig. 61 D) endemic to areas of thorny scrub in southern Madagascar. A more imposing forest tree. *Euphorbia abyssinica* (Euphorbiaceae), which conforms to Rauh's model, has been described by H.O., 1970, pp. 86–87. This cactus-like tree of East Africa has winged succulent photosynthetic stems and reduced, caducous leaves, but still reaches a height of 30 m, showing the rhythmic growth and tiered branches of the model in a very regular fashion.

2. Ferns. A creeping fern *Oleandra pistillaris* (Polypodiaceae, Indonesia) serves to illustrate the possibilities of the model in herbaceous plants (Fig. 60). The "trunk" is here horizontal and root-bearing but shows rhythmic growth, the branch tiers are all negatively geotropic and appear as small individuals which repeat the model since the equivalence of all branch meristems is expressed precisely in this example.

Variations. From the example of this fern it can be appreciated that the physiognomic possibilities of this model are unlimited. A species of *Clusia* (Guttiferae) from the mountains of Martinique and Guadeloupe (French Antilles) shows one possibility. Plants form a short trunk with the lowest branch tier much more expanded than the uppermost tiers, so that a cushion-shaped tree develops. The lower branches may take root and so propagate the tree if the trunk dies. In this kind of habitat the convergence of different models towards the same cushion shape is noteworthy (RAUH, 1939b).

Despite the simple structural features of this model, the expressed range in details is considerable. The unbranched seedling axis may be quite long, e.g., up to 4 m in *Hevea* and *Aucoumea klaineana* ("okoumé", Burseraceae, Gabon), but the longest are in the larger and commercially important Meliaceae like *Entandrophragma, Khaya, Swietenia* in which the monoaxial state may persist to a height of 10 m. The epicotyledonary axis has a massive primary diameter (up to 5 cm) and proportionately large leaves (up to 2 m in *Khaya ivorensis*), but these dimensions are reduced in successive orders of branch axes following Corner's rules.

Variation in the periodicity of rhythmic growth is considerable. It is often correlated with season, as is most obvious in temperate trees, which are also mainly deciduous. With decreasing latitude the tendency to produce more than one flush of growth per season is noticeable, e.g., in South Florida an evergreen oak, *Quercus virginiana* ("live oak", Fagaceae, eastern United States), will show as many as three growth increments each year which are not necessarily synchronous. Periodic growth in nonseasonal climates indicates an endogenous control of shoot extension; one of the best studied examples is *Hevea brasiliensis*, which has a regular cycle of mitotic activity repeated every 40 days (HALLÉ and MARTIN, 1968). This cycle can be modified by the environment, so that a dry season extends the period of mitotic inactivity. This periodicity in *Hevea* is expressed morphologically by the variation in leaf size and internode length, allowing one to recognize "morphogenetic units", the trunk being made up of a linear series of such units (Fig. 6). Similar units can be recognized in all examples of Rauh's model and their length is correlated to some extent with leaf size (i.e., surface area); the average length of the unit in large-leaved species like *Cecropia* and *Khaya* is 1 m; it is 50 cm in rubber with trifoliolate leaves, but scarcely 25 cm in simple-leaved species like *Quercus sessiliflora.*

Branch development is closely correlated with rhythmic growth of the axis, an essential feature of Rauh's model. In temperate species branches develop mainly by prolepsis, from dormant lateral buds close to the resting terminal bud. This familiar feature of temperate trees can be seen in many tropical species, e.g., in Burseraceae, Meliaceae, Moraceae. *Swietenia* species (mahoganies) provide good examples, with the resting terminal buds protected by bud-scales, much as one would see in an ash or maple. In contrast branching may be by syllepsis, with the lateral axis developing during the phase of extension of the terminal bud, on the current shoot. The branch tier then tends to be more diffuse. Avocado (*Persea americana*) provides a good example.

Inflorescence position is consistently lateral in this model, but varies considerably in relation to extension growth. In avocado it is pseudoterminal, because the flowers are on the first part of the renewal shoot to expand, their position as lateral appendages becomes evident when the distal, leafy part of the shoot elongates. The situation described earlier for sipo is similar but distinctive, in that flowers expand well before the terminal buds. The most common arrangement is for flowers to accompany the new growth; in *Carpotroche* aff. *amazonicum* (Flacourtiaceae, South America) the flowers occur in the axils of foliage leaves, near the branch apex; more usually the flowers are at the base of the renewal shoot, subtended by scale leaves, as in *Hevea* and in many temperate examples. Flowers may be restricted to older defoliated parts, as in *Henriettella patrisiana* (Melastomaceae), an understorey treelet to a height of 5 m in the Guianese forest, which is a spectacular sight with its leafless axes covered with snowy white flowers in the short dry season of March. In temperate Myricaceae (e.g., *Myrica cerifera*), flowers develop on the current-year shoots but do not expand until the following year. Cauliflory is represented by *Couroupita guianensis* ("cannon-ball tree", Lecythidaceae) and *Artocarpus heterophyllus* ("jak-fruit", Moraceae).

These examples are sufficient to show the wide range of biological possibilities which lateral flowering permits in this model and which undoubtedly contribute to its ecological adaptability.

Strategy of the Model. The chief reason for the evident success of this model lies not so much in its inherent simplicity of expression as in its ability to regenerate readily. This topic is dealt with in greater detail elsewhere and only a brief commentary is offered here. Regulation of the growth pattern of such trees depends on the apical meristem of the trunk. The tree may grow precisely according to the model throughout its life-cycle, as is common in weed trees like *Cecropia* and *Macaranga.* However, if the trunk meristem is destroyed, it is readily replaced, usually by the uppermost lateral meristem or, if the damage is more extensive, by the uppermost branch which rapidly substitutes as a leader. This is possible because all meristems are equivalent, regeneration then is carried out with a minimum of growth disturbance. The growth pattern in examples of Rauh's model may be said to be "supple". A walk through a temperate woodland will demonstrate this clearly since it is almost impossible to find an individual of ash, oak, or maple which conforms precisely to the model, so readily are young trees damaged. (Pines are different, maybe because their short-shoot pattern plays a distinctive role.) Nevertheless, this does not reduce the competitive ability of the tree. Oak trees are particularly distorted in the way—as witness the irregular, broken crown of an old oak. Red oak (*Quercus rubra*) in Massachusetts never has a straight trunk, the sinuous shape reflects the continuous readjustment and replacement of the axis in its vigorous passage to the canopy (OLIVER, 1975).

In the tropics we can compare trees representing Rauh's model with examples of Aubréville's model in which the replacement of a terminal meristem is a less direct and undoubtedly slower process. Both, however, have rhythmic growth allowing them to suspend meristematic activity during regular (seasonal) or irregular periods of environmental stress. In models of the same group, those with terminal inflorescences regularly lose vegetative apical meristems by sexual differentiation and cessation of vegetative growth is definitive (Scarrone's model). When rhythm is lacking, there is no programmed means of suspending meristem activity and this could explain the diminished success of such trees in all environments except the most stable ones (Attims' model).

Taxonomic List of Examples (Rauh's Model)

PTERIDOPHYTES

Oleandraceae:
[H] *Oleandra pistillaris* (Sw.) C. Chris. (Fig. 60), Indonesia.

GYMNOSPERMS

Araucariaceae:
**Araucaria araucana* (Molina) Koch, Temp. S. America / **Araucaria bidwillii* Hook., Australia / *Araucaria cunninghamii* Sweet., "hoop pine", New Guinea / *Araucaria hunsteinii* K. Schum., "klinki pine", New Guinea.

Pinaceae:
(Most species of *Pinus* exhibit this model, the following are merely representative.) **Pinus caribaea* Morelet, "Honduran pine". Honduras / *Pinus elliottii* Engelm., "slash pine", S.E. United States / *Pinus merkusii* Jungh. and de Vries, Sumatra / **Pinus radiata* D. Don, "Monterey pine", California, widely cultivated / *Pinus silvestris* L., "Scots pine", Europe / *Pinus strobus* L., "white pine", E. United States.

Podocarpaceae:
Podocarpus salicifolius Kl., Martinique.

DICOTYLEDONS

Aceraceae:
Acer pseudo-platanus L., "sycamore", Europe / *Acer rubrum* L., "red maple", E.N. America, WILSON, 1966.

Apocynaceae:
Alyxia clusiophylla Guill., New Caledonia, VEILLON, 1976 / *Couma guianensis* Aubl., Trop. S. America.

Aquifoliaceae:
Ilex mitis Auct., Madagascar / **Ilex paraguaiensis* A. St.-Hil., "maté", S. America / *Ilex* sp., (F. Hallé 1972), New Guinea.

Bombaceae:
Eriotheca sp., (Oldeman 2155), French Guiana.

Burseraceae:
Aucoumea klaineana Pierre, "okoumé", W. Africa / *Canarium schweinfurthii* Engl., Trop. Africa / *Dacryodes klaineana* (Pierre) Lam., Trop. Africa / *Pachylobus edulis* G. Don., W. Africa / *Tetragastris altissima* (Aubl.) Swart, French Guiana / *Trattinickia* cf. *demerarae* Sandw., (Oldeman 2279), Guianas.

Casuarinaceae:
Gymnostoma deplancheana Auct., New Caledonia, Veillon, 1976.

Crassulaceae:
Kalanchoë beharensis Drake (Fig. 61 D), Madagascar.

Epacridaceae:
Styphelia pancheri (Brogn. and Gris) F. Muell., New Caledonia, Veillon, 1976.

Ericaceae:
Erica arborea L., Europe to E. Africa, Temple, 1975 / [H] *Erica herbacea* L., C. Europe, Temple, 1975 / [H] *Erica multiflora* L., Mediterranean, Temple, 1975 / [H] *Erica vagans* L., W. Europe, Temple, 1975 / [H] *Calluna vulgaris* Salisb., Europe, Temple, 1975.

Erythroxylaceae:
Erythroxylum mannii Oliv., Trop. Africa.

Euphorbiaceae:
Cocconerion balansae Baill., New Caledonia, Veillon, 1976 / *Elaeophorbia grandifolia* (Haw.) Croizat, W. Africa / *Euphorbia abyssinica* J.F. Gmel., E. Africa / *Euphorbia candelabrum* Trémaut, E. Africa / *Euphorbia didiereoides* N. Denis and Humbert, Madagascar, Cremers, 1976 / *Euphorbia durani* Ursch. and Léandri, Madagascar, Cremers, 1976 / *Euphorbia enterophora* Drake, Madagascar, Cremers, 1976 / +*Euphorbia excelsa* W.D. and S., Transvaal / *Euphorbia leucodendron* Drake, Madagascar, Cremers, 1976 / *Euphorbia oncoclada* Drake, Madagascar, Théodore, 1969 / +*Euphorbia xylophylloides* Auct., Madagascar / *Hevea brasiliensis* Muell.-Arg., "hevea rubber", Trop. S. America, Hallé and Martin, 1968 / *Macaranga aleuritoides* F. von Muell. (Fig. 61 B), New Guinea / *Protomegabaria stapfiana* (Beille) Hutch., Trop. Africa / *Ricinodendron heudelotii* (Baill.) Pierre ex Pax, Trop. Africa / *Spondianthus preussii* Engl., Trop. Africa / *Uapaca bojeri* Baill., Madagascar / *Uapaca guineensis* Muell.-Arg., Trop. Africa.

Fagaceae:
**Lithocarpus teysmannii* Rehd., Java / *Quercus rubra* L., "red oak", E.N. America / *Quercus sessiliflora* Salisb., "sessile oak", Europe / *Quercus subsericea* Camus, Malaysia / *Quercus virginiana* Mill., "live oak", S.E. United States (Probably most species of *Quercus* exhibit this model).

Flacourtiaceae:
Caloncoba welwitschii Gilg, C. Africa / *Carpotroche* cf. *amazonicum* Mart., (Oldeman 2534), Trop. S. America.

Gesneriaceae:
[H] *Boea suffruticosa* Ridley, Malaysia, Burtt, 1964.

Goodeniaceae:
Scaevola subcapitata F. Br., Marquesas.

Guttiferae:
**Mammea americana* L., "mamee apple", Trop. America / *Montrouziera cauliflora* Planch., New Caledonia, Veillon, 1976 / *Pentadesma butyracea* Sabine, Trop. Africa.

Illiciaceae:
**Illicium anisatum* L., Temp. Asia.

Lauraceae:
**Actinodaphne* sp., Malesia / *Aniba bracteata* Mez, Martinique / *Aniba rosaeodora* Ducke, Trop. S. America / *Aniba* sp., (Oldeman 2187), Guianas / *Persea americana* Mill., "avocado", Trop. America / *Persea borbonia* (L.) Spreg., "red bay", S.E. United States.

Lecythidaceae:
Couroupita guianensis Aubl., "cannon-ball tree", Guianas.

Leguminosae – Caesalpinioideae:
Cassia occidentalis L., Pantropical.

Leguminosae – Papilionoideae:
Sesbania grandiflora (L.) Poir., Indonesia.

Magnoliaceae:
Talauma plumierii DC., Martinique.

Melastomaceae:
+*Henriettella* cf. *patrisiana* (DC.) Naud., (de Granville 50), Guianas.

Meliaceae:
Entandrophragma angolense (Welw.) C.DC., Trop. Africa / *Entandrophragma utile* (Dawe) Sprague (Fig. 61 A), "sipo", Trop. Africa / *Khaya ivorensis* A. Chev., W. Africa / **Swietenia macrophylla* King, "mahogany", C. America / *Swietenia mahagoni* (L.) Jacq., "West Indian mahogany", W. Indies / *Trichilia monadelpha* Auct., Trop. Africa.

Melianthaceae:
Bersama abyssinica Fres., Trop. Africa.

Moraceae:
Artocarpus heterophyllus Lam., "jak-fruit", Trop. Asia / *Artocarpus utilis* (Park.) Fosb., "bread-fruit" (Fig. 61 C), S.W. Pacific / *Cecropia palmata* L., Martinique / **Cecropia peltata* L., Trop. America / *Cecropia sciodaphylla* Mart., Trop. America / **Cecropia surinamensis* Miq., Trop. America / *Ficus aurea* Nutt., "strangler fig", W. Indies / *Ficus citrifolia* Mill., "shortleaf fig", W. Indies / *Ficus vogelii* (Miq.) Miq., Trop. Africa / *Musanga cecropioides* R. Br., "umbrella tree", Trop. Africa.

Myoporaceae:
**Bontia daphnoides* L., W. Indies.

Myricaceae:
Myrica cerifera L., "wax myrtle", N. America.

Myrsinaceae:
Cybianthus cf. *nitidus* Miq., (Oldeman 3069), French Guiana, Oldeman, 1972 / *Tapeinosperma viellardii* Hook., New Caledonia, Veillon, 1976.

Myrtaceae:
Callistemon pancheri Brongn., New Caledonia, VEILLON, 1976.
Oleaceae:
Fraxinus americana L., "white ash", E. United States, GILL, 1971a / *Fraxinus excelsior* L., "European ash", Europe.
Rosaceae:
Hagenia abyssinica J.F. Gmel., E. Africa.
Rubiaceae:
Bikkia tubiflora Schl., New Caledonia, VEILLON, 1976 / *Mantalania sambiranensis* Cap. ex. J. F. Leroy, Madagascar, LEROY, 1974a.
Sapotaceae:
Planchonella kuebiniensis Auct., New Caledonia, VEILLON, 1976 / *Trouettea heteromera* (Vink.) Aubr., New Caledonia, VEILLON, 1976.
Sonneratiaceae:
Sonneratia griffithii Kurz., Malaysia.
Sterculiaceae:
Cola nitida (Vent.) Schott. and Endl., "kola nut", Trop. Africa / *Hildegardia barteri* (Mast.) Kosterm., Trop. Africa / *Triplochiton scleroxylon* K. Schum., W. Africa.
Tiliaceae:
Christiana africana DC., Trop. Africa.

Attims' Model

Definition. The architecture is determined by axes with continuous growth, differentiated into a monopodial trunk and equivalent branches; branching takes place either continuously or diffusely. Flowering is always lateral and does not affect shoot construction.

This model is close to Rauh's model, but differs in the continuous activity (i.e., nonrhythmic growth) of the meristems which make up trunk and branches. We have mentioned some tentative reasons why the model is relatively uncommon (p. 226), especially in comparison to Rauh's model.

The model is named after Y. ATTIMS, since it is expressed so clearly in the mangrove species *Rhizophora racemosa* studied by her (ATTIMS and CREMERS, 1967).

Example. We illustrate the model by one species from several of the mangrove genera which conform to it, i.e., *Lumnitzera racemosa* (Combretaceae), widely distributed in the mangal of southeast Asia[10]. This makes a low dense-crowned tree, "little more than a shrub" according to WATSON (1928). However, it develops a single trunk (Fig. 62C) with continuous growth of the terminal meristem, the widespread but semi-erect branches produced in a diffuse manner. These repeat the essential pattern of the parent axis but with lateral racemes of flowers within the leafy region. A related species *Lumnitzera littorea* (Scarrone's model) has terminal inflorescences of conspicuous scarlet flowers.

Fig. 62A–E. Attims' model. ▷
A *Geniostoma ligustrifolium* A. Cunn. (Loganiaceae, New Zealand, from a specimen in cultivation in J. Marnier-Lapostolle's Botanic Garden, Saint-Jean-Cap Ferrat, France). A shrub, 2 m high, flowering on the leafless parts of trunk and branches; a sucker shoot system conforming to the model, and not the whole tree is represented.
B *Crossostylis biflora* Forst. (Rhizophoraceae, Hiva-Oa Island, Marquesas, French Polynesia, *F. Hallé 2112*). A tree, to 5 m high, with stilt roots common in montane rain-forest.
C *Lumnitzera racemosa* Willd. (Combretaceae, southeast Asia). A small shrubby tree, up to 4 m high, growing in the mangrove forest; branching is diffuse. Attims's model seems to be dominant in the mangrove communities throughout the tropics.
D *Phyllanthus polygonoides* Nutt. ex. Spr. (Euphorbiaceae, California and Mexico). A herbaceous species, 30 cm high (BANCILHON, 1971).
E *Pemphis acidula* Forst (Lythraceae, Polynesia). A shrub, up to 4 m high, growing on dry elevated coral reefs in the western Pacific

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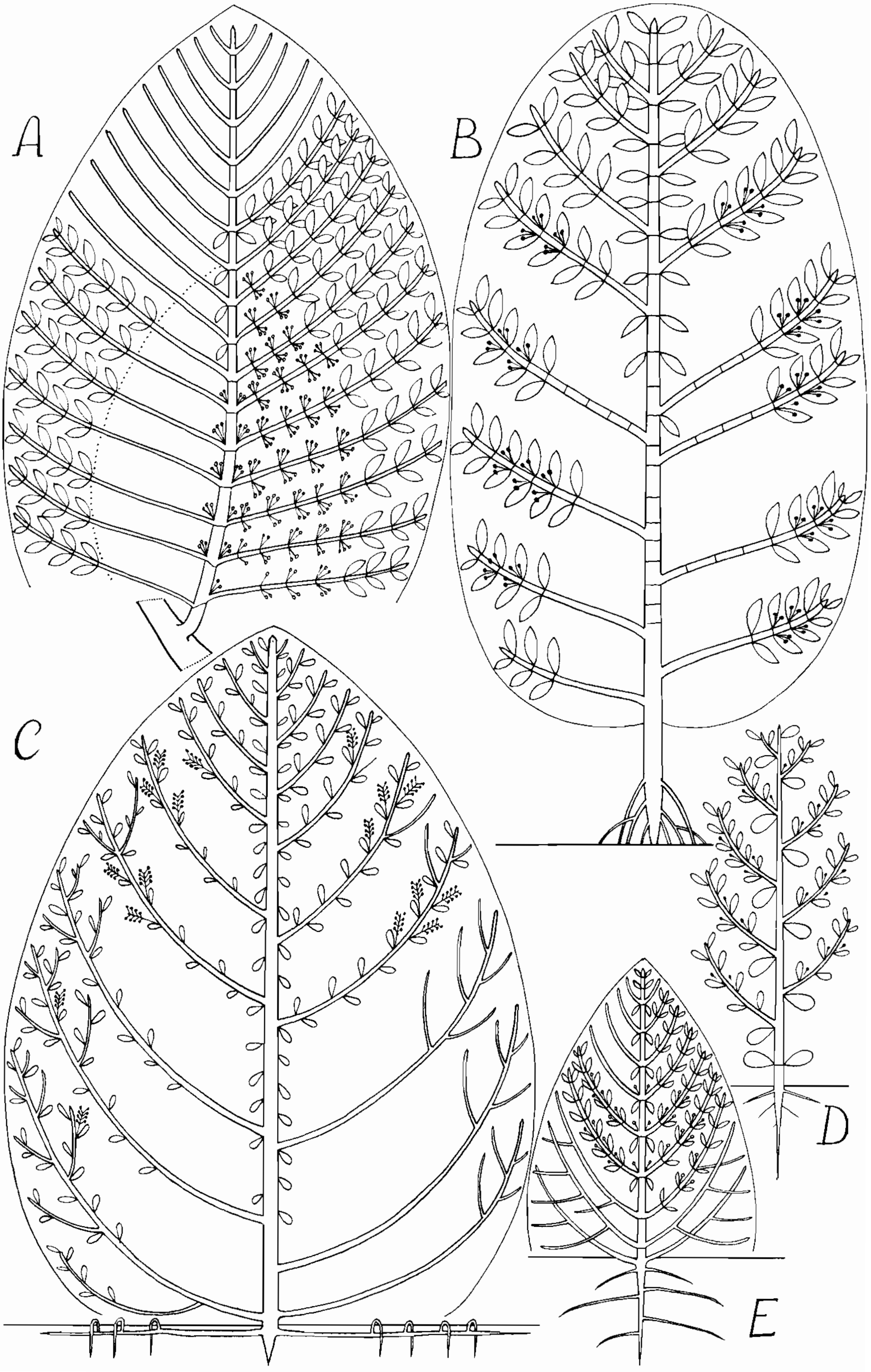
[10] The specific epithet "racemosa" is frequent among species representing this model and indicates indeed that their branching is profuse.


A
B
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E

Other Examples. Some emphasis on the family Rhizophoraceae is inevitable in describing this model since all species of *Rhizophora* exhibit it well, e.g., *R. racemosa*, as illustrated by H.O. (1970, p. 90), and *R. mangle* (GILL and TOMLINSON, 1969, 1971 b). *Rhizophora racemosa* is of interest because it provides an example of natural "marcottage" (discussed on p. 310). *Rhizophora mangle* varies enormously in its stature, from spider-like shrubs scarcely 2 m high with disproportionately developed stilt roots to tall trees reaching a height of 25 m. All this variation may be expressed while still in conformity with the model. Readers familiar with *Rhizophora* will know that the distal parts of older branches can be readily confused with modular "Terminalia-branches" such as occur in Aubréville's model (see Fig. 12A, B). However, the orthotropy of *Rhizophora* branches is clear in young branch complexes near the trunk apex. In damaged trees a broken leader is readily replaced by an adjacent lateral. Species of *Ceriops* from the mangrove communities of the Asian tropics are identical with *Rhizophora* in architecture. The same family is also represented here by *Crossostylis biflora* (Fig. 62B), but in the quite different habitat of montane forest in the Marquesas Islands where it makes a small tree up to 5 m high, with short stilt roots. Branching is diffuse, but regular; the axes are marked by the prominent stipule scars.

Geniostoma ligustrifolium (Loganiaceae, New Zealand) represents the model as a low shrub scarcely 2 m high in forest undergrowth, with continuous branching (Fig. 62A). It is unusual in that the flowers appear on the older, leafless parts of the branches so that there is a cone of flowers within the leafy crown. Another shrubby plant with continuous branching is *Pemphis acidula* (Lythraceae, Polynesia) which is characteristic of dry elevated reefs on Pacific Islands (Fig. 62E) and may be described as a mangrove associate.

Herbs are likely to exhibit Attims' model; we have illustrated *Phyllanthus polygonoides* (Euphorbiaceae, California and Mexico, Fig. 62D), whose architecture has been described by BANCILHON (1971).

In seeking examples of large trees which conform to Attims' model we probably need to look no further than the genus *Eucalyptus* which, despite its commercial importance, remains architecturally little known (JACOBS, 1936). *Eucalyptus globulus* has been referred to this model (H.O., 1970, p. 88) and *E. regnans* is seemingly the same, from the description of CREMER (1972). The existence of pronounced differences between juvenile and adult phase is well known in *Eucalyptus* and is of interest in combination with the essentially continuous growth and branching of such trees. In the Guianese rain-forest a large tree is *Dipteryx odorata,* "gaiac" (Leguminosae – Caesalpinioideae). This forms stilt roots of spectacular dimensions, which with age become elliptical in section by secondary growth. Their physiognomy may also be that of buttresses hollowed out at the base.

The frequent existence of species in this model which possess stilt roots deserves comment; the feature is, of course, not exclusive to the model, but there is certainly a concentration here. Other models which notably include stilt-rooted species are those of Rauh and Troll.

Variations. The activity of meristems in this model is described as continuous, but this does not imply a uniform rate of growth. Fluctuation in growth rate is evident in plants growing in seasonal climates, as has been measured by GILL and TOMLINSON (1971 b) for *Rhizophora mangle.* In *Eucalyptus regnans,* although the rate of growth was not measured, there is a suggestion by CREMER (1972) that there is cessation of growth in winter. Unlike the situation in Rauh's model periodicity is not endogenous. This is reflected by a constant bud composition, both in the *Rhizophora* and *Eucalyptus* species, which seems an important criterion for recognizing continuous growth: as one leaf expands outside the bud it is essentially replaced by a primordium initiated at the shoot apex.

Strategy of the Model. The number of known species in this model is low in comparison with Rauh's much more successful model. We have already suggested (p. 36) that an endogenous resting phase, which is the key difference, is a very significant one even in trees of nonseasonal climates. In our later discussion (p. 273) we will show that *Rhizophora mangle* further reduces its adaptability by the loss of reserve buds with age. Continuous growth, which is characteristic of Attims' model, seems to account for the large number of its examples in the relatively uniform environment of tropical mangroves (it is known so far in the genera *Rhizophora, Ceriops, Laguncularia, Lumnitzera, Avicennia, Sonneratia*). Mangrove vegetation offers some of the best examples of a biotope saturated by monospecific populations with a zonation from species to species (Chapman, 1976). Such plants are characterized by a high output of propagules which is often continuous. Perhaps we should look to the world of weeds, those population-oriented organisms in optima forma, for more information about the ecological significance of Attims' model (Jeannoda, 1977).

Taxonomic List of Examples (Attims' Model)

Avicenniaceae:
Avicennia germinans (L.) L., Mangroves of Trop. America and W. Africa (Possibly all *Avicennia* species exhibit the same architecture).
Betulaceae:
Alnus incana Medici, Europe.
Campanulaceae:
Lobelia scaevolifolia Roxb. [= *Trimeris scaevolifolia* (Roxb.) Mabb.], St. Helena, Mabberley, 1974a.
Casuarinaceae:
Casuarina equisetifolia L., "whistling pine", Australasia, commonly cultivated.
Combretaceae:
Lumnitzera racemosa Willd. (Fig. 62C), Trop. Asia.
Compositae:
Senecio redevivus Mabberley, St. Helena, Mabberley, 1975.
Cornaceae:
**Corokia virgata* Turrill, New Zealand.
Cunoniaceae:
Weinmannia sp., Madagascar.
Dilleniaceae:
Hibbertia coriacea Gilg, New Caledonia, Veillon, 1976.
Euphorbiaceae:
+ *Euphorbia canariensis* L., Canary Islands / *Euphorbia stenoclada* Baill., Madagascar, Thomasson, 1972; Cremers, 1976 / [H] *Phyllanthus lacunarius* F. Muell., Australia, Bancilhon, 1971 / [H] *Phyllanthus polygonoides* Nutt. ex Spr. (Fig. 62D), Mexico, Bancilhon, 1971.
Fagacaceae:
Trigonobalanus verticillatus Forman, Malaysia.
Guttiferae:
Calophyllum sp., New Guinea / **Garcinia gnetoides* Hutch. and Dalz., Trop. Africa / *Rheedia* cf. *macrophylla*, (Oldeman 2479), French Guiana / **Tripetalum cymosum* K. Schum., New Guinea.
Icacinaceae:
Cassinopsis madagascariensis Baill., Madagascar.
Leguminosae – Caesalpinioideae:
**Dipteryx odorata* (Aubl.) Willd., Trop. S. America.
Loganiaceae:
**Geniostoma ligustrifolium* A. Cunn. (Fig. 62A), New Zealand.
Lythraceae:
Pemphis acidula J.R. and G. Forst. (Fig. 62E), New Guinea-Polynesia.
Myrsinaceae:
Maesa lanceolata Forsk., Madagascar / *Rapanea asymmetrica* Mez, New Caledonia, Veillon, 1976.

Myrtaceae:
**Eucalyptus globulus* Labill., Australia / *Eucalyptus regnans* F. Muell., Australia, CREMER, 1972.
Onagraceae:
[H] *Jussiaea abyssinica* (A. Rich.) Dandy and Brenan, Trop. Africa.
Rhizophoracae:
Anopyxis klaineana (Pierre) Engl., Trop. Africa / *Ceriops tagal* (Perr.) C.B. Rob., Trop. Asia / *Crossostylis biflora* Forst. (Fig. 62B), Marquesas / *Rhizophora mangle* L., Trop. America and W. Africa, GILL and TOMLINSON, 1969 / *Rhizophora racemosa* Meyer, Trop. America and W. Africa, ATTIMS and CREMERS, 1967. (All *Rhizophora* species have an identical architecture).
Rubiaceae:
Morierina montana Viell., New Caledonia, VEILLON, 1976.
Rutaceae:
Euodia madagascariensis Baker, Madagascar / **Euodia suaveolens* Scheft. var *ridleyi* (Hochr.) Bakh. f., New Guinea.
Sonneratiaceae:
Sonneratia caseolaris (L.) Engl., Trop. Asia.
Strasburgeriaceae:
Strasburgeria robusta (Viell. ex Panch and Seb.) Guill., New Caledonia, VEILLON, 1976.
Theaceae:
Archboldiodendron cf. *calosericeum* Kobiski, New Guinea.
Turneraceae:
[H]**Turnera ulmifolia* L., Trop. America, commonly cultivated.

3. Trees with Mixed Axes — an Introduction

The final tree models differ from all those previously described in that their architecture is determined by axes which have been defined as mixed (H.O.),1970; p. 114). Trees belonging to previous models (except McClure's model) are constructed by meristems which determine either wholly orthotropic shoots, or there is a combination of meristems which produce either orthotropic or plagiotropic shoots, the former trunk, the latter branch axes.

In the remaining models single meristems determine both trunk and branch axis, for example, by primary growth, as in Mangenot's model, where growth in height is determined by an initial orthotropic phase which is followed, usually abruptly, by a plagiotropic phase. In this remarkable phase change, there may even be a change of phyllotaxis (from spiral to distichous). Total growth in height of the plant is effected simply by superposition of such units, the early phase producing a segment of the trunk axis, the later phase initiating a branch complex.

In the following two models, a similar effect is produced by secondary changes. The axis may be essentially orthotropic, bending secondarily under its own weight, as in Champagnat's model. In Troll's model, by contrast, the axis is essentially plagiotropic and height growth is determined by secondary erection of part of the axis. This model represents the culmination of a trend towards the elimination of orthotropy in this group of trees. It is not always easy to distinguish between these last two models, but we believe that the differences are sufficiently clear cut to require that the two should be separated. Difficulties are again due to an incomplete understanding of plagiotropy and orthotropy (p.48, Fig. 12). It is quite clear that the trunk and branch segments of each unit in trees with mixed axes are not always readily distinguishable. Equally the level of outgrowth of a new relay axis is determined largely by an ill-defined region of maximum curvature (most obvious in Mangenot's model). Consequently it is not always easy to distinguish architectural branching from reiteration. In Troll's model particularly this apparent lack of precision provides some of the plasticity which accounts for part of the ecological success of its examples.

Mangenot's Model

Definition. Axes are mixed, the apical meristem producing initially a basal vertical part, followed by a distal horizontal part, often associated with a change from spiral to distichous phyllotaxis, and from small to large leaves. Indefinite superposition of such axes at the level of transition builds the architecture of the tree, with the trunk made up of successive proximal vertical parts, the branches of horizontal distal parts.

In this model orthotropy of each axis is significant in producing a tree since growth in height is established precisely by its vertical part. This is evident because the reorientation of the axis is very abrupt, the radius of curvature at the level of change usually being very short. The level of emission of each "branch" from the "trunk" is thus very precisely established. The renewal shoot, of which there is usually only one, originates on the curve (Fig. 63). Some similarity with the models of Massart and Roux is evident in the marked differentiation between orthotropic trunk and plagiotropic branch. However, in these two models the two types of axis are produced by two different types of meristem, whereas in Mangenot's model they are produced by one and the same meristem.

The model is named after GEORGES MANGENOT, since it was he who first described it in his study of the African *Dicranolepis persei* (Thymeleaceae, MANGENOT, 1965; see H.O., 1970, p. 122). This species is not an arborescent element of West African forests; we have made an exception by illustrating this model by means of a temperate example.

Fig. 63. Mangenot's model, *Dicranolepsis persei* Cummins (Thymeleaceae). Seedlings showing initial axis plagiotropic distally, the renewal shoot of the next relay axis just extending

Nontropical Example. Vaccinium corymbosum (Vacciniaceae, widely distributed in eastern North America as one of the "blueberries") is a constituent of the understorey of mixed hardwood forests but with a strong predilection for open situations. It forms a deciduous shrub or low tree to a height of 4 m with a characteristic tiered appearance (Fig. 64A). Rhythmic growth, related to the marked seasonality of its environment, is pronounced.

Growth in height is produced by axes which are initially orthotropic but during their first season of extension they curve fairly abruptly (Fig. 64C) and certainly by the end of the second season have a permanent plagiotropic orientation. Shoots are sympodial by abortion of the terminal bud each fall. The onset of winter dormancy may occur with the axis in any orientation, but subsequent growth by the substituting lateral meristem always completes the plagiotropic response. This is true also for renewal shoots stimulated by damage to the axis. Branching is other-

Fig. 64A–C. Mangenot's model, ▷ *Vaccinium corymbosum* L. (Ericaceae, "highbush blueberry", eastern North America).

A Habit of a small tree, 2.5 m high with typical irregular trunk and pronounced branch tiers. The abrupt junction of orthotropic and plagiotropic portions of single axes is evident in several places.

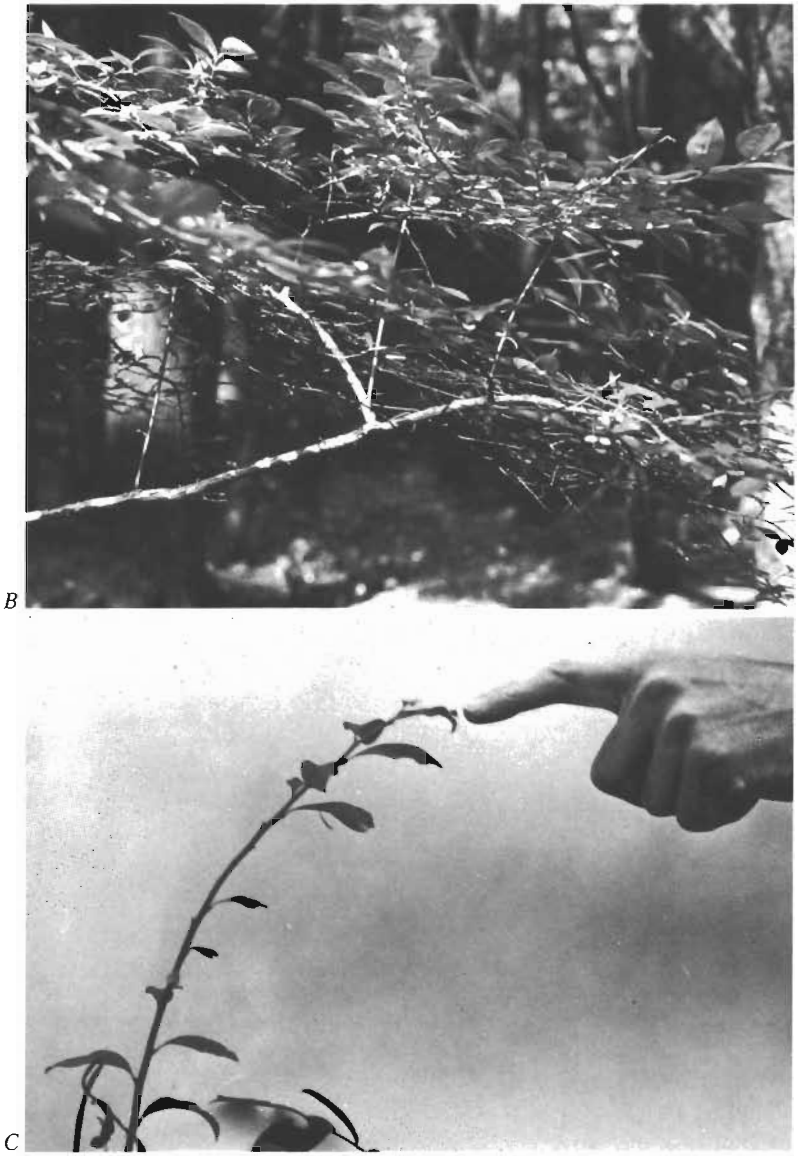
B Detail of distal branch complex including three recent orthotropic renewal shoots.

C Single orthotropic axis showing early development of plagiotropic distal portion (*finger*). This shoot represents one season's growth

wise initiated only in the second season of growth, and the resulting second-order and subsequent axes are always horizontal so that a branch complex of interwoven axes is developed within two or three seasons, with lateral clusters of flowers. This architecture is less precise than most of the tropical examples in that the position of insertion of erect renewal axes is not obvious, so that a distinct trunk axis is either not developed or is at most very irregular (Fig. 64A). Renewal shoots may also occur distally on the branch complex (Fig. 64B); their number suggests reiteration.

Phyllotaxis is spiral throughout and secondary orientation of leaves is responsible for the marked plagiotropy of distal portions of the shoot system. Irregularity of the shoot system in closed natural environments is undoubtedly related to the damage sustained by these low trees from falling branches.

Tropical Examples and Variations. Mangenot's model is not common in the New Caledonian flora (Veillon, 1976), but a good example there is provided by *Jambosa longifolia* (Myrtaceae) where the genus *Jambosa* is here regarded as distinct from *Syzygium*. This forms a tree to a height of 5 m (Fig. 65A) with the pendulous distal part of each unit forming a drooping branch. It is cauliflorous. An interesting biological variation of this model is found in *Rhyticarium longifolium* (Icacinaceae, New Guinea) in which the



mixed axes are determinate since they end in a terminal inflorescence (Fig. 65B). The distal part of each relay axis is self-pruning so that a trunk is formed. However, this rarely reaches a height of more than 3 m and a shrubby habit is predominant since basal branching, representing reiteration, is common.

When the basal orthotropic portions are long they may become very elaborate, as described in *Mouriri* (Melastomaceae, French Guiana) by Oldeman (1974a). Here branching occurs as in Massart's model on the basal portions of the mixed axes, until they differentiate apically and form a branch segment, which on older parts of the tree appears as an isolated plagiotropic branch between tiers of apparently equivalent branches.

In a later discussion of lianes (p. 251) the frequency of distinct juvenile phases is commented upon. We have shown this juvenile phase here for an unnamed species of *Strychnos* (Loganiaceae) from French Guiana (Fig. 65C) which in the sterile juvenile condition represents Mangenot's model precisely. The adult phase has not been seen, but it is likely to be a climber, as is characteristic of most species of the genus, some of which are known to conform to this model. Differentiation of the distal, plagiotropic part of each mixed axis may become pronounced and *Canthium orthacanthum* (Rubiaceae, Congo) illustrates this (Fig. 65Da). This forms a small tree with conspicuous pairs of spines. The distal part of each unit has the longer branches orientated more or less in a single plane with the foliage borne by specialized short shoots which also bear the flowers (Fig. 65Db).

As with the previous model the height to which each orthotropic axis grows before it turns horizontal determines the habit of the plant, rather than the number of relay axes. Where it is short (50 cm or less), a low shrub develops, as in *Dicranolepis, Maieta, Siparuna* and *Vaccinium*. Small trees are developed in a few genera in which the orthotropic segment is longer (over 1 m) as in *Guatteria, Memecylon*, and *Vismia*. Otherwise trees of any stature are rare in this model, but *Okoubaka aubrevillei* (Octocnemaceae, West Africa) and *Mouriri crassifolia* (Melastomaceae, American tropics) are exceptions. The architecture, however, seems well adapted to the development of lianes (see p. 254) as in species of *Atroxima* (Polygalaceae), *Rhaphiostylis* (Icacinaceae) and *Strychnos* (Loganiaceae). *Rhapiostylis beninensis* is reported to have the habit of a tree on occasions and shows the adaptability of the model. In general the lianescent habit is promoted by the prolongation of the orthotropic phase and may be associated with morphological specialization, e.g., tendrils in *Strychnos*.

The transition from orthotropy to plagiotropy is commonly associated with a change in phyllotaxis from spiral to distichous (e.g., in *Dicranolepsis, Rhaphiostylis*) with the leaves on the trunk segment being smaller than those on the branches. In *Siparuna cristata* leaves are decussate throughout, dorsiventrality on the plagiotropic segment being achieved by twisting of internodes. In this species there is a suggestion of rhythmic growth since series of close-set leaf scars, which may correspond to a dormant phase, alternate with leaf-bearing regions of the stem. The abrupt bend in the axis seems consistently to be associated with a series of scars.

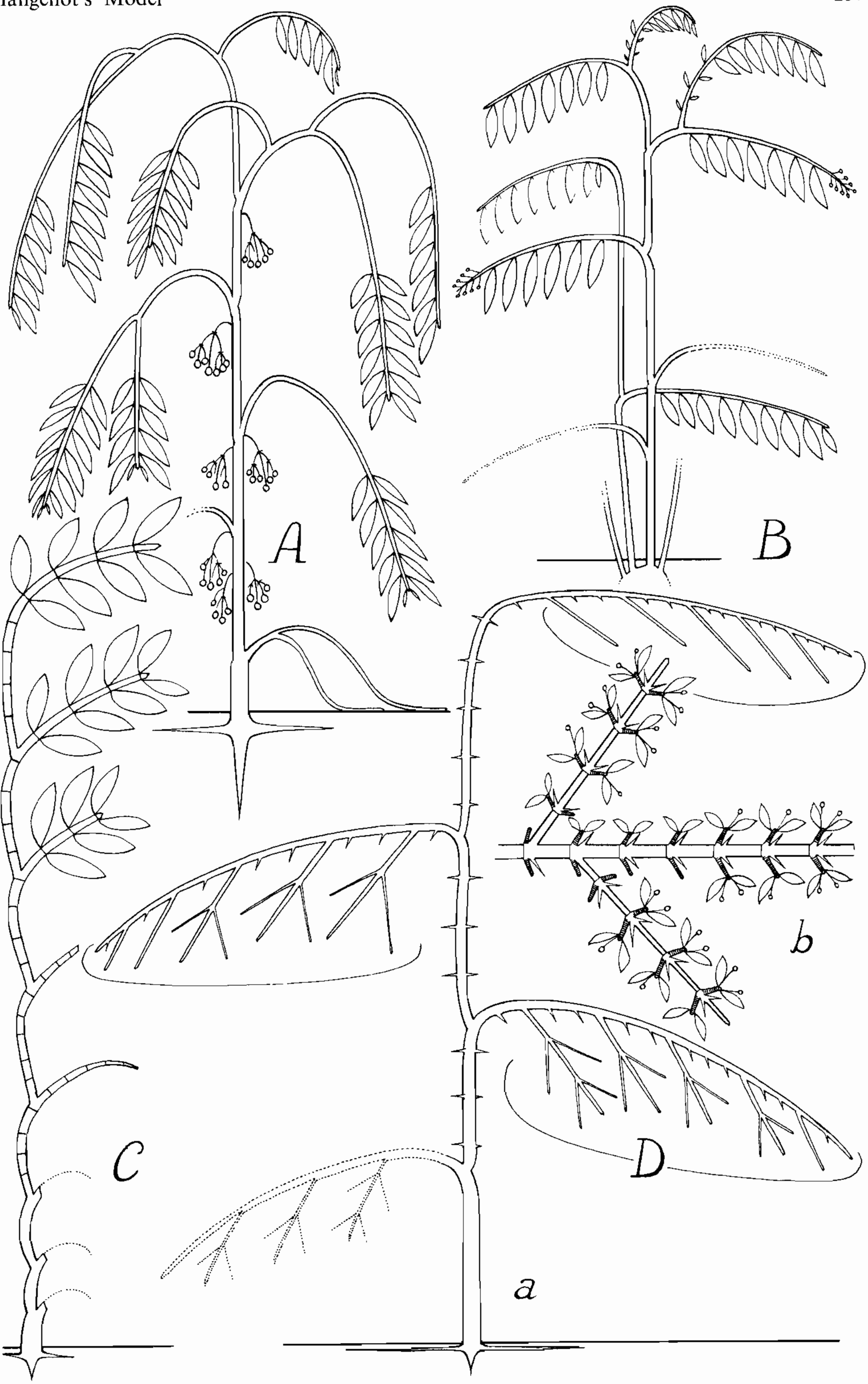
Fig. 65A–D. Mangenot's model. ▷

A *Jambosa longifolia* Brongn. (Myrtaceae, New Caledonia). A small tree, 5 m high, cauliflorous, with the successive apices growing into long pendulous twigs. This architecture is quite unusual in the New Caledonian flora.

B *Rhyticarium longifolium* K. Schum. and Lauterb. (Icacinaceae, New Guinea). A small treelet, 3 m high, in the forest margin; inflorescences are apical, and the plagiotropic apices are self-pruning.

C *Strychnos* sp. (Loganiaceae, Saül, French Guiana, *F. Hallé 2274*). The juvenile form; this sterile young plant reaches 2 m high, and it is likely that the adult is a climber.

D *Canthium orthacanthum* (Mildbr.) Robyns (Rubiaceae, M'Bila forest, Congo, *F. Hallé 1611*). A small tree, 5 m high, of the forest undergrowth. *a* General architecture showing the successive axes; *b* the plagiotropic part of the axis, seen from above, to show the spines, and flowers on short shoots


A
B
C
D
a
b

Growth of the branch portion of the axis is also quite variable. In *Dicranolepis persei*, for example, the branch grows monopodially but with frequent abortion of the terminal bud.

Strategy of the Model. Examples of Mangenot's model are characteristic of forest environments, usually occupying the undergrowth in which pronounced differentiation of plagiotropic branches seems adaptive, much as in Massart's and Roux's models. This environment also seems appropriate for the development of a scandent habit.

Taxonomic List of Examples (Mangenot's Model)

Annonaceae:
Guatteria sp., (Oldeman 1931), Guianas.
Buxaceae:
**Sarcococcus confusa* Sealy, China.
Ericaceae:
Vaccinium corymbosum L. (Fig. 64), "high-bush blueberry", E.N. America.
Guttiferae:
Vismia confertiflora Spruce ex H.G. Reich., Trop. S. America / *Vismia* cf. *ferruginea* H.B.K., (Oldeman 2857), Guianas.
Icacinaceae:
[L] *Desmostachys vogelii* (Miers) Stapf, Trop. Africa, CREMERS, 1973, 1974 / [L] *Rhaphiostylis beninensis* (Hook.) Planch. (Fig. 69H), W. Africa, CREMERS, 1973 / *Rhyticarium longifolium* K. Schum. and Lauterb. (Fig. 65B), New Guinea.
Loganiaceae:
[L] *Strychnos congolana* Gilg., Trop. Africa, CREMERS, 1973 / [L] *Strychnos variabilis* De Wild., C. Africa / [L] *Strychnos* sp. (Fig. 65C), (F. Hallé 2274), French Guiana.
Melastomaceae:
Maieta guianensis Aubl., Trop. America / *Memecylon guineensis* Keay, W. Africa / *Mouriri crassifolia* Sagot, Trop. S. America / *Mouriri francavillana* Cong., French Guiana / **Mouriri guianensis* Aubl., Trop. S. America.
Monimiaceae:
**Matthaea calophylla* Perk., Borneo / *Siparuna cristata* D.C., Trop. S. America.
Myrtaceae:
Eugenia jambolana Lam., Marquesas / *Jambosa longifolia* Brongn. (Fig. 65A), New Caledonia, VEILLON, 1976.
Octocnemaceae:
Okoubaka aubrevillei Pellegr. and Normand, W. Africa.
Polygalaceae:
Atroxima liberica Stapf, Trop. Africa, CREMERS, 1973.
Rosaceae:
Hirtella cauliflora Hub., French Guiana.
Rubiaceae:
Canthium orthacanthum (Mildbr.) Robyns (Fig. 65D).
Theaceae:
**Eurya japonica* Thunb., Japan.
Thymeleaceae:
Dicranolepis persei Cummins (Fig. 63), W. Africa, MANGENOT, 1965 / *Dicranolepis stenosiphon* Gilg., Congo / *Dicranolepis* cf. *vestita* Engl., Congo.

Champagnat's Model

Definition. Architecture is determined by the indefinite superposition of mixed orthotropic axes with spiral phyllotaxis, each relay axis becoming pendulous distally by its own weight, the renewal shoot then arising on the upper surface in the initial curve of the pendulous axis. The part distal to the renewal shoot becomes a branch of the tree, the part proximal to the renewal shoot becomes part of the trunk.

This model represents the simplest construction amongst trees with mixed axes, since there is no morphological distinction between distal and proximal parts of each axis, although such a distinction may develop secondarily. Since the curvature of the axis is gradual, relay axes tend to proliferate over a considerable length of the zone of curvature, but always proximal rather than distal. A dominant "leader" in the construction the tree is seldom apparent and many examples of this model correspond to the generalized concept of a shrub (Fig. 66). Nevertheless, trees of appreciable size are sometimes developed.

This model shows most affinity to those described earlier in which the axes are all equivalent and orthotropic; namely the models of Corner, Leeuwenberg, and Rauh, but differs in the diminution of the amount of primary and secondary supporting tissue. Some intermediate forms are described below.

The model is named after PAUL CHAMPAGNAT, specialist in the morphology of woody plants in Europe, including *Rosa, Rubus,* and *Sambucus,* which represent the architecture well (CHAMPAGNAT, 1947, 1949, 1954a, 1965). However, examples of this model are known in the tropics, being particularly common in dry tropical areas, notably the African sahel.

Examples. The commonly cultivated Calabash tree *Crescentia cujete* (Bignoniaceae, native to tropical America) serves to exemplify this model (Fig. 66C). It is a small, cauliflorous tree rarely exceeding a height of 10 m. The axes are thick and widespreading, rapidly becoming rough-barked and corky with age. The overall architecture is readily appreciated because foliage is largely borne on sessile short shoots, which become embedded in the bark; consequently long shoots which add to the architecture of the tree are produced infrequently. A short trunk will develop as older branches are lost. Flowers are borne on the older wood and may produce the large woody fruits. These are berries with a woody epicarp; when the pulp is removed a handy vessel is produced. *Balanites aegyptica* (Zygophyllaceae, African sahel) illustrates the model in a different setting (Fig. 66Aa). The distal parts of old shoots are often quite pendulous. The spiny young shoots (Fig. 66Ab) and microphyllous habit reflect the dry conditions under which the tree grows. In *Salvadora persica* (Salvadoraceae) of the same general area, the older twigs will root distally (Fig. 66Da). This plant is scarcely a tree, rarely exceeding 3 m in height.

Other Examples and Variations. The habit of plants which conform to this model depends largely on the rigidity of the axes and the level at which relay axes are inserted. Many examples are shrubs which are characterized by the tendency to produce vigorous basal sprouts, as in *Abuta concolor, Carpotroche longifolium,* and *Thunbergia erecta.* This habit is, of course, familiar in temperate representatives like *Rosa, Rubus,* and particularly *Sambucus.* On the other hand, if the curvature of axes is less pronounced and the height at which branching occurs is greater, larger or smaller trees develop, as in *Andira, Crescentia, Guarea,* and *Lagerstroemia.* In the other direction we have lianescent species, with a generally sprawling habit. We have illustrated *Oxera palmatinervia,* a verbenaceous climber from New Caledonia (Fig. 66B). This grows to a height of 15 m, with the orthotropic part of each axis tending to twist around the support. Flowers occur only on the older parts. In appropriate ecological circumstances such lianes are capable of growing quite tall if supported by surrounding vegetation, and may even develop a thick trunk, as in *Alchornea cordifolia* and in the familiar *Bougainvillea spectabilis.* The latter is provided with stout branch-spines which serve as grapnels and represent modified inflorescences. In *Alloplectus coccineus* (Gesneriaceae) the habit is quite variable, the plant forms a low shrub, but is lianescent and even epiphytic in appropriate conditions (LEEUWENBERG, 1958).

We have emphasized the uniformity of the axes in Champagnat's model, with no difference between base and apex, but some tendency towards distal dorsiventrality is noticeable in some species (e.g., in *Thunbergia* and *Lagerstroemia*). This is shown in distal parts by some asymmetry of leaves on upper and lower surfaces or by an occasional but not regular twisting of internodes which puts leaves in one plane. The slight differentiation between axes is indicated furthermore by the tendency of branches to acquire some degree of plagiotropy according to whether they arise on a horizontal axis or not. Young shoots in *Salvadora persica* show distal plagiotropy, as we have illustrated (Fig. 66Db). This reflects a tendency towards the architecture of Troll's model. Indeed, the continuum between these two models is very evident, as exemplified by *Psidium guajava* ("guava", cultivated throughout the tropics) which represents a borderline case.

Taxonomic List of Examples (Champagnat's Model)

Acanthaceae (or Thunbergiaceae):
Thunbergia erecta (Benth.) T. Anders., W. Africa, Prévost, 1965.
Apocynaceae:
[H] *Lochnera rosea* (L.) Reichenb. f., Pantropical, in cultivation.
Bignoniaceae:
Crescentia cujete L. (Fig. 66C), "calabash tree", Trop. America.
Boraginaceae:
**Cordia bantamensis* Bl., Indonesia / *Cordia macrostachya* (Jacq.) Roem. and Sch., Pantropical / *Cordia tomentosa* Lam., French Guiana, Oldeman, 1974a.
Caprifoliaceae:
Sambucus nigra L., "elderberry", Europe, Asia, Rauh, 1939a; Champagnat, 1954a.
Convolvulaceae:
**Ipomoea arborescens* Don, C. America.
Didiereaceae:
+*Decarya madagascariensis* Choux., Madagascar.
Euphorbiaceae:
Alchornea cordifolia (Schum. and Thonn.) Muell.-Arg., Trop. Africa / **Euphorbia fulgens* Kasw. ex Klotzsch., Mexico.
Flacourtiaceae:
Carpotroche longifolium (Poepp. and Endl.) Benth., Guianas, Ecuador.
Gesneriaceae:
[L] *Alloplectus coccineus* (Aubl.) Mart. ex G. Don, Trop. S. America, Leeuwenberg, 1958.
Labiatae:
[H]**Orthosiphon grandiflorus* Bold., S. E. Asia.
Leguminosae – Caesalpinioideae:
Caesalpinia pulcherrima (L.) Swartz, "Pride of Barbados", Pantropical in cultivation / [L] *Cassia chrysocarpa* Desv., Trop. S. America.
Leguminosae – Papilionoideae:
**Andira inermis* (Sw.) H.B.K., Trop. America and W. Africa / **Andira surinamensis* Splitg., Guianas.
Lythraceae:
Lagerstroemia indica L., "crêpe myrtle", China.
Meliaceae:
**Guarea guara* (Jacq.) P. Wilson, Trop. America / *Turraea heterophylla* Sm., W. Africa.
Menispermaceae:
Abuta cf. *concolor* Poepp. and Endl., (Oldeman 2766), Trop. America.
Nyctaginaceae:
[L] *Bougainvillea spectabilis* Willd., "bougainvillea",

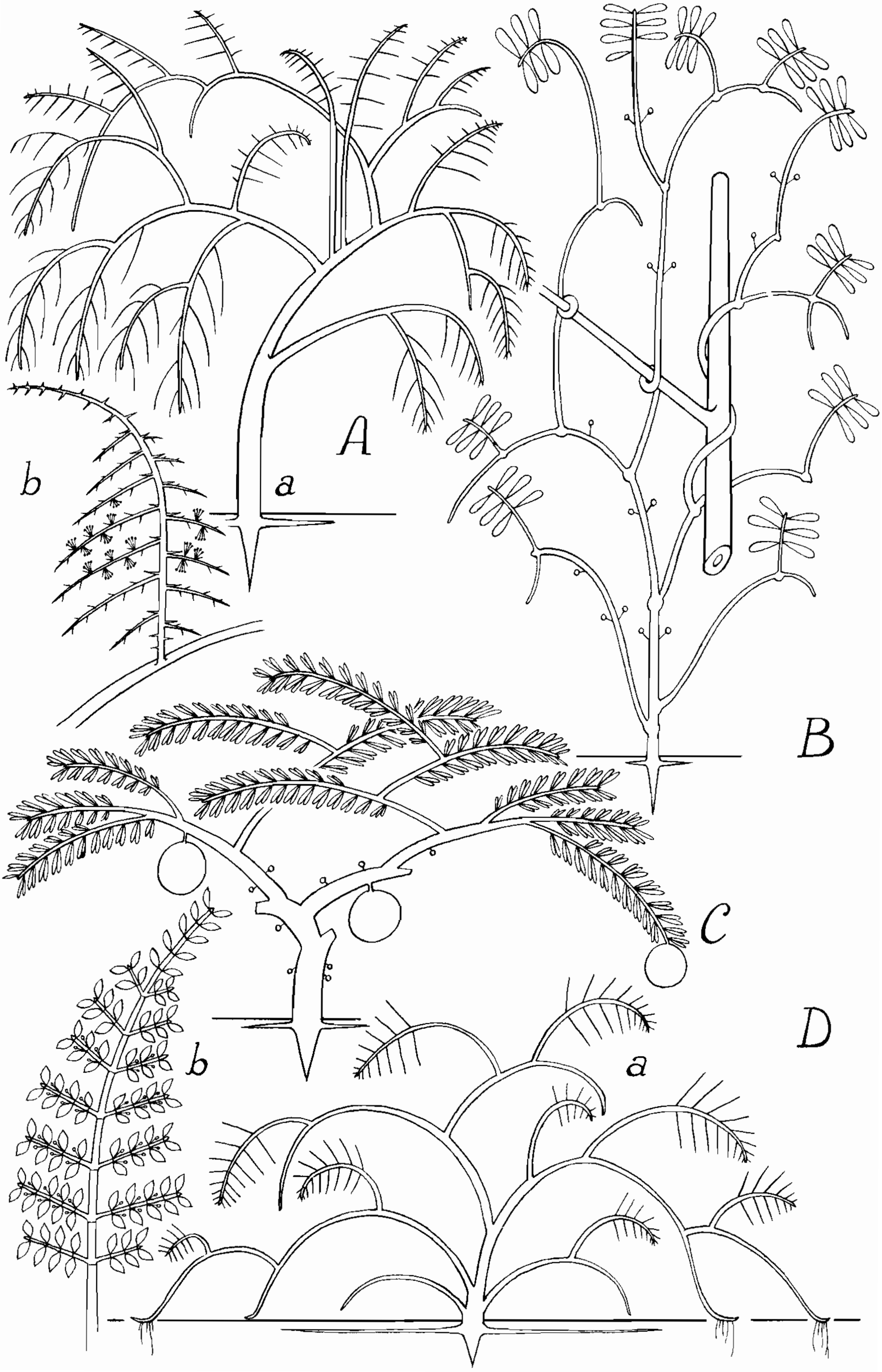
Fig. 66 A–D. Champagnat's model. ▷

A *Balanites aegyptica* (L.) Del. (Zygophyllaceae, dry savanna around N'Djamena, Tchad, *F. Hallé 2341*). A small spiny tree, 10 m high, common in the African sahel. *a* General architecture of the young tree, showing the old axis bending towards the ground; *b* the young shoot, with its spines and axillary flowers; the small bifoliate leaves, 2 cm long, are not represented.

B *Oxera palmatinervia* Dubard (Verbenaceae, New Caledonia, *J.M. Veillon 1036*). A climber, reaching 15 m high; the vertical part of every shoot is twining, the flowers are borne on old wood (Veillon, personal communication).

C *Crescentia cujete* L. (Bignoniaceae, tropical America, the common "calabash tree"). A small cauliflorous tree, less than 10 m high, with a characteristic form.

D *Salvadora persica* L. (Salvadoraceae, between N'Djamena and Lake Tchad, *F. Hallé 2337*). A shrubby bush, 3 m high, with the older twigs rooting in the ground (Lebrun et al., 1972). *a* General architecture; *b* the young shoot, showing small plagiotropic branches and axillary flowers


A
b
a
B
C
D
b
a

Brazil / [L] *Bougainvillea glabra* Choisy, "bougainvillea", Brazil.

Olacaceae:

Ximenia americana L., Trop. America and Africa.

Rosaceae:

[L] *Rosa canina* L., "eglantine", Europe / *Rubus idaeus* L., "raspberry", Europe / *Rubus saxatilis* L., "bramble", Europe.

Rubiaceae:

Nauclea latifolia Sm., Trop. Africa, Menaut, 1971.

Salvadoraceae:

Salvadora persica L. (Fig. 66D), C. Africa.

Sterculiaceae:

Scaphopetalum amoenum A. Chev., Trop. Africa.

Verbenaceae:

[L]+*Oxera palmatinervia* Dubard (Fig. 66B), New Caledonia.

Zygophyllaceae:

Balanites aegyptica (L.) Del. (Fig. 66A), C. Africa.

Troll's Model

Definition. Axes are all plagiotropic, the architecture being build by their continual superposition; main-line axes contribute part trunk, part branch, the proximal part becoming erected, most often secondarily after leaf fall. The distal part of each axis is then a branch with or without determinate growth, bearing lateral axes which often do not form a basal erected portion.

The model is named after Wilhelm Troll, who has described precisely this construction of a tree from plagiotropic axes in his description of the growth of the European *Ulmus effusa* (Troll, 1937). Tropical examples are abundant, however, and constitute a majority among all trees.

How does such a tree with wholly plagiotropic axes grow in height? Two processes are involved: first, the indefinite superposition of similar axes and second, the ability of the basal part of each shoot to become erected after leaf loss by secondary growth. This implies that reaction anatomy of secondary wood is involved in architecture, a consideration we have encountered only once before, in Koriba's model. The close relationship between this model and that of Mangenot is indicated by the frequent development of a short orthotropic axis in the seedling and juvenile phases of growth, but which is rapidly lost in later relay axes. In species which conform exactly to the above definition, plagiotropy is complete, even in seedling axes. Examples are given below.

It is possible also to compare Troll's model with that of Roux, not merely because the two models are frequently found

Fig. 67A–E. Troll's model. ▷

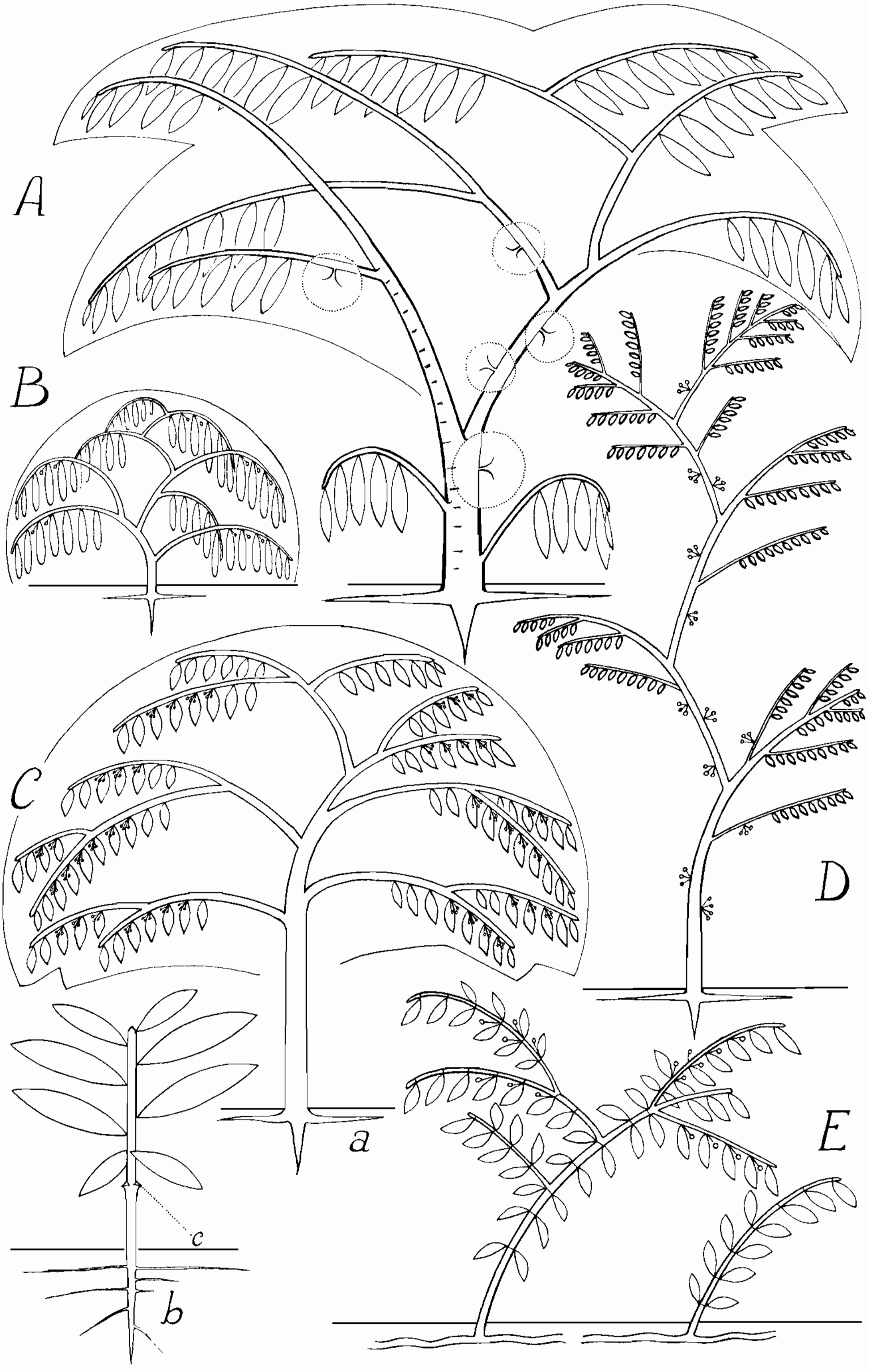
A *Saraca thaipingensis* Cantley (Leguminosae – Caesalpinoideae, Malaysia). A small plagiotropic tree, 8 m high, which exemplifies the main architectural model of the family Leguminosae.

B *Phyllanthus myrtifolius* Moon (Euphorbiaceae, Sri Lanka, from a specimen cultivated in the Papeari Botanic Garden, Tahiti, Polynesia). A plagiotropic shrub, less than 2 m high, with axillary flowers on phyllomorphic ramuli.

C *Chrysophyllum cainito* L. (Sapotaceae, tropical America, the "star-apple"). *a* General architecture of this frequent fruit-tree; *b* the young seedling showing that, except for leaves 3 and 4, all the leaves of the primary axis are in the cotyledonary plane; *c* cotyledon scars.

D *Anaxagorea acuminata* (Dun.) St. Hilaire (Annonaceae, French Guiana, *R.A.A. Oldeman 2189*). A small cauliflorous tree of the forest undergrowth, 6 m high, which exemplifies the main architectural model of the family Annonaceae.

E *Psidium guineense* Sw. (Myrtaceae, one of the wild guava trees of tropical America, from specimens growing as weeds on Hiva-Oa Island, Marquesas, French Polynesia, *F. Hallé 2110*). Root suckers in which the original architecture of the tree is preserved; in contrast to other examples, this species has decussate, not distichous phyllotaxis


A
B
C
D
E
a
b
c

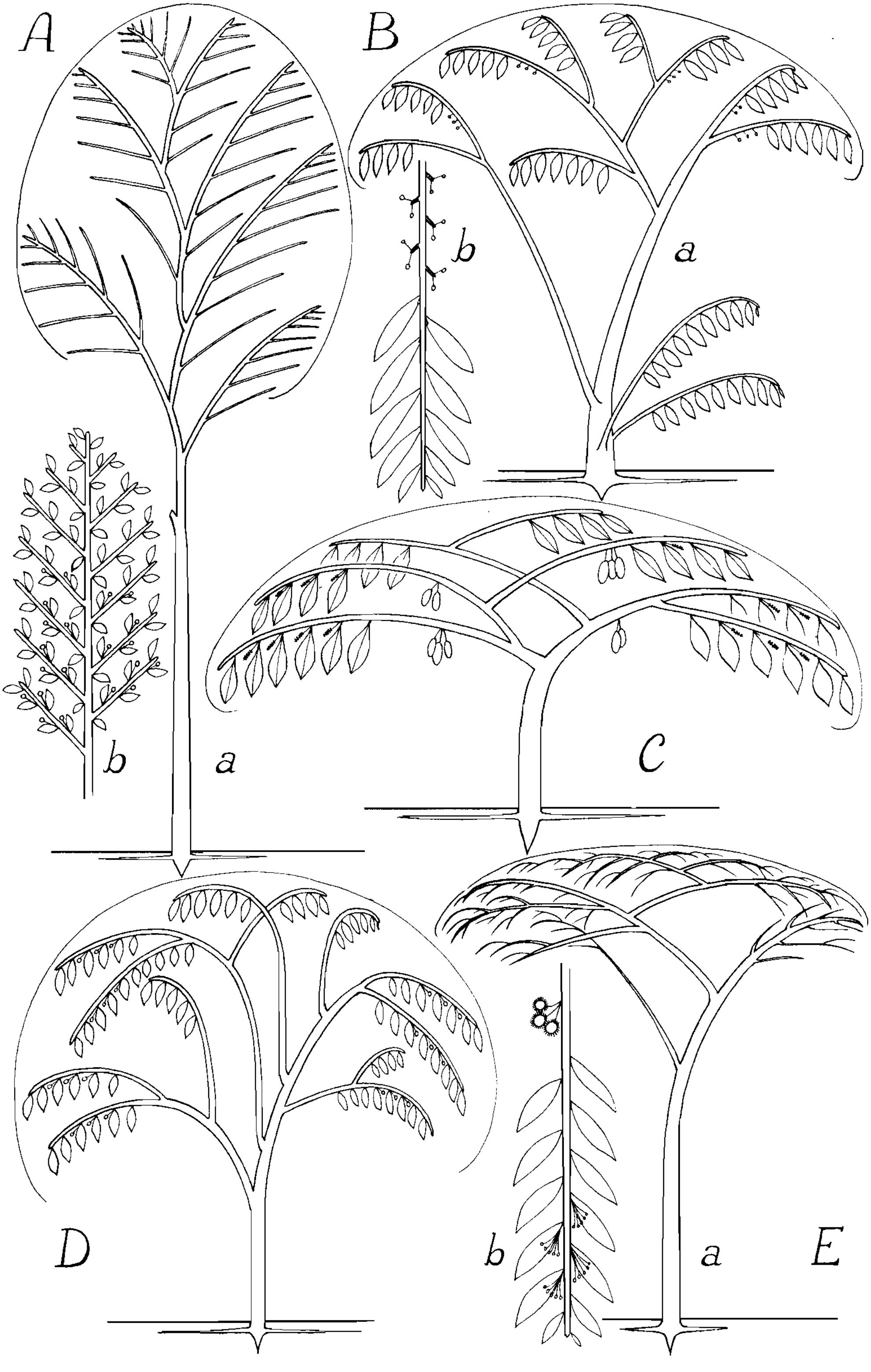
in different species of the same genus (e.g., *Celtis, Chrysophyllum, Chlorophora, Heisteria, Phyllanthus, Siparuna, Vismia*), but also because the branches in Roux's model are comparable to the mixed axes in Troll's model. In the latter all those characters which we have learned to associate with plagiotropic differentiation (i.e., horizontal growth, dorsiventrality, distichous phyllotaxy or at least a disposition of leaves in one plane, assymetry of leaves and ability to form flowers in the adult state) are here essential features of all axes.

Examples. The main architectural model of the family Leguminosae is here represented by *Saraca thaipingensis* (Caesalpinioideae), a small tree native to Malaysia but which is commonly grown as an ornamental tree (Fig. 67A). Flushing growth is striking in this species since the young leaves expand rapidly but hang limp and reddish before later becoming green and erect. Conspicuous globose inflorescences of yellow flowers occur on the older parts. Axes are initially plagiotropic but a short trunk is developed by late erection of the basal parts of successive axes. As in many leguminous trees grown in the open, plagiotropy so dominates the architecture that the tree remains low and spreading.

Further examples from different regions of the tropics serve to illustrate the diversity of families in which this architecture is to be found and some of their biological peculiarities. One species of *Phyllanthus* (Euphorbiaceae) distinguished by its marked shoot differentiation can be included here. *Phyllanthus myrtifolius* from Sri Lanka shows plagiotropy of axes, the ultimate branchlets being represented by phyllomorphic shoots with axillary flowers (Fig. 67B). The shrub scarcely reaches 2 m. *Chrysophyllum cainito* ("star-apple", Sapotaceae, tropical America) is quite widely cultivated for its edible ridged fruits. The arching pendulous branches are distinctive (Fig. 67Ca).

Another family which commonly exhibits Troll's model is Annonaceae, here illustrated by *Anaxagorea acuminata* (Guianas). This cauliflorous tree reaches a height of 6 m but the individual mixed axes are usually quite distinct (Fig. 67D). Annonaceae generally show long arching branches with distichously arranged leaves, the visible and persistent expression of their pronounced plagiotropy. In all these examples distichous phyllotaxis is characteristic. Myrtaceae – Myrtoideae are distinguished by a decussate shoot system but may show the same dorsiventrality, readily seen in the commonly cultivated guavas (*Psidium* spp). Here we illustrate *Psidium guineense* (tropical America) by means of root suckers which retain the original architecture of the tree

Fig. 68 A–E. Troll's model (further examples). ▷
A *Trymatococcus oligandrus* (R. Ben.) Lang. (Moraceae, Brazil and Guianas). *a* General architecture of the tree, 17 m high and 15 cm in basal diameter; *b* a leafy part, seen from above, to show the axillary inflorescences.
B *Rinorea bengalensis* Kuntze var. *disticha* Boerl. (Violaceae, Indonesia). *a* General habit of this small tree, 3 m high; *b* leafy part, seen from above, showing the distichous phyllotaxis and axillary inflorescences.
C *Averrhoa carambola* L. ("carambola", Oxalidaceae, tropical Asia). A small fruit-tree, less than 10 m high, with purple axillary flowers, and delicious fruits on the defoliated parts of the twigs.
D *Heisteria parvifolia* Smith (Olacaceae, tropical West Africa). A treelet of the secondary forest undergrowth.
E *Commersonia bartramia* Merr. (Sterculiaceae, Polynesia). *a* General architecture of this small flat-topped tree, 5 m high, occurring in the mountain rain-forest of the high islands; *b* leafy part, seen from above, showing the distichous phyllotaxis and the axillary flowers


A
b
a
B
b
a
C
D
b
a
E

(Fig. 67E). Plagiotropy in this example is maintained by twisting of alternate stem internodes and reorientation of leaf blades.

An unusual and interesting example is in Moraceae, as shown here by *Trymatococcus oligandrus* (Fig. 68Aa, Brazil and Guianas). The distal part of each axis (Fig. 68Ab) shows marked dorsiventrality with the branches regularly disposed and orientated in one plane. Further families represented here are Violaceae (*Rinorea bengalensis,* Indonesia, Fig. 68B); Oxalidaceae (*Averrhoa carambola,* the commonly cultivated "carambola" from tropical Asia, Fig. 68C); Olacaceae (*Heisteria parvifolia,* tropical West Africa, Fig. 68D), and Sterculiaceae (*Commersonia bartramia,* Polynesia, Fig. 68E). The surface views of the shoots shown in Figures 68Ab, Bb, and Cb express the pronounced dorsiventrality of the distal part of each axis very well.

Other Examples and Variations

1. Gymnosperms. Monopodial trunk structure is so pronounced a feature of conifers that one scarcely expects to find examples with mixed axes. However, eastern hemlock [*Tsuga canadensis* (L.) Carr., Pinaceae] is familiar in the eastern United States with its drooping leader which MERGEN (1958) has shown to become secondarily erected in association with development of compression wood on the lower side of the curve. Cause and effect have not clearly been differentiated, but it seems likely that erection of the leader is a consequence of the development of compression wood. The drooping leader strongly suggests sympodial growth and Troll's model, but we still lack clear evidence that there is periodic substitution of the leader. *Callitris cupressiformis* Vent. (New South Wales and Queensland, Cupressaceae) is a subtropical example with a similar drooping leader.

2. Dicotyledons. We have included as examples of this model a number of species in which an initial tendency for axes to develop an orthotropic segment shows a feature comparable to Mangenot's model. The character which allows us to distinguish these two models is that later-formed axes lose this tendency, though it may reappear in reiterated shoots. In *Delonix regia* ("poinciana", Leguminosae – Caesalpinioideae), for example, the first aerial axis is practically orthotropic throughout, but in later axes there is progressive change to the plagiotropic condition. In the adult tree all axes are plagiotropic. This leads to the development of the low, spreading crown which is so characteristic of many leguminous trees, and which is notable in species of *Acacia* (Leguminosae – Mimosoideae) in drier environments, as in East Africa and the drier parts of Ecuador and Peru. The same architecture, however, can lead to the development of tall forest trees as is shown by *Parinari excelsa* (Rosaceae), ranging from Africa to the American tropics. Here the orthotropic phase of the seedling axis is marked by small, spirally inserted leaves which contrast with the distichous, larger leaves of the plagiotropic phase. This orthotropic phase is progressively lost in succeeding relay axes; growth in height is then provided by the secondary erection of the basal part of each new axis. By this method a tree is developed which ultimately may reach, in Africa, a height of 25 m, with a basal trunk diameter of 1.5 m (H.O., 1970, p. 127).

The orthotropic segment is equally evident in the epicotyledonary axis of a number of other examples, e.g., *Averrhoa carambola* (Oxalidaceae), *Strephonema pseudocola* (Combretaceae), *Vouacapoua americana* (Leguminosae – Caesalpinioideae) where it may be 15–30 cm long, with at least ten leaves (including the cotyledons) showing a spiral arrangement prior to the transition to distichy. In *Ulmus foliacea* (Ulmaceae), described by SCHOUTE (1937), the orthotropic phase is briefer, with six spirally arranged leaves preceding the distichous condition. *Holoptelea grandis,* an African member of the same family, is similar. In *Chrysophyllum cainito* ("star-apple", Sapotaceae) there is a pair of leaves at right angles to the cotyledons after which the distichous arrangement is established in the cotyledonary plane (Fig. 67Cb). In *Sapium cornutum* and *Pedilanthus tithymaloides* (both Euphorbiaceae) the orthotropic phase is represented by the cotyledonary axis. In a species of *Lecythis* (=*Eschweilera,* Lecythidaceae) from French Guiana even the cotyledons are distichous, although this condition seems exceptional. Most examples express a degree of orthotropy in the seedling axis which reflects the differentiation sequence imposed on the apical meristem by the sexual process of seed development, and beginning with a dedifferentiated, orthotropic phase, even if short. As we will show later, the length of this axis may be correlated with seed size.

The method of trunk development and resulting growth in height admits some variation. In general, the trunk is produced by sympodial growth and the elm, *Ulmus effusa,* described by TROLL (1937), is a familiar example. Here the terminal bud of the seedling is abscised at the end of the first year of growth, to be substituted in the following spring by a lateral meristem which in its turn functions for a year. Many tropical trees resemble the elm in their abscission of the terminal bud and consequent sympodial trunk, although the periodicity of growth is not necessarily annual (e.g., *Anaxagorea acuminata,* Annonaceae, Fig. 67D; *Apeiba burchellii,* Tiliaceae; *Averrhoa carambola,* Oxalidaceae, Fig. 68C; *Heisteria parvifolia,* Olacaceae, Fig. 68D; *Parinari excelsa,* Rosaceae; *Strephonema pseudocola,* Combretaceae; *Trymatococcus oligandrus,* Moraceae, Fig. 68).

In contrast, in other species the trunk is monopodial, because the epicotyledonary meristem persists indefinitely. Although this axis is plagiotropic, growth in height is produced by the constant erection of the older parts, after loss of the leaves. *Cleistopholis patens* (Annonaceae, West Africa) provides a good example (H.O., 1970, p. 133), but others are provided by *Annona paludosa* (also Annonaceae), *Gilbertiodendron splendidum* (Leguminosae—Caesalpinioideae) and *Treculia africana* (Moraceae).

Once established as a "branch", the further behavior of the distal plagiotropic portion is largely determined in its growth by the position of inflorescences. When these are terminal, growth is sympodial, at least towards the periphery of the crown. Examples include *Parinari excelsa, Apeiba burchellii, Delonix regia,* and species of *Bauhinia* (Leguminosae—Caesalpinioideae). The situation in many Annonaceae is distinctive (e.g., *Annona arenaria,* Central Africa) since the terminal inflorescence is displaced very early and occupies a pseudolateral position. The length of the vegetative phase between successive inflorescences varies widely. In this family the single prophyll usually occupies an adaxial position and the distichy remains uninterrupted, so that the sympodial nature of the axis may be obscured. In other families the inflorescences are lateral and growth of the axis is indeterminate, as in *Bridelia micrantha* (Euphorbiaceae, tropical Africa), *Baphia nitida* (Leguminosae—Papilionoideae, West Africa), *Chlorophora excelsa* (Moraceae, tropical Africa) and *Chrysophyllum cainito.* This disposition, of course, admits of ramiflory and even cauliflory as in

Heisteria cauliflora (Olacaceae, tropical America) and *Swartzia prouacensis* (Leguminosae – Caesalpinioideae, tropical America).

Variation in the degree of differentiation of the plagiotropic phase is considerable and must be considered carefully since this is the critical feature of Troll's model. Frequently the aerial meristem is bilaterally symmetrical, the leaves are distichous, often with associated asymmetry (e.g., many Ulmaceae, Tiliaceae) so that dorsiventrality is a primary feature of growth. In other examples the meristem is primarily radial in its construction, with spirally arranged leaves, but bilateral symmetry is a result of secondary torsion of the axis. This is seen in many Leguminosae (e.g., *Albizzia, Delonix, Pentaclethra*) but also in *Strephonema* (Combretaceae), *Vismia guineensis* (Guttiferae). A similar reorientation in a decussate system has been mentioned for *Psidium*.

It would seem appropriate to mention examples of this model in which dorsiventrality is expressed further in the flattening of the axis itself. This is a primary feature in *Muehlenbeckia platyclados* (Polygonaceae, Solomon Islands but frequently cultivated for its bizarre aspect), as well as in some epiphytic Cactaceae (species of *Rhipsalis* and *Zygocactus*). In lianescent members of the genus *Bauhinia* (Leguminosae – Caesalpinioideae) the old stems are ribbon-like and become flattened at right angles to the original plane of distichy by secondary growth.

3. *Monocotyledons.* If, as we suggest, Troll's model exists as a consequence of secondary reorientation of woody trunks, there may be a simple anatomical explanation for the absence of it in monocotyledonous examples: most woody monocotyledons lack secondary vascular tissue. A secondary change from plagiotropy to orthotropy is not possible in such plants[11]. Where secondary tissues are present, as in some Agavaceae, Xanthorrhoeaceae and a few Liliaceae (*Aloë* species) there is a close developmental relation to the primary vascular system (ZIMMERMANN and TOMLINSON, 1970). Secondary growth in monocotyledons has little influence on their architectural models, as our earlier examples have shown. Furthermore, there is no record of reaction wood in monocotyledonous stem tissue (SCURFIELD, 1964), the basic mechanism for secondary stem reorientation thus seems absent. It should be mentioned again that reaction fibers have been described for monocotyledonous leaves, for *Xanthorrhoea* by STAFF (1974), where their biological significance is clear in positioning older leaves in very crowded crowns.

Strategy of the Model. This model is undoubtedly the most frequent of all those we have recognized, indeed we estimate that about 20 to 30% of all trees conform more or less closely to it. For this reason the following list of examples is very incomplete and, for convenience, we have indicated only one species in large genera where we know the model to be represented by many other species.

The reason for this abundance is undoubtedly the extreme individual plasticity of the resulting architecture. This is mainly because of the general "freedom" of the model (which is not to say that it lacks organization – quite the reverse). However, the extent to which each relay axis contributes to growth in height, the position of the relay axis and the lateral extent of the branch phase of each relay axis are all variable and can adjust to environmental influence. This is best seen in the ability of a species to exhibit a low, dome-shaped crown in the open in contrast to a narrow, conical crown which

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[11] This, of course, does not exclude the possibility of a primary change as in McClure's model.

may be shown by the same species in the forest. Many Leguminosae exhibit this individual plasticity well. The total height which a tree can achieve is readily adapted to existing circumstances. Such a tree will compete vigorously by resistance to overtopping in crowded communities. Equally well pronounced is the reiteration ability of the individual, to the extent that it may be difficult to distinguish the relay axes of the model from reiterated shoots in a given tree. An orthotropic initial phase, as in the seedling axis, provides evidence for reiteration. This adaptability bears comparison with Rauh's model, and undoubtedly accounts for the frequency of these two models in temperate floras. Both provide good examples of well-developed individual-centered strategies.

Morphogenesis in the Model. The apparent lack of precision in organization in this model is misleading. Examples undoubtedly offer scope for morphogenetic analysis. For example, we have commented on the extended orthotropic seedling axis in certain species, notably of *Parinari.* This may be determined by the amount of food reserve in the seed. If this amount is reduced by severing the seedling from the seed before the reserves are used up, the length of the orthotropic shoot is proportionately reduced. At the other end of the scale, seedlings with little or no food reserves provide examples of the early onset of the plagiotropic phase. This is notable in many Gesneriaceae. In *Sida carpinifolia* (Malvaceae), a woody herb, the orthotropic phase has been extended by Bancilhon (1974, unpublished) by growing the plant in a very rich medium.

Little has been said in the previous description of the level of insertion of the relay axis. This seems imprecise, though undoubtedly the phenomenon of epinasty is involved. Experimental demonstration of controlling factors should be sought.

Finally our description of the secondary reorientation of trunks needs amplification. It seems clear that it usually does not commence prior to leaf fall. What prevents erection continuing in the "branch" portion of the axis, once this is delimited by a new relay axis? Is there some form of control of the older axis by the younger axis, once this is established?

Taxonomic List of Examples (Troll's Model)

Annonaceae:
Anaxagorea acuminata (Dun.) St.Hil. (Fig. 67D), French Guiana / *Annona arenaria* Thonn., C. Africa / *Annona muricata* L., Trop. America / *Annona paludosa* Aubl., French Guiana / *Cleistopholis patens* (Benth.) Engl., W. Africa / *Exalobus crispiflorus* A. Rich., Congo / *Monodora myristica* (Gaertn.) Dunal., Trop. Africa.

Apocynaceae:
**Wrightia religiosa* Benth. and Hook., Siam / **Wrightia tomentosa* Roem. and Sch., India.

Aristolochiaceae:
**Aristolochia arborea* Lind., India / **Aristolochia tricaudata* Auct., Mexico.

Burseraceae:
Protium sp., (Oldeman 2146), French Guiana.

Capparidaceae:
[L] *Capparis corymbosa* Lam., Chad.

Combretaceae:
Strephonema pseudocola A. Chev., W. Africa.

Ericaceae:
Leucothoë catesbaei Gray, N. America, Temple, 1975.

Erythroxylaceae:
Erythroxylum coca Lamk., "coca", Trop. America.

Euphorbiaceae:
**Antidesma montanum* Bl., Java / *Breynia nivosa* (W.G. Sm.) Small, Polynesia, Roux, 1968 / *Breynia patens* (Roxb.) Benth., Trop. America / *Bridelia micrantha* (Hochst.) Baill., Trop. Africa, F. Hallé, 1971 / *Emblica officinalis* Gaertn., Trop. Asia, Bancilhon, 1971 / *Pedilanthus tithymaloides* (L.) Poit., C. America / [H] *Phyllanthus alpestris* Beille, Trop. Africa / *Phyllanthus caroliniensis*

Walt., Antilles, Venezuela, BANCILHON, 1971 / **Phyllanthus myrtifolius* Moon (Fig. 67B), Sri Lanka / *Sapium cornutum* Pax, Trop. Africa.

Eupomatiaceae:

Eupomatia laurina R.Br., New Guinea.

Fagaceae:

Fagus grandifolia Ehrh., "American beech", N. America / *Fagus sylvatica* L., "beech", Europe, RAUH, 1939a.

Flacourtiaceae:

Aphloia theaeformis Benn., Madagascar / *Banara guianensis* Aubl., Guianas / *Dovyalis zenkeri* Gilg., Trop. Africa / **Flacourtia inermis* Roxb., Widely cultivated.

Gesneriaceae:

[H] *Columnea* sp., (F. Hallé 2304), French Guiana / [H] *Drymonia* sp., (Pasch 4/51), French Guiana / [H]**Klugia* cf. *notoniana* Auct., Sri Lanka.

Guttiferae:

Vismia guineensis (L.) Choisy, Trop. Africa.

Hamamelidaceae:

**Loropetalum chinense* Oliver, China.

Icacinaceae:

Alsodeiopsis stadtii Engl., Trop. Africa.

Irvingiaceae:

Irvingia gabonensis (Aubry) Baill., Trop. Africa.

Lecythidaceae:

Lecythis (=*Eschweilera*) sp., (Oldeman and Sastre 183), French Guiana, OLDEMAN, 1971 / **Lecythis* cf. *pisonis* Camb., Guianas.

Leguminosae – Caesalpinioideae:

Bauhinia blakeana Dunn., "Hong Kong orchid tree", Hybrid origin, cultivated / *Bauhinia hookeri* F. Muell., Australia / *Bauhinia purpurea* L., Trop. Asia / *Bauhinia rufescens* Lam., W. Africa / *Cassia javanica* L., "Judas tree", Java / [H] *Cassia mimosoides* L., Trop. Africa / *Delonix regia* (Boj.) Raf., "poinciana", Madagascar / *Didelotia brevipaniculata* Léon., Trop. Africa / *Gilbertiodendron splendidum* (A. Chev.) Léan., Trop. Africa / *Hymenaea courbaril* L., "copal", Guianas / *Saraca thaipingensis* Cantley (Fig. 67A), Malaysia / *Swartzia prouacensis* (Aubl.) Amsh., Trop. S. America / *Vouacapoua americana* Aubl., French Guiana.

Leguminosae – Mimosoideae:

Acacia pinnata, French Guiana / *Albizzia adianthifolia* (Schum.) Wight, Trop. Africa / *Albizzia julibrissin* Durazz., Tropics, cultivated widely / *Albizzia lebbek* (L.) Benth., India / *Pentaclethra macrophylla* Benth., Trop. Africa / *Piptadeniastrum africanum* (Hook. f.) Brenan, Trop. Africa.

Leguminosae – Papilionoideae:

Baphia nitida Lodd., W. Africa / *Milletia laurentii* De Wild., C. Africa / **Pterocarpus indicus* Willd., Malaysia / *Pterocarpus officinalis* Jacq., Trop. America.

Loganiaceae:

[L] *Strychnos* spp., Trop. Africa, LEEUWENBERG, 1969 / [L] *Strychnos* sp., (Oldeman 2614), Guianas.

Lythraceae:

[H] *Cuphea carthagenensis* (Jacq.) McBride, French Guiana.

Malvaceae:

**Hibiscus grewiaefolius* Hassk., Java / [H] *Sida carpinifolia* L.f., Pantropical weed, BANCILHON, 1974.

Meliaceae:

**Turrea sericea* Sm., Madagascar.

Moraceae:

Bosquiea angolense (Welw.) Ficalho, Trop. Africa / *Chlorophora excelsa* Benth. and Hook., "iroko", Trop. Africa / *Craeterogyne kameruniana* (Engl.) Lanjouw, Trop. Africa / *Neosloetiopsis kamerunensis* Engl., Trop. Africa / *Treculia africana* Decne., Trop. Africa / *Trymatococcus oligandrus* (R. Ben.) Lang (Fig. 68A), Guianas.

Myrtaceae:

Psidium guineense Sw., Trop. America / *Psidium guajava* L. (Fig. 67E), "guava", Trop. America, PRÉVOST, 1965.

Olacaceae:

Aptandra zenkeri Engl., Trop. Africa / *Heisteria cauliflora* Smith, Trop. America / *Heisteria parvifolia* Smith (Fig. 68D), Trop. Africa / *Olax viridis* Oliv., Trop. Africa.

Oxalidaceae:

Averrhoa carambola L. (Fig. 68C), Trop. Asia.

Piperaceae:

[H] *Piper* sp., (F. Hallé 2235), French Guiana.

Polygalaceae:

Carpolobia lutea G. Don, Trop. Africa / [L] *Securidaca longepedunculatus* Fres., Trop. Africa.

Polygonaceae:

**Muehlenbeckia platyclados* Meissn., Solomon Islands.

Rhopalocarpaceae:

**Rhopalocarpus lucidus* Bojer, Madagascar.

Rosaceae:

Couepia cf. *versicolor* R. Ben., (Oldeman 2145), Guianas / *Hirtella velutina* Pilg., Guianas / *Licania* cf. *ovalifolia* Kleinh., (Oldeman 2159, 2160), French Guiana / *Parinari excelsa* Sabine, Trop. Africa and America.

Rubiaceae:

**Adina fagifolia* Val., Amboina / [H] *Argostemma involucrata* Hemsl., Malaysia.

Sapotaceae:

**Chrysophyllum cainito* L. (Fig. 67C), "star-apple", Trop. America / *Chrysophyllum olivaeforme* L., "satin leaf", W. Indies.

Scytopetalaceae:

Rhaptopetalum beguei G. Mangenot, Trop.

Africa / *Scytopetalum tieghemii* (A. Chev.) Hutch. and Dalz., Trop. Africa.

Sterculiaceae:

Commersonia bartramia Merr. (Fig. 68E), Tahiti / *Leptonychia pubescens* Keay, Trop. Africa / *Pterospermum semisagittatum* Buch.-Ham. ex Roxb., India / *Rulingia madagascariensis* Bak., Madagascar.

Tiliaceae:

Apeiba burchellii Sprague, Guianas / **Luehea speciosa* Willd., Brazil / **Muntingia calabura* L., Trop. America / *Tilia platyphyllos* Scop., "linden", Europe, RAUH, 1939a.

Ulmaceae:

Celtis australis L., Europe, MASSART, 1923 / *Celtis zenkeri* Engl., Trop. Africa / *Holoptelea grandis* (Hutch.) Mildbr., W. Africa / *Ulmus americana* L., "American elm", N. America / *Ulmus effusa* Sibth., "elm", Europe, TROLL, 1937 / *Ulmus foliacea* Gilib., "elm", Europe, SCHOUTE, 1937.

Urticaceae:

[H] *Pilea microphylla* (L.) Liebm., Trop. America.

Violaceae:

**Rinorea bengalensis* Kuntze var. *disticha* Boerl. (Fig. 68B), Indonesia / **Rinorea javanica* Kuntze, Java.

D. Architecture of Lianes

In our previous descriptions of models we have included, where appropriate, a few examples of woody climbing plants or lianes. This approach will have indicated that many of our tree models can be recognized in climbing plants, and we devote this chapter to a discussion of the subject. However, this can only be brief and preliminary; first, because the topic is somewhat outside the scope of this book and secondly, because our knowledge of lianes is still very incomplete. The study of tropical lianes remains a major area for biomorphological and other research.

The existing literature on lianes is not large and has mainly emphasized their anatomy because it is so distinctive (e.g., RADLKOFER, 1895; PFEIFFER, 1926; OBATON, 1960) or has been concerned with the biological methods of anchorage, i.e., by adventitious roots (WENT, 1895), tendrils, hooks, grapnels, or simply by twining of stems and petioles (SCHNELL, 1970; N. HALLÉ, 1973b). The investigation of *Parthenocissus tricuspidata* (S. & Z.) Planch. (Vitaceae) by CRITCHFIELD (1970) is a pioneering effort in its concern with overall growth strategy and in studies on tropical species it might be used as a guide.

The strategy of lianes is essentially one which economizes on trunk-making and they have to be viewed in this way, not as pauperate or incomplete entities. The energetic "compensation" made possible by this habit is suggested by Critchfield's measurements; in *Parthenocissus* he recorded one shoot which produced 352 expanded leaves on three orders of laterals during one growing season in Cambridge, Massachusetts. Anatomy is one of the more obvious adaptive features of these plants since mechanical tissues are virtually eliminated and the axis functions largely as a translocation "pipe". The role that lianes play in the bioenergetics of a forest is a distinctive one because they largely substitute for an equivalent amount of tree canopy in terms of biomass, as the measurements of KIRA et al. (1969) show. The efficiency of lianes is revealed by the ease with which many of them can be grown on an artificial support in a botanic garden, or with which they themselves find such artificial supports in disturbed situations, e.g., via telephone poles and wires. Not all lianes can do this and one has to distinguish between forest-dwelling climbers and those of early successional phases.

Recently CREMERS (1973, 1974) has provided the foundation for an understanding of the architecture of woody climbing plants in the tropics and his observations serve as a basis for our own discussion. He described examples of lianes from tropical Africa, but his conclusions seem generally applicable throughout the tropics; he was able to recognize examples from 13 tree models. Following him we may recognize two main groups, essentially distinguished by whether they conform closely to known tree models or not.

I. Lianes with an Architecture Conforming Closely to That of Tree Models

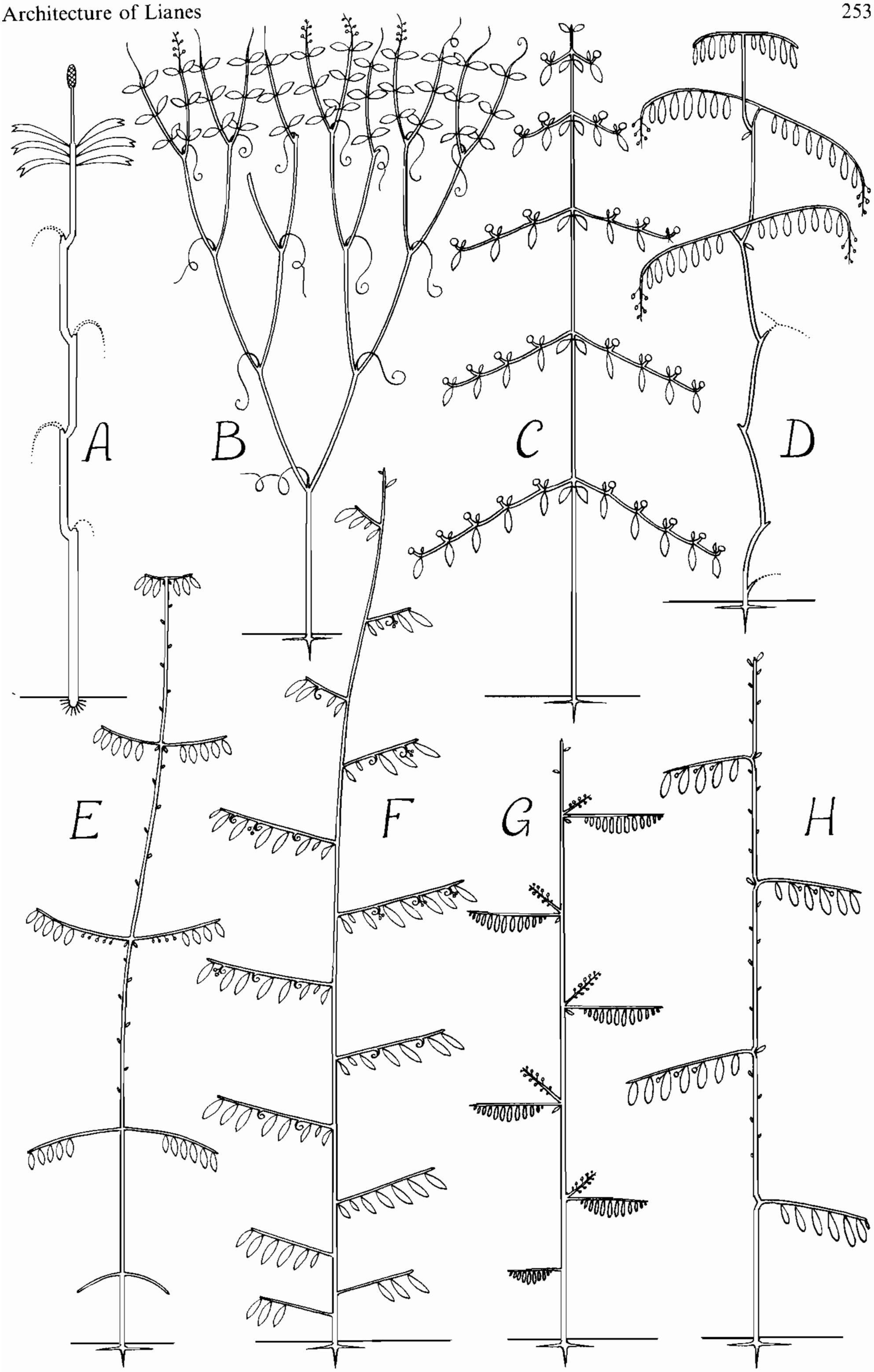
Examples have been cited throughout the earlier part of the text. Adaptations in such plants are simply quantitative changes which permit a scandent habit. Apart from the reduction in mechanical tissues so that the plant is no longer self-supporting, internodes or modules (at least in the adult phase) are usually elongated and specialized anchorage organs are developed. In some lianes of this type, the habit is facultative, so the same species may grow as a climber, or a treelet (e.g., *Mabea taquari,* Euphorbiaceae, Guianas; *Chiococca alba,* Rubiaceae, West Indies; *Allamanda cathartica,* Apocynaceae; *Tecoma* spp., Bignoniaceae).

Some examples of this kind of architecture may be described briefly, after CREMERS (1973) (see Fig. 69). *Landolphia dulcis* (Apocynaceae, West Africa; Leeuwenberg's model; Fig. 69B) shows an initial juvenile axis with short internodes and several flushes of growth, but terminating in a tendril, which thus marks the limit of the first module. Succeeding modules constitute the adult lianescent stage, each produced sympodially singly or in pairs below a terminal tendril, or in the distal parts below a terminal inflorescence, as is more usual for this model (p. 145). The homology between tendril and inflorescence is quite obvious. Other species of *Landolphia* and of *Dictyophleba* in the same family are similar.

We have listed *Pycnanthus dinklagei* (Myristicaceae, West Africa) as an example of Massart's model (Fig. 69E) and a more extended description is appropriate. The epicotyledonary axis is orthotropic with spirally arranged leaves and at the end of its first flush of growth produces a tier of plagiotropic branches as is characteristic of the model. The first tier is produced at a height of between 20 and 50 cm, but subsequent ones are separated by up to 3 m of unbranched stem. The leaves on the orthotropic axis are small, 10–15 mm long, and caducous so that assimilation is carried out by the large leaves of the plagiotropic branches. The seedling axis itself is capable of reaching the canopy if supported and produces tiers with larger numbers of branches as it grows taller. Otherwise, it bends under its own weight but will continue to produce plagiotropic tiers. Leaves are very flexible on these branches and readily reorientate themselves into a horizontal position by twisting of the petioles.

Fig. 69A–H. Lianes conforming to known tree ▷ models. (After CREMERS, 1973).

A Chamberlain's model, e.g., *Carludovica palmata* (Cyclanthaceae), a root climber.
B Leeuwenberg's model, e.g., *Landolphia dulcis* (Apocynaceae), climbing by tendrillous stem tips.
C Petit's model, e.g., *Atractogyne bracteata* (Rubiaceae), supported by divergent branches.
D Nozeran's model, e.g., *Mabea taquari* (Euphorbiaceae), supported by divergent branches (OLDEMAN, 1974a).
E Massart's model, e.g., *Pycnanthus dinklagei* (Myristicaceae), supported by divergent branches.
F Roux's model, *Artabotrys insignis* (Annonaceae), climbing by inflorescence hooks.
G Cook's model, e.g., *Phyllanthus muellerianus* (Euphorbiaceae), supported by divergent branches.
H Mangenot's model, e.g., *Rhaphiostylis beninensis* (Icacinaceae), supported by divergent branch portions of mixed axes


A
B
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H

Reiteration from these prostrate plants is abundant, usually by epinasty so that new erect shoots are developed, increasing the chance of the plant finding support. These reiterated shoots repeat the architecture of the seedling axis. Flowers are eventually produced on older branches as axillary, pendulous panicles. Anchorage is provided by the sharp angle between trunk and branch and not by any specialized organ.

A third example illustrates a climber with mixed axes, provided by *Atroxima liberica* (Polygalaceae, West Africa), which conforms to Mangenot's model. The juvenile phase consists of an axis with an initial vertical portion bearing scale leaves, followed abruptly by a plagiotropic portion with foliage leaves, the phyllotaxis changing from spiral to distichous. A new module is initiated at the level of the reorientation of the axis, from one of the three serial buds in each leaf axil. Two or three such modules are produced before the lianescent adult form is developed. This consists of a series of modules, each with an orthotropic, scale-bearing proximal portion, followed by long internodes. Distally the axis becomes twining and leaf development is delayed until support has been established, in the manner of twining plants. The lower scale and transitional leaves subtend short shoots, each with two foliage leaves produced during their initial phase of growth. The renewal shoot or shoots develop from the region of curvature of the preceding module. Short shoots resume rhythmic growth when the parent long shoot has itself ceased to grow. They eventually produce flowers in axillary spikes. In this species only the juvenile axis corresponds precisely to the definition of Mangenot's model, the adult phase is somewhat different, although its sympodial construction is very obvious.

One notes in the examples described by CREMERS (1973) that the juvenile and adult phase are usually distinct from each other, with something of a transition between them. Commonly features of the adult architecture produce some deviation from a strict conformity to the model. For example *Cuervea macrophylla* corresponds to Roux's model except that the trunk becomes sympodial. In *Rhaphiostylis beninensis* (Mangenot's model; Fig. 69H) growth in height is achieved by marked extension of the orthotropic segment of each unit. In *Icacina mannii,* which belongs to the same model, the plagiotropic segment often becomes vertical if the plant finds support. Here also there is frequently the development of several simultaneous relay axes, not one as in the model. This may be a form of reiteration, as indicated by OLDEMAN (1974a).

List of Architectural Models Shown by Lianes. (From CREMERS, *1973, Except Where Otherwise Stated)*

HOLTTUM'S MODEL

Palmae – Lepidocaryoideae:
Plectocomia griffithii Auct., Malay Peninsula (see p. 104).

CORNER'S MODEL

Aspidiales – Lomariopsidaceae:
Lomariopsis guineensis Auct., Tropical Africa.

TOMLINSON'S MODEL

Palmae – Lepidocaryoideae:
Calamus deeratus Mann, Tropical Africa.

CHAMBERLAIN'S MODEL

Cyclanthaceae:
Evodianthus funifer (Poit.) Lindm. (Fig. 69A), Tropical America.

LEEUWENBERG'S MODEL

Apocynaceae:
Dictyophleba leonensis (Stapf) Pichon, Tropical Africa / *Dictyophleba stipulosa* (Moore ex Wernb.) Pichon, Tropical Africa / *Landolphia dulcis* (R.Br. ex Sabine) Pichon var *barteri* Stapf (Fig. 69B), Tropical Africa.
Bignoniaceae:
Tecoma sp. (OLDEMAN, 1974a), Tropical America.
Liliaceae:
Gloriosa superba L. (H.O. 1970), Tropical Africa.

SCHOUTE'S MODEL

Flagellariaceae:
Flagellaria indica L. (TOMLINSON, 1970b), Old World Tropics.

PETIT'S MODEL

Rubiaceae:
Atractogyne bracteata (Wernh.) Hutch. and Dalz. (F. HALLÉ, 1967) (Fig. 69C), West Africa.

NOZERAN'S MODEL

Euphorbiaceae:
Mabea taquari Aubl. (OLDEMAN, 1974a) (Fig. 69D), Guianas.

MASSART'S MODEL

Myristicaceae:
Pycnanthus dinklagei Warburg (Fig. 69E), West Africa.

ROUX'S MODEL

Annonaceae:
Artabotrys insignis Engler and Diels (Fig. 69F), West Africa.
Hippocrateaceae:
Cuervea macrophylla (Vahl) R. Wilczek ex N. Hallé, West Africa.

COOK'S MODEL

Euphorbiaceae:
Phyllanthus muellerianus (O. Kuntze) Exell (ROUX, 1968) (Fig. 69G), Tropical Africa.
Rhamnaceae:
Ventilago africana Exell, Tropical Africa / *Zizyphus papuanus* Ltb., Australia, New Guinea.

CHAMPAGNAT'S MODEL

Apocynaceae:
Allamanda spp. (OLDEMAN, 1974a), Tropical America.

MANGENOT'S MODEL

Icacinaceae:
Icacina mannii Oliver, West Africa / *Rhaphiostylis beninensis* (Hook. f. ex Planchon) (Fig. 69H), West Africa.
Loganiaceae:
Strychnos congolona Gilg, West Africa.
Polygalaceae:
Atroxima liberica Stapf, West Africa.

TROLL'S MODEL

Leguminosae – Caesalpinioideae:
Bauhinia sp. (OLDEMAN, 1974a), Tropical America / *Lonchocarpus* cf. *chrysophyllus* Ducke (OLDEMAN, 1974a), Tropical America.

II. Lianes with an Architecture Not Conforming to That of Known Tree Models

Knowledge of such plants is still insufficient to permit the recognition of architectural categories since CREMERS (1974) has described only eleven species, all from West Africa. Nevertheless, he recognized three groups, as follows:

1. Juvenile form orthotropic, the climbing adult form is a monopodium, not interrupted by flowering or other structural modification.

The juvenile form is often characterized by its large leaves, short internodes and thick primary axis; growth is very slow, the stem is self-supporting and often remains unbranched. In the adult these characters are reversed, i.e., the axis grows rapidly, remaining slender so that it is no longer self-supporting, and climbs. The climbing axis is usually abundantly branched and, of course, ultimately bears flowers or flowering shoots. In the examples described by CREMERS serial buds are common and "replacement shoots" are frequent, apparently representing reiteration. This kind of axis in its early development usually shows a return to the juvenile condition.

Example. Gouania longipetala (Rhamnaceae) serves to illustrate this condition. The seedling axis grows erect to a height of 20 or 30 cm, bearing a spiral series of leaves separated by short internodes. Within three months there is a transitional phase recognized by the development of branches beginning in the axil of the 10th or 11th leaf. The first branches are short, producing two scale leaves and one foliage leaf before they end in a tendril. The adult form is recognized by the development of a lateral tendril in the axil of the uppermost foliage leaf and below the aborted terminal bud. With sexual maturity of the plant this bud does not abort but becomes a terminal inflorescence. Flowering does not begin until the plant is 3 to 4 m high and well supported by surrounding shrubs. The architecture of the transitional and adult phases is made quite complex by the development of additional branches from the series of buds subtended by each leaf.

Other Examples. Contrast between juvenile and adult forms may involve differences in leaf form, as in *Crossostemma laurifolium* (Passifloraceae) where the seedling leaves are lobed, unlike the adult. Here the juvenile leaf form is repeated at the base of the "replacement shoots", providing a good demonstration of reiteration. In *Hugonia planchonii* (Linaceae) the juvenile phase is protracted and may last for 15 months, when the seedling may still be only 18 to 25 cm high, in contrast to the 7 m it can attain as an adult.

Branch specialization in relation to climbing is often marked in these lianes. Extremes are provided in the West African flora by the family Dioncophyllaceae, exclusively lianescent. In *Triphyophyllum peltatum* for example (Fig. 70A) the leaves themselves are highly modified; they may be normal ovate, entire foliage leaves but otherwise either with terminal hooks or with a peculiar long glandular apex (MENNINGER, 1965). Of especial interest are those lianes with basal branches which are initially stoloniferous before they find support around which they can twine. *Neostachyanthus occidentalis* and *Pyrenacantha mangenotiana,* both of the Icacinaceae, provide good examples. In *Dioscoreophyllum cumminsii* (Menispermaceae) the stoloniferous branches produce subterranean offshoots which become tuberous. CREMERS (1974) showed by pruning experiments that it is possible to transform a stoloniferous shoot into a tuberous shoot. This is but one example of the way in which these lianes are capable of morphogenetic analysis by simple experimental procedures.

Taxonomic List of Examples (All After CREMERS, *1974)*

Dioncophyllaceae:
Triphyophyllum peltatum (Hutch. and Dalz.) Airy Shaw (Fig. 70A), Sierra Leone to Ivory Coast.
Icacinaceae:
Neostachyanthus occidentalis Keay and Miège, Ivory Coast to Nigeria / *Pyrenacantha mangenotiana* Miège, Ivory Coast to Ghana.
Linaceae:
Hugonia planchonii Hook. f., Guinea to Nigeria.
Menispermaceae:
Dioscoreophyllum cumminsii (Stapf) Diels, Guinea to Zaïre.
Passifloraceae:
Crossostemma laurifolium Planch. ex. Benth., Guinea to Ghana.
Polygonaceae:
Afrobrunnichia erecta (Aschs.) Hutch. and Dalz., Sierra Leone to Zaïre.
Rhamnaceae:
Gouania longipetala Hemsl., Guinea to Zaïre.
Sapindaceae:
Paullinia pinnata L., Old and New World Tropics.

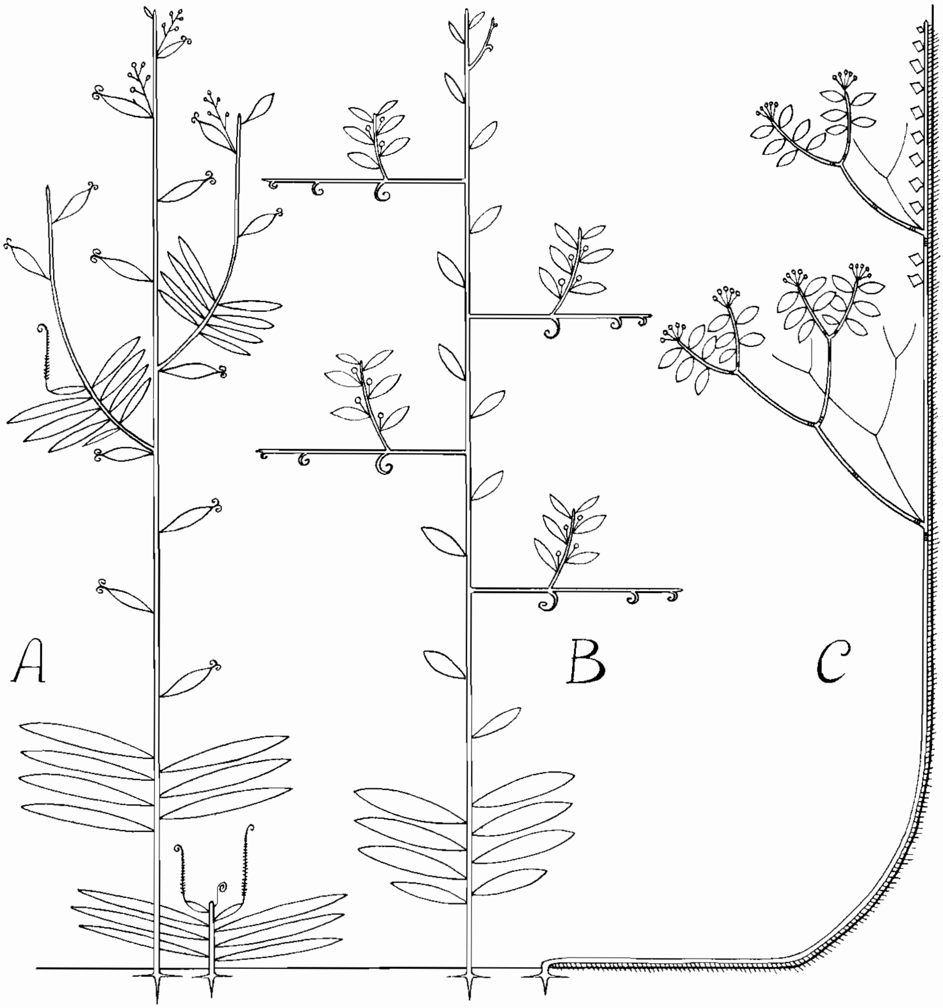

Fig. 70A–C. Lianes not conforming to known tree models. (After CREMERS, 1974).
A *Triphyophyllum peltatum* (Hutch. and Dalz.) Airy Shaw (Dioncophyllaceae), climbing by pairs of hooks on apex of certain leaves.
B *Ancistrocladus abbreviatus* (Ancistrocladaceae), climbing by axis hooks.
C *Hedera helix* (Araliaceae), a root climber

2. Juvenile form orthotropic, climbing adult form sympodial by substitution below flowering axes.

Example. Species of *Ancistrocladus* (Ancistrocladaceae, an exclusively lianescent, Old World family) show this behavior well, but with a complex sympodial development (Fig. 70B). The juvenile form is erect with large leaves and short internodes, reaching a height of 60–100 cm and persisting upwards of one year. During this period rhythmic growth of the axis is marked, with up to 15 foliage leaves per flush, each flush separated by three or four reduced leaves. There is a rapid transition to the adult phase distinguished by the development of a sympodial complex where successive axes end in a hook. In the sexual phase flowering axes are associated with this grapnel-like organ whose morphology is not well understood. Essentially, however, the lianescent axis is made up of a series of determinate units of which the proximal leafy portion provides for growth in height.

Other Examples. We have commented elsewhere and briefly on *Iodes liberica* in our description of Schoute's model (p. 132). Again the adult lianescent form is sympodial, each segment of the sympodium terminating in a tendril with which is always associated an inflorescence.

Taxonomic List of Examples

Ancistrocladaceae:
Ancistrocladus abbreviatus Airy Shaw (Fig. 70B) / *A. barteri* Sc. Elliott, Sierra Leone and Ivory Coast.
Icacinaceae:
Iodes liberica Stapf, widely distributed in West Africa.

3. Juvenile form plagiotropic, with adventitious roots, often stoloniferous, the adult climbing form similar but with roots largely functioning as anchoring roots.

This category includes large numbers of species generally described as root climbers and it is sufficient here to list a few examples to indicate their taxonomic diversity. In individual ontogeny there may be either a direct transition to the adult phase, marked by a change in leaf size, loss of adventitious roots and the development of flowers (e.g., *Hedera helix,* Araliaceae, Fig. 70C) or the adult phase is represented by flowering, plagiotropic branches which are essentially a fertile accessory of the lianescent stage (e.g., many Marcgraviaceae). Juvenile and adult phases in these plants are so well differentiated and so constantly retain their characteristics after vegetative propagation that they provide a classic demonstration of topophysis (p. 17) and have been the subject of a number of experimental studies (e.g., Doorenbos, 1954; Robbins, 1960).

Taxonomic List of Examples

Araliaceae:
Hedera helix L. (Fig. 70C), "European ivy", North temperate region.
Ericaceae:
Pieris phillyreifolius Hook., Southeastern United States.
Marcgraviaceae:
Marcgravia spp., Tropical America.
Moraceae:
Ficus repens Rottb., Asia.
Myrtaceae:
Metrosideros scandens (J.R. and G. Forst.) Druce (Dawson, 1967), New Zealand.
Pandanaceae:
Freycinetia spp., Asian tropics.

The scope for biological and morphogenetic research on lianes in the tropics is enormous, but the preliminary descriptive phase, which establishes their architecture, has only just begun. Autoecological investigations with any precision simply do not exist at all, as far as we know, in the field of lianes.

E. Architecture of Herbs: Miniaturization in Relation to Tree Models

1. Miniaturization of Models

Size does not enter into the definition of a model so we have felt free to include herbaceous examples in a number of our descriptions which otherwise concern trees. However, the architecture of herbs is not well known and, in fact, represents a fertile field for future research (BUDELMAN, 1974; JEANNODA, 1977). Nevertheless, it seems appropriate to discuss the relation between herbs and trees on the basis of present knowledge of architecture since where the subject has been considered by earlier authors the emphasis has been anatomical (e.g., SINNOT and BAILEY, 1914). Perhaps this concern for anatomical "reduction" chiefly seen as a "loss" of cambial activity avoids the real issue, which is architecture. Tropical "herbs" are, in fact, usually quite woody. A feature of the herbaceous habit is the production of large numbers of sexually determinate shoots, ending in flowers or inflorescences. A plant in many instances is "herbaceous" because its strategy includes neither the production of a long-lived vegetative meristem like the "leader" of a tree, nor the ability indefinitely to superimpose short-lived meristems as in trees with modular construction. This consideration immediately suggests that the architecture of many herbs will be found to be different from that of trees.

From our current treatment of woody plants it becomes possible to discuss the problem in two quite different contexts: first, the phylogenetic one which is concerned with the evolutionary relationship between herbs and trees, i.e., to what extent the one is derived from the other; second, the ontogenetic one which also is hypothetical but open to experimental analysis; it considers the way in which during the individual development of the tree reiterative complexes are progressively reduced in size (p. 279). Both may be regarded as the consequence of a general reduction in size ("miniaturization", H.O., 1970; p. 139). Our preliminary discussion, obviously highly speculative, is concerned mainly with the first process.

a) Reduction in Size

In drawing attention to the existence of herbaceous examples of models which we have cited from time to time, two purposes have been served. First the examples show that the concept of "model" does not involve size and second they also provide clues as to the possible phyletic connection between related herbs and trees. This relationship has been discussed by several authors (e.g., CORNER, 1966; MANGENOT, 1964) with the general suggestion that many temperate herbs are derived from ancestral tropical trees as part of a general tendency for diminution in the size of vascular plants. This relationship does not conflict with our earlier discussion of the composition of tropical floras.

In tree examples of Tomlinson's model one can already recognize much of the morphology of herbaceous monocotyledons and these are best considered as examples of neoteny, as is discussed later.

The evolutionary picture in the Gramineae is peculiarly interesting. Tufted and rhizomatous grasses provide numerous examples of Tomlinson's model. However, the "arborescent grasses", i.e., bamboos, have been ascribed to a distinctive model, McClure's model, reflecting their peculiar growth and reproductive strategies. Herbaceous examples of McClure's model are represented by a few small bamboos and one looks in vain for examples among the true grasses. If the bamboos are ancestral to herbaceous grasses, simple reduction in size does not account for habit evolution. To find herbaceous examples of McClure's model one has to look for the specialized forms in the Costaceae, Marantaceae and Philesiaceae which have been cited. Species of *Asparagus* (Liliaceae) and *Ruscus* (Ruscaceae) also correspond to the definition of the model.

Leeuwenberg's model is quite common in herbs. We have illustrated *Acanthospermum hispidum* (Compositae, p. 150). In Euphorbiaceae many species of *Croton* (e.g., *C. hirtus*) provide examples. One would not expect Koriba's model to occur in herbs, since its essence is the secondary erection of successive modules as trunk units, but we have said that tropical herbs can be quite woody. We suspect examples in Nyctaginaceae and *Solanum* species. Can one say the same thing of Troll's model, which is also dependent on secondary changes for its architecture? Woody herbs which conform to this model do occur, the best examples being species of *Sida* (Malvaceae), which are common weeds of the tropics. The evolutionary relationships are here obscure because arborescent members of the Malvaceae, as far as we know, do not produce examples of Troll's model.

One finds as a fairly general rule that herbaceous examples are most likely in models where the tree representatives are themselves never of considerable stature. We can cite in support of this statement Petit's model (illustrated earlier by *Waltheria indica,* Sterculiaceae p. 176), Scarrone's model (illustrated by *Bidens* sp., Compositae, p. 214). Examples of Stone's model in dicotyledonous herbs have been provided for a number of New Caledonian species by VEILLON (1976). Contrast this with Prévost's, Fagerlind's, Aubréville's, Massart's, and Nozeran's models, which seem exclusive to sizeable trees. The explanation here seems to be that these models all exhibit rhythmic growth, which is not possible in the above-ground parts of herbs. In contrast we find in the models of Cook and Roux genera which include within the tropics a range from trees to herbs where the transition seems to be effected without change of architecture. *Phyllanthus* (Euphorbiaceae) provides a familiar example with a wide range in stature mostly conforming to Cook's model (e.g., *P. distichus,* a treelet versus *P. nuriri,* a weedy herb). This genus has, indeed, already attracted attention as a source of information about herb-tree relationships (ROUX, 1968; WEBSTER, 1967; BANCILHON, 1971).

Attims' model includes a wide range in sizes, since we have contrasted *Eucalyptus* on the one hand with *Phyllanthus polygonoides* on the other. In view of what we have just said about rhythmic growth it is not surprising that erect herbs are not known in Rauh's model. However, if one accepts the concept of "prostrated parallels" (JEANNODA, 1977), as in the description of *Oleandra pistillaris* (p. 224), then Rauh's model is likely to occur frequently in plants with a rhizomatous habit.

In plants with mixed axes, as represented by Mangenot's and Champagnat's models, the trend may be towards the shrubby or lianescent habit rather than the herbaceous habit by reduction in size.

b) Neoteny

The concept of early sexuality and elaboration of early ontogenetic phases in organisms as a medium for evolutionary change is familiar to zoologists in the processes of neoteny and paedomorphosis (DE BEER, 1958). TAKHTAJAN (1976) has suggested that neoteny has played a part in the origin of flowering plants, but we lack other than circumstantial evidence. In the future the concept of architecture is likely to be of considerable help in this kind of evolutionary analysis. CARLQUIST (1962) for example, has applied the principle of paedomorphosis in wood anatomy, but MABBERLEY (1974b, c) has questioned this, mainly on the grounds of gross morphology.

In plants neoteny involves the rapid, essentially precocious sexuality of most or all of the aerial axes. This change is all the more evident when the primary axis of the tree remains sterile but becomes fertile in the herbaceous equivalent. Evidently the model is expressed in a modified form and may even become completely obscured. Thus the neotenous development of a tree as a herb can only be recognized when the model remains clearly visible. This may occur in existing trees, as SCARRONE (1969) has shown in neotenous individuals of mango (*Mangifera indica*) which produce a terminal flower or inflorescence on a monocaulous seedling less than a meter high. This observation suggests that experimental induction of neoteny may be possible in other species, and BANCILHON et al. (1974) has come close to this in her work on *Phyllanthus distichus*. The herbs exemplifying Stone's model also show a terminally flowering main axis in many cases (JEANNODA, 1977). This eventuality therefore figures in the definition of that model.

Probably the best examples of neotenous expression in evolutionary terms are those herbaceous monocotyledons which conform to Tomlinson's model, but with a pronounced development of the underground parts as rhizomes, whereas the aerial parts are reduced by early terminal flowering. Within the order Zingiberales, most members are rhizomatous and have specialized (i.e., evolutionarily advanced?) flowers, but the Strelitziaceae are predominantly arborescent and have less specialized (primitive?) flowers. It seems difficult to avoid the conclusion that the arborescent habit is primitive in this order (TOMLINSON, 1962) and that the rhizomatous habit is derived by neoteny.

The dicotyledonous family Guttiferae provides comparable examples. *Symphonia globulifera* (Roux's model) may be regarded as an arborescent ancestral type, characterized by its trunk and branches without determinate growth since flowers occur laterally on the branches. Herbaceous forms may be represented by species of *Hypericum* which are common in temperate floras. Here the overall stature of the plant is reduced because both trunk and branch are determinate by flowering. This example is not well documented because we lack knowledge of intermediate forms. This shows that if neoteny obscures the original model and intermediate forms are lacking the original architecture of a herbaceous descendent is no longer recognizable. It might become so if experimental means were devised to postpone flowering in neotenous species.

An example which is probably more correctly referred to as paedomorphosis, in which extant intermediate forms are available, is provided in the possible origin of *Tillandsia usneoides* (Spanish moss, Bromeliaceae, tropical and subtropical America). The forms involved are all herbaceous epiphytes in the genus *Tillandsia*, but it seems clear that evolution has involved the modification of early seedling stages (TOMLINSON, 1970a, pp. 224–229).

c) Fragmentation

In many tree models the architecture involves rhythmic growth of the trunk (which may branch either monopodially or sympodially) and the tree is built up of distinct *structural* units (not to be confused with modules which we have defined as *developmental* units, p. 5). Tree models of this type include those of Aubréville, Fagerlind, Nozeran, Prévost, Massart, and Rauh. Herbaceous examples may be derived essentially by the indefinite propagation of one of these units. Since the herbaceous derivative is equated with only part of an original tree model, we may refer to this process as "fragmentation".

The best examples are provided by large genera which include both trees and herbs as in *Euphorbia* (Euphorbiaceae). Thus *E. abyssinica* (East Africa) represents Rauh's model clearly, as a tree, whereas the architecture of many herbaceous species of *Euphorbia* (and its segregate genus *Chamaesyce*) which have a creeping habit might be regarded as one branch complex of a woody ancestor. The distinctive morphology of certain herbaceous Zygophyllaceae, notably *Tribulus terrestris* (FUKUDA, 1974) may be compared to one plagiotropic branch tier of woody members of the same family, e.g., species of *Bulnesia* and *Guaiacum*. The similarity is emphasized by the peculiar phyllotaxis in both trees and herbs, involving pairs of leaves in one plane. Here the morphology of both herb and tree is so complex that detailed comparative studies should be very illuminating. Within the Rubiaceae, herbaceous forms like *Geophila* bear comparison with one branch of a *Psychotria* species belonging, for example, to Roux's model.

The process may have occurred within a single genus, as is suggested by species of *Cornus* in eastern North America. Most *Cornus* species are small trees with monopodial trunks showing rhythmic growth, the branches mostly with substitution of terminal inflorescences, as in Fagerlind's model (e.g., *C. alternifolius, C. florida*). However, in *Cornus canadensis* the creeping, somewhat woody axis may be equated with one branch of a tree ancestor. The superficial similarity is enhanced by the development of foliage leaves in distinct rosettes along the horizontal axes in both forms.

In such examples, if this interpretation is correct, there should be some evidence of the orthotropic trunk of the parent model in the epicotyledonary axis. A comparison of seedling stages would, therefore, be informative. Within the wholly herbaceous monocotyledonous family Commelinaceae this transition seems to have occurred, since some taxa have orthotropic shoots (e.g., *Palisota*), others have an ephemeral orthotropic axis with spiral phyllotaxis in the seedling phase, although the adult plants have plagiotropic stems with alternate leaves (some *Callisia* and *Cyanotis* species). There is a hint in this family that many species have acquired their plagiotropic features by fragmentation (CLARK, 1904).

The above examples are not intended to show that the process of fragmentation is restricted to the models we have named, it is just that the process can only be recognized clearly in plants of known architecture. It might, for example, occur equally well in trees with "mixed" axes, in which case there would be a simultaneous reduction in size, i.e., the plagiotropic portion of the axis would become propagated indefinitely. In *Annona*, which includes many examples of Troll's model, this tendency occurs in savannah species of northern Brazil, according to the descriptions by FRIES (1959).

d) Loss of the Original Orientation of the Trunk

We have seen in our discussion of Schoute's model that *Nypa* can be equated with a *Hyphaene* which has lost its orthotropic orientation. *Serenoa* is perhaps another palm which grows horizontally rather than vertically. This suggests a simple method of derivation of herbs from trees, if the process is accompanied by some reduction in size. *Remirea maritima* (Cyperaceae), a common sedge of open beaches throughout the tropics, and *Honckenya peploides* (Caryophyllaceae), a coastal plant of cliffs and dunes in Europe, may have originated by this loss of tropism. Their architecture otherwise resembles Stone's model.

Diodia maritima and *Diodia vaginalis* (Rubiaceae) bear consideration in the same context. They also are coastal plants, the former species occurs both in Africa and America.

2. Origin of New Models

The probably evolutionary processes referred to above can be related to known described models, but this does not exclude the existence of other series of architectures exclusive to herbs. When more is known about the subject we may be in a position to recognize "models" which may be fitted into the architectural continuum of trees, or more likely, extend it. Since there is genetic continuity throughout the plant kingdom it will be a matter for future analysis to establish how new series of architecture may become evident from the cumulative results of some of the processes we have considered or which exist because they are the persistent herbaceous examples of models which have become extinct as trees. Since there are numerous habitats from which trees are virtually excluded these are reasonable assumptions. One may, therefore, look for distinctive architectures in montane vegetation above the tree limit, in many deserts, savannahs and tundras, in coastal habitats such as sand dunes and temperate salt marshes and in seagrass communities. Certain biotopes rich in herbs may be included, e.g., epiphytic vegetation, as also would ephemeral weeds of arable farmland.

F. Architecture of Fossil Trees[12]

The stature and habit of many of the more common fossils are known from reconstructions and allow a certain degree of comparison with living trees. Strictly we should not refer to the "model" of a fossil because we have emphasized the dynamic nature of this concept. A reconstruction of a fossil is usually a static image, representing the plant at only one architectural stage of its development – usually a late stage. Only rarely are the dynamics of its growth envisaged (e.g., *Lepidophloios pachydermatikos*, Lepidodendraceae; ANDREWS and MURDY, 1958; ANDREWS, 1967). We must, therefore, accept that our discussion of fossils remains at a hypothetical level, but not entirely so since it is often possible to establish the architecture of a tree belonging to one of the simpler models without studying its ontogeny, as with palms, or the monocaulous species of *Chytranthus* in the rainforest. A certain amount of deductive reasoning is, therefore, possible. In this sense we are forced to conclude that the architecture of several fossil trees is better known than that of most existing tropical trees by virtue of the careful investigations of the one in contrast to the neglect of the other (e.g., various Lepidodendraceae, EGGERT, 1961; ANDREWS and MURDY,

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[12] This chapter represents an expansion of the topic as discussed in H.O., 1970, pp. 135–142, using the same illustrations.

1958; or progymnosperms, FLORIN, 1944; BECK, 1962).

We may, therefore, briefly review the kinds of models recognizable amongst fossil trees, giving the source of their reconstructions.

1. HOLTTUM'S MODEL

Isoetales:

Pleuromeia sternbergi (Munster) Corda (Fig. 71 A), Lower Trias of Germany, HIRMER, 1933.

2. CORNER'S MODEL

This is well represented by numerous monoaxial fossil trees in which sexuality does not interrupt the growth of the trunk.

Bennettitales:

Cycadeoidea jenneyana Ward, Lower Cretaceous of Dakota, WIELAND, 1916 / *Williamsonia sewardiana* Sahni, Jurassic of India, SAHNI, 1932.

Cycadales:

Palaeocycas integer (Nath.) Florin, Trias of Sweden, MORET, 1949.

Marattiales:

Caulopteris sp., Carboniferous or Permian, CORSIN, 1948 / *Hagiophyton* sp., Carboniferous, CORSIN, 1948 / *Megaphyton* sp. (Fig. 71 B), Carboniferous, CORSIN, 1948 / *Psaronius* sp., Carboniferous of Illinois, MORGAN, 1959.

Osmundales:

Thamnopteris schlechtendalii (Eichwald) Brong., Permian of the Urals, EMBERGER, 1968.

Pteriodospermales:

Lyginopteris oldhamii (Binney) Potonie, Carboniferous of England, EMBERGER, 1968 / *Medullosa noei* Steidtmann, Carboniferous, STEWART and DELEVORYAS, 1956.

All these trees possessed large, densely arranged leaves which were often very dissected. *Megaphyton* (Fig. 71 B) and *Hagiophyton* had distichous leaves, comparable to *Wallichia*. Support, in part, of the trunk might have been provided by a root mantle as in the fossil Marattiales which thus resemble existing tree ferns, while others had stilt roots (*Lyginopteris, Medullosa*) like *Pandanus*.

3. TOMLINSON'S MODEL

Equisetales:

Stylocalamites Weiss. (Fig. 71 C), Westphalien of the Ruhr, BOUREAU, 1964.

4. LEEUWENBERG'S MODEL

Bennettitales:

Wielandiella augustifolia Nath. (Fig. 71 D), Trias of Sweden, NATHORST, 1909 / *Williamsoniella coronata* Thomas, Jurassic of England, THOMAS, 1915.

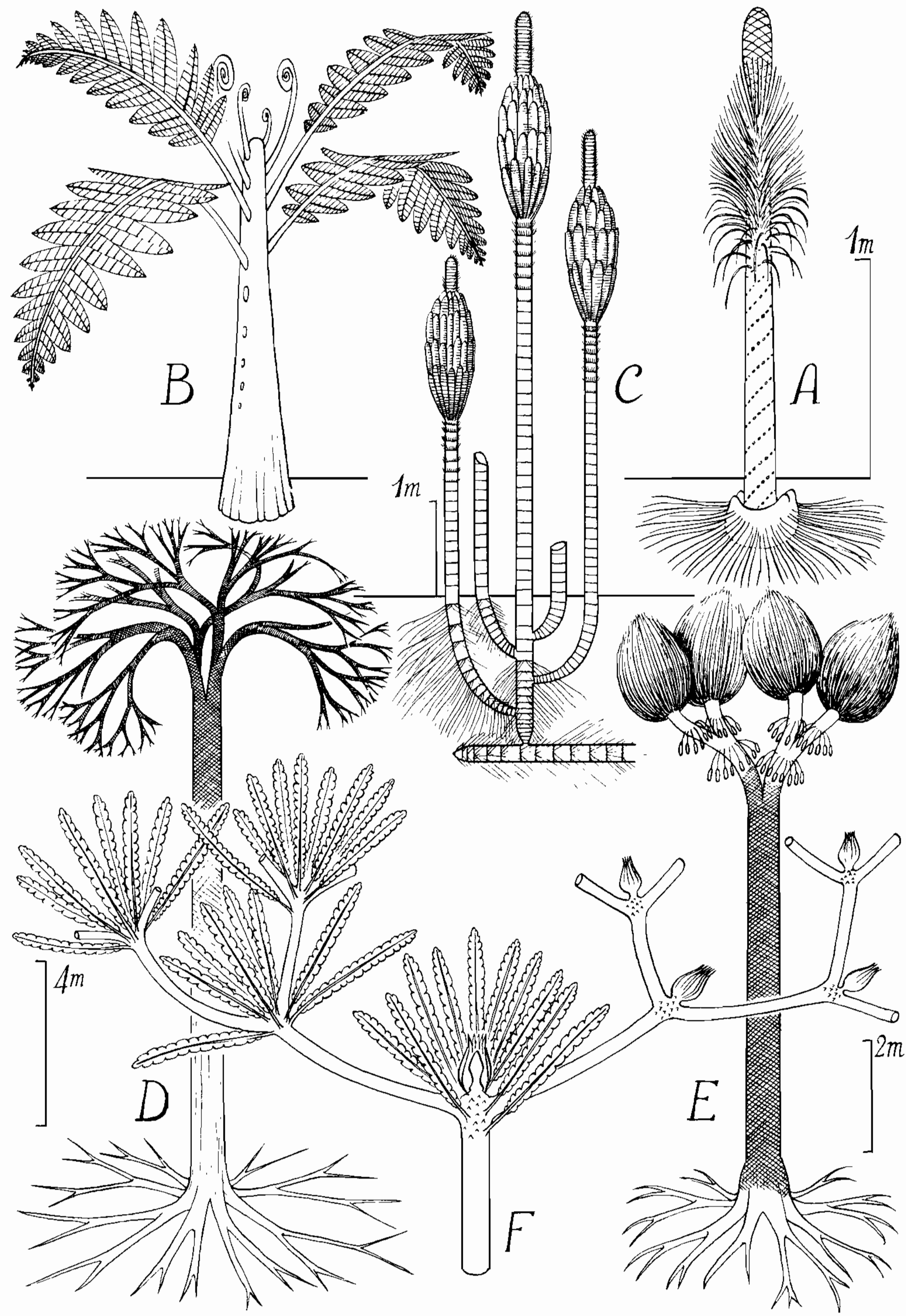
This model is indicated by the modular construction, each module terminating in a complex reproductive axis.

5. SCHOUTE'S MODEL

This model is rare amongst living trees, as we have seen, but may have been very common in arborescent Lepidodendrales of the Carboniferous, if one can judge from published reconstructions. All available evidence indicates that branching was by an equal division of the apical meristem (e.g., MORET, 1949; ANDREWS and MURDY, 1958; EGGERT, 1961; ANDREWS, 1967; EMBERGER, 1968), in precise accordance with our definition of this model. The dichotomy was not necessarily followed by symmetrical development of the resulting axes.

Fig. 71 A–F. Architecture of fossil trees. (From H.O., 1970, Fig. 74). ▷

- *A* *Pleuromeia sternbergi* (Munster) Corda, Isoetales – Pleuromeiaceae (after HIRMER, 1933); Holttum's model.
- *B* *Megaphyton* sp., Marattiales (after CORSIN, 1948); Corner's model.
- *C* *Stylocalamites* sp., Equisetales – Calamitaceae (after BOUREAU, 1964); Tomlinson's model.
- *D* *Wielandiella augustifolia* Nath., Bennettitales (after NATHORST, 1909); distal parts showing branching according to Leeuwenberg's model.
- *E* *Lepidodendron* sp., Lepidodendrales – Lepidodendraceae (after EGGERT, 1961); Schoute's model.
- *F* *Sigillaria elegans* Brongniart, Lepidodendrales – Sigillariaceae (after HIRMER, 1927); Schoute's model


B
C
A
1m
1m
D
E
F
4m
2m

Lepidodendrales:

Bothrodendraceae:

Bothrodendron minutifolium Auct., Carboniferous, Hirmer, 1927.

Lepidodendraceae:

Lepidodendron sp. (Fig. 71 E), Carboniferous, Eggert, 1961 / *Lepidodendron* sp., Carboniferous, Hirmer, 1927 / *Lepidophloios pachydermatikos* Andrews and Murdy (Fig. 72 A), Carboniferous of Kansas, Andrews and Murdy, 1958; Andrews, 1967.

Sigillariaceae:

Sigillaria elegans Brongniart (Fig. 71 F), Carboniferous, Hirmer, 1927.

Ulodendraceae:

Ulodendron major Lindl. et Hutt, Carboniferous, Hirmer, 1927.

It is presumed that the Lepidodendraceae lived in swamps or lagoons in a uniformly warm and humid climate. These trees attained heights of 30-35 m, with a basal trunk diameter of 2 m. The young stages were monocaulous and up to 30 m tall (Andrews, 1967). This late branching suggests, from our knowledge of living tropical trees, that their environment was that of dense forest. The juvenile form bore large leaves, up to 1 m long and densely inserted according to a numerically complex phyllotaxis (Dickson, 1873). When branching began it was marked by a progressive decrease in diameter of successive orders of axis, by a simplification of their vascular anatomy, by a numerical simplification of the phyllotaxis and a decrease in leaf size (Fig. 72 A). Such changes in fact provide an independent corroboration of Corner's rules. It would appear that this principle has already been accepted by palaeobotanists, applied by them in their reconstruction, and termed apoxogenesis (Eggert, 1961).

6. RAUH'S MODEL

Equisetales:

Calamites, subgenus *Calamitina* Weiss (Fig. 72 B), Carboniferous, Boureau, 1964.

This assignation refers only to the aerial parts, since the erect trunks arose from an underground rhizome system and, therefore, are with little equivalence to any of our models (but cf. Tomlinson's and McClure's model).

7. ATTIMS'S MODEL

Equisetales:

Calamites, subgenus *Crucicalamites* Gothan and *Diplocalamites* Gothan (Fig. 72 C), Carboniferous, Boureau, 1964.

These *Calamites* reached a height of 30 m, with a basal trunk diameter of 1 m. They apparently lived in swampy forest and the frequent presence of stilt roots may have produced a mangrove-like aspect in the community.

Coniferales:

Cordaites Permian (Fig. 72 D), Carboniferous, Grand'Eury, 1877; Cridland, 1964.

The generalized reconstruction of these trees, with monopodial trunks to a height of 30 or 40 m, suggests this model. A *Rhizophora*-like appearance is again indicated by the presence of basal stilt-roots.

8. MASSART'S MODEL

Cordaitales:

Lebachiaceae:

Lebachia piniformis (Schloth.) Florin (Fig. 72 E), Permian, Florin, 1944.

This species, from its reconstruction, would be so categorized, a conclusion supported by precise evidence for foliar dimorphism related to axial dimorphism, which is a frequent phenomenon in examples of Massart's model.

Fig. 72 A–F. Architecture of fossil trees (further examples). (From H.O., 1970, Fig. 75). ▷

A *Lepidophloios pachydermatikos*, Lepidodendrales – Lepidodendraceae, Schoute's model. *a* Young unbranched individual (after Andrews and Murdy, 1958); *b* older, branched individual (after Andrews, 1967).

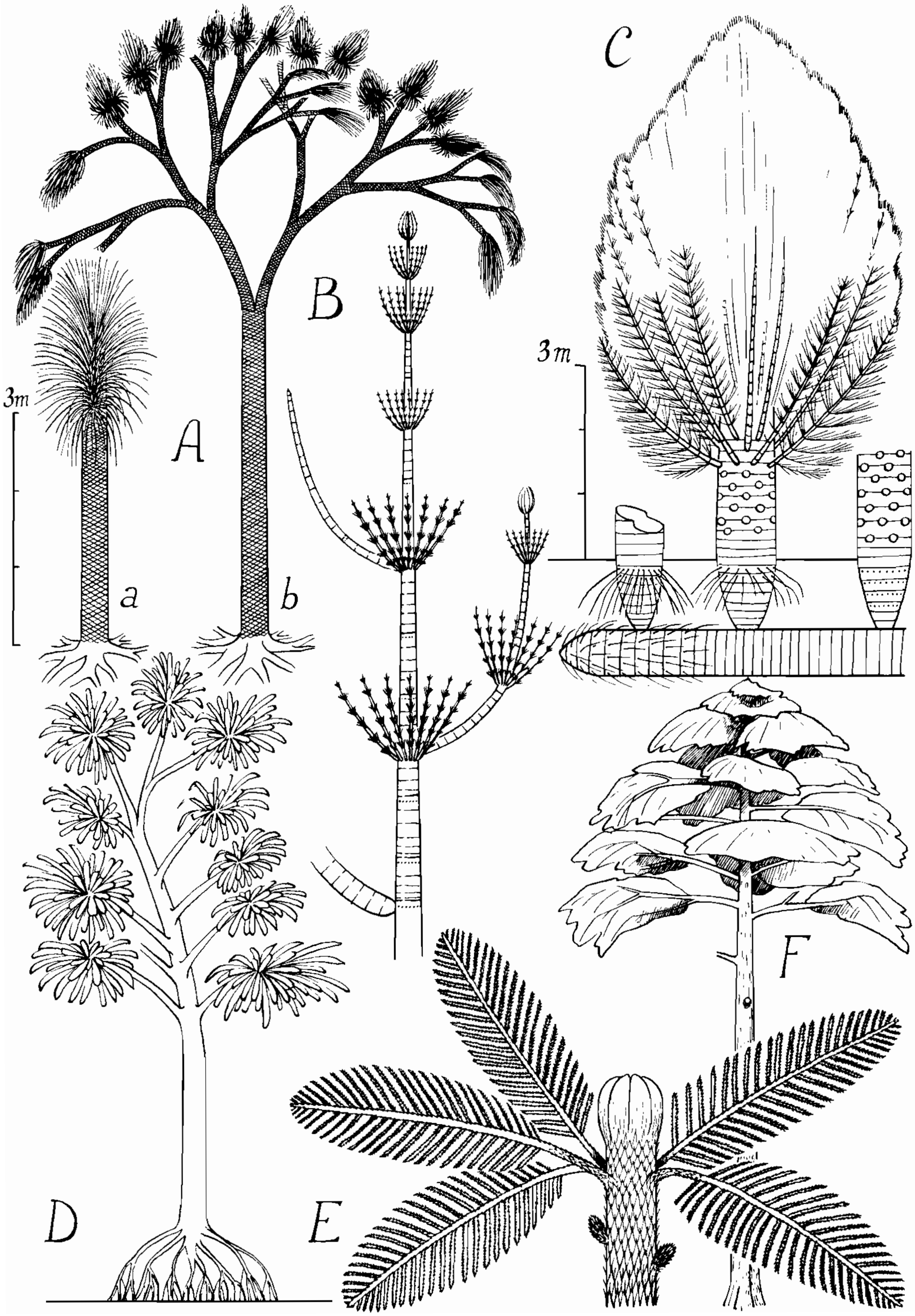
B *Calamitina* sp., Equisetales – Calamitaceae (after Boureau, 1964); Rauh's model.

C *Crucicalamites* sp., Equisetales – Calamitaceae (after Boureau, 1964); Attims's model.

D *Cordaites* sp., Cordaitales, generalized reconstruction of a member of this group (after Cridland, 1964); Attims's model.

E *Lebachia piniformis*, Coniferales – Lebachiaceae (after Florin, 1944); Massart's model.

F *Archaeopteris macilenta*, Archaeopteridales (after Beck, 1962); Roux's model


C
3m
B
3m
A
a
b
F
D
E

9. ROUX'S MODEL

Archaeopteridales:

Archaeopteris macilenta Lesq. (Fig. 72F), Upper Devonian, North America, BECK, 1962.

This tree exceeded a height of 30 m; its monopodial trunk with regularly produced horizontal branches seems to satisfy the definition of Roux's model.

In conclusion it seems significant that fossil trees can be ascribed with reasonable precision to models which correspond to those found in existing trees and that this equivalence goes back as far as the Devonian. This indicates the repeated appearance of the same model in successive groups of vascular plants whose abundance has waxed and waned and which, in many cases, have eventually become extinct. We cannot, therefore, say that architecture alone determines the supremacy of the angiosperms since many of their models preceded them, but it seems reasonable to conclude that the angiosperms owe at least part of their success to the great diversity of growth models they exhibit.

The question of reiteration (p. 269) in fossil trees can be discussed with even less certainty than architectural models. It seems that reiteration at least could occur in fossils, but we lack examples. It would be an attractive hypothesis to suggest that existing dicotyledonous trees again owe at least part of their greater success to their greater ability to adapt through reiteration, but our present state of knowledge does not allow us to discuss this idea. It should, however, be considered as an important evolutionary factor, since it plays so important a role in community interaction, as the last part of this book shows.

Chapter 4 Opportunistic Tree Architecture

A. Reiteration

Trees in the forest rarely exist in the ideal state we have provided for them in our preceding description of architecture. A reader therefore may have had difficulty in recognizing the architectural features we have outlined even with access to tropical species in which there is greatest architectural variety. This is simply because trees rarely conform completely to their model. In the undergrowth of the tropical rain-forests, where microclimatic conditions appear to be optimal for the functioning of trees (CACHAN and DUVAL, 1963), numerous environmental factors still modify their development. Branches are broken mainly by the fall of limbs from trees higher in the canopy, as was shown by HARTSHORN (1972) in his study of the population dynamics of *Pentaclethra macroloba* and *Stryphnodendron excelsum* in Costa Rica. Trees are subject to insect and fungal attack, larger twigs are broken and eaten by arboreal herbivores like sloths, bears and monkeys as OPPENHEIMER and LANG (1969) have shown in their study of *Gustavia*. Moreover, the tree crown, during its lifetime, crosses successive levels in the vegetation, each of which has its distinct pattern of energy supply. Nevertheless, architectural models are inherent in the development of all trees and provide the analytical key to the interpretation of actual tree shape. The process of architectural adjustment by which the damaged tree accommodates itself to its environment is here called *reiteration*. The term may be defined as any modification of the tree's architecture not inherent in the definition of its model and which is occasioned by damage, environmental stress or supraoptimal conditions. Reiteration usually involves the bringing into activity of resting apical meristems not normally involved in the expression of the model, but can also involve change in the orientation of a shoot, e.g., from plagiotropy to orthotropy. The implications of reiteration for an understanding of tree growth are treated in detail in this section. We first will move to a more practical plane in explaining the growth of the individual tree by gathering the architectural evidence inherent in simple and directly observable phenomena.

I. *Reiteration as a Morphological Phenomenon* (Fig. 73)

A walk through a forest will reveal how architectural principles relate to what is visible among existing trees. In small undergrowth trees one frequently notes trunks with pronounced articulations which resemble the attachment of a bayonet to a rifle (Fig. 73C). The same "bayonet-joints", as they may be termed, are also common on wider trunks in taller trees although, in the tropical forest, the screen of lower vegetation will have to be cleared to reveal them. Evidently such joints represent levels where the terminal meristem of an initial trunk has been broken or aborted leading to its substitution by another trunk. In some cases this is simply the relay mechanism involved in the building of a sympodial trunk in conformity with the architectural model, as, for example, in the models of Chamberlain, Nozeran and Troll. In other cases it is not and in these alternative examples it is readily appreciated that disruption of the growth pattern has occurred and effectively *a second tree, showing the same model* has been substituted for the first. However, whereas the initial model originated from a seed and had developed a root system, the second comes from a lateral meristem, previously in a latent or subordinate condition, but now released or given an opportunity for more vigorous development by some activating influence. The second axis usually does not produce an independent root system since it is inserted on an axis of the previous model. The illustration (Fig. 73C) shows this construction in a diagrammatic way, with the bayonet-joint shown by the arrow.

Trees with forked trunks may represent the same phenomenon, but with two instead of one substitution trunk (Fig. 73D), excepting those in which this forking is inherent, as in Leeuwenberg's and Schoute's models. More than three substitution trunks at one level are not often encountered in the young trees here considered, although overall there may be no limit to the total which can appear in one tree.

Where a tree is thrown askew, for instance by the weight of detritus falling from the canopy or by partial uprooting, more or less complete models originating from lateral meristems may develop by the process generally described as *epitrophy* and here included as part of our concept of reiteration. This response is readily observed in trees which hang over a river where a near-horizontal trunk or low branch throws up a series of vertical axes which decrease in size distally. This "river-bank effect" is very important in understanding the reactions of trees surrounding holes in the canopy, human settlements, roads and any other discontinuity of the vertical structure (see p. 365). Similar growth phenomena can be promoted, either experimentally or in horticulture, by bending a young tree in an arc (Fig. 73A).

Sucker sprouts generally conform to this pattern of renewal, whether they arise from the trunk of a broken tree (Fig. 73B) or from roots (Fig. 73F). Stem sucker sprouts usually develop from dormant buds, but they may be adventitious, arising from a callus (MOLD and LANNER, 1965). Root suckers normally develop their own root systems independent of that of the parent tree and constitute a more complete expression of the model. The ability to produce root suckers varies widely in trees and is evidently determined genetically (KORMANIK and BROWN, 1967). The general horticultural practice of vegetative propagation from stem cuttings makes artificial use of these several reiterative abilities in plants (Fig. 73E).

The term reiteration of the model, or more concisely reiteration (after OLDEMAN, 1974a), that we use here to refer to these processes, is not to be confused with another general term, regeneration. Regeneration is undoubtedly an important ecological process, especially in temperate trees where it is a major determinant of tree shape, but it does not cover all possibilities. Reiteration is the mechanism by which regeneration of a *damaged* tree takes place, and in this precise case the two notions more or less cover each other. But reiteration is also the mechanism by which trees adjust to their environment *without* the intervention of mechanical disturbance, as will be seen later (p. 280). Reiteration thus is a morphogenetic process not necessarily implying the

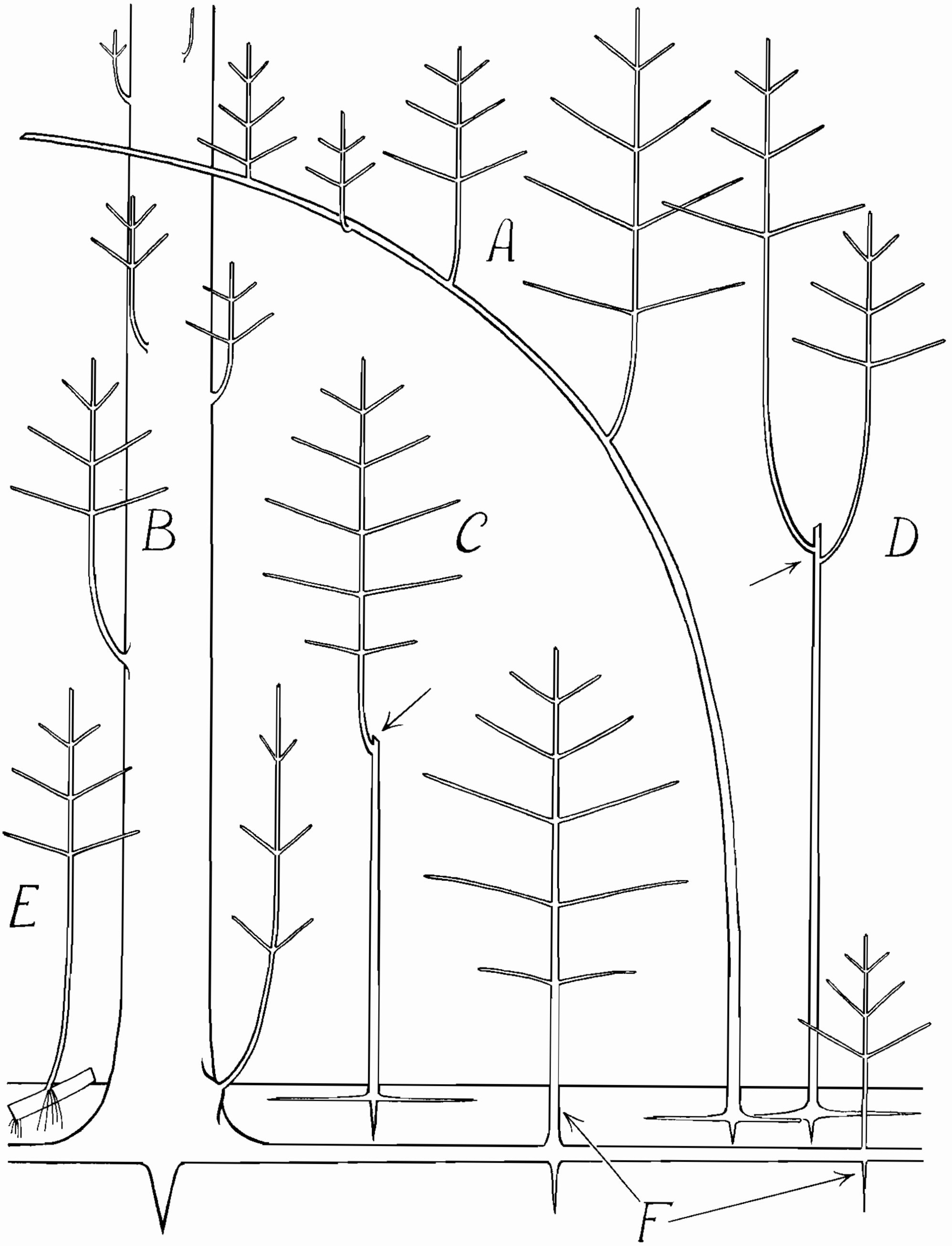


Fig. 73A–F. Reiteration in the lower storeys of the forest.
Diagrammatic representation of morphological features visible in trees, regarded as examples of reiteration usually involving reactivation of latent meristems.

- *A* Reiteration, on an arched trunk.
- *B* As stem suckers on an old tree.
- *C* As a mechanism for regeneration, "bayonet-joint" (*arrow*).
- *D* Same but twice, producing a fork (*arrow*).
- *E* From a cutting.
- *F* As root suckers

"repairing" of a previously disturbed organic system; it refers to genesis, whereas regeneration indicates the *re*-establishment of something lost, the concept most acceptable to agronomists (e.g., ODEGBARO, 1973). As such, the notion of reiteration covers a field much wider than mere regeneration. Contrariwise, it is much narrower than "repetition"; just as "replication" has been coined for repetitive genetic processes, "reiteration" specifically refers to the repetition of overall plant growth patterns starting from meristems. With this important qualification in mind we can elaborate, explain, and apply the concept of reiteration.

Reiteration implies the addition to the initial tree of a new shoot system, in general conforming rather closely to the architectural model which had previously been expressed by the same tree. Some change in architecture is implicit in this process because the new "tree" has not originated from a seed, but since most changes are quantitative and involve changes in size or growth vigor of the newly added part (e.g., especially stump sprouts) and since neither of these parameters has entered into the definition of the original model, we can accept that the reiterated shoot conforms to the same model as the parent. This is readily observed in terms of the diagrams which form Figure 73, but is best appreciated in many published illustrations of trees. Occasionally reiteration does result in modification sufficiently extreme to provoke recognizable change from one model to another. For example, trees of *Perebea guianensis* (Moraceae) which reach a height of 12 m in the forest, normally conform to Roux's model, characterized by continuous branching (Fig. 52). Suckers originating from a fallen trunk have been observed, however, to conform to the architecture of Massart's model by a change-over towards rhythmic branching. The development of trunks in specimens of *Hevea brasiliensis* which lack branches completely (HALLÉ and MARTIN, 1968) involves a change of equal magnitude, but from rhythmic towards continuous growth. However, such a change of model within the development of an individual tree is rare. What is usually reiterated is another copy of the same model, more or less complete.

Tree models with differentiated branches always possess a morphologically distinguishable trunk so that if we recognize new models among lateral architectural complexes formed as the individual develops, it is possible to recognize several trunks on one tree. Our architectural analysis and its expression in terms of reiteration permits us to do so, without contradicting a physiognomic definition of a tree as a tall plant with a single trunk. After the early establishment of the tree conforming to its model, we may find that reiteration establishes new trunks, supernumerary with reference to the initial, seed-originated model and constituting the first step in a reconditioning of the overall growth pattern.

On this basis it becomes possible to distinguish two basic kinds of branching, depending on whether we are dealing with a tree which conforms to its initial model, or whether branching is in part a consequence of reiteration. Following OLDEMAN (1974a), with a slight change of wording which does not change the meaning, we have the following definitions:

Branching, in the most general sense, is the appearance of a lateral axis on another axis.[13] This definition corresponds, of course, to common usage. The concepts of architectural model and reiteration allow one to distinguish in a

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[13] Equal dichotomy is a rare exception (TOMLINSON, 1978), not readily catered for by this definition.

general way the two following expressions of branching. *Sequential branching* refers to the successive and orderly appearance of lateral axes according to the regularly unfolding sequence of the architectural model. Generally, in trees originating from a normal seed in a normal biotope, this is the only kind of branching (*initial* model of the individual tree). *Reiteration of the model* is the appearance of lateral axes according to the potential and latent sequences of meristems generated during growth corresponding to the model but expressed later: such sequences may be lateral, may result from dedifferentiation of terminal meristems or may be due to neoformation of meristems, but in any case they lead to a (generally delayed) phase of growth completely or partially expressing the same growth pattern as the initial model. Such branching may be distinguished readily from those trees with modular construction since reiteration is neither regular nor predictable.

The complete definitions have been given here so as not to separate their different aspects in the text, but we will explain them step by step, dealing first with the simplest condition. This is reiteration by meristems which were initiated during the expression of the initial model, but remained latent without contributing to its architecture.

In many tropical trees (and a few temperate trees) the difference between the two kinds of branching is very clear because it corresponds to the difference between sylleptic and proleptic branches defined earlier and usually recognized by consistent morphological differences (p. 42). In *Rhizophora mangle* (Attims' model) for example all sequential branching is by syllepsis. Prolepsis occurs when a terminal bud is damaged and a latent lateral develops. In this particular case, reiteration theoretically permits regeneration of a damaged architecture by activation of a latent meristem, a process which is easily recognized by the morphology of a proleptic shoot. In nature prolepsis actually plays little role even in reiteration of *Rhizophora,* first because of the limited life span of latent meristems, and second because of the frequent dedifferentiation of terminal meristems so that a shoot destined to become plagiotropic in the architecture of the tree is able to remain orthotropic. Another example of proleptic reiteration, this one familiar to temperate foresters, is the development of lammas shoots on oaks in stands that are thinned too thoroughly. Here, reiteration is in no way related to tree regeneration, but is entirely due to a modified supply of radiant energy in the stand and, maybe, redistribution of water and nutrients in the soil. Lammas shoots are a spectacular case of proleptic nonregenerative reiteration.

Indeed, if one examines architectural models on the basis of their sequential branching one can often establish that branching in conformity with the model is entirely sylleptic. Table 9 summarizes this information in a very generalized form.

In models with mixed axes (Champagnat, Mangenot and Troll) exclusive prolepsis is common in many temperate trees but less common in tropical trees.

It can be recognized intuitively that the activation of a meristem and its subsequent continued activity cost energy and, in the same quantitative terms, the more vigorously a plant grows, the more meristems it can activate and continue to support. This statement will be more formally expanded in a further section on bioenergetics (p. 302). However, even in its simple form, the assertion implies that the normal expression of a model requires a specific "standard vigor" at germination and that there is a subsequent "normal" increase in vigor in order to allow the

Table 9. Sequential branching within models

A. Branching absent:		
	Holttum	Corner
B. Branching ± exclusively by syllepsis (rarely by dichotomy):		
	Schoute	Roux
	Chamberlain	Cook
	Koriba	Attims
	Fagerlind	Scarrone
	Stone	Aubréville
C. Branching ± exclusively by prolepsis:		
	Tomlinson	McClure
D. Branching both by prolepsis and syllepsis:		
1. Variation within the same *model*		
	Rauh	temperate species by prolepsis, tropical species often by syllepsis;
	Leeuwenberg	temperate species by prolepsis, tropical species often by syllepsis;
2. Variation within the same *individual*		
	Prévost	trunk modules proleptic, branch modules sylleptic;
	Nozeran	trunk modules proleptic, branch modules sylleptic;
	Massart	trunk and axes branching either by prolepsis or syllepsis, sometimes both

functioning in most models of an ever-enlarging number of aerial meristems in a preestablished order (sequential branching). The same, of course, is true of underground meristems, mainly those of roots, although we know virtually nothing of their architecture.

That there is a standard vigor at germination for a given species is amply demonstrated by the very uniform mean seed weight in the higher plants, although the total range for all species is 10 orders of magnitude. This constancy (HARPER et al., 1970) in turn leads to seedlings of very uniform morphology again characteristic for each species. In the subsequent development of the tree, vigor is no longer determined by food reserves in seeds, but by successful energy absorption from the environment. Where this energy input is itself relatively constant, the "normal" increase in vigor of a tree is well expressed. In these simple qualitative terms we can grasp in a general way why the remarkably uniform microclimatic conditions of the tropical rain-forest explain the relatively large number of trees in this biotope which conform to their model. We can say that the energy balance established by the model is closely and constantly maintained.

However, in a forest the canopy is likely to change, often abruptly as when a tree, or a large branch, falls. Consequently the energy input into lower trees may abruptly surge upwards and their vigor changes accordingly. Even at maximum performance, the number of model-determined meristems may not now be sufficient to accommodate this increased amount of energy. Consequently growth activities not found in the normal developmental sequence of the model can be started. Meristems may undergo dedifferentiation as when a branch-forming meristem becomes a trunk-forming meristem, e.g., in *Rhizophora* mentioned above. Equally, latent meristems previously held in check may also be activated and neoformation of meristems may occur, as in the initiation of adventitious shoots like root suckers. These responses fall into our generalized concept of reiteration. Reiteration can now be seen to be any general morphogenetic departure from the "standard" developmental sequence of the model.

In our usage, it is an assumption that reiteration reproduces partially the original model, but we cannot specify to what quantitative extent a reiterated model is functionally similar to the basic model. Where there is a marked phase change from juvenile to adult in the parent model, juvenility may not be expressed very completely in a reiterated shoot. Sexuality offers a particular problem, since a reiterated shoot complex may flower much earlier than a seedling, as shown by COMBE and DU PLESSIX (1974) in *Hevea*. This aspect is important in our later discussion of tree construction. Consequently, we recognize that our concepts are no panacea for all problems, and that many questions will remain unanswered, for instance until the physiology of meristem interaction in developing trees is better understood.

For the moment, we need not discuss the concept of "vigor" further, but we will return to it later (p. 310).

II. The Organ Complexes Built by Reiteration

1. The Tree in the Forest (Fig. 74)

Foresters have a physiognomic concept of a tree, combining size and age, with reference to its potential size (cf. AUBRÉVILLE, 1963). The connotation of reiteration perhaps brings some difficulties to the use of the word "tree", since it considers individual woody plants as having, in many cases, several trunks, but in fact this semantic problem provides no obstacle to the understanding of tree growth as long as we refer to the whole organism as a tree, i.e., as long as we clearly distinguish the tree's trunk from a model's trunk. If one adopts a developmental approach, such a tree may go through two phases, the first of which is determined by the initial model and the second by reiteration of this model. The units developed during these two stages are architectural *complexes* of organs, and in order not to burden the text with lengthy circumscriptions we will distinguish between an *initial complex* of a tree, which is the architecture unfolding after germination, and a *reiterated complex*, referring to the architecture resulting from the activity of one of its supernumerary meristems. Morphologically the two complexes may or may not be easily recognized. In trees which conform to their model the initial architecture dominates subsequent development, with reiteration being a supplementary process. Otherwise, the presence of reiterated complexes in a tree implies, either that it has suffered major damage and regenerated by reiteration, or that it has altogether left the phase in which the initial model alone, or one regenerated model, determines its growth. Henceforth, a collection of models constitutes the tree. If this approach is accepted there should be no confusion produced by using expressions like "the small trees making up the whole tree" instead of "the reiterated complexes making up the tree".

One should not confuse this concept with that of juvenility versus maturity (p. 16), since such a phase change is considered to be a normal part of the tree's architecture. In fact, "reversion to the juvenile condition" can be one of the best indications of reiteration.

For graphic purposes (Fig. 74) we chose an example corresponding to ROUX's model, i.e., with clear differentiation between trunk and branch, since this most clearly allows one to distinguish between the model and its reiteration. An instance might be *Durio zibethinus*, of the Malayan forest, but other species and other models could be substituted.

In the undergrowth of the forest, the tree has an architecture conforming to the model (Fig. 74A) and we have here an initial complex. Since the sapling is likely to be damaged, it then is regenerated by reiteration of new models, their levels of insertion often indicated by bayonet-junctions. These joints become obscured in time by secondary growth and only dissection can reveal them. The tree is monocaulous, but not monoaxial. Reiteration at this level replaces but does not profusely multiply trunks because the tree is "suppressed" in the forester's sense (e.g., RICHARDS, 1952; LINDEMAN and MOOLENAAR, 1959; OLIVER, 1975). In fact, its architecture is still governed by one single model, the initial one, even if parts of it are regenerated by reiteration. Quantitatively the tree may reduce its architecture by net loss of leaves and branches.

The following diaries over a period of seven months in 1965 for trees on the Rorota Plateau, near Cayenne, French Guiana, give some idea of how little growth there can be in such a suppressed tree:

Example 1: Virola surinamensis (Myristicaceae, Massart's model), tree initially 2.6 m high with only four plagiotropic branches of the uppermost tier persistent. Several bayonet-junctions indicate earlier regeneration.

April 15–June 15: no change
June 15–September 13: apical growth of 3 cm, almost all leaves shed from the branches
September 13–November 14: no further trunk extension, but sympodial extension of branches

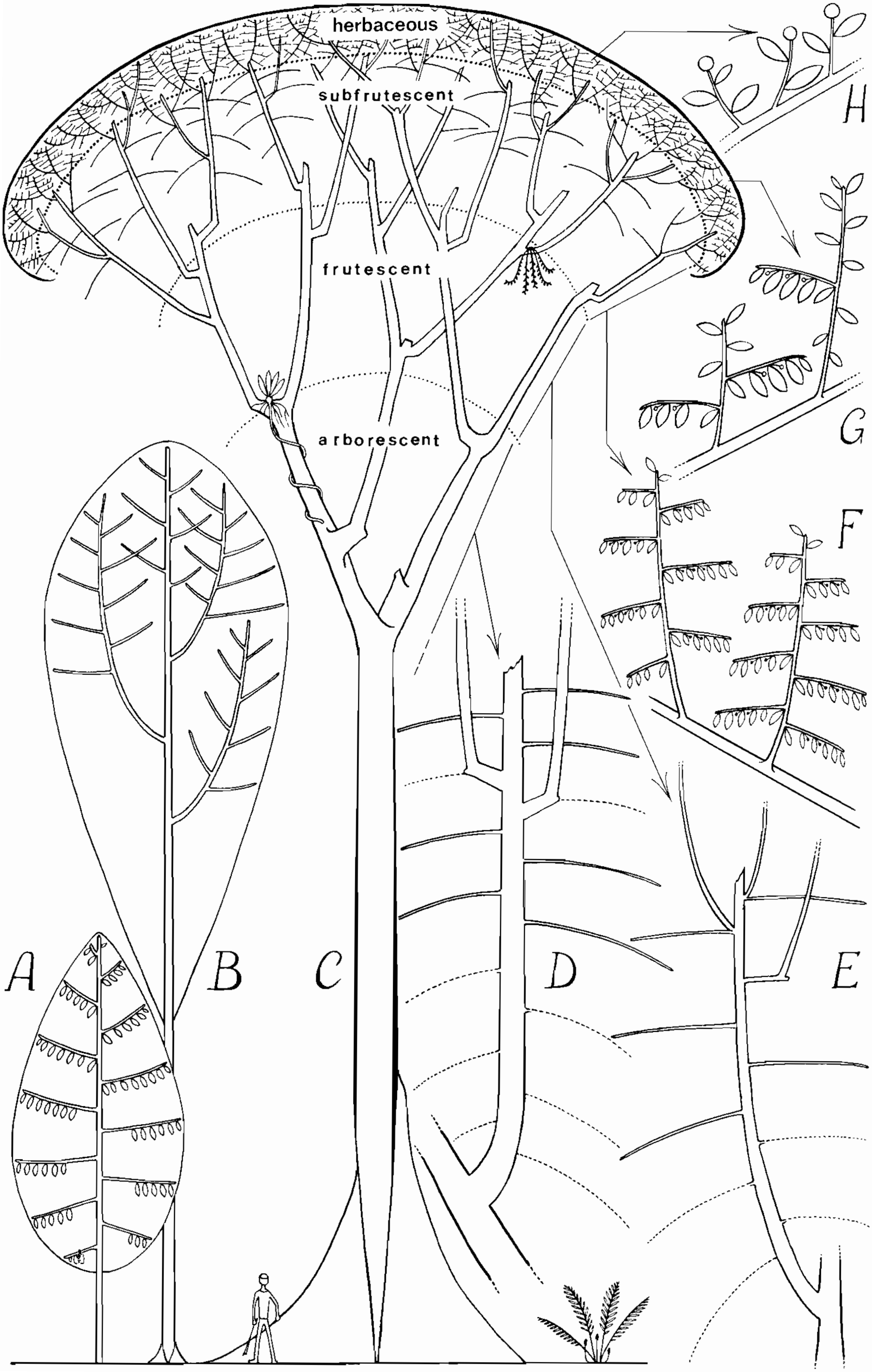
Since growth of branches within the model is monopodial, this represents regeneration by partial reiteration of the model. At the last stage examined the photosynthetic apparatus of the tree consisted of 15 leaves.

Example 2: Cordia exaltata (Boraginaceae, Prévost's model), tree initially 2.5 m high; one fork, with a living and a dead trunklet; two tiers each with three branches, on the uppermost part of the living half of the fork.

April 15–June 30: no change
June 30–August 8: branch extension with up to nine new leaves on the new modules, with a total of 30 new leaves
August 8–September 13: no change
September 13–October 1: some branch extension
October 1–November 14: no change

These are but two examples from a total of 12 trees (seven individuals of *Virola*, five of *Cordia*) which were followed over this period, with the rainy season beginning in June and ending in September. The amount of growth varied. Although the two detailed examples showed only branch extension, other trees formed new branch tiers, while only the most vigorous showed both branch and trunk extension. In comparison trees of the same two species in the ORSTOM Botanic Garden in Cayenne showed over the same period productivity measurable in terms of numbers of whole tiers, rather than in leaves and internodes as observed in the suppressed trees. Suppressed trees, as these examples show, have growth rates which are marginal to survival; a slight detrimental change will kill them. However, there seems to be no precise infor-

Fig. 74A–H. Reiteration in a forest tree. ▷
A Initial model (e.g. Roux's model).
B First spontaneous reiteration.
C Fully mature tree showing the traces of successive waves of reiteration.
D–H Details to show successive morphological features of each phase, with progressively diminished capability. *D* Arborescent reiteration, resulting in a "tree"; *E* frutescent reiteration, resulting in a "shrub"; *F* subfrutescent reiteration, resulting in an "undershrub"; *G* and *H* herbaceous reiteration, resulting in "herbs", the ultimate reduction *H* involving precocious flowering by neoteny. Further explanation in the text


herbaceous
subfrutescent
frutescent
arborescent
H
G
F
A
B
C
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E

mation as to how long such trees may survive.

Improvement in the level of available energy, most usually light energy resulting from some change occurring in the higher levels of the canopy, will promote growth at a more rapid rate. At first, this continued growth will be expressed in the more rapid development of the model. If the architecture of such a tree was much reduced quantitatively during the suppression period, few meristems included in the model complex may have persisted, but an improvement in conditions may still allow them to be activated. Sooner or later the moment comes when active meristems inside the model function at their maximum capacity, so that they cannot translate into production any more increase in energy offered from outside. Any excess of energy which could not otherwise be used by a model tree is then taken up by reiteration, as is explained more fully on p. 290. The tree now develops the first trunks which are supernumerary with reference to the initial model (Fig. 74B). From this point on, the development of the tree can only be understood in terms of reiteration and its architecture must be described in terms of reiterated complexes. Terminology and bioenergetic interpretation aside, the phenomenon is not in doubt and can be demonstrated easily.

Further development of the forest tree is a perpetual adjustment of its architecture to its surroundings. As will be seen in a later chapter on sylvigenesis (p. 366ff.), trees grow up to the canopy in more or less regular gaps successively opening above and beside their crowns, dicotyledonous emergents often being left over from a destroyed canopy and not always having emerged from a pre-existing forest as their name suggests[14]. The consequence of this series of successive improvements and declines in available energy is tree development in "waves" of reiteration, which for the sake of clarity are schematically represented in a symmetric manner in Figure 74C, but which in reality, owing to the occurrence of lateral openings, can be very lopsided. Seasonal fluctuations in macroclimate would come into play in many regions, codetermining phases of stagnation and release of reiteration, but they can be discounted in nonseasonal tropical rain-forest.

Intuitively we can appreciate that the chance of survival of the tree is increased after each wave of reiteration, since more meristems are made available. Demographic studies (e.g., SARUKHÁN, 1978) show that the older and taller a tree becomes the more likely it is to survive. This suggests that every phase of vigorous growth, determined either by the model or by its reiteration, heightens the chance of survival. Eventually by continued accretion of new reiterated complexes, together with some loss, but a net gain, the ultimate result is a big forest tree (Fig. 74C). Again we cannot exclude the possibility of trees reaching large proportions while still conforming to their model, but examples seem to be few (e.g., *Araucaria hunsteinii,* New Guinea – a photograph of an undoubtedly model-conform emergent in WHITMORE, 1975, his Fig. 14.7).

Studying the development of a common big forest tree it can be seen that each

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[14] In the absence of any reliable method for ageing tropical trees, this statement might be contentious. In the temperate eastern United States, where tree age can be determined, *Liriodendron* in old forest can be an emergent younger than surrounding canopy trees. *Pinus strobus* may become an emergent simply because it can grow taller than hardwoods in certain types of mixed deciduous forest. Some models may provide real emergents more readily than others.

new wave of reiteration produces more numerous and smaller organ complexes than the preceding one on which they are inserted essentially as progressively higher branch orders. The smaller complexes generally have a shorter period of development, a shorter life-span and a limited biomass. Ultimately they exist as an axis or a complex of axes with living cambium, and the next generation of reiteration meristems. The reiterated complexes pertaining to successive waves of reiteration can be compared to the architecture of an individual which has originated as a seed meristem. Reiterated complexes borne by the trunk or the thickened branches of the initial model-conforming tree develop like small trees, as shown in Figure 74D. We can conveniently refer to this as "arborescent reiteration", and such a unit is responsible for the larger limbs of the developing tree. In later waves of reiteration the units are smaller and by analogy with seed-originated shrubs we can speak of "frutescent reiteration" (Fig. 74E). These reiterated shrubs are borne on the trunks or branches of previous arborescent complexes. In their turn, shrubby complexes support reiterated "undershrubs" (Fig. 74F) and yet smaller and more numerous, miniaturized complexes resulting from "herbaceous reiteration" (Fig. 74G). The model is now expressed in its smallest proportions commensurate with its definition and still recognizable by its architecture.

The architecture at first is still sufficiently clearly expressed in herbaceous reiteration for its model to be recognized. However, further reduction, as by a few branches or internodes, renders the pattern incomplete. This is effectively what happens in the ultimate stages of herbaceous reiteration (Fig. 74H) when only parts of the model are expressed. This partial reiteration may involve fragmentation of the model or a process parallel to neoteny, where the model is represented largely by its flower or inflorescence. This process, in fact, is one cause of the difficulties the morphologist has in circumscribing the "inflorescence" in woody plants (VAN STEENIS, 1963). A flower or flower-bearing branch is usually an intrinsic component of the model and its position can be important in the definition of the model. If the model is reduced to little more than the reproductive axis, the relationship of parts becomes obscured.

An important difference between seed-originated and reiterated architectures is their relation to the root system. Though some observations do suggest that the capacity for aerial root formation in association with reiterated complexes does exist in *Ficus*, *Rhizophora* and *Clusia*, the anatomical data are lacking which one would need to acquire a general understanding of these phenomena. We do not know the precise stimuli needed for aerial root initiation in tropical trees. The exploitation of light resources in the environment, on the contrary, is remarkably comparable in herbs, shrubs, trees, and their reiterated equivalents. The ontogenetic process is evident but needs extended analytical investigation.

In the short functional life-span of the individual units this wave of herbaceous reiteration is also comparable to a population of herbs. This is important, because it signifies that the tree has reached its maximum dimensions. Herbaceous complexes can add no more massive structures to the tree, so it maintains a constant size. The upper layers of the tree crown thus behave like a field of weeds in the ultimate stage of growth, but lacking a root system. Indeed the appearance of a flat-crowned tree with a dense shoot system has already suggested this analogy in the creole name "cour-macaque" ("monkey playground") for large mimosaceous trees such as *Newtonia suaveolens* in the Guianas.

The next question to be asked obviously is, "How long does the tree maintain itself at this stage of growth?" Furthermore, "what factors may contribute to the decline and loss of reiterated complexes"? This process of elimination is considered later (p. 325ff.), but it seems quite possible for trees to maintain themselves in this state of dynamic equilibrium for extended periods. This is a highly subjective statement, since tropical trees cannot be dated and the necessary prolonged measurements have not been made.

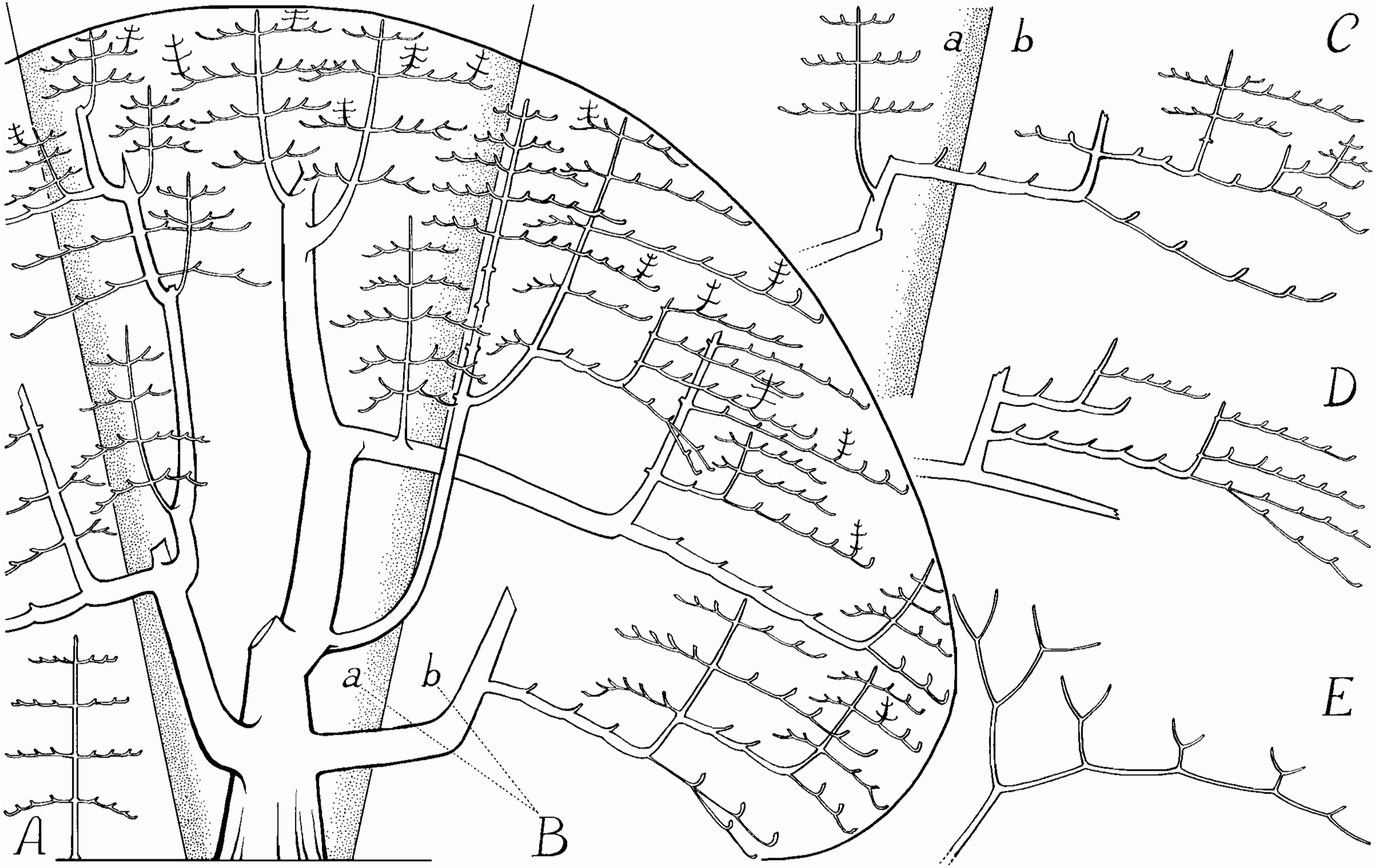
2. The Free-Standing Tree (Fig. 75)

A tree in an open field, not in competition with other trees, behaves differently from a forest tree which is more or less uniformly shaded by the crowns of its larger neighbors throughout most of its life. In free-standing trees the effect we have spoken of as the "river-bank effect" (p. 270), which results from the availability of light or other ecological factors in a lateral direction (OLDEMAN, 1972), plays an important and permanent role. To exemplify the processes of development in a free-standing tree we have here chosen Aubréville's model (Fig. 75A). Initial conformity with the model is short.

In many instances, the initial model has not yet been completely expressed when reiteration sets in. Examples are provided by Scarrone's descriptions (1969) of the precise morphogenetic development of young mango trees (*Mangifera indica*, Scarrone's model) in young plantations that are under a high light regime. Only rarely does the initial model go as far as two branch tiers. Most often branches after the first tier rapidly start to behave like trunks, and in very rare cases the seedling axis flowers terminally (neoteny). Scarrone's description does not consider development after this flowering phase; is it lethal, so that Holttum's model is substituted for Scarrone's model, or are there subapical buds starting postfloral reiteration?

In the schematic representation of processes in Figure 75, reiteration starts early because the available level of light energy is high. The model itself develops insufficient active meristems to utilize this energy fully, even at maximal growth performance, so that the set of active meristems in the model is supplemented by reiteration processes. Generally, these are proleptic or occur by dedifferentiation of terminal meristems. Subsequent asymmetric growth of reiterated complexes is next promoted, since the crown develops more in width than in height. The result is a tree lower than that in the forest, with a crown possessing a capacity of light interception comparable to that of a big forest tree, but a more hemispheric or ovoid crown and an obviously much shorter trunk (compare Figs. 74C and 75B). This last illustration shows the resulting architectural complex, and it is easily appreciated that the tendency to dorsiventrality is pronounced in the lower and peripheral parts of the crown, at (b)

Fig. 75A–E. Reiteration in a free-standing tree ▷ (or in the crown of an emergent tree).
A Initial model (e.g. Aubréville's model).
B Mature free-standing tree and its reiteration complexes; *a* central zone of the crown comparable to that in a forest tree; *b* periphery of crown, with river-bank effect.
C Contrast in reiterated complexes of center *a* and periphery *b* in the crown.
D Plagiotropy and pronounced asymmetry in lower part of crown, owing to river-bank effect.
E Example of secondary dorsiventrality (by apposition) in margin of crown of a tree conforming to Leeuwenberg's model. Further explanation in the text


a
b
C
D
E
a
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A
B

whereas in the center of the crown, at (a) ascending axes are promoted. The central portion, in fact, is a microcosm of whole forest canopy and conditions here are comparable with those for a forest dwelling tree. The river-bank effect is most pronounced in the lower, peripheral portions of the crown, with pronounced dorsiventrality, and the architectural complex at different heights is shown in Figure 75C and D. Herbaceous reiteration may so incompletely express the model and dorsiventrality may be so pronounced that only one or two erect internodes develop. Even where no axial plagiotropy within the models exists, as in models like those of Rauh, Attims, Scarrone and Leeuwenberg, a pronounced dorsiventral organization is induced. Orthotropic axes start to grow obliquely into the free lateral space, a process which occurs in trees along river-banks, with axes growing toward the water (OLDEMAN, 1972). Leeuwenberg's model, where radial symmetry of shoots is otherwise particularly well expressed, shows pronounced dorsiventrality in riverside trees (Fig. 75E). In Aubréville's model, where plagiotropy is inherent, for it forms part of the definition of the model, the river-bank effect stimulates the development of supplementary branch modules towards the outside of the crown. This can easily be seen in *Terminalia catappa* grown as a decorative tree.

Even in the forest itself, the river-bank effect is present at least in parts of the crowns of most trees at some time or another, if not repeatedly, where they find themselves adjacent to gaps or chablis[15], or next to human settlements, roads or other interruptions of the forest. It is likely that many forest trees cannot reach the higher regions of the forest without receiving some light laterally. Forest trees do not grow straight up, their crowns zigzag to higher levels. The sinuous course of the crown in its upward growth may even be reflected in trunk shape, as suggested by OLIVER (1975) for red oak (*Quercus rubra*) in Massachusetts. The frequency of chablis in determining the ever-changing mosaic of succession in tropical forests is particularly significant where macroclimatic and geological catastrophes like hurricanes and earthquakes are rare and where disturbance is minimal. This is certainly the case in French Guiana where probably less than 40% of forests are in old and well structured stages, a proportion which can be measured on analytical transects such as "Mt Galbao" (OLDEMAN, unpublished). This situation should be contrasted with that in the western Pacific, where cyclones are frequent and catastrophic disturbances of varying intensity play a large part in forest succession (WHITMORE, 1974).

Free-standing and forest trees thus represent two extreme ways in which reiter-

Fig. 76a–f. Forest clearing, showing form of ▷ trees which can be understood according to the reiteration processes, Orapú River, French Guiana. *From left to right: a* broken fluted trunk; *b* foreground, abundant reiteration with loss of synchrony of reiterated complexes; note the lianes on the trunk of this tree with their large leaf mass just below the leafy crown; *c* immediately behind, a flat-topped crown with reiteration according to the river-bank effect; *d* asymmetric leafless crown; *e* large tree in the foreground with abundant reiteration; *f* medium-sized tree with a bayonet-joint (*arrow*) in the trunk, the newly developed rounded crown above the remains of an old one, its regular shape suggesting model conformity

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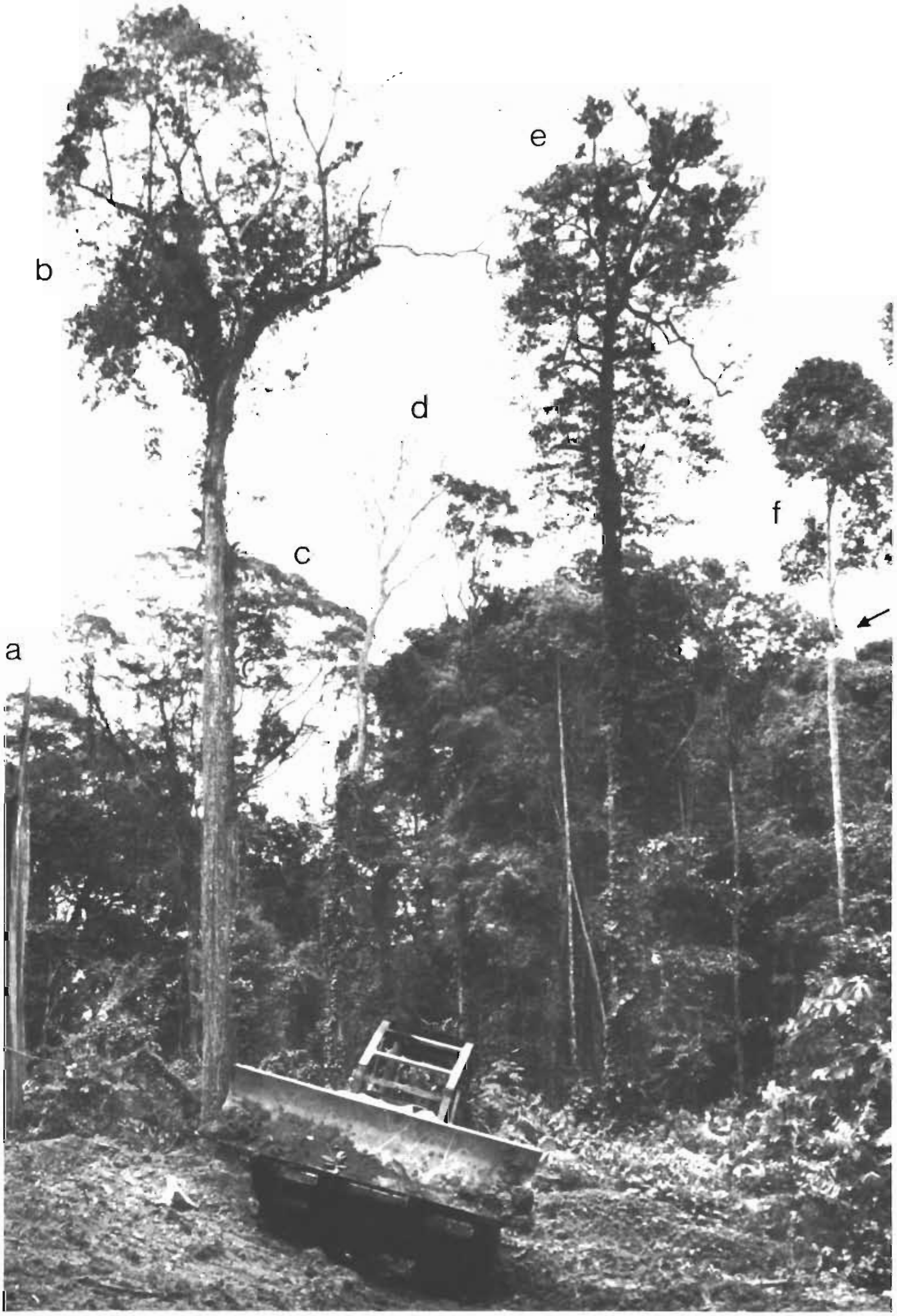
[15] "Chablis" is a convenient but untranslatable term of long usage by French foresters. It means the fall of a tree in itself as well as the resulting situation in the forest, a light-admitting gap in the canopy, the piled-up debris on the soil, and the surviving, more or less damaged trees of all sizes (see p. 368).


a
b
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ation determines the development of a tree. Other intermediate possibilities exist, depending on the ecological circumstances and the capacity of more or less profuse reiteration of the tree. The *constant* feature in this developmental process is the inherited architectural model.

If the analysis of tree form is therefore approached with the twin concepts of architecture and reiteration at hand, the observer is presented with powerful techniques which admit a qualitative interpretation of the overall physiognomy of the tree. This is evident in Figure 76 where a clearing of the undergrowth has exposed several trees, at different stages of development (a process to be discussed in further detail later). Here their shapes (a–f) can be readily interpreted in terms of reiteration complexes. In contrast, Figure 77 shows the forest margin from the river. The canopy comes down to the water's edge due to pronounced horizontal extension of branches, via the riverbank effect. The old emergent specimen of *Vochysia* behind has a much reiterated crown with nonsynchronous behavior of the different complexes.

Reiteration, in fact, goes a long way to account for the nonsynchronous behavior of the crown of certain tropical trees frequently commented upon (e.g., LONGMAN and JENÍK, 1974, p. 144), where different parts, at any one time, may be in different stages of development, most strikingly illustrated by leaf flush, senescence or loss, or nonsynchrony in flowering and fruiting. This is well shown in Figure 78 which obviously represents a much reiterated tree with complexes variously flushing, flowering or with mature foliage. If such events are determined primarily by endogenous rhythms it is not surprising that successive reiterated models could get out of step with each other, either progressively or abruptly, and show striking lack of synchrony. A careful analysis of such a nonsynchronous tree crown, in architectural terms, would obviously be needed to substantiate our suggestion. The process is capable of being overridden by climatic influence. SCHULZ (1960) has indicated that flowering in *Tabebuia serratifolia*, the tree illustrated in Figure 78, is promoted by water stress. However, as we will see later, water stress can also be different from one reiterated complex to the next, by the effects of unequal distribution of sap streams inside the whole tree.

B. Energetics

I. Trees in Their Environment

1. Energy Exchange

The preceding section on reiteration has broached the topic of vigor and energy distribution within the tree, together with that of energy exchange between trees and their environment. The former approach is essentially that adopted by SHINOZAKI et al. (1964) in their analyses of trees according to the pipe model theory. Mathematical models by ODUM and PIGEON (1972) also consider the interaction between trees and their environment in terms of energetics. However, in these publications energy flows are not linked to the architecture of the tree.

Fig. 77. Oyapock River, Ilets Yacarescin, French ▷ Guiana, showing in the foreground the canopy coming down to the water's edge via the riverbank effect. The large, old tree in the background (*Vochysia* sp., Vochysiaceae, probably Massart's model) shows a much reiterated crown with nonsynchronous behavior of the reiterated complexes

We now need to consider both aspects, one physiological, the other ecological, in order to obtain insight into the way in which tree architecture controls basic patterns of mass distribution and mass energy flow. The situation is self-regulating in the sense that architecture functionally balances and expresses with great accuracy internal and external levels of energy and in so doing determines the way in which the subsequent architectural stage is built. Our object is to present an integrated picture. This contrasts with the more usual approach where individual topics are treated in isolation, for instance physiologists have considered water transport or nutrient translocation, or respiration, or photosynthesis, each apart; ecologists and foresters, on the other hand, have concerned themselves with biomass production, canopy structure, age distribution and floristic diversity. Where an attempt is made to link topics, as CARLQUIST (1975) does with xylem specialization, water transport and ecology, a synthetic air of completeness may be generated, but essentially this is the sum of different specialized data. Our attitude *begins* with an overall image, of which all these subjects are aspects, although for the time being we omit reproductive processes (flowering, fruiting and seed set) for purposes of simplification. This use of topics as analytical criteria is analagous to the way in which the study of the architecture of whole trees borrows analytical criteria from descriptive organ morphology. Our approach is primarily qualitative since there is little available information which quantifies the approach we adopt.

2. *Energetic Efficiency*

Surface area and volume of a tree are well adjusted to each other, the former reflecting exchange capacity of the tree with its environment, the latter representing the medium of internal redistribution of energy resources made available to the tree. Each architectural model represents a solution to the equilibrium problem so posed. In evolutionary terms selection pressures will have worked towards an efficient solution to these problems in a given set of environmental circumstances. Since diverse anatomical and morphological combinations may be accommodated within a single model, there can be alternative ways of achieving this equilibrium. Tree ferns, monocotyledonous trees and woody dicotyledons present different solutions to the problem of internal transport because their stem anatomy is so different. Nevertheless representation of each anatomical group may occur within one architectural model (e.g., Corner's model). Similarly gymnospermous needle leaves, monocotyledonous megaphylls and the mesophylls of dicotyledons can occur on different trees representing the same model (e.g., Stone's model). Accidental defoliation of a tree, as by a hurricane or by chemical defoliants, which is lethal, indicates an extreme upset of the normal equilibrium. In normally deciduous trees the leafless state is not lethal because changes in transport capacity and leaf shedding are temporary and synchronized.

In establishing an energetic balance, and not only establishing it but maintaining it during active growth, the tree is governed by the simple physical rules which determine relative changes in vol-

Fig. 78. Tabebuia serratifolia (Bignoniaceae, Koriba's model), Cayenne, French Guiana, a much reiterated tree in a private garden. This shows complete nonsynchrony of reiterated complexes, with both flowering, early flush and late flush complexes

ume and area. These relations have, of course, long been of interest to biologists (e.g., THOMPSON, 1917).

Internal redistribution is a function of fluid mechanics and so depends on volume, exchange with the environment depends on the limits of surfaces and is measurable in terms of areas. Volume growth is a third-degree function and surface extension is a second-degree function. We can consider the changing relations of these functions in terms of a uniform cylinder by which we represent a tree trunk, but similar considerations apply for any simple shape, a cone or a sphere. We might consider then the cambium as a surface (in this instance a producing and not an exchanging surface) in contrast to the volume of the wood it produces. The volume (V) and surface (S) of a cylinder are expressed by the formulas

$$V = \pi R^2 h \qquad \text{and} \qquad S = 2\pi R h$$

in which R is the radius and h the height. In a cylindrical growing organ, R and h change, but of course remain the same in the two functions, of which the comparison then becomes:

$$\frac{V}{R} = \frac{\pi \cdot R^2 \cdot h}{2\pi \cdot R \cdot h} = \frac{R^2}{2R}.$$

The functions $f_s(R) = 2 \cdot R$ and $f_v(R) = R^2$ are represented graphically in Figure 79. The vascular cambium must have an inherent limit to its ability to produce tissue. At first, increased nutrient input results in increased output of derivatives, but beyond a limiting threshold, the value of which depends on the organization of the cambium initials, the cambium is unable to react to an increased nutrient supply (Fig. 79, inset). The production of the cambium at that moment represents its intrinsic maximal performance (in $cm^3/cm^2/h$), which can be called M, a value varying from species to species. Once this limit is reached by a cambial cylinder of given diameter biomass production is also limited according to the function $F'_v(R) = 2R + M$. If the surface area changes so that it is no longer that of a cylinder, the impasse may be partially surmounted, and this occurs in fluted, buttressed or fenestrated trunks. We have commented on the frequency of fluted trunks in tropical American trees which conform to Massart's and Nozeran's models and illustrate this here with the striking example of *Minquartia quianensis* (Fig. 80). In general these species are rather slow-growing, with hard wood and stem diameters narrow in proportion to their height, suggesting that the "M-factor" in cambial activity would be low. We have here a hint of the correlation between bioenergetics and architecture.

However, fenestrated trunks are rare even in tropical trees and buttresses are usually limited to the base of the tree (Fig. 81). They are also most characteristic of trees in tropical lowland swamp forest. SMITH (1972) in discussing this problem has provided a descriptive model for the accurate estimation of surface area and enclosed volume of buttressed tree bases which, in principe, treats the trunk as an inverted frustum of a right circular cone and the buttresses as prisms. Using this model he found in measured trees that the surface area of the buttressed base was from three to nine times greater than in a hypothetical cylindrical base, i.e., if the base of the same tree were cylindrical and not buttressed. He suggests that buttressing is absent from temperate trees because they have a negative selective value in stressed climates. His hypotheses imply that energy exchange factors are part of the advantages of buttressing, but he points out that testable data are, as yet, unavailable.

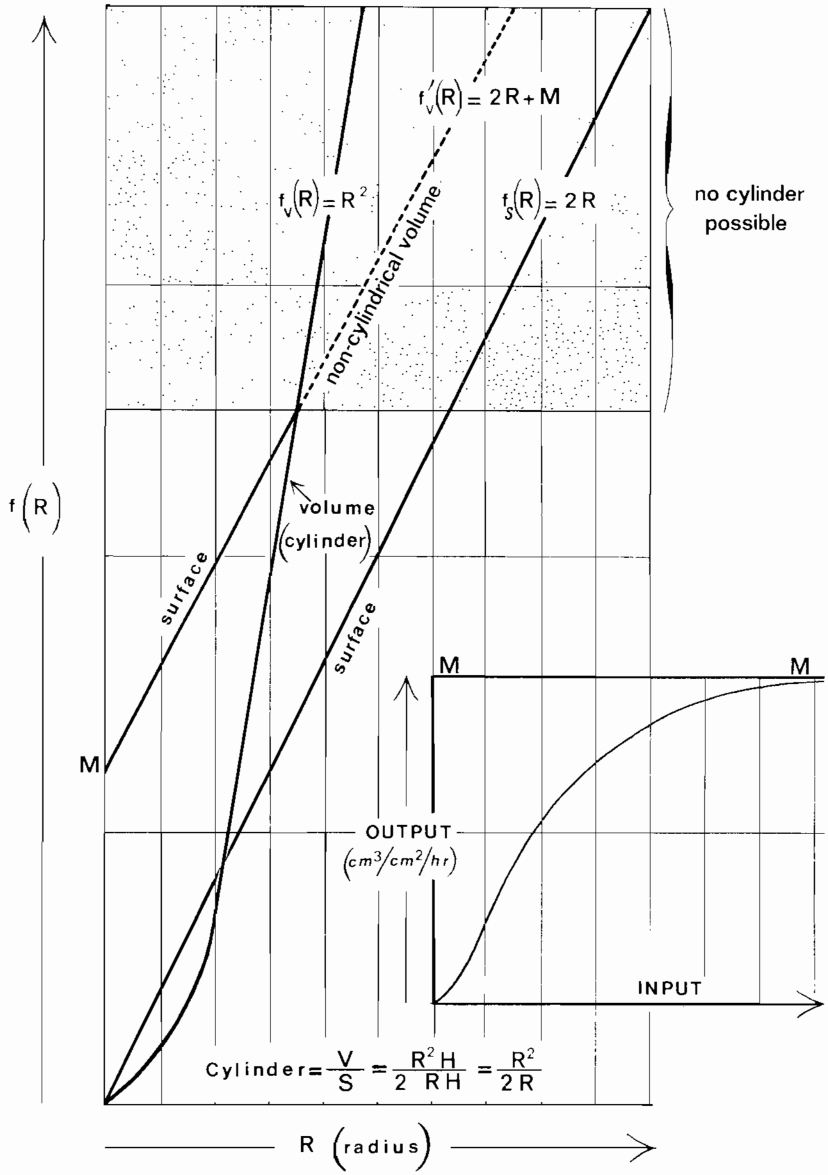


Fig. 79. Surface–volume relations in cylinders indicating the way in which factors depending on surface area (f_s) and volume (f_v) are related by geometrical considerations. M: maximum capacity for production ($cm^3 \cdot cm^{-2} \cdot h^{-1}$). Beyond a certain radius, determined by M, the biological production of a cylinder becomes impossible and form changes (*shadowed part*). *Inset:* the relation between energetic input (calories, lux, ergs, HP) and productive output (volume, mass) is always asymptotic, the asymptote determing M. Further explanation in the text

Volume–surface relationships enter into a consideration of branching, whether this be within the model, or as a result of reiteration. Both effect the equilibrium within the trunk and crown, effectively substituting many narrow cylinders for one wide one. It will be of interest to examine more carefully the development of the tree, in architectural terms, and the initiation of buttresses. If there is any correlation one would expect to find buttresses to be largest and most frequent in reiterated trees. Preliminary, but very incomplete data from French Guiana suggest that this is so. The vertical localization of transport channels could be an important factor in buttress development. In ring-porous trees ZIMMERMANN and BROWN (1971, p. 172) indicate that it may be possible to kill a limb by interrupting xylem and phloem in a peripheral sector of the trunk since water movement is axial. A knowledge of the orientation and degree of interlinkage between vessels is evidently important – here morphology and physiology are closely interdependent. Dye injection gives preliminary information.

In leafy shoots the volume–surface relationships involve a trade-off between capturing light and losing moisture. Here the exchange equilibrium must be optimized, mediated by the stomatal mechanism. Dorsiventrality of branch systems is the morphological expression of this relationship with the highest efficiency achieved in leaves, but probably also in those models with fixed plagiotropy of their branches. Here volume is minimized by the limited cambial activity indicated by NOZERAN et al. (1971), and in the most specialized instances (Cook's model) the branch itself is relatively short-lived.

Analogies may be sought in some pneumatophore-bearing root systems which are architecturally dorsiventral and simultaneously promote gas exchange and liquid absorption in the oxygen-rich surface layers of otherwise anaerobic substrates (TROLL and DRAGENDORFF, 1931).

From these introductory remarks we can appreciate that the problems of surface–volume relationships are geometrical and clearly in the province of architecture. We shall now try and analyze some of these geometrical problems in terms of the different architectures we encounter in tropical forests.

3. Energetic Economy in Whole Architecture

We have suggested that the integration between surface and volume takes place within the totality of the tree's architecture, whether the tree is conforming to its model or undergoing reiteration. Branching represents a redistribution of volume production so that every branch, whether it is produced sequentially or by reiteration, represents a regression or downward displacement along the theoretical curves shown in Figure 79. The displacement can be thought of as a move to a "younger" level. Sequential branching, i.e., that within the model represents a standard response to a narrow range of optimal conditions, reiteration is a more opportunistic response to a greater diversity of conditions. Differentiation of branches is the most specialized solution to the problem of energy exchange. Plagiotropic branches are specialized for photoassimilation and sexual reproduction, the trunk is the organ for mechanical support and transport. The model, recog-

Fig. 80. Minquartia guianensis Aubl. ("méquoi", Olacaceae; Nozeran's model). Extreme example of a fluted trunk, in places one can see completely through the center of the tree ▷

nizable by its architectural phases, represents a specific inherited solution to the integration of surface and volume production. The process of adjustment of overall architecture to the local, changing conditions encountered by the tree no longer involves the number and size of organs inside the model but the number and size of reiterated models in the tree.

In some models the differentiation sequence is such that trunk and branch are not well defined (e.g., Troll's model), the model is "vague" and it is not always easy to distinguish a sequential branch from a reiterated complex. This can occur also in models with diffuse branching (e.g., Attims' model) since the position and number of orthotropic axes in the system is in no way fixed, and because the differentiation between trunk and branch is often easily reversible.

One can suggest that the energy exchange requirements are somewhat different for orthotropic axes, i.e., with a maximizing of volume production for support and conduction compared with plagiotropic axes with an emphasis on surface production. If this is so, then obviously architectural analysis is a necessary preliminary to a study of energetics. One can appreciate this contrast in the examples of Attims' model (e.g., *Rhizophora*) where plagiotropy is imitated by orthotropic axes in the periphery of the crown (Fig. 12A, B). One feature of this process is the overall decrease in internode length, a measure of the decrease in volume of the branch system. Concurrently, the relative amount of leaf area is increased. However, the architectural model alone does not permit a too rigorous application of such principles to energetic analysis, since it gives a clearly useful outline but still tolerates a considerable degree of variation as we have described. The object here is to suggest approaches which might be adopted.

The discussion so far has centered on trees with secondary thickening, but the meristematic features common to all trees can be viewed in very simple terms of "transfer of functions". Apical meristems produce leaves; the cambial system of trees with secondary thickening is an extension of or delegation of the "mass-producing" function of such a meristem. In palms and tree ferns, the apical meristem gradually organizes the capacity for "mass-production" during establishment growth of the seedling and the two functions of surface and volume growth are subsequently combined in the massive meristematic crown.

4. Spatial Disposition of Surface in Tree Crowns

The overall shapes of tree crowns are reflected in the terms used to describe them, as round, cylindrical, umbrella-shaped, weeping, etc. (e.g., Bremekamp, 1936; Corner, 1952; Sarlin, 1954).

In our models the disposition of all the leaves together can be reduced to rather simple overall stereometrical surfaces. We suggest that these overall surfaces, built by one model or another, represent all geometrical possibilities compatible with biological means of construction. Crown shapes in palms are very easily reduced to rotation surfaces and Figure 82 represents some of these as funnels, spheres, hemispheres and discs. The funnel shape (Fig. 82A) formed by the leaf mosaic is most often found in the forest (e.g., *Astrocaryum*, *Manicaria*), the spherical or hemispherical occurs most often in palms growing in open biotopes (e.g., date palm, *Washingtonia*, oil palm) and is particularly characteristic of fan-palms. The umbrella shape (Fig. 82B), well-represented by many arecoid palms, is an intermediate type. A flat disc (Fig. 82C) occurs in a

Fig. 81. Large buttressed trees in forest plot with undergrowth cleared. Plateau de la Douane, Saül, French Guiana. *Background: Terminalia amazonia*; *foreground: Enterolobium* sp. *Scale:* bent-over man to the right of *Terminalia*'s base

number of forest palms (e.g., *Iriartea* sp.) and is a modification of the funnel.

Some dicotyledons with orthotropic axes and large peltate leaves also produce the spherical or hemispherical surface (Fig. 82D) as in *Schefflera* (*Didymopanax*) *morototoni*. In the same family (Araliaceae) simple variations of this are the cylindrical (Fig. 82F) and flat-topped (Fig. 82E) crown. These shapes may be seen as a unit of construction in branched trees. A funnel-shaped crown (Fig. 82G) can be seen in dicotyledons with large, elongated leaves, e.g., *Clavija* (Theophrastaceae). We can continue this analysis of models as expressions of the compromise between surface volume ratios and recognize other shapes: cones, spiral bands and folded laminar surfaces (Fig. 82H). Combining these, the regularly tiered or continuously branching tree models can be represented as a series of superimposed discs, circles, inverted cones, or a spiral band (Fig. 82 I K).

We can combine the elements of the pipe model theory of tree form developed by SHINOZAKI et al. (1964) to interpret further the variety of constructional compromises effected by tree models. This theory interprets the plant in terms of *unit* *pipes* of stem or branch tissue, each supporting a unit amount of photosynthetic organs. The theory is based on the observation that the amount of leaves existing above a certain horizontal level in a plant community was always proportional to the sum of the cross-sectional area of the stems and branches found at that level. In plagiotropic branches the pipe system demands a limited amount of secondary thickening, minimal in phyllomorphic branches which are determinate in space and time. In trees with this kind of branch (models of Nozeran, Roux, Massart) there are as many big pipes as there are branches and an abrupt change in diameter from branch to trunk. The assimilating surfaces in such a system are clearly in contrast with orthotropic systems. A further contrast is provided by wholly plagiotropic models, such as in Troll's model where a gradual volume increase of pipe systems from twig towards trunk occurs, without abrupt diameter changes at the points of branching, so that the whole tree sometimes acquires the overall form of a leaf, as in *Annona paludosa* (cf. Fig. 82H).

These overall surfaces by which the models can be represented are all rotation surfaces (in Troll's model the rotation is not complete). No systematic treatment of these surfaces is here attempted or intended, but we suggest that further detailed analysis, for instance along the lines suggested by STEVENS (1974), is likely to demonstrate that trees realize all possible rotation surfaces within the limits set by their surface/volume relationships. The best treatment of this problem in terms of photosynthetic efficiency is that of HORN (1971) who has shown that in temperate trees (mainly Rauh's model) the average light intercepted over the day by a tree is proportional to its peripheral surface. He distinguishes two types (monolayer and multilayer) according to the distribution of leaves within the crown, which is shown to be important in successional interaction (HORN, 1975).

5. *Height-Diameter Relationship in Trees*

It is of interest to see if there is any fixed relation between parameters by which surface and volume can be expressed and which can be measured easily. For trees, one of the simplest relationships is between height (H) and diameter (d) and this has been considered by several workers with different approaches (e.g., SCHULZ, 1960; ATTIWILL, 1962; BERLYN, 1962; COBBLE, 1971). The basic interest is in developing models by means of which one easily measured parameter can be used to estimate values less easily obtained, for example what can a measurement of the diameter of a trunk or branch tell of the biomass or leaf surface it supports. This is one of the objectives of the pipe model theory (SHINOZAKI et al., 1964). Engineers have provided particularly useful analyses in their assessment

Fig. 82A–K. Spatial distribution of surface in tree crowns, represented as different kinds of rotation surfaces and planes. ▷

A–C The crown of palms represented as a funnel *A*, umbrella-shape *B* or a more or less flattened disc *C*.

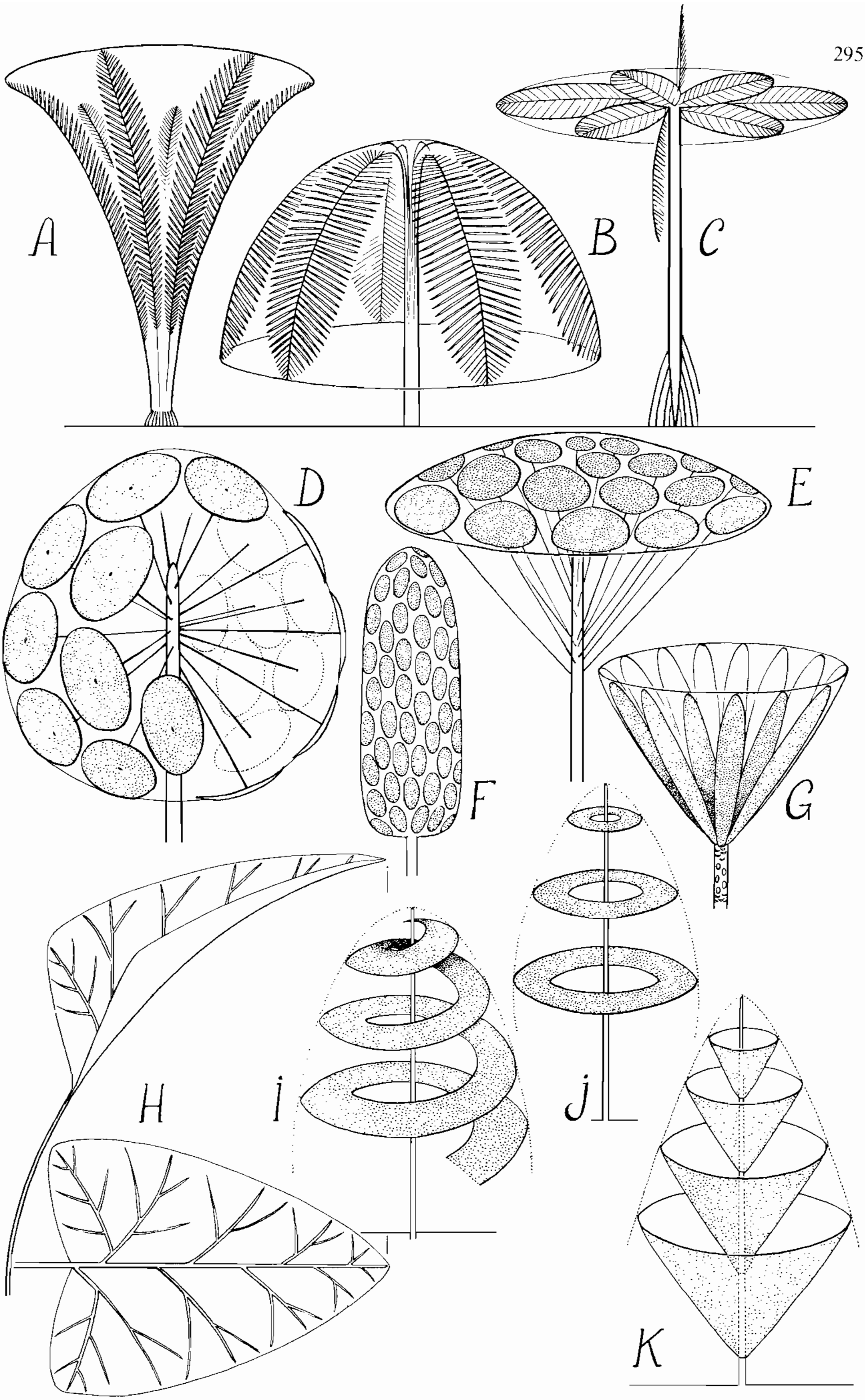
D–F Crown shape in dicotyledons with orthotropic axes and large peltate leaves representing a sphere or hemisphere *D*, flat-topped disc *E* and cylinder *F*.

G Funnel-shaped crown in a dicotyledon with large leaves.

H A folded laminar surface, representing the whole tree crown (e.g., certain examples of Troll's model, in early development) or a single plagiotropic branch complex.

I Crown shape in tree with continuous branching represented as a spiral band.

J and *K* A series of superposed disks *J* or funnels *K* characterizes branch tiers in models with rhythmic plagiotropic branches


A
B
C
D
E
F
G
H
I
J
K

of the elastic properties of trees (e.g., McMahon, 1973) and have established a power law relationship which is expressed simply as $d = K_2 \cdot H^{3/2}$, where trunk diameter at a standard height has been plotted for known trees, as in Figure 83 which represents primarily values for 576 champion trees of the United States taken from the American Forestry Association's records. In principle, this means that trees become proportionally broader as they increase in height, a principle also revealed by Kira (1978). The values obtained are always less than the proportions which calculation shows would lead to buckling, as of course would be expected (Fig. 83). However, these values relate to the maximum stature of trees presumably of considerable age, and probably in most cases much reiterated and having reached a steady state. What is the circumstance throughout the entire life-span of the tree, from sapling to maturity?—especially if mechanical constraints are not necessarily limiting factors.

In making forest inventories on the basis of ecological plots, some of which will be described later, and in making inventories of model-conforming trees for H.O. (1970), a useful empirical rule was established: the relationship $H = 100d$ was expressed fairly constantly for model-conforming trees where d is measured above the influence of any pronounced root buttresses. That this rule of thumb only concerns the model is shown by Fig-

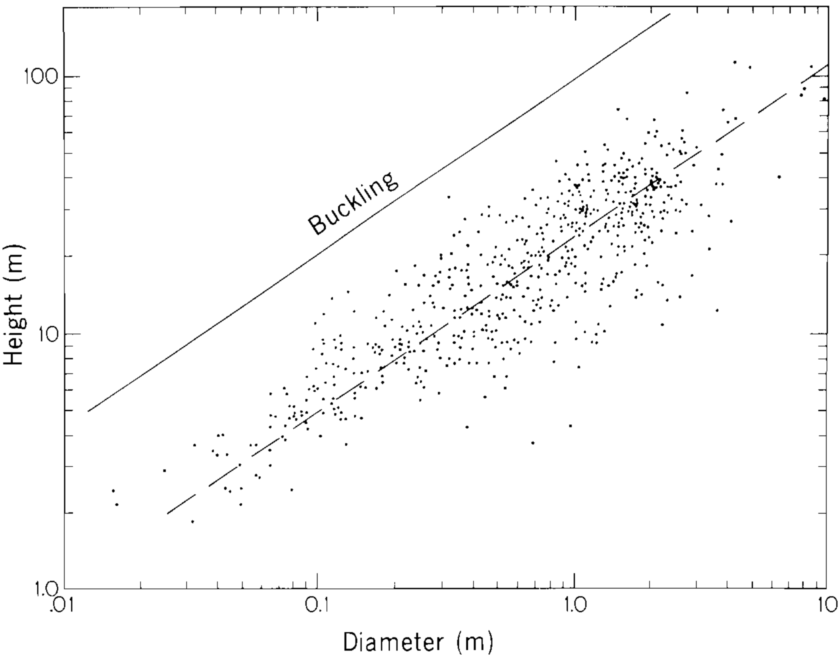


Fig. 83. Log overall height vs. log base diameter of 576 record trees representing nearly every species found in the United States (from McMahon, 1973). This is used to demonstrate that trunk proportions are limited by elastic buckling criteria, since no points lie to the left of the solid line which represents calculated limiting values for uniform wooden cylinders loaded under their own weight

ure 83, since most points fall well below the line $H = 100d$, but we must emphasize again that these are adult, steady state trees. The highest tree on this figure which shows $H = 100d$ is a little over 30 m high; all others are smaller.

We have accepted the empirically obtained simple relationship between tree height and trunk diameter as being an expression of harmonious relationships within the model. On this basis, deviations from it can be used as a crude measure of deviations from the model. Again empirical observations of the following relationships seem constant, and are also intuitively acceptable:

$H > 100d$ when the tree has effected pronounced trunk regeneration by reiteration. The excess of height is produced by the distal establishment of a new model.

$H < 100d$ when the tree has entered a phase of profuse reiteration which eventually ends with herbaceous reiteration. An example would be the trees illustrated at (b) or (e) in Figure 76. There may be little or no increase in height, although trunk thickening continues. This represents the relationship expressed by the power law and evaluated in terms of mechanical stress. It is also the normal relationship found in forest trees in the canopy which rarely conform to their model very long into adult life.

Figure 84A, B represents actual shapes for H/d relationships for two species (*Quararibea turbinata*, Fagerlind's model and *Croton* sp., Koriba's model) based on measurements obtained in French Guiana (after OLDEMAN, 1974a).

In this and other examples trees still conforming to their model may show a height exceeding a hundred times their basal diameter, i.e., in a manner suggestive of regeneration. Morphological analysis may explain this as when, for example, either (a) "bayonet-joints" within the model resemble those developed through reiteration, as is most evident in Chamberlain's model (e.g., *Talisia* spp., Sapindaceae) or (b) the tree is growing in an ecological chimney, i.e., a narrow funnel or cylinder under a slight gap in the canopy through which the light energy level is raised, but is insufficient to trigger reiteration. Under the last circumstance trees may be released from suppression, but continue to grow slowly and conserve a narrow crown which, in terms of the necessary sap supply, does not demand a stem of very wide diameter.

For trees grown in the open, the general shape of the H/d relationship is such that the onset of the phase in which $H < 100d$ occurs is at much lower heights (Fig. 84C, R_1) compared with forest-grown individuals (Fig. 84C, R_2). This confirms our qualitative contrast of trees in closed and open communities which was expressed earlier. A broken tree might be expected to go through a cycle of development represented in Figure 84D.

Graphs in the ecological literature which represent the changing proportions of plant parts and between plant parts with age, sometimes give evidence of changes occurring in a way which could easily be linked to the changes in H/d relationship here described (OLDEMAN, 1974a).

6. *Flexibility and Rigidity in Volume-Surface Integration*

The problem of energy interchange in trees can be simplified by considering the tree as a system in which as large a surface as possible must be irrigated with the minimum production of volume,while at the same time guaranteeing the evacuation of absorbed energy (in the form of chemical bonds in assimilates) towards other parts of the plant.

The enormous variety in leaf forms and dimensions shows the biological diversity which these constraints still permit; these are discussed on the basis of sharply contrasted examples (Fig. 85). Plants, like palms with rigid volume-producing patterns, cannot reiterate. Such plants either remain vegetatively unbranched (Corner's and Holttum's models) or branch sequentially in very restricted and stereotyped ways (Tomlinson's model). In the last example branches acquire energetic autonomy by the formation of adventitious roots and the result is essentially clonal production of separate trunks. These physiological problems were discussed earlier when trees without secondary thickening were described. The photosynthetic unit of such plants is invariably large so that rigid surface production, in the form of regular unfolding of megaphylls, goes well with rigidly programed volume production with fixed numbers of meristems and a constant vascular system (Fig. 85 B). In some dicotyledons with megaphylls this rigidity is reflected in peculiar vascular development, *Carica papaya* (Corner's model) providing a familiar example. Otherwise in megaphyllous trees with a more standard secondary vascular anatomy the flexibility is seen to increase with age. *Carapa guianensis* and many related Meliaceae show gigantic leaves in the monocaulous juvenile stage, with decreasing leaf size when branching is initiated, in accordance with Corner's rules (p. 81). In a few compound leaves there is a degree of internal adjustment provided by periodic extension of the leaf axis, as in species of *Guarea*, *Chisocheton* (Meliaceae) and *Sclerolobium* [(Caesalpinioideae); Fig. 4]. From these few observations the relationship between branching and leaf dimensions which has been commented upon in various parts of this book can now be seen from the viewpoint of harmonization of volume and surface. Leptocaul trees with small leaves are more elastic than monocaul or pachycaul trees with large leaves. This is only true, however, up to a certain point where leaves become so small that their surface is but little different from that of small axes with the same volume, e.g., needle-units. The rapid organization of large numbers of meristems which would be needed to adjust a photosynthetic surface consisting of huge numbers of needle leaves to abruptly increased light energy levels would be inefficient. Flexibility would eventually be lost if leaf size were reduced below a certain level.

In gymnosperms cambial activity is harmonized to the slow cadence of surface increase, because it is geared to the production of narrow, short and uniform transport units, the tracheids, with a relatively large volume of wood functioning in water transport (Braun, 1963, 1970). In a typical gymnosperm both the vascular cambium and the apical meristems have to undergo a long and vigorous period of growth in order to produce simultaneously an equally substantial increase in axial transport capacity and photoassimilating area (Fig. 85 C). The ring-porous tree is the extreme converse, since it produces each year the whole of its water transport system very rapidly in relation to a rapid expansion of assimilating surface. The gymnosperm stresses safety in its surface/volume relationships, the ring-porous tree sacrifices safety in favor of efficiency (Zimmermann, 1978). The assimilating surface of most gymnosperms is long-lived, growth is steady, regular but unelastic. We probably have here an element of explanation of the quite usual "model conformity" of conifers (cf. Massart's model). From the energetic viewpoint, it is not surprising that in many gymnosperms needles are concentrated on short shoots in which formation of stem tissue (volume production) is mi-

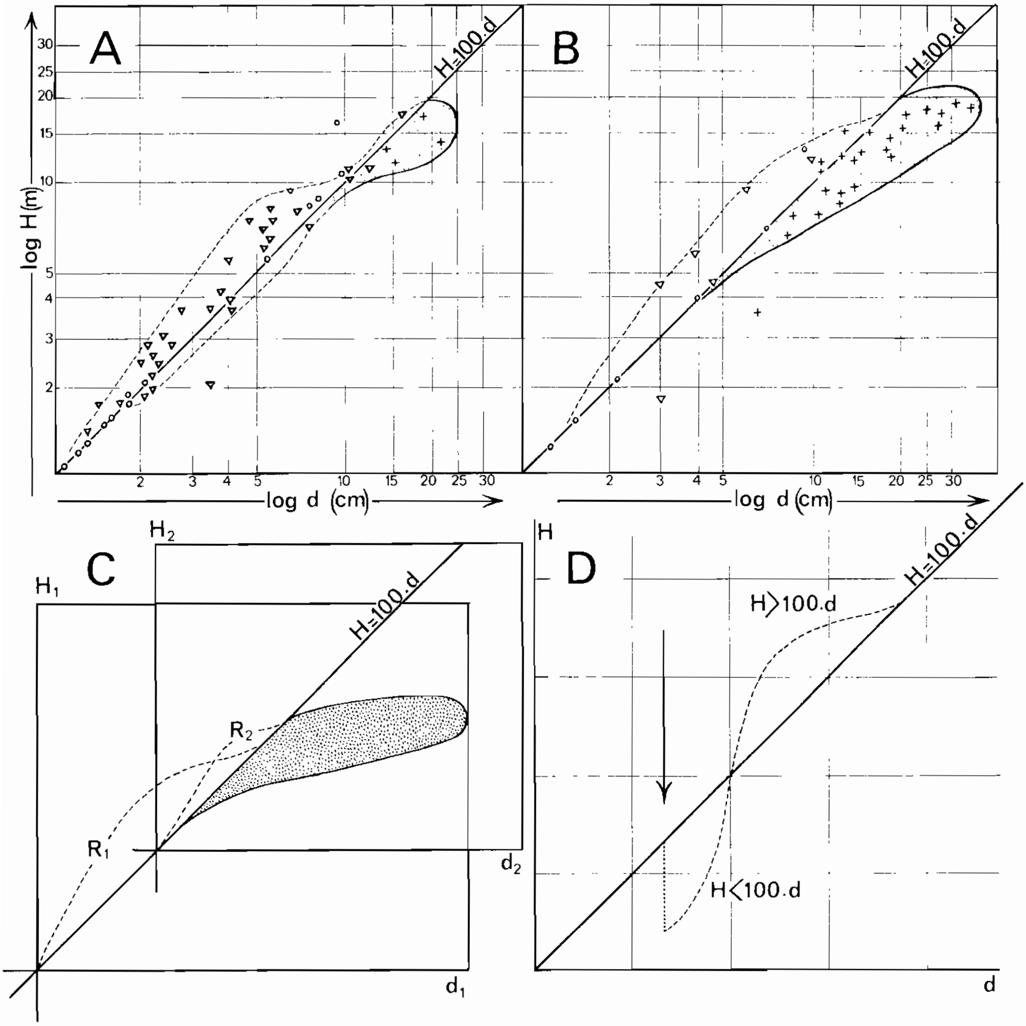


Fig. 84A–D. Relation between height (H) and basal diameter (d) from field measurements of

A *Quararibea turbinata* (Bombacaceae, Fagerlind's model).

B *Croton* sp. (Euphorbiaceae, Koriba's model). *Circles*, trees conforming precisely to the model; *triangles*, trees showing early regeneration by reiteration (trunk axes); *crosses*, trees showing abundant ("herbaceous") reiteration.

C Suggested height-diameter (H/d) relationship of an open-grown (R_2) compared with a forest-grown tree (R_1) to reflect the differing times at which reiteration is expressed. The shaded area to the right of the line H = 100d reflects the power-law relationship shown by adult trees (cf. Fig. 79).

D Suggested changes in H/d relationship during regeneration of a broken tree, showing fluctuation in relation to the line H = 100d.

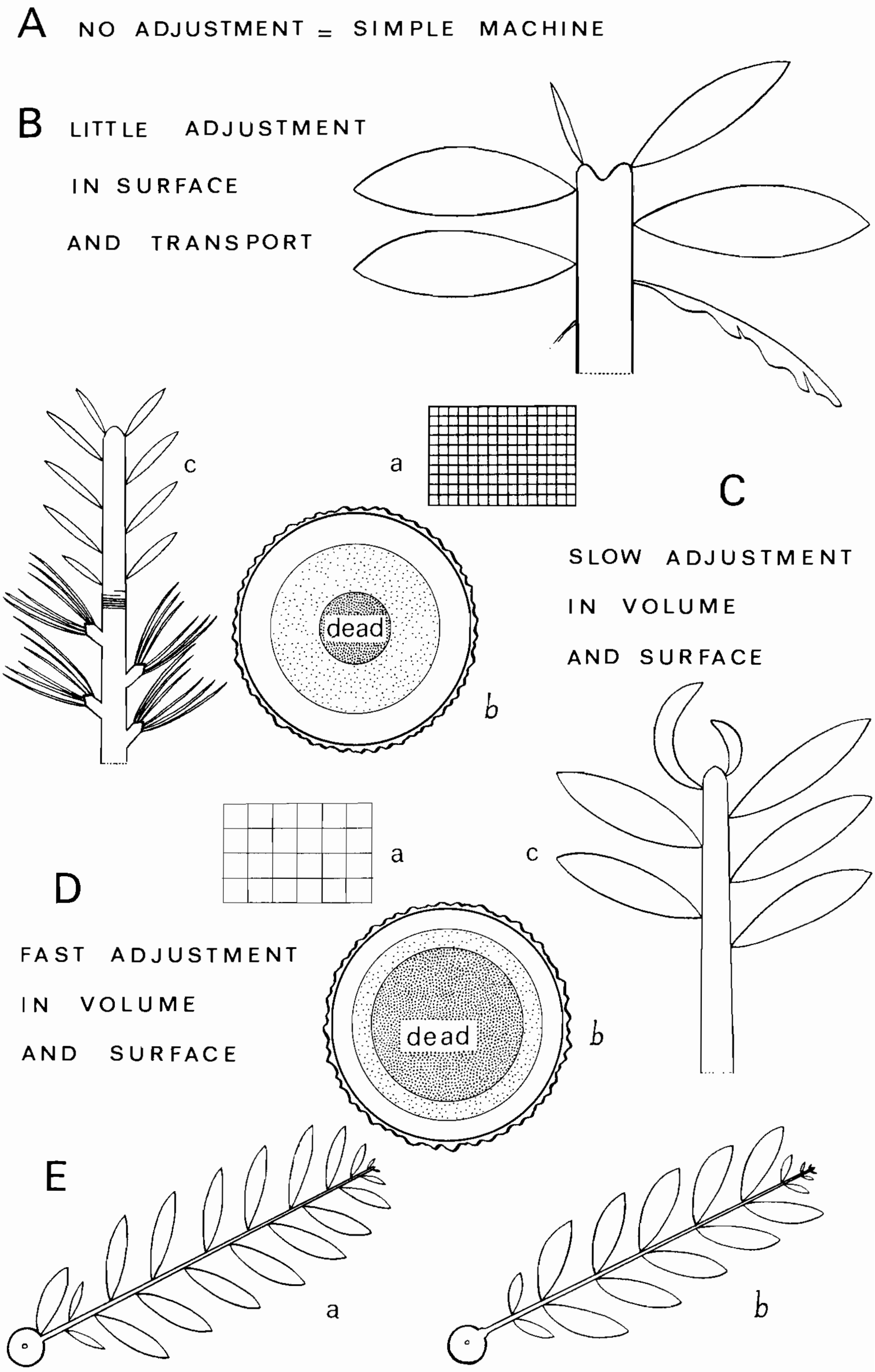
A–C After OLDEMAN (1974a)

nimal. It is surely no accident that the rare deciduous gymnosperms in which there is a total and synchronous shedding of needles or leaves either have the leaves clustered in short shoots (*Larix*, *Pseudolarix*, *Ginkgo*), or shed units larger than single needles (*Taxodium*, *Metasequoia*). Conversely the only mesophytic gymnosperms with vessels are broad-leaved (*Gnetum*) and admit the scandent-habit. Tropical gymnosperms tend to be broad-leaved (*Agathis*, *Podocarpus*) and have wide tracheids (CARLQUIST, 1975). Tropical pines produce multiple tiers of branches in a single year, indicative of their greater plasticity. The conifers tend to be more successful than broad-leaved trees at high altitudes and latitudes, where short conducting elements (which localize embolism) and a minimized assimilating surface have selective advantages. This is not the place to discuss these considerations in detail, but the nonuniform distribution of trees bearing different kinds of leaf is surely capable of explanation in terms of the topics we have raised. The subject is discussed in ZIMMERMANN and BROWN (1971) and ZIMMERMANN (1978).

The intermediate condition represented by broad-leaved dicotyledonous trees with some degree of branching in their aerial architecture is an effective compromise. Their construction and adaptability allows for rapid adjustment in volume and surface (Fig. 85D). In tropical trees regulation of crown assimilation is reached largely by variation in the growth rate of apical meristems. Reiteration allows the tree to react to revolutionary changes in the environmental energy level. As we have seen, transformation of a certain "normal" amount of assimilated energy is taken care of in a preprogrammed way in the model. Under the lower limit of this normal amount pauperate forms (p. 310) show readjustment for survival; beyond the upper limit either resting meristems are mobilized or existing meristems adjust their activity so that the model reiterates. This architectural adjustment effectively reharmonizes volume/surface relationships and when the adjustment is rapid, maximum advantage can be taken of supplementary energy sources suddenly made available in a competitive environment. This rapid adjustment is only possible when leaves are large enough to allow the rapid extension of new assimilating surfaces, but small enough not to extend cambial activity beyond its maximal capability during the production of the anatomical units needed to serve the in-

Fig. 85A–E. Diagrammatic representation of flexibility in certain contrasted systems. >

- *A* A simple machine has no capability to regulate itself internally.
- *B* Pachycaulous, megaphyllous axis, as in a palm, little improvement on a simple machine because adjustment in surface area via increase in numbers of individually large leaves cannot be effected without major adjustment in stem volume (i.e., transport capacity), which is scarcely possible. Palms thus provide good examples of continuous uniform growth.
- *C* Gymnosperm such as *Pinus*; since the transport capacity involves large numbers of small units *a*, i.e., tracheids and a relatively large volume of functioning xylem *b* together with large numbers of small surface units *c*, i.e., needle leaves, whose integrated organization is complex, adjustment of surface-volume relationships can be effected only slowly.
- *D* Angiosperm has maximum flexibility since the transport units can be large *a*, i.e., vessels, the transport capacity is determined by a relatively narrow zone of functioning xylem *b*, and the surface units are of moderate size *c*. The ring-porous tree is the extreme example of rapid adjustment.
- *E* A phyllomorphic branch *a* and a compound leaf *b* with limited capability for growth to illustrate functional convergence in surface features of morphologically dissimilar organs with little capability for volume increase


A NO ADJUSTMENT = SIMPLE MACHINE
B LITTLE ADJUSTMENT
IN SURFACE
AND TRANSPORT
c
a
C
SLOW ADJUSTMENT
IN VOLUME
AND SURFACE
dead
b
a
c
D
FAST ADJUSTMENT
IN VOLUME
AND SURFACE
dead
b
E
a
b

creased area. The mesophyllous tree deals in moderate currency units so that it can handle sums of almost any size. Reiteration is the key to this process and its predominance in medium-leaved dicotyledonous trees should be contrasted with its infrequency in or even absence from many gymnosperms, woody monocotyledons and dicotyledonous weeds.

In tropical forest trees architecture can be used as an indicator of the previous "ecological" history of the tree and can also serve for the estimation of its potential for further development. The further extension of this process is then to assemble the history of the forest from an analysis of its individual units. This becomes the basis for our later discussion of the forest. In this section we have attempted to show how surface and volume are important when one talks about the relationship between architecture and energy exchange, i.e., the "usefulness" of certain architectures and the adaptive value of reiteration. Since we have involved ourselves in a discussion of biomass we must now consider in architectural terms how the tree functions in assembling its biomass.

II. Energy Exchange and Production

In general change in volume can be used as a measure of production, since its increase implies an increase in weight and changes in these values approximately run parallel to each other, whereas (wood) volume is often more easily measured in intact trees than weight. Where curves of one value are used to represent those of the other, this will be stated.

In order to obtain an overall picture of production in a tree (OLDEMAN, 1974a, Chap. 2), such an organism can be considered as consisting of three producing units; first, the leafy crown (plus young twigs, cf. PERRY, 1971) where photoassimilation takes place; second, the cambial cylinder where conducting tissues are produced; and third, the root system where metabolic processes, like synthesis of nitrogenous substances (cf. ZIMMERMANN and BROWN, 1971, p. 317) takes place. In the group of trees without secondary thickening the cambium is represented by the massive apical meristems. This very generalized model is represented in the form of an energy flow chart in Figure 86.

The term "energy flow" is used to refer to any transfer of any kind of energy between the tree and its environment or inside its body. The different forms of energy considered include radiant energy, such as is absorbed by leaves, the chemical bonds shifted by enzyme-triggered processes, and the direct transport or absorption of molecules bearing energy-rich bonds. Transformation of radiant energy and shifting of bonds occur in the three blocks (subsystems or cybernetic "black boxes") at the periphery of the circle and flow of energy-bearing molecules is represented by the arrows within it (Fig. 86). Arrows at the outside of the circle indicate exchange of biochemical and physical energy with the environment.

Increase or decrease of activity in any one subsystem provokes reciprocated changes in the others and results in a general amplification or decline of the whole system's activity. By this series of feedback mechanisms incorporated into the system, internal self-regulation is guaranteed. Every producing organ has an inherent maximum rate of performance which we already discussed for the cambium (p. 289). This upper limit in any one unit has the effect of a governor on the whole machine. Growth of the tree can be viewed as taking place in a series of steps, moving from one equilibrium level to another, but with increasing age of the

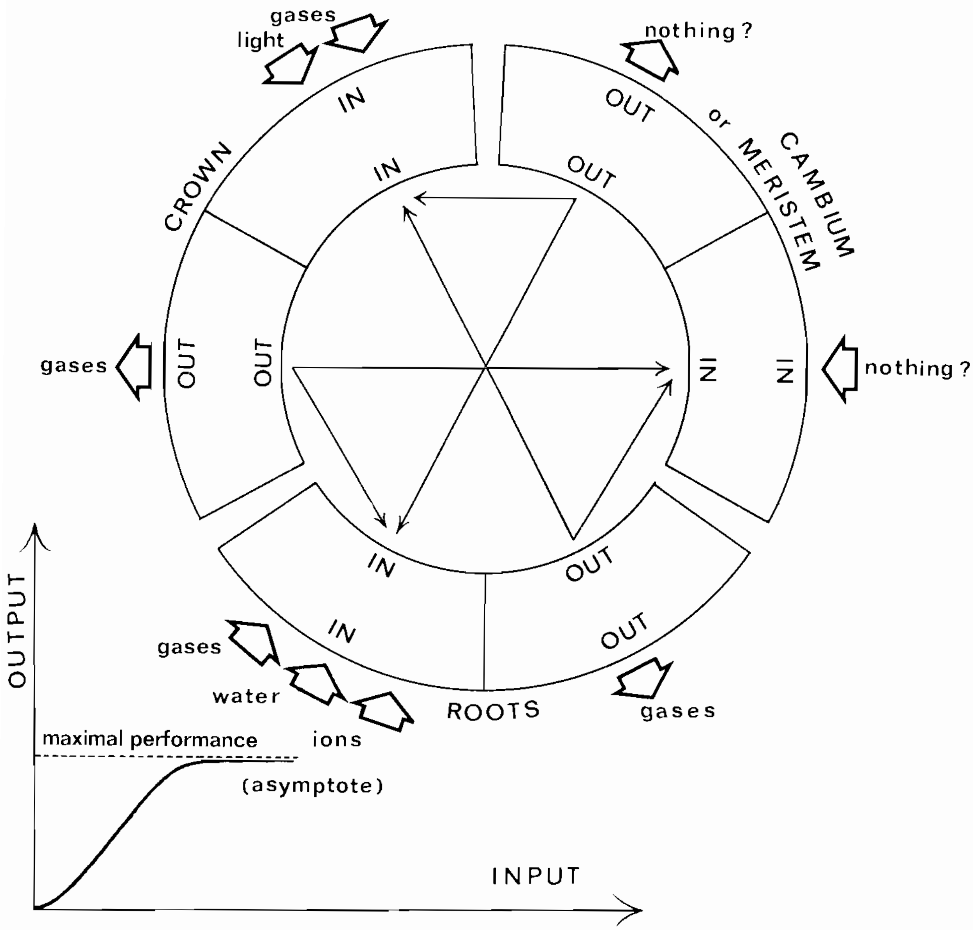


Fig. 86. Simple flow chart to show relationships between the three major producing units of the tree, i.e., crown, cambium, and root system, here considered as "black boxes". *Inset*, relation between input and output into any one system expressed graphically to show that each has a maximum output, represented by the asymptote of this hypothetical curve (cf. Fig. 79). Further explanation in the text

tree the number of interacting units increases with an inevitable and perceptible degree of hysteresis. The inherent limit to production in any one synthesizing unit is represented by the inset diagram in the flow chart (Fig. 86), in which the input/output curve is represented as having an asymptotic value.

The biological answer to limits of performance set for individual units is to increase the numbers or size of the producing organs so that larger quantities of incoming energy can be handled. Branching and reiteration in the leafy crown are examples of this process; they probably have their counterparts in root proliferation, but this still remains to be demonstrated as a general phenomenon, although VEILLON (1976) gives some observations on taproot reiteration in *Arauca-*

ria. We have already expressed the notion that branching within the model is a standard solution to bioenergetic relationships, whereas reiteration allows for ecological opportunism.

The cambial cylinder takes a special place in this system. As far as we know, it admits of no direct energy exchange with the external environment, its responses to climatic change are therefore all indirect (cf. PHILIPSON et al., 1971). Because it receives its energetic supply solely from the other subsystems, cambial activity can be taken as a measure for overall growth in the tree. Indirectly, of course, its activity can be a very sensitive measure of climate, a property exploited by dendrochronology. However, the cambium is not usually multiplied; although fluting of axes can allow quantitative geometric increase. In optimal conditions of illumination, soil fertility, soil permeability and water supply it is the cambium that imposes limits to total tree growth. When this process of endogenous limitation is very slow, as in the coastal redwoods of California (*Sequoia* spp.), the tree never dies a physiological death; it dies by some external accident before it has the time to die for endogenous reasons.

The unique apical meristem of palms is equally distinctive. Feedback mechanisms are such that the increase or decline in its activity are reflected in the rate at which trunk tissues are added. This fluctuation is evidently registered in palms initially by changes in internode length but ultimately in diameter, changes which accurately record fluctuation in ecological amplitude of environmental parameters. HOLTTUM (1955) suggested that the lifespan of palms is limited by the amount of root-producing surface at the base of the trunk; ZIMMERMANN (1973) indicated that phloem transport capacity of the trunk is also a limiting factor, gradually leading to starvation of the crown. Cambium-less trees have to anticipate this gradual loss of efficiency: palms represent ideal organisms for experimental research on production interactions since their units are large and simple, their meristems do not multiply except in the integrated way proper to their growth model, and most of the functional trunk biomass is retained throughout the life of the tree.

Curves of biomass production and of amounts of accumulated biomass against time have a standard pattern which can be represented in the same way for all levels of biological organization – cells, organs, organisms, populations. The pattern is shown schematically in Figure 88. In tree trunks there is a good reason for using volume as a measure of mass increase because we know that the specific gravity of wood (but perhaps not bark) is relatively constant throughout a single tree. Girth increment curves for trunks of forest trees from Surinam, published by SCHULZ (1960), can be analyzed in this manner, since volume is directly proportional to the square of the diameter.

Figure 87 represents one example of the observations made by this author and our interpretation. *Ocotea rubra* (Lauraceae), which was the object of this scrutiny, is a high forest tree which can become 40 m high. We will see (Fig. 92) that such trees grow up into the canopy through alternating stages of suppressed and released growth, the latter being most often promoted by an increase of light through a damaged canopy. This is translated by the oscillating curve. The general shape of our basic curve is similar for the trees of one species growing on different soils, which could be expected since it represents the average functioning of a cambium with the same organization. For trees in different edaphic situations the fundamental parameters would not change, only the numerical value of appropriate constants.

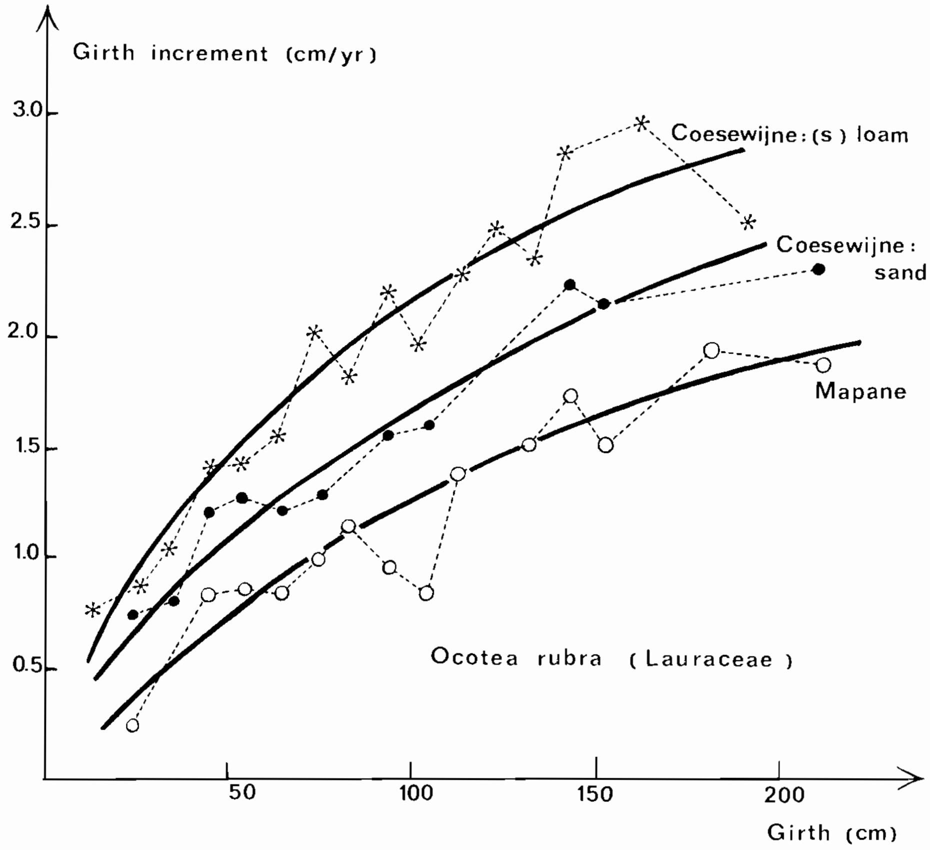


Fig. 87. Fluctuation in rate of girth increment of *Ocotea rubra* (Lauraceae) in relation to increase in girth, from data presented by SCHULZ (1960). The *dotted line* follows the points for the actual data, the *solid line*, which it fluctuates about (drawn in free-hand), representing the presumed hypothetical base-line. The three curves represent three different sites, the points are averages for from 40–80 trees. Further explanation in the text

In none of these curves is there evidence of the cambium functioning near its asymptotic performance.

Up to a girth of 65 cm (d=appr. 20 cm), the behavior of the trees in the three forests is remarkably similar. *Ocotea rubra* conforms to its model, somewhat transitional between Aubréville's/Rauh's model, for an extended period, so that we may say that this diameter corresponds to a height of 20 ± 3 m ($H = 100d$; for estimated deviation see OLDEMAN (1974a; his Figs. 51, 60, 84, 87, 91). A phase of rapid production brought the trees from a level between 5 and 15 m ($5 < d < 10$ cm), where they were suppressed as can be seen by the rather constant growth rate increasing more slowly than the basic curve, to a further suppression phase between 12 and 23 m high ($12 < d < 20$ cm). Above the average level of 20 m (between 17 and 23) growth waves become more erratic, which can be understood by the damage that these trees suffer from when they start to penetrate the canopy. As we will see, the less regular growth pulsations in this part of the graph correspond to waves of reiteration, because cambial activity gives a measure for total growth activity. The fact that the graph represents observations of populations of 40 to 80 trees on different substrates, and not successive phases in the growth of a single tree, certainly also contributes to this irregularity.

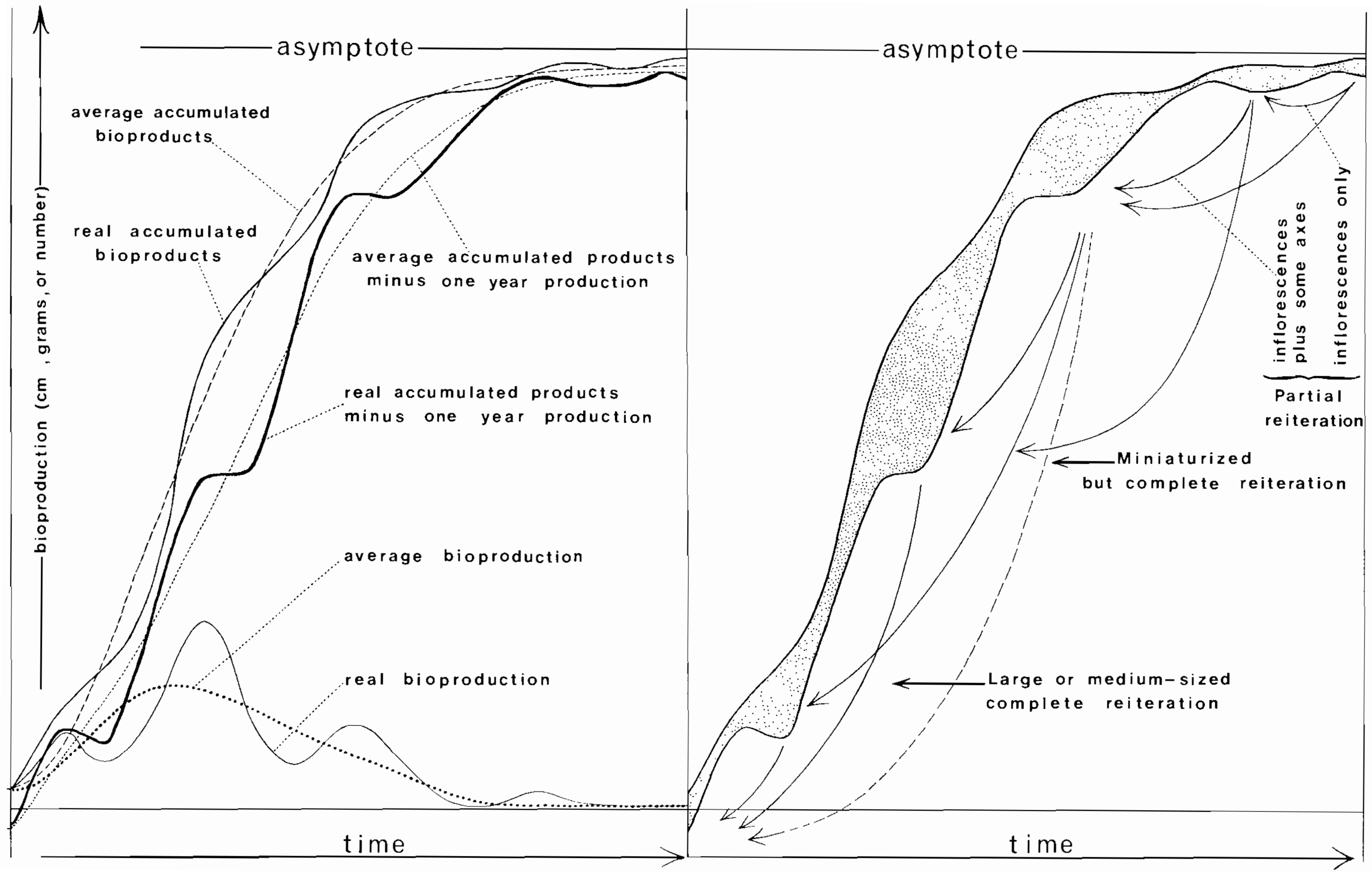
An inherent advantage in working with trees is that much of the biomass produced during its life is retained in the trunk as the nonmetabolic part of the wood (heartwood). Both production and accumulated mass can be established by direct measurement. Values are most accurate for palms, as we have mentioned. For short-lived organs like leaves, flowers, fruits, twigs which are shed, one can make estimations of total mass (e.g., HUTTEL and BERNHARD-REVERSAT, 1975; KLINGE and RODRIGUES, 1973; MÖLLER et al., 1954). The same is true for parts of the root system which are short-lived and difficult of access.

Since the developmental relations between these directly and indirectly measurable parameters remain of diagnostic value throughout the life of the tree, the rate of growth and the mass development in its trunk provide a measure of the mass increase of the whole tree, with the formation of mass, volume, and surface being harmonized by its architecture. Since the cambial system is not influenced by direct energy exchange with the exterior, it can be used as a measure of the metabolic performance of the whole tree. This can be quantitatively ascertained by measures of diameter increase either at intervals or continuously with the aid of permanent recording devices (BREITSPRECHER and HUGHES, 1975).

With a tree, however, one also has to make a distinction between metabolic and nonmetabolic mass; it is only the former which is significant in production, i.e., energy exchange with the biotope and energy distribution within the plant. To distinguish this "living" part of total biomass it is represented by the shaded zone under the curve for accumulated mass (Fig. 88, right). Its area is established here on the assumption that biomass lives, i.e., remains metabolically functional, for one year, and by subtracting the accumulated value of the production of the previous year from the value of the total accumulated biomass in any given year.

We recognize that the functional lifetime of different tissues varies widely for different species. BRAUN (1963) provides fairly direct information about the lifespan of the conducting hydrosystem in the xylem. BARKER (1953) cited figures of 50 years for the upper age limit of ray parenchyma cells in *Tilia*. The graph would clearly have to be corrected for every special case, but each would be only a variant of the general one. Figure 88 (left) represents both the real and average production of living mass against time. In Figure 88 (right) the resulting biological situation is represented by showing the amount of living mass in periodic oscillation around the means we have represented on the left side of this figure.

Fig. 88. Schematic, graphic representation of ▷ production within a single cell, tissue, organ or (here) tree during the course of its development. *Left:* Production with time, the lower curve representing the rate of production, fluctuating about a hypothetical mean, upper curves representing accumulated products, as indicated. *Right:* The curves for accumulated biomass, with the amount representing recent, metabolically still active biomass stippled, in relation to the process of reiteration. *Arrows* represent the processes of reiteration with increasing time as a return to an earlier level of production


asymptote
average accumulated bioproducts
real accumulated bioproducts
bioproduction (cm , grams, or number)
average accumulated products minus one year production
real accumulated products minus one year production
average bioproduction
real bioproduction
time
asymptote
inflorescences plus some axes
inflorescences only
Partial reiteration
Miniaturized but complete reiteration
Large or medium-sized complete reiteration
time

This fluctuation is the result of rapidly produced quantities of mass in the tree, which are more or less contemporaneous, and cease to be metabolically significant in the same contemporaneous way. Meanwhile, production of tissues may have slackened or accelerated so that the dying mass is replaced by a different amount of young metabolic active mass. On the seasonal scale this is most evident in temperate trees, over a longer period and in trees of nonseasonal climates this is reflected in the waves of reiteration we have already described. *The dynamic image that has to be emphasized is that of the environment yielding not steady, but pulsating, energy flows to the plant and of the latter's response by a pulsating, not steady, production pattern.* This is represented in Figure 88 and exemplified by Schulz's observations (Fig. 87).

The progressive decrease in the size of the pulsations in the shaded part of the graph indicates that the amount of free energy available for morphogenetic increase progressively decreases and becomes less effective. Since each wave of reiteration represents a kind of partial rejuvenation of total architecture, consequent on the development of a new model from a meristem with biomass close to zero, there is a progressive displacement of points towards lower time/mass levels in the graph. The potential size of each new reiterated complex is, however, progressively reduced and the waves of reiteration, drawn as arrows, represent collections of arborescent, frutescent, subfrutescent and herbaceous models successively built into the whole tree. Speaking qualitatively one can say that vegetative rejuvenation becomes more and more difficult as the tree ages.

That this difficulty is also organizational is emphasized by the fact that reiterated complexes in one tree behave more and more like a population, as is reflected in the tropics by their unsynchronized phenology, which has been often observed and termed "erratism" of branches (e.g., by SCARRONE, 1969, in *Mangifera indica*). We have shown this phenomenon in a specimen of *Tabebuia serratifolia* (Bignoniaceae) in Cayenne (Fig. 78), in which some reiterated complexes are leaf-bearing, others bare except for inflorescences, and still others in the postfloral stage. This behavior is regarded as a difference between different reiterated complexes.

In these graphs (Fig. 88) the origin can be regained only by seed formation and the profuse flowering of miniaturized and fragmented models reiterated on old trees represents the biological compensation for loss of vegetative capability. The ultimate size of the individual plant is represented by the asymptote of maximum accumulated biomass. In terms of mass and energy the analogy between reiterated complexes and individual shrubs, undershrubs and herbs is complete. It is reasonable to hypothesize that as total accumulated biomass at the end of the lifespan decreases from species to species or from a reiterated complex to the next (i.e., the asymptote in Fig. 88 becomes lower), rapidity of growth, i.e., the steepness of the curve in its initial part, increases with every further step towards the herbaceous. This is almost self-evident since herbs are so defined by their minimal amount of conductive tissues (equals accumulated biomass). One difference between a herb and a whole tree may be determined by the different way energy distribution is mediated (see MANGENOT, 1969).

These facts make it possible to understand the one essential difference between individual herbs and reiterated "herbs" (i.e., reiterated herbaceous complexes in trees), which lies in the input of root-originated forms of biochemical energy.

Reiterated "herbs" depend for this input on a long tapering transport channel throughout a whole tree, whereas individual herbs receive this input directly from their autonomous root system. Where rooting is easy, stem cuttings made from reiterated "herbs" often can grow up rather easily into trees conforming to a tree model, whereas individual herbs are permanently consigned to a life form which may not be found in trees.

The brief and generalized discussion of production given here is sufficient for our purpose of linking architecture and energetics. The central point is that each wave of reiteration requires an increase of transport tissue. Eventually the ability to build this becomes limiting. Growth slows and finally ceases because reiterated complexes compete in an inhibiting way for light, transport capacity or root assimilates.

III. Size and Architectural Proportions

We have earlier discussed the simple relations between axes and appendages in plants which have been expressed qualitatively in Corner's rules. It is of interest to consider the limits which may be set to the size of plants, as determined by these rules. We have repeatedly emphasized that our definitions of models do not implicate size, and have supported this by examples in our lists of both herbs and trees conforming to the same model. At the same time, species do have a characteristic upper size limit. Sizes range from the smallest *Phyllanthus* species to large Dipterocarps, as in Roux's model, which seems to belie the statement of STEVENS (1974, p. 16): "We find, however, that the geometric relations that arise from a difference in size affect structural behavior ... We also find, as a corollary, that in order to maintain the same structural characteristics a difference in size must be accompanied by a difference in shape." The contradiction, however, is only apparent, because in plants size is broken up into small manageable units; cells at one level, organs at the next, organ complexes at the highest one. In this manner, they can span sizes from the multicellular to the megaphytous scale without changing their basic organization and adjusting only the number of units at each level, or even the character of these units. In the tree model the number and character of organs, and in reiterating trees the number and character of reiterated models can be adjusted. As our study covers tree models and reiteration we can now ask the question: are there upper and lower limits to the size that may be covered by trees built according to these standards?

The answer concerning the lower limit of architectural model size is implicit in what has been said – as soon as organs cannot reach the minimal number in order to form the model, the latter is imperfect. This phenomenon has been observed in miniaturization followed by fragmentation of the model in individual herbs, as discussed earlier. It is also seen in the progressive size reduction of reiterated complexes in the development of the tree. Miniaturizing the organs can lead to further miniaturization of the model, so that herbs like *Biophytum* spp. (Corner's model) and *Phyllanthus* spp. (Cook's model) form scale models of trees.

As to the upper limit of size that can be reached by plants initiating one model and then reiterating it, no definitive answer can as yet be given in architectural terms (but see CHUAH, 1977), since the limiting factors are perhaps mechanical (McMAHON, 1973).

Within a single species, the individual maximal size depends on an interaction between size of parts, rapidity of growth and architecture. An example of this is the comparison between a free-standing and a forest specimen of the same species (Figs. 74 and 75); rapid growth occasions early profuse reiteration and a smaller overall size in the free-standing tree, and slower growth of the forest tree delays the prolific reiteration phase so that a larger overall size is reached. When a tree reaches its maximal size, it is bound to die sooner or later—this leads us to a discussion of vigor and death in trees.

IV. Vigor and Death in Forest Trees

In general, only metabolically functional tissues (Fig. 88) have any importance for the continued growth of a plant. This includes the conducting tracheary elements, exceptional because their functioning in transport is dependent on the loss of their cytoplasm. The morphogenetic performance of a tree is dependent on the productivity of meristematic tissue present, and the balance between growth rate and death rate of particular tissues may be taken as a measure of the tree's vigor. When production is high and senescence and death of large masses of previously produced tissue is lower than new growth there is a net increase. In the inverse case a net decrease is the result. A balance may be struck where production and loss are equal, we can refer to these three states as high and low vigor for the first and second condition, with the third representing an intermediate condition of stability. At the highest rate of net increase compatible with the definition of the model, a maximum number of organs is present. When net productivity declines, growth is slow and a minimum number and volume of organs is present.

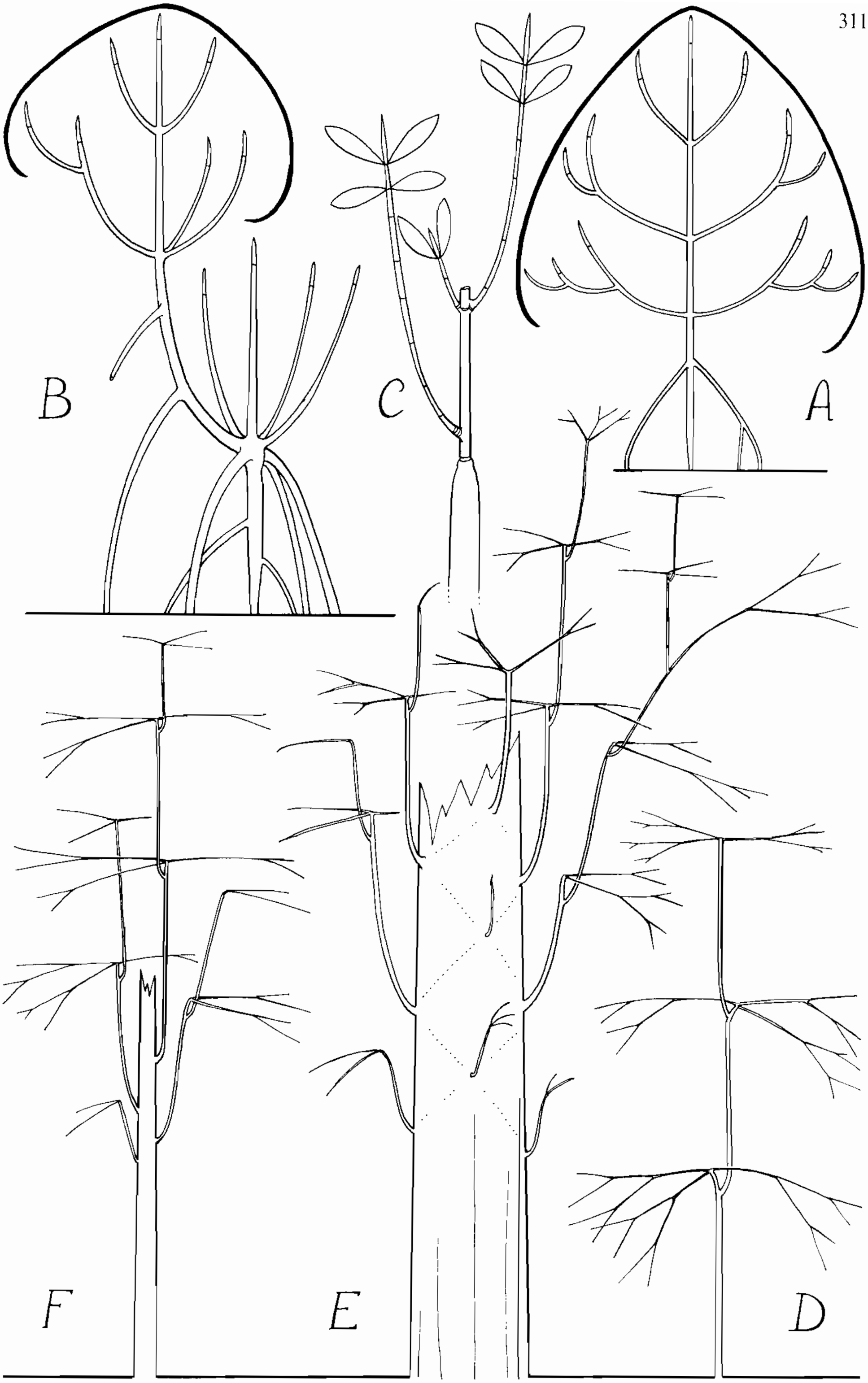
Where production is insufficient to sustain the complete expression of the model we may speak of "pauperization" of the model—too few branches and smaller leaves are realized (Fig. 89). This pauperization, for example, can be seen well in dwarf or scrubby trees of *Rhizophora mangle* (Fig. 89B, C) in which the architecture conforms to the model on a reduced scale, but the model may also become unrecognizable (Fig. 89C). Pauperization of another model, that of Nozeran, in reiterated complexes on an old broken trunk of *Minquartia guianensis* is represented on the same figure (Fig. 89E, F). Oldeman (1974a) used the expression "level of latency" to denote a state of low vigor associated with a high number of resting meristems in a pauperized tree. If this level decreased further, death would result.

Vigor can be visibly ascertained by its result, which is rapid growth such as it is currently appreciated in horticultural practice (Champagnat, 1954b). Therefore we can express the dynamic tendencies in the proportion between functional and nonfunctional biomass in a graphical way (Fig. 90). This remains hypothetical, however, in so far as no measured values are available to tie model to vigor in the case of a real example

Fig. 89A–F. Pauperization of the model when vigor is very low. ▷

A–C Rhizophora mangle (Rhizophoraceae, Florida); *A* Attims' model; *B* the pauperized reiterated model on the left is still recognizable, the other axes may be trunks or branches; *C* the model, reduced to a small number of internodes and leaves, cannot be recognized any more.

D–F Minquartia guianensis (Olacaceae, French Guiana); *D* Nozeran's model; *E* reiteration of still recognizable models at the top, unrecognizably pauperized model at lower heights, on the broken trunk of an old tree; *F* same on a younger broken tree, which may regenerate completely, however, by the upper reiterated complex

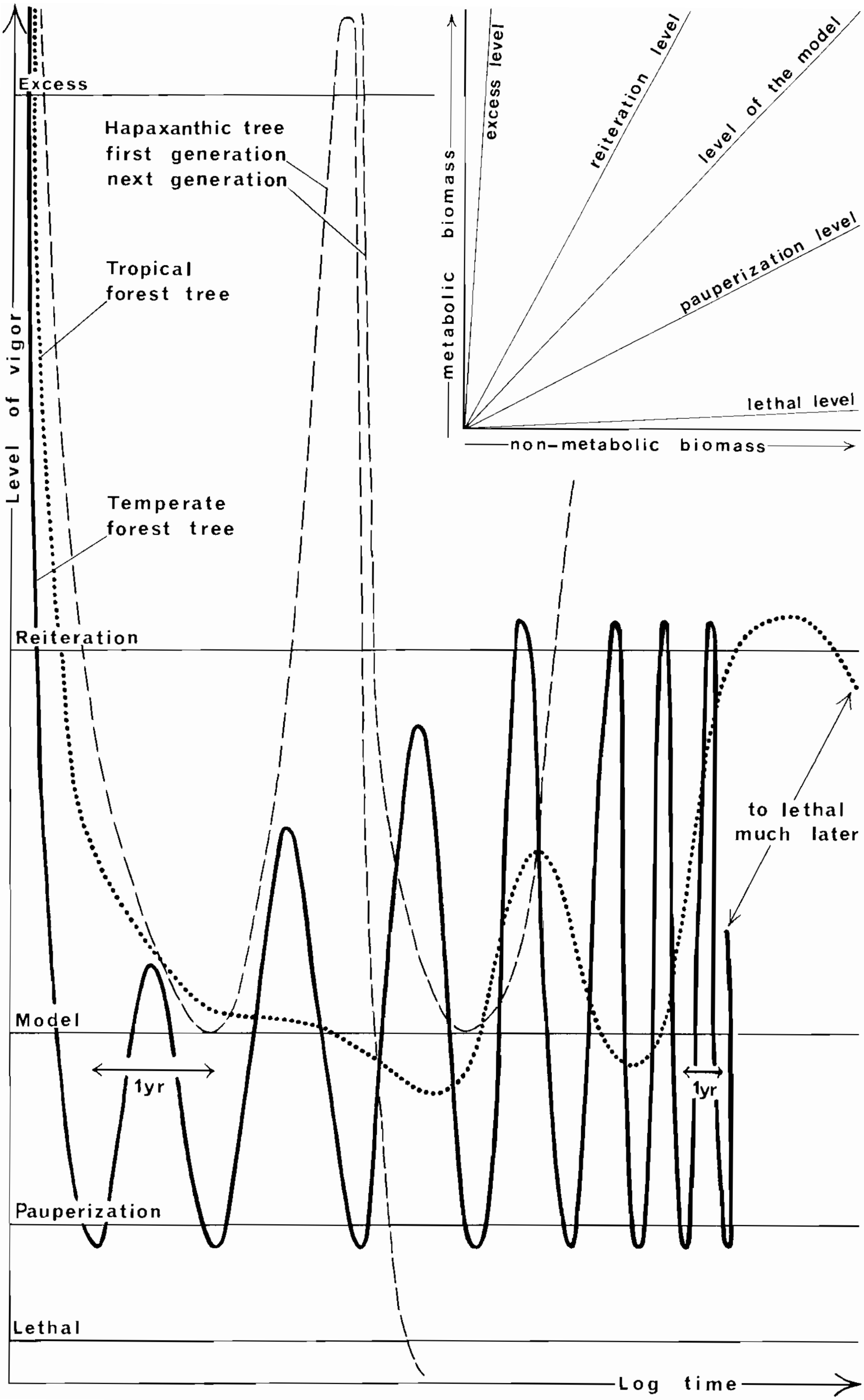

B
C
A
F
E
D

allowing a scale to be put on abscissa and ordinate. In Figure 90 (inset) five levels of vigor are arbitrarily indicated by lines representing respectively lethal, pauperization, model, reiteration and excess levels. In the larger Figure 90 where these same levels are represented by horizontal lines between which the plant oscillates during its individual development, the values chosen are again arbitrary in the absence of actual measurements.

In this figure the course of development of three kinds of tree in relation to these levels of vigor are shown. All seedlings are in the zone of excess vigor. Effectively during germination and shortly afterwards all of their biomass is functional. With rapid accumulation of nonfunctional biomass there is a rapid drop to the level of the model. The rate of fall is represented arbitrarily and in reality may have very different values for different trees. On reaching the level of the model, vigor then follows different paths in different species belonging to different biological types. The simplest condition is probably represented by hapaxanthic trees (Holttum's model) when the model level of vigor is steadily maintained owing to the unbranched state, to be completed by a sudden mobilization and expenditure of reserves. Morphogenetically this is represented by the initiation and activation of numerous floral meristems. This excess vigor is followed by its abrupt depression to a sublethal level, followed by the death of the plants. Meristems survive solely in the form of seeds ("next generation").

In a tropical forest tree, development in relation to different levels of vigor may be represented graphically as in Figure 90 (dotted line) and should be compared with the morphological events associated with reiteration shown in Figure 74. In the post-seedling stage, the curve descends steeply to the model level, just as in hapaxanthic plants. This level is then maintained approximately, the slight oscillation in vigor from one side to the other being reflected in the number and length of branches on the trunk, or the total number and surface of leaves in a monocaulous tree. In the forest this phase can be long, but the horizontal time scale in the illustration is logarithmic. Undue protraction of this phase may cause the vigor to descent via pauperization to the lethal level. We have described the visible symptoms of this in *Virola surinamensis* and *Cordia exaltata* on p. 276. In a surviving forest tree the curve of its vigor, following generally an increase in irradiation occasioned by some opening up of the forest canopy, goes up to the reiteration level. Subsequently it may be depressed again if the tree is overtopped leading to loss of reiterated parts and a return to the level of the model (but not necessarily the precise architecture of the model, which by now has been disrupted). This is effectively pauperization of the whole tree and is essentially the reverse of regeneration. This fluctuation continues to be repeated with the possibility of death of the tree consequent upon any fall in level of vigor to the lethal level. Conversely survival of the tree, dependent upon successive phases of light increase and successive phases of reiteration, carries the tree crown into the canopy. Here it remains for a long time until the curve is depressed irreversibly towards the lethal level, since

Fig. 90. Graphic representation of changes in > "vigor" of a tree in relation to age. In the absence of any quantitative estimates the values chosen are arbitrary. *Inset, top right,* vigor (expressed as the relation between metabolic and nonmetabolic biomass) at five different levels of performance for individual trees. *Larger figure, lower left,* changes in vigor of three kinds of tree (hapaxanthic, tropical forest and temperate forest) with time. Further explanation in text


Excess
Hapaxanthic tree
first generation
next generation
Tropical
forest tree
Temperate
forest tree
Level of vigor
Reiteration
Model
1yr
Pauperization
Lethal
Log time
1yr
to lethal
much later
excess level
reiteration level
level of the model
pauperization level
lethal level
metabolic biomass
non-metabolic biomass

vigor is ultimately no longer determined by the external energy source, as is explained later (see Trees of the Present, p. 322).

In the temperate forest tree, or the tree of tropical savannas, vigor drops seasonally to the level of pauperization, owing to the unfavorable changes in climate, either to winter or to a dry season. Bud and cambial dormancy and leaf shedding are responses to these environmental pulsations, representing temporary levels of adjustment with a minimum of structural damage. A rapidly oscillating pattern of vigor is then expressed, as shown in Figure 90. The abundance of sympodial substitution in temperate trees, expressed by the existence of "homogeneous apical groups" of branches, a phenomenon considered normal by temperate physiologists (cf. CHAMPAGNAT, 1954b), may be a consequence of this oscillation, because in temporarily pauperized trees there are not only many resting meristems but also many meristems that die.

The major source of oscillations illustrated for tropical forest trees in Figure 90 is microclimatic and determined by local conditions. Detailed phenological studies of individual "ever-growing" trees over extended periods in nonseasonal climates which would provide a measure of these changes are nonexistent. The study of GILL and TOMLINSON (1971b) on rates of leaf production of *Rhizophora mangle* in South Florida provides some quantitative information on leaf renewal in an ever-growing tree which demonstrates the effect of macroclimatic fluctuations.

The gradual decline in vigor of a tropical forest tree after it has remained a long time at a "reiteration level" of vigor has its explanation in architectural terms as a result of the progressive decrease in size of the reiterative complexes we have previously described. This decline is quite independent of the architectural model to which the tree conforms. Reiteration, as we have seen, is first arborescent, then frutescent and finally herbaceous. The overall result for the vigor of the tree is change from reiteration level to pauperization level. On the contrary, the "individual" curves of each reiterated complex begin to resemble that of a hapaxanthic plant – we have already drawn an analogy to neoteny in establishing the morphology of these distal parts (Fig. 74H). The mass of the inflorescence becomes large in comparison with the vegetative parts of the complex. If one views the old tree as a large population of meristems, its low total vigor is the sum of high but ephemeral activity of the total of individual herbaceous complexes of which its crown is made, largely as a consequence of mobilization of reserves. Seed production is the consequence of this effect.

CARR and PATE (1967) have claimed that in plants death is preprogrammed. All evidence summarized in the preceding pages of this book indicates that death is the failure of growth programs (e.g., our growth models) to provide for individual survival. When the program for individual survival fails, a program for population survival can take its place. In Tomlinson's model, a clone is established, by the death of parts in the architectural model. In branched dicotyledons and some gymnosperms abundant seed production consequent on herbaceous reiteration promotes the sexual method of survival. The strategy involved in survival of meristems by clonal means is most clearly expressed in rhizomatous herbs and the analysis of *Medeola* by BELL (1974) may be cited as a very precise example.

V. Ecological Strategies of Trees

Strategy, in an economic or military sense, is the reciprocal set of actions and reactions between two conflicting groups directed to the attainment of their ends by each group. The concept has been used widely in animal ecology where active strategic patterns of behavior are most readily recognized and has recently penetrated the fields of plant ecology and evolution. One can, in fact, recognize without any teleological interpretation that the "ends" sought by plants are very simple, they preserve their genotype and to do this occupy as large a part of the available biotope as is necessary. For trees, occupation of space is an inherent mechanism without which a population cannot survive, and it is towards the interpretation of such mechanisms that much of the concept of strategy in plant ecology is directed.

The efficiency of strategy in a plant species, as in animals, is a question of the classic "trial and error" approach of evolution. Since this is the method of screening successful strategies, species without an efficient strategy cannot exist. The concept of the tropical rain-forest as a "museum" of accumulated inefficient woody species suggested by some authors (e.g., MANGENOT, 1964; STEBBINS, 1974) is therefore appropriate only in the sense that in such a forest conditions prevail where strategies are successful that would not be so elsewhere.

For the present purpose of tree and forest architecture our concern is with the ecological aspects of strategies, i.e., how does tree architecture contribute to tree survival in the forest? The evolutionary aspect, briefly considered in the discussion of fossil trees, as to how these strategies arose, is outside the scope of this book. Initially we deal with the strategy of individual trees, the problem in the context of forest architecture and sylvigenesis is discussed in a later section. This accent on short-term considerations is clearly a voluntary restriction and we appreciate that its separation from long-term evolutionary considerations is artificial (cf. BLONDEL, 1975).

The idea of two main trends in selection of specific strategies arises from the work of animal biologists (MACARTHUR and WILSON, 1967), developed recently by the ornithologists PIANKA (1974) and BLONDEL (1975), the last of whom has incorporated the time and energy allocation theory of CODY (1966). The views of these workers have to be considered critically before being accepted for plant populations and this may account for some differences between the source of ideas in the zoological literature and our application in the following pages (see also discussion under Holttum's model).

Essential for the comparison of the two main strategies mentioned are the notion of r, which is the intrinsic rate of population increase, and K, the equilibrium population size attainable in a given environment under specified restrictions. MACARTHUR and WILSON define K for an island, since their work deals with theoretical island biogeography. We can compare this to the "forest biotope" referred to here; the concept can be modified by the introduction of "temporal islands", which result from forest succession. In addition, we have to use the notion of "ecotope", the combination of niche and habitat favored by ecologists (e.g., WHITTAKER et al., 1973; OLDEMAN, 1974b). The rate of population increase r is the difference between λ, the per capita birth rate, and μ the per capita death rate. According to MACARTHUR and WILSON the chance of an individual propagule leaving descendants which will eventually grow to the maximum population size K is about r/λ, and the average survival time of a population already at the size K is about λ/r times the average life span of a propagule and its descendants.

These basic relationships interact differently according to the environment a plant population has to exploit. If this environment is relatively empty, the function r/λ will be maximized in order to attain a maximum value of K since initially the equilibrium population size is virtually unlimited. An intrinsic high value for population increase, r, is thus favorable to a maximum rate of biotope invasion. This condition is achieved when every individual plant of a colonizing species is given to reproduction. Selection under these circumstances would favor individuals with a high reproductive capacity, less prolific individuals would be at a selective disadvantage from generation to generation. We can, therefore, think in terms of "r selection" working towards high reproductive values. It would be expected that the effect could be reinforced if μ, the per capita death rate, were reduced, but for the extension of the life span of individuals, the energy allocation principle of CODY (1966) has to be considered. This says: "It is possible to think of organisms as having a certain limited amount of time or energy available for expenditure, and of natural selection as that force which operates in the allocation of this time and energy in a way which maximizes the contribution of a genotype to following generations." This implies that priority to reproductive behavior leaves less time and energy available for building a large, long-lasting vegetative body; μ, if anything, is likely to increase with r, after a certain threshold.

In contrast, in an environment which is biologically full, the equilibrium population size K is limited by lack of space, its maximum value is reduced. The total biotope is, in fact, reduced and split into a number of contrasting ecotopes. The inverse function λ/r now has to be maximized, emphasis being now placed on the longevity of individuals which are specialized to meet the requirements of the specialized ecotopes. This specialization involves a diversion of energy resource towards vegetative growth leaving a relatively small amount of the total budget for energy and time available for reproduction. Vegetative architecture is then designed to allow spread of a moderate reproductive effort (see production) in time. Species of this kind are said to owe their existence to "K selection" during evolutionary time. The extended life-span and the specialized architecture of trees undoubtedly provide a prime example of the results of this process.

In the preceding section on bioenergetics it was stated that architectural tree models each represent standard solutions to the utilization of energy offered by the environment. We can now appreciate that each of these models is more or less suited to an r-determined or K-determined life cycle as has been briefly discussed in each of the model descriptions. We are in accord with PIANKA (1974) in thinking of an r to K selection continuum along which an organism can have a different position according to the particular environment. Most tree models can be recognized as intermediates between extreme r and K plants.

The size of trees is such that always a considerable amount of energy is devoted to the construction of vegetative parts. This is true even in Holttum's model, which is represented by trees most orientated towards an r strategy. In *Corypha elata* the inflorescence forms a large part of the plant body and still reproductive biomass only involves of the order of 10–15% of total biomass (TOMLINSON and SODERHOLM, 1975).

BLONDEL (1975), on the basis of the three-dimensional graphs of CODY (1966) and the data of McNaughton and Wolf (1973), considers available energy to be allocated between "competition", "reproduction" and "fighting (avoiding) predators" (Fig. 91A). Competition and predator avoidance represent *K*-orientated energy use while reproduction is *r*-orientated. Predator-avoidance in plants is passive and involves the production of protective organs, toxic distasteful and fungistatic substances, reserve meristems and large seed populations. Janzen (1970b) gives theoretical distribution patterns of seedling predators of forest trees. The patterns of distribution of a predator (e.g., insect) population, however, are not necessarily in direct relation to the population of seedlings but are certainly to a large extent determined by other circumstances, e.g., weather conditions, or the breeding patterns of the insects themselves (den Boer, 1968, 1972; Andrewartha, 1970). This fluctuation with weather has been seen for instance in butterflies in French Guiana (successful and unsuccessful years with abnormal seasons, for collectors) and might be expected to occur in seed predators. Similar fluctuations could occur in pollinating insects, or in mammals which ensure the dispersal of seeds. Janzen's theoretical patterns are very probably in existence, but they are more likely to determine insect strategy rather than tree strategy. The disconnection between seed and tree at the time of fruit fall means that no direct feedback is possible; the blind character of "trial and error" processes is here particularly evident.

A direct feedback certainly exists between leaf predators and trees. A diminishing leaf surface can stimulate growth of new leaf-bearing axes, this increase in food resource stimulates the increase of

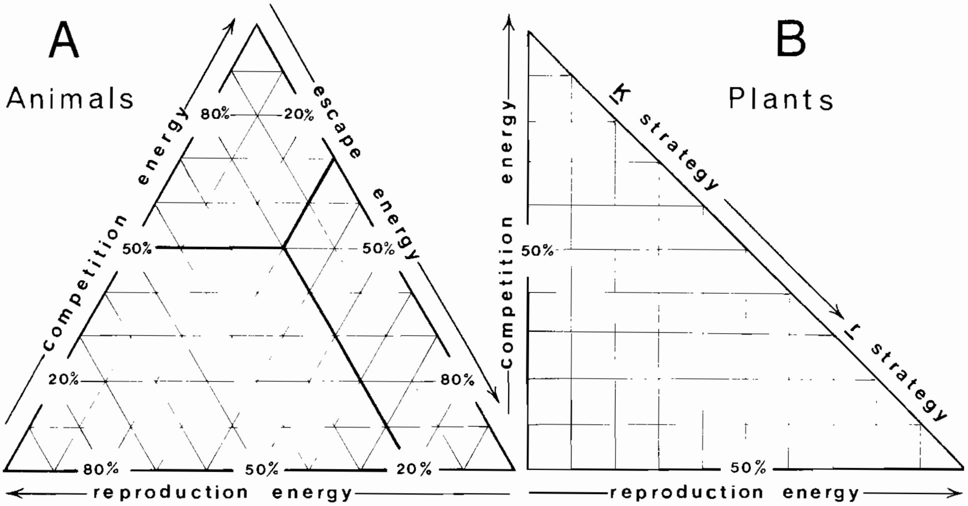


Fig. 91A and B. Energy allocation in animals *A* and trees *B* compared (*A* after Blondel, 1975). In animals energy is assumed to be consumed in 3 major directions – for reproduction, competition and escape. In woody plants the last parameter is considered to be lacking or at most included in the competitive factor. Reiteration, from arborescent to herbaceous, causes a big forest tree to "slide" from a *K* strategy when young toward an *r* strategy when old (*arrow*) insect populations. A commercial analogy would be the process of tea plucking. Flower and fruit predators are less likely to promote the same response.

For trees, the simplified version of Blondel's graph (Fig. 91 B) is a useful representation of the energy distribution between vegetative (*K*-orientated) and reproductive (*r*-orientated) strategies, with any defense against predators incorporated into the complex of *K*-orientated (competitive) factors. Because of a tree's immobility, physical flight from predators is possible only in the seed-phase and is then linked to the reproductive (*r*-orientated) behavior of the tree.

As long as a tree conforms to its initial model, where vegetative growth and sexual reproduction are integrated in a standard pattern, its place along the *K* to *r* line of Figure 91 B is fixed. We have not attempted to place our models precisely on this line because in very few examples do we have quantitative data to produce the necessary analysis. The parameters involved in addition to the branching pattern of the tree would be: overall shape, distribution of leaves within the crown, reproductive periodicity, seed crop size and ability to reiterate. This type of approach would lead to an understanding of the ecological strategy or strategies of the model and its rigidity or flexibility. The subject will obviously have to be developed. When reiteration starts, the position the model occupies in the *K*-*r* slope of Figure 91 B is displaced because we have seen that reiteration represents a shift towards more abundant flowering and fruit-set, a result of the progress towards neoteny in the successive reiterated models, which we have described earlier. Since the individual tree becomes a complex of reiterated models, the increase in numbers of models permits this quantitative shift. Reiteration in the form of root-suckers which become independent eventually achieves the same effect, since a clone is a population of individuals. The increasing proliferation of models involves a shift from arborescent towards herbaceous units, and we can now equate this with a shift towards an *r* strategy. The multitude of "herbaceous" reiterated complexes can indeed be closely compared to a true population of herbs (p. 308).

This is true in an ecological as well as an ontogenetic sense. In its first stages of growth the tree grows in the lowest layers of the forest where biotope diversification is greatest, though average overall conditions are remarkably constant, and where specialization of vegetative architecture is indispensable. Growing up, the tree approaches and finally enters into or even penetrates the canopy which is the contact surface between the forest and the macroclimatic environment. This environment is in sharp contrast to that of the forest-floor; it has all the characteristics ornithologists have associated with a biotope suited to an *r* strategy, i.e., it is relatively uncrowded and population-independent unpredictable forces, sometimes of a catastrophic nature, freely act upon it. The correlates of *K* and *r* selections as expressed by Pianka (1974) and reproduced here in Table 10 clearly apply to reiterated complexes as well as individual plants.

The population unit seen in this light seems clearly the meristem, regardless of whether it is produced vegetatively or by a seed, but taking into account its differentiation (e.g., plagiotropy). The model would come off second best as a population unit, because it integrates a number of functional meristems in a strict pattern which, however, may quantitatively change during successive waves of reiteration, becoming more elusive than meristems to the science of numbers that is population biology. The complete tree ap-

Table 10. Some correlates of r and K selection. (After PIANKA, 1974; Table 4.4, put in a botanical context)

r selection	*K selection*
Climate	
Variable and/or unpredictable; effects uncertain. Open tropical country or forest canopy, e.g., many temperate regions.	Fairly constant and/or predictable; effects more certain, e.g., undergrowth of the tropical rain-forest.
Mortality	
Often catastrophic, nondirected, without relation to the biology of the plant.	More directed, often by bioregulation effecting the microclimate.
Survivorship	
Probably: short but concerning the largest part of the seedling population.	Probably: long but concerning a very small part of the seedling population.
Population size	
Variable in time, not of an equilibrium level; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecologic vacuums; recolonization annual, seasonal or successional.	Fairly constant in time, at an equilibrium level; at or near carrying capacity of environment; saturated communities; no recolonization but gradual replacement of dying individuals.
Intra- and interspecific competition	
Variable, often lax.	Usually strong.
Selection favors	
1. Rapid growth. 2. High maximal rate of reproduction, r_{max} (seed production). 3. Early reproduction. 4. Small body size (shrubs, herbs) either as individuals, or reiterated models; clones as populations. 5. Continuous high reproduction rate, reproductive events single or few.	1. Slower growth. 2. Greater competitive ability (complex vegetative architecture). 3. Delayed or extended reproduction. 4. Larger body size (trees), usually individuals: clones as surviving parts of an individual. 5. Relatively low rate of reproduction, reproductive events repeatedly at wide intervals.
Length of life	
Short; annuals or biennials, or relatively short ("pioneer species", "nomads").	Longer, decades or centuries.
Leads to	
"Profligacy", vagrancy.	"Parsimony", permanency.

pears the least suited to be the unit in population studies as it changes very much over its lifetime. In the next chapter it will be seen how this can be taken into account in the analysis of forest architecture.

C. Growth Potential of Forest Trees

Having discussed the architectural and related properties of individual trees we are now in a position to evaluate their role as building elements of the forest. One should bear in mind, however, that the following statements essentially refer to dicotyledonous forest trees with a branched architectural model. As a tree grows its potential for further expansion is gradually lost when it approaches a maximum size, for the reasons related to energy exchange with its environment and energy distribution within its own body, which were presented earlier. In the forest, trees coexist in different phases of development, some cannot expand further, having reached the limit of their size, others still retain their potential for enlargement while yet others have been so broken up that they cannot recover and are slowly eliminated from the vegetation. A simple but fundamental device in our later analyses of forests is to consider trees as belonging to three different classes whose sylvigenetic roles are distinct.

Trees that lack any potential for further expansion, but exist at a stationary height (which may range from about a meter up to 80 m) without adding to this dimension or to the width of their crowns, generally determine or dominate the architecture of the forest they are living in, at any one moment, provided this forest is not subject to frequent and violent total destruction (e.g., by hurricanes). As no further "promotion" to a "higher" rank is possible for them, they will be called *trees of the present*. In contrast, trees in the lower reaches of the forest that are either in a phase of vigorous expansion, or suppressed and waiting for conditions which will promote resumed growth, still have a potential for future expansion. These may be termed *trees of the future*. It must be emphasized that such trees can be recognized only in terms of their *potential* for development; their life-span may be ended by precocious death and their potential future never realized. Lastly, trees may be damaged beyond repair so that neither potential for future development, nor possibility for survival in a stationary state are left to them. They have played their rôle in sylvigenesis and there is nothing left for them but eventual elimination from the forest. These are *trees of the past*. Again size is not a necessary criterion for recognizing them, the causes of their decline are bioenergetic ones.

These phases in the life of a single tree have been drawn schematically in Figure 92. We will now discuss their individual properties.

I. Trees of the Future
(Fig. 92, left)

In chronological order the tree of the future is represented by the first stage of development when it either conforms to its original model, though often more or less pauperized, or is regenerated by reiteration. Reiteration in this life class is, however, never profuse, as in the succeeding one. In tropical forest trees this phase is extended, in nearly all free-standing dicotyledonous trees with a branched model, it is short. In temperate forest trees the phase of total conformity to the initial model in nature may be so ephemeral as to remain unrecognized, though experimental work in which seedlings are grown in controlled or uniform environments can allow the model to be expressed more clearly, as in the studies of LAVARENNE-ALLARY (1965) on *Quercus sessiliflora* (Rauh's model) or in temperate oaks grown in a nonseasonal climate in Java. Temperate trees in nature are otherwise so soon regenerated by reiteration that it is frequently difficult to establish what is "normal" in the growth pattern. For this reason the relationship $H = 100\,d$, which we have accepted as diagnostic for the model is not often observed, although it is more frequently encountered in tropical forest trees.

In a tropical tree of the future, after it has been damaged and its top broken off, the change in the H/d relationship is indicated in Figure 84D. Breakage means an abrupt fall to a level where $H < 100\,d$, reiteration corrects this, with some overshoot ($H > 100\,d$) since a root system is available which is more extensive than in the seedling. Later the relation $H = 100\,d$ can be restored and the bayonet-joint becomes hidden by secondary growth, a process which may be very slow in a suppressed tree.

Free-standing trees behave differently since profuse reiteration is precocious and vigorous secondary growth then brings the relation down to $H < 100\,d$. A free-standing tree is, therefore, a tree of the future only for a relatively short period; it soon realizes its potential.

As we have already stated, trees of the future may be either suppressed or rapidly growing. The latter phase is normally brief in comparison with the first, since it is but a step to the next period of suppression. By this stepwise process of longer periods of suppression and brief spurts of more vigorous growth the stage is gradually approached when we can categorize the tree as "tree of the present". Quite obviously there is a transition state (Figs. 92 and 102, the hickory (*Carya*) near mark 15); or the larger anacardiaceous tree near mark 20 (Fig. 98). Representation of these trees as a tree of the present or the future may seem subjective, but more objective criteria will become apparent when we have examined the architecture of the forest as a whole.

The suppressed tree of the future is worthy of some discussion because it shows a characteristic state of energy exchange with its environment. The average conditions of the lower layers of the tropical forest are remarkably uniform, as numerous observers have commented (e.g., RICHARDS, 1952, 1970; BUDOWSKI, 1961; CACHAN and DUVAL, 1963; OLDEMAN, 1974b).

Diversification, however, is provided, just as in temperate forests, by factors like canopy-determined sun flecks, dry soil patches between buttresses, "biotic heterogeneity" (BARKMAN, 1970) and others (SCHULZ, 1960; WHITTAKER, 1970). This local diversification is important in the establishment of seedlings and herbs of the forest floor. Our concern, however, is with the average constancy in relation to the bioenergetics of the suppressed tree of the future. The atmospheric conditions are characterized by windlessness (PIANKA, 1974), a high CO_2 concentration by respiration of many organisms and decomposition of dead matter without evacuation by moving air currents, and a high relative humidity due to persistence of water vapor in still air. Elevated CO_2 concentrations favor photoassimilation at a constant light intensity level (HUGHES, in BAINBRIDGE et al., 1966); at submaximal light intensity, photosynthesis is at its maximum with high transpiration rates (ASLYNG, 1956). Soil humidity in the rain forest is nearly always at or near the field capacity, and cambium production can adapt itself to the transport capacity that the crown needs in the suppressed phase. Consequently, the rate of overall production of the tree remains low, but is geared by feedback mechanisms between roots, cambiums and crown (Fig. 86) to optimalize its performance in the given limiting external circumstances.

The stagnant phase of development, however, may be changed in diverse ways. Most obviously and very often the overtopping canopy is disturbed and more light is admitted. Wind penetration may be aided by the fall of a large but not too distant tree – a higher transpiration rate may result. Soil fertilization may be caused by the decomposition of a nearby fallen stem. Root and light competition, as that of a climbing plant may be lessened by the death of a climber which breaks under its own weight or is eaten by herbivores. Each of these changes in the pattern of available energy permit the tree to penetrate higher into the forest where there are more sun flecks. The tree is larger, but the level of equilibrium is increased.

Sometimes there is a situation where very gradual amelioration of conditions allows the tree a slow, continuing development, during which it not only keeps conforming to its model, but also does not increase its total leaf area much. There is mainly extension growth, in these cases, but no significant changes in the cross-sectional transport area of the trunk are necessary. Secondary thickening lags behind, and these trees, though conforming to their model, are higher than 100 times their diameter. This has been infrequently, but regularly observed in French Guiana for forest trees of different species growing in "ecological chimneys" (OLDEMAN, 1974a).

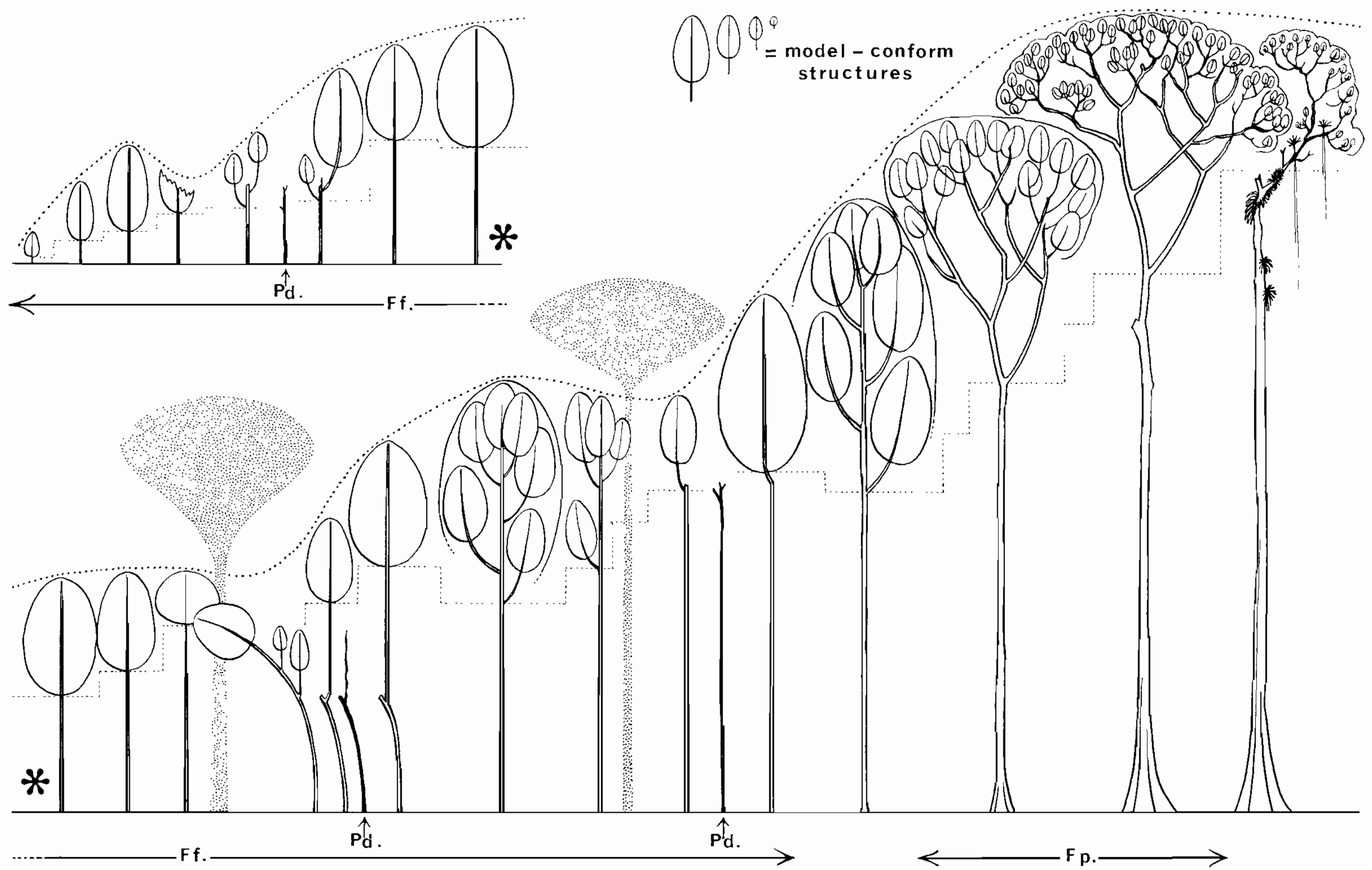
Some species appear to be exclusively adapted to grow in this way; they generally remain in conformity with their model, reiterating little, if at all. They are characteristic of early forest succession where the canopy is relatively open and we have called them "sciaphilous nomads" (see p. 383). They may be exemplified by *Iryanthera* spp. (Myristicaceae, Massart's model, Guianas), *Duguetia* spp. (Annonaceae, Roux's model, Guianas) and *Polyalthia* sp. (Annonaceae, Roux's model, Gabon).

Sooner or later, however, reiteration of the surviving nonnomadic tree of the future becomes pronounced and these successive waves of reiteration establish the tree of the present.

II. Trees of the Present
(Fig. 92, right)

Survivors from the earlier phase of development can be recognized as trees of the present according to the reiterative principles we have discussed earlier. There the architecture was examined in detail and the waves of reiteration progressing from "arborescence" to "herbaceousness" were described, both for forest and free-standing trees. The tree of the present, considered as a whole, shows *no* regeneration in an architectural sense, since neither additions nor losses in its architecture

Fig. 92. Schematical representation of phases ▷ in the life of a single forest tree. As a tree of the future (Ff) it has a potential for further develop into a tree of the present (Fp), unless it meets a precocious death (Pd) after suppressed periods or damage. Between the states "of the future" and "of the present" there is a transitional phase, reiteration being abundant but not as yet frutescent or herbaceous. *At the extreme right,* senescence has transformed the tree of the present into a tree of the past. *Shadowed:* other, overtopping trees which cause the suppressed periods. *Lower dotted line:* the morphological inversion layer (p. 358)


= model - conform structures
*
Pd.
Ff.
*
Pd.
Pd.
Ff.
Fp.

tend towards recovery of earlier forms. Rather the tree has now established a new energetic balance in an environment where the total light energy received by the tree is no longer the principal limiting factor. This steady state is achieved according to the feedback principles discussed earlier; root development and cambial activity are promoted. Exploitation of the soil layers may be reflected in certain architectural features of the root system (OLDEMAN, 1971). It is suggested by the layering of roots which has been demonstrated in certain forest soils (e.g., HUTTEL and BERNARD-RÉVERSAT, 1975; LONGMAN and JENÍK, 1974). The ability of the root system to supply water and mineral nutrients may, however, eventually become the factor limiting the growth of a tree of the present, and this is clearly the situation where a tree grows in unfavorable soil conditions – its size then is less than the maximum for a species. The particular limits which the soil can impose on roots are discussed later when intertwined structural sets of trees are described (p. 364). No limits seem to exist to the architecture and the photosynthetic capacity of the crown, by virtue of the huge number of meristems produced. Limits, however, are frequently imposed on root absorption by unfavorable soil or water conditions, though endogenous limits to its growth are probably absent, as in the crown. Crown size is then determined by the highest total leaf area possible with a limited rate of transpiration, and this, of course, is seen in the oft cited predominance of sclerophyllous leaves in the upper layers of the rain-forest (e.g., SCHIMPER, 1903; RICHARDS, 1952).

Reiteration in trees of the present finally becomes "herbaceous" because of interaction between the numerous reiterated complexes and rationing of resources, mainly transpirational water.

An analogy may be sought in the populations of herbaceous epiphytes growing in the very canopy made up by "herbaceous" reiteration in the highest trees of the present. Automatic adjustments to the macroclimatic conditions which correspond to the small increases and decreases in vigor in the extreme right-hand part of Figure 88 are not inherent in the model and do not manifest themselves in trees of the future, but they greatly enhance the life span of the tree of the present.

The difference between tropical and temperate trees in the time span during which the tree remains relatively free of macroclimatic constraints can readily be appreciated in this context. A forest cannot keep heavy frost from penetrating its lower layers, but in the tropics it can and does effectively control the absolutely limiting microclimate of the understorey. Differences between trees of the future and trees of the present are more extreme in the tropics than in temperate regions.

Though it has come to terms with its environment, the tree of the present has a limited life, ending when its architectural capabilities cannot adjust any more to climatic exigencies. This moment coincides with either a diminishing production of new meristems during the current wave of "herbaceous" reiteration, or a diminishing cambial activity, or both. Progressively less foliage or conducting tissue is produced, production is gradually diminished and death ensues. In very long-lived trees, there is a greater chance of a sublethal accident before endogenous factors nullify the growth potential. Such accidents are the source of surviving but maimed trees which form the next category.

III. *Trees of the Past*

In natural forests, trees of all sizes are frequently uprooted, thrown askew or broken, as a consequence of some interaction with their biotic and physical environment, e.g., the fall of a neighboring tree, diseases, herbivorous parasites, frost damage, or undermining of the roots by run-off. These processes, which are correctly referred to as disturbances or perturbations if one thinks of the interrupted developmental process (cf. BUDOWSKI, 1961; WHITTAKER, 1970; DRURY and NISBET, 1973), are sometimes seasonal and may be statistically more or less predictable. This ecological fact makes the concept of strategy so eminently suitable for the understanding of organisms and their life-cycle.

Trees of the future, when so damaged, most often regenerate their initial model by reiteration, because they still retain the considerable architectural plasticity shown by all trees of the future, even to some degree in quite sizeable trees which have not yet attained their maximal expansion (Fig. 89F). In a tree of the present no capacity for architectural regeneration persists, neither before it is damaged, as we have seen already, nor after. Dormant meristems may be mobilized, but the considerable reserves of the extensive root system and the often substantial fragment of the trunk that is left are exhausted before a competitive tree crown can be formed. The level of balanced production (Fig. 90) lowers drastically, and consequently it is commonly seen that such large damaged trees bear a cluster of rather humble reiterated complexes at or below the level where the trunk is broken. None of them is capable of reconstituting the old trunk. Even the most vigorous only partially succeed in closing the newly made gap in the forest canopy; however, they do not suppress but only slow down the growth of trees of the future underneath, which, after overtopping the impaired tree, overshadow and eliminate it.

Trees of the past are very much lower than 100 times their diameter, and thus can be mostly recognized readily on *H/d* graphs. They show no particular response to the outside energy offer of the space they abruptly occupy after the disturbance; their roots and the old trunk-fragment are adapted to a crown that functioned at a certain level of energy-exchange, whereas the new and meager crown adjusts to another pattern of energy exchange. The resulting architectural chaos, therefore, is the accurate reflection of an internal functional chaos. Consequently, such trees are eliminated, a process that may be hastened by the installation of creepers and lianes. Large trees of the past are not very frequent in the forest, suggesting that their elimination takes relatively little time. By virtue of this low frequency they provide so little impediment to sylvigenesis that they need not enter into our later discussion on this topic.

IV. *The Morphological Inversion Point*

At every moment in the life of the tree expansion and elimination of parts of the crown strike an energetic balance in which cambial productivity is also involved. The crown changes both in width and height according to this balance, the overall change in shape being controlled by the phase of development of the tree. Architecturally the most significant morphological feature of the tree is the lowest major branch, and as branches are progressively shed so the crown is gradually displaced vertically. The shed branch may belong to the sequential system of the model itself, or be a reiterated trunk bearing reiterated complexes. Even in its final phase as a large forest tree of the present, the crown may still change shape by loss of lower branches, although total height remains constant: the crown then becomes shallower (Fig. 92).

In most dicotyledonous trees of the present, but less commonly in gymnosperms, the lowest branch is a reiterated trunk. This first fork, which is the level of origin of the oldest living reiterated complex, represents the location of an inversion in size of morphological units. Up to the level of this fork the vegetative complex is distinguished by a single large unit, the trunk; beyond it the reiterated complexes are smaller and smaller as is self-evident when one examines tree form. Where trees still conform to their initial model the same principle can be applied, the distal branches are progressively smaller. It is convenient to refer to this level, characterized by the first living branch or reiterated trunk, as the morphological inversion point (OLDEMAN, 1974a).

OGAWA et al. (1965) have already stressed the importance of the location of the lowest living branch when analyzing tropical rain-forest in Thailand (Fig. 105). Estimation of leaf area index (LAI), a technique suited to and devised for low growing vegetation or crop stands (COWAN and MILTHORPE, 1968; MONSI, 1968) proves to be inappropriate in the rain-forest and the procedure adopted by OGAWA et al. was to substitute crown depth (measured from the first living branch to the tree top) for LAI in order to obtain an estimate of forest photoassimilation.

Our viewpoint, considering the configuration of axes in trees of the future and of reiterated complexes in trees of the present as summarized by the morphological inversion point, which measures their energetic status, is at an intermediate scale between the more overall approach of OGAWA et al. and the more detailed view of HORN (1971), who considered the disposition of leaves on branches. Hence he treated branch disposition in the crown statistically, i.e., the differentiation sequence was not used as an integrating principle. Two fundamentally different configurations of leaves, referred to as "monolayer" and "multilayers" were recognized, the first without reciprocal overlapping (corresponding to a LAI close to one), the second with several superimposed layers spaced vertically in such a manner that lower layers profit from the diffuse light that passes through the higher ones.

It is clear that architectural models themselves can accommodate multilayered and monlayered arrangements, and indeed we have drawn attention to contrasted types which are precise demonstrations of those in our discussion of Fagerlind's model (p. 183). Reiteration favors multilayers, as is certainly the case when there is a crowded multitude of herbaceous reiteration complexes. In both cases crown depth seems proportional to the tendency to increase the number of leaf layers, for in a deeper crown the statistical chance as well as the architectural tendency of overlapping is greater than in a shallower one with the same architecture.

The usefulness of the morphological inversion point is that it provides an easily measurable value for the ratio between crown depth and total height, and so of the bioenergetic status of a tree. Empirically we have established that a value for this ratio greater than one half, whereby the crown begins somewhere in the lower half of the tree, indicates a free-standing tree, or at least a tree not shaded by taller vegetation. A value of one half suggests a forest tree having entered recently a vigorous phase of growth, or for trees of the present, a recent establishment in the canopy. A value less than one half, whereby the crown is shallower than half the total height, is evidence of diminished vigor, most often by suppression in trees of the future, or by senescence in trees of the present. A tree initiating a period of rapid growth conserves initially its inversion point at its starting value lower than one half total height, but this changes rapidly. As a generalized statement when dealing with a large number of trees this rule is undoubtedly useful, but one should, of course, not expect it to give what it does not possess, i.e., a precise explanation of every particular case.

Application of these facts in forest analysis must be preceded by an examination of the interaction between trees.

V. Gymnosperms and Forests

Since we have considered forests in the preceding pages using fundamental parameters like form, mass, and energy, we are confident that any vegetation type can be analyzed in the same way. Considerable emphasis has been put on form and in this respect a very great difference is found between forests dominated by gymnosperms and those dominated by broad-leaved trees, of which several are represented in this book by profile diagrams. Unfortunately we do not know enough about the architecture of gymnospermous trees, as represented mainly by conifers, to explain this evident difference very completely, but a brief speculative discussion may be useful in drawing attention to a comparative problem.

In most gymnosperms, model conformity is much stronger than reiteration. This produces trees of predictable appearance which is the foundation of their horticultural use in landscaping. Species of *Araucaria*, for example, precisely display Massart's model, in which there is a very fixed morphogenetic expression of plagiotropic branch symmetry. Even where reiteration does occur, as described by VEILLON (1976, 1978), it is partial and the effect is to produce a secondary crown by the addition of reiterated plagiotropic branches. Trees of this genus which have produced reiterated trunks are so rare as to be objects of curiosity, and show a pronounced loss of the harmonious shape which renders this tree such an attractive ornamental. Most pines show little tendency for reiteration (cf. data in MIROV, 1967). They conform to Rauh's model since short shoots are architecturally not significant. Pine plantations are noted for their monotony, because all trees conform rather precisely to the same model, e.g., *Pinus pinaster* (parasol pine of the Mediterranean), *P. caribaea* (Honduras pine, planted in many parts of the tropics), *P. elliottii* (slash pine of the southeastern United States), *P. radiata* (Monterey pine extensively planted in New Zealand). One may still find contrast between *Pinus sylvestris* (Scotch pine) in plantations with trees growing in open or exposed habitats, as in Auvergne (France) or on the sand plains of the Veluwe (Netherlands) where reiteration does produce a bushy crown. *Pinus strobus* (white pine of New England) frequently produces reiterated trunks and old trees with low forked trunks are known as "cabbage trees". They usually reflect a tree with the leader shoot destroyed by a parasitic moth when young, but which has survived with several trunk axes. In pine forests, however, as in plantations, the canopy which forms the unique structural ensemble (see Fig. 96) of this community is made of crowns conforming to the model and reiteration does not necessarily enter into the growth pattern of the tree of the present. A morphologically precise inversion point represented by a major fork is not present but may be established as the level of the lowest major assimilating branch, corresponding to the point defining crown depth according to OGAWA et al. (1965; see our Fig. 105). In trees of the present, this point is always high up in the second half of the total height, since their crowns are shallow except during the dynamic phase of the forest (see p. 326). In this respect pines can be considered to behave much like any other tree. Pines in general are markedly heliophilous pioneer plants, intolerant of competition and with a preference for permeable and relatively infertile soils. In the Guianas, *Pinus caribaea* gives good results on sandy ridges of the savannas of the coastal plains, in environments comparable to its natural sites, but performs badly on richer inland soils. *Pinus strobus* is known locally in New England as "old field pine" since it rapidly dominated farmland abandoned by (human) pioneers in favor of the fertile midwestern United States in the nineteenth century. Despite their distinctive short shoot morphology, many pines show features in common with tropical heliophilous nomads like *Cecropia* and *Musanga*, not the least of which is their relative rapidity of growth, high in comparison with other conifers, which makes them commercially so valuable.

We may contrast pines with hemlock (*Tsuga canadensis*). Branches of higher orders show pronounced (secondary) dorsiventrality so that they approach the phyllomorphic branches such as we have described in Cook's model (p. 206). The extreme tolerance of this tree to shade and competition is indicated in the profile diagram at Harvard Pond, reproduced in Figure 93. In this forest they represent the whole set of the future and relatively vigorous growth is indicated by the position of their morphological inversion points, below the middle of their total heights. We have suggested in the section on bioenergetics (p. 301) that trees with tracheids and needle leaves are designed for regular and sustained model growth neither adapted to nor too much disturbed by fluctuations in energy supply. OLIVER (1975) shows that hemlocks indeed keep growing steadily under the broad-leaved forest that has overtopped them and has entered into its homeostatic phase. This suggests that the microclimatic conditions determined by the temperate hardwood forest do not control the growth of hemlocks in any major way. Hemlocks eventually overtop and smother the present broad-leaved canopy by virtue of the dense shade they cast, eventually to form hemlock forest 60 m high, such as still exists in protected valleys in Massachusetts where there is escape from devastating hurricanes. *Tsuga* is directly comparable to tolerant dicotyledonous species of late successional stages described elsewhere, because it is a leptocaul gymnosperm in which reiteration and sequential branching are hard to distinguish, as has already been emphasized by OLDEMAN (1974a, b) for dicotyledons showing Troll's model, whereas hemlock may show Mangenot's model (EDELIN, personal communication). *Tsuga* shows in its generalized overall volume-surface relationships similar properties to dicotyledons so that its successional response is very different from *Pinus*.

The physiological condition necessary to mobilize resting meristems for reiteration is reached when meristems and cambium are driven to their maximal intrinsic performance. Dicotyledons are capable of reacting rapidly in this way to bioenergetic stimuli and reiterate readily. Coniferous plants can be considered more sluggish in their reactions and thresholds of reiterative response are less often reached. In many instances it seems, indeed, that they are never attained. In trees like *Arau-*

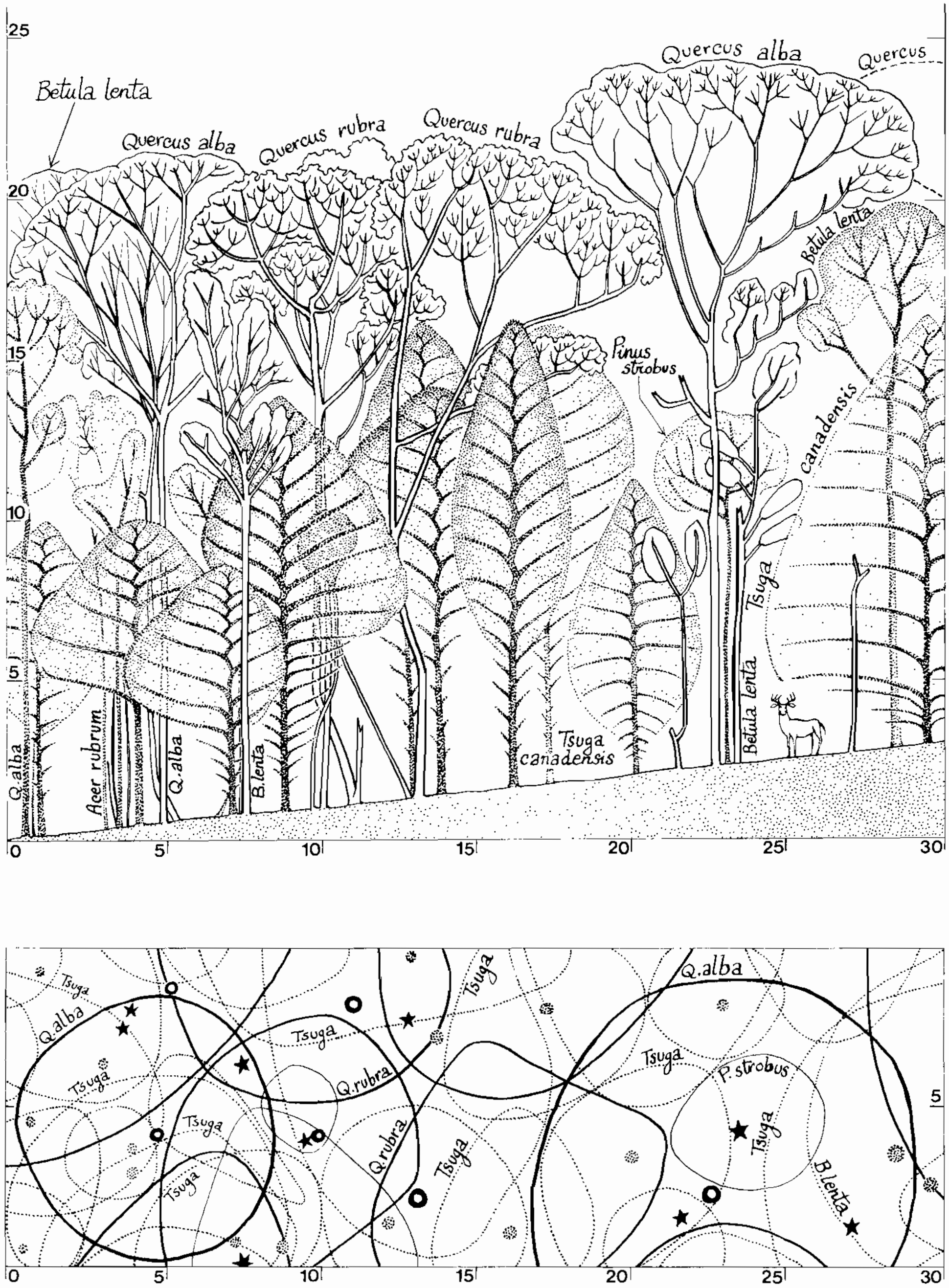


Fig. 93. Profile of a forest plot 10 × 30 m at Harvard Pond, Harvard Forest, Petersham, Massachusetts, USA, prepared by the methods described in this book. Trees of the present (*in outline*) dicotyledons; trees of the future (*densely stippled*) mainly *Tsuga canadensis*, most understorey dicotyledons are being smothered. Compare this figure to Figure 85 in order to understand slow, steady growth of gymnosperms. Further explanation in the text

caria, Pinus, Abies, Picea, complexes of *sequential* branches of smaller and smaller size have the same function as *reiterated* "treelets", "shrubs", "undershrubs", and "herbs" in woody dicotyledons. In gymnosperms, the organization of these complexes within the tree coincides with strict model organization, whereas they have considerably more freedom in the overall constitution of a whole dicotyledon (Figs. 74 and 75) which thus has greater liberty to cope with and take advantage of unexpected environmental change. This produces trees of dissimilar aspect, both representing adaptive solutions to environments which only overlap partially. Further architectural analysis of gymnosperms along these lines is likely to be informative of their ecological strategy.

D. A Note on Floristics

In previous pages we have identified where possible the plant species serving as examples in our architectural analyses and do so in subsequent pages as encountered in our forest plots. Sometimes, however, we have managed only generic or even familial identification. We can defend this apparent lack of precision by pointing out that our approach lies fundamentally outside the field of floristics. This is a consequence of our methods being of tropical origin and representing means of dealing with problems involving multitudes of species, many not yet delineated with any taxonomic precision. If, in order to tackle botanical problems in tropical regions, one had to wait until the tropical flora was completely described, this book could not have been written for perhaps another century. Where practical problems necessitate the avoidance of traditional taxonomic procedure as a first approximation, the results obtained by approaching ecological problems in a nonfloristic way should justify the procedure. Floristics become a necessity at a certain level of precision. But so long as this level is not approached, satisfactory results can still be obtained. It is by a demonstration of the value of results obtained by this prefloristic approach that one determines the level of floristic refinement needed. Plants are integrated into ecological communities as individuals and only subsequently as species.

Since Linnaeus the species has more and more exclusively been delineated by its peripheral organs, mainly leaves, flowers and fruits and with the development of microscopical technology the precision with which this is done has increasingly necessitated an emphasis on smaller parts. This is certainly appropriate where the object is to obtain greater refinement in the recognition of taxa. But a corollary of this fact is that the statistical distribution and frequency of species now mean little more than the count of groups of certain leaves, flowers and fruits (pertaining to individual plants) and their diffusion in the vegetation, and such data refer to symptoms rather than causes. When modern phytosociologists try to fit these groups of organs into horizontal and vertical patterns no answer is found to the question why one species of leaf, flower, and fruit occurs here and why another kind occurs elsewhere. There is, indeed, a correlation between such statistical patterns and organization in nature, but as far as the explanation of its guiding principles is concerned the road ends there.

Clouds of leaves, flowers, fruits, trichomes, and other diagnostically useful parts do not hang somewhere in the air but form part of whole organisms. The architectural method attempts to fill a taxonomic gap by establishing the organic continuity which determines the distribution of otherwise disparate parts. The morphology and morphogenesis of leaves, flowers, and fruits are specifically diagnostic and genetically determined. But so also are growth model and architecture, rate and periodicity of growth, capacity and rate of reiteration. The one can be conveniently represented and stored in a herbarium, the other cannot. "Classical" taxonomic characters provide parameters whereby we can make inferences about adjustments for light interception and moisture conservation, about sexual reproduction, dispersal and likely evolutionary events. The architectural features sum up the parameters which determine the role of the plant in vegetational superstructure. One can understand the function of vegetative architecture without necessarily knowing the behavior of the smaller organs, but one cannot fully comprehend assimilation and reproduction without any knowledge of their architectural coherence. Different systems have been devised by several workers who understood this predicament and used a physiognomic analytical approach (e.g., RAUNKIAER, 1934, for plants; RICHARDS, 1952, for forests; AUBRÉVILLE, 1965, for tropical vegetation). Essentially these all stand outside conventional floristic analysis.

Replacing physiognomic methods by architectural ones heightens the precision of the approach to a level consistent with what is usual in morphology and taxonomy without losing their applicability to macroaspects of ecosystem analysis. The methods also permit a better definition of floristics since they distinguish the exact role of a species in vegetation and in the successional mosaic and its seral position with regard to other species.

An integration of the architectural and floristic methods has been tried by BUDELMAN in his studies of Compositae as elements of pioneer vegetation in the interior of Surinam. His diagram (BUDELMAN, 1974, pp. 25–27), which he called a model of the relation "dispersal mechanism-habitat-growth model" takes the form which is here exemplified by the one he used for anemochores:

Open field — Wind
Habitat — *Dispersal agent*
Examples: *Eupatorium odoratum* L.
Erechthites hieracifolia (L.) Rafin. ex D.C.
Growth model — *Dispersal mechanism*
"Cymous model" — Pappus

His growth models are established by parameters different from those used by us for, as the name "cymous model" indicates; he reasoned from the inflorescence down to the plant, whereas we build the model from the seed and its germination on. Even if, in herbs, the inflorescence takes a preponderant importance (*r* strategy!), in our opinion following plant development from germination to seed-set allows the growth pattern to be more surely established than tracing it back from its final result, which may mirror the effects of environmental conditions which no longer exist at the time an analysis is made.

Chapter 5 Forests and Vegetation

A. The Architecture of Forest Plots

Architecture is a concept that can be applied not only to individual plants or their parts, but to all living systems. For example, it has been used by ROLLET (1974) to indicate the population characteristics of forests, whereby mathematical relationships are expressed graphically.

In our use of the term, architecture has been referred to momentary form complexes, and the processes which determine the change from one architectural phase to another have been represented by a growth model. It is useful to speak of *forest architecture* and *sylvigenetic model* by analogy with *tree architecture* and the *tree model,* with reference to their differences of scale and controlling factors. In a single tree, the model includes a set of axes organized according to the differentiation sequence. This sequence is what the tree has in excess of the mere sum of its axes, i.e., what distinguishes it from an arbitrary collection of axes. At the scale of the forest, the model includes a set of trees aggregated as vegetation by interaction between a diversified set of trees. This coherent diversification, which has been expounded in the preceding sections on trees of the present, the future and the past, is what the forest has in excess of the mere sum of its trees, i.e., what distinguishes it from a collection of arbitrarily chosen trees.

In the present chapter we look at forest architecture of an area sufficiently small to be capable of analysis because it represents a uniform architectural phase. Our method is quite unstatistical, just as it was for individual trees, where not the average, but the rare tree was studied, conforming to and so revealing its initial model. Intact architecture is less easy to detect at first sight in forests than in individual trees, and indeed, of the examples presented later in this chapter nearly all show some aberrant features.

In this respect, it might have been some help to study tree plantations which are artificially homogeneous, but no such cultures were established in French Guiana where the analytical method originated. Some of the schematic diagrams from the treatise on temperate sylviculture by HOUTZAGERS (1956), representing technical sketches of planted forest before thinning or harvesting, effectively correspond to simplified versions of the natural temperate forest, e.g., that represented by Figure 102.

The size of the natural forest plots examined in this chapter has been empirically determined, and coincides rather well with the smallest sample (plot or "station") in statistically oriented vegetation analysis as for example by GODRON (1971), although here we do not establish plot size by a statistical method. In a plot of 20 × 30 m, in tropical rain-forests with maximum tree heights of between 30 and 50 m, and considering only those trees higher than 10 m, two important factors were evident. The first of these concerns disturbances and horizontal gradients. In general, over an area of this size, the forest is either intact or shows only one disturbance, such as a recently fallen tree, or one gradient, e.g., soil depth, so that the effect of this one factor alone could be studied. The second advantage is that these plot dimensions make for an easily designed and easily legible profile diagram. For forests in New England, the practical dimensions proved to be of 10 × 30 m where the trees were up to 25 m high.

As a general rule, this gave as the useful dimensions for profile plots a width of between one-third and two-thirds of the height of the forest, and a length at least equal to this height. In tropical rain-forests higher than 30 m, the profile is not made longer, to minimize the risk of introducing more than one disturbance. To construct plots of a 10 cm high lawn by analogy, the dimensions according to this rule would be 5 × 10 cm. In unpublished studies of rain-forest undergrowth DE GRANVILLE (personal communication, 1973) used plot sizes of 5 m wide for the forest layer of trees between 10 and 5 m high, 2 m wide for the layers with a height from 5 to 2 m, and so on. In the present book, the different components of forests are treated according to this principle, and it is also relevant for discussions on succession. We appreciate that this method of sampling is crude, but it permits useful comparative data to be gathered.

I. The Layered Forest

Usually rain-forests, and more and more often other vegetation types (cf. WHITTAKER, 1970), are described as "stratified", i.e., made up of discrete "strata", the concept being an old one; RICHARDS (1952), in his lengthy discussion goes back at least as far as 1919. More recently ROLLET (1974) has indicated how extensive is the literature on this topic. From it three areas of common agreement emerge: (1) it is more or less irrelevant whether strata exist (GODRON, 1971) or not (RICHARDS, 1969; SCHNELL, 1970), but convenient for analysis to treat vegetation as if they existed; (2) strata are subdivisions of the whole plant population of the forest (BUDOWSKI, 1961; RICHARDS, 1970; SCHNELL, 1970; GODRON, 1971; SHIMWELL, 1971); (3) strata are horizontal (see notably the schematic drawings of RICHARDS, 1970).

The concept of stratification though often disputed is so firmly established in ecological discussion of tropical forest that writers may assume its presence and misread descriptions where it is not intended. Thus ROLLET (1974, p. 32) seems to have mistaken the description by OLDEMAN (1974a) of inversion surfaces (discussed in this book on p. 356) for "strata", though the two should not be confused. Our opinion is that there are *no strata in the forest as subdivisions of the total population,* but that in certain plots there are demonstrable horizontal "sets" composed of trees of the present. For this reason we have sparingly used the word "layer", even then with some apprehension, but repeat that our layers do not correspond to the strata (real or imagined) of previous ecologists but refer to aggregations at certain levels of particularly built trees, not to the total tree population. Before we describe this in detail, we permit ourselves a few comments about topographic "strata".

Those who believe in general "stratification" of vegetation prefer either to exaggerate its stability or to have no concern for the time-consuming way in which a tall forest grows. It is assumed that "disturbances" in the rain-forest are rare, for if they were more frequent "stratification" could not be as general as presumed – the frequent breaking open of the canopy would obscure it. Few tropical or temperate botanists, to our knowledge, have commented on the enormous abundance of fallen trees on the forest floor; it is tacitly assumed that the turnover of tropical forest trees was small with the occasional death of a tree by parasite attack or disease. In height–frequency curves, for example, no author as far as we know has ever distinguished trees in the vicinity of large fallen trunks from those more remote from dead and fallen wood, which otherwise would have been a logical thing to think of when one looks for "undisturbed" rain-forest. Even then, there would remain the possible time lag between total decomposition of a fallen tree and complete reconstitution of the damaged forest. In 1933/1934, DAVIS and RICHARDS initiated the excellent profile-diagram method which, applied with the desired degree of precision, leaves nothing to the imagination. Among the profile diagrams produced since then, a number of which are reproduced and commented on in OLDEMAN (1974a), few, in fact, represent undamaged forest structures.

We must remember at all times that tropical foresters lack that one most valuable tool which their temperate counterparts take for granted, the existence of datable growth rings in the secondary wood. A precise time scale is thus lacking for demographic studies in tropical forests.

A consideration of the concept of the "emergent" tree, so frequently discussed by tropical ecologists, will demonstrate this static approach. Emergent trees are regarded as rising above the existing canopy; still, they most often show the crown characteristics of a forest-grown and not a free-standing tree. How can such trees "emerge"? If they indeed did emerge and grow further up into full sunlight, they would enjoy enormous biological advantages but, nevertheless, in nature they are so rare as not to form a closed forest canopy. Some attempts have been made to ascribe the discontinuity of emergents to their frequent wind-throw (AUBRÉVILLE, 1965), but this would not be consistent with a widespread existence of undamaged lower strata. The existence of emergents seems a very strong argument against "stratification" as a constant characteristic of tropical forests in general, at the level of emergent crowns as well as lower down.

"Strata" are thought to be horizontal. However, there was no published analysis of "stratification" on slopes, although there is mention (as by SCHNELL, 1971) of frequent tree-fall on steep hillsides. If the "continuous canopy" is at 30 m from the ground on top of a hill of 200 m high, it would have to be at 230 m at the base of that hill; this clearly cannot be. Two possible explanations exist: either "stratification" is not horizontal, or the canopy is made up of a roofing-tile sequence of horizontal canopies, which better fits the circumstances as we will show (p. 360). Consequently height–frequency curves would have to be established exclusively on flat country to serve as proof for or against "stratification". Descriptions of tropical lowland forest have placed little emphasis on the role of micro-relief and its interaction with forest structure. In most of tropical South America, forest "lowland" closely resembles pea soup in which the peas, half floating, are steep little hills, and the more or less swampy valleys between them are the soup.

For the foregoing reasons, the most-used elements in discussions on "stratification", height–frequency curves, are not relevant proof, even if thorough and extended like those of ROLLET (1974), who analyzed 3000 km^2 in Venezuela. Research along these lines is not likely to yield any new information on the subject. The only convincing demonstration of "stratification", up till now, has been direct observation, as in layered early successional forests (BUDOWSKI, 1961) or layered species-poor forests (RICHARDS, 1952). Secondary vegetation has been thought to be rare in nature, and mainly to result from disturbance by man (VAN STEENIS, 1956a; BUDOWSKI, 1961), as has also species-poor tropical forest (RICHARDS, 1952). This could lead to the idea that "stratification" is correspondingly rare.

The most serious handicap in studies of layering is, that they do not incorporate precise ideas on the growth and form of individual trees. The gap between interpretation of growth processes, according to concepts like apical dominance on the one hand, and the structure of the forest on the other, has not been bridged. Approaches which attempt this are found in the pipe model theory of SHINOZAKI et al. (1964) and HORN's (1971) study of principles of leaf distribution. The crown-depth diagrams of OGAWA et al. (1965) are promising means for the analysis of forest structure, but they do not clarify concepts of stratification (see OLDEMAN, 1974b).

It will be seen later in this book that layering is shown by forest phases occupying a minority of the total forest surface (p. 366ff.), and that the "layered climax" covers an even smaller portion. Nevertheless, the understanding of these parts of the forest, in which layering constitutes a functionally very important aspect of the mechanism of homeostasis, appears to be essential for subsequent comprehension of nonlayered parts of the forest. "The" forest is neither uniformly layered, nor uniformly unstructured, nor vertically homogeneous; parts of each arrangement enter into its construction, intermixed in diverse ways. This concept is, therefore, no longer simplistic, but how much more fascinating it becomes! We have to examine each arrangement in turn, beginning with the simplest – the layered forest plot.

II. The Architecture of Homeostatic Forest Plots

Where the forest has reached a stable state which may be termed homeostasis (cf. VAN DER PIJL, 1969 and further discussion on p. 370ff.) its architecture can be represented by the schematic profile diagram of Figure 94 where the trees are distinguished simply as those of the present, future, and past, recognized by the criteria we established in the previous section. Field examples of precise plots drawn in the same way are shown in the following section (Figs. 98–103) and in OLDEMAN (1974a, b). They provide specific examples of the totality we think of as "the forest". The method is currently restricted to dicotyledonous forests, but there is no reason to believe that it is not applicable to all types of vegetation, once appropriate architectural studies of individual plants have been made. We still lack very comprehensive studies of gymnosperms and herbaceous plants, for example.

To make the transition from the individual tree to the scale of the forest plot, trees of each category will be considered as a *set* (assemblage or *ensemble*). Consequently we have a set of the trees of the present, a set of the trees of the future, and a set of the trees of the past, referred to simply as set of the present, future, and past, respectively. It is the interaction between trees which determines each set, and between sets which determines the creation and control of microclimate within the forest, at the scale of one plot. Since it is made up of the largest trees, the set of the present determines overall architecture and the main modulations of the vertical light gradient. The set of the future contains a potential forest of tomorrow, i.e., those among its members which do not die precociously, filling in the holes in the existing architecture and codetermining the main modulations of the vertical gradient of relative atmospheric humidity, since the transpiring crowns of its members occur throughout the forest. The set of the past provokes transient irregularities in this pattern. The three sets need separate discussion before we examine overall architecture. This is done on the basis of the descriptive model in Figure 94.

1. *The Set of the Present*

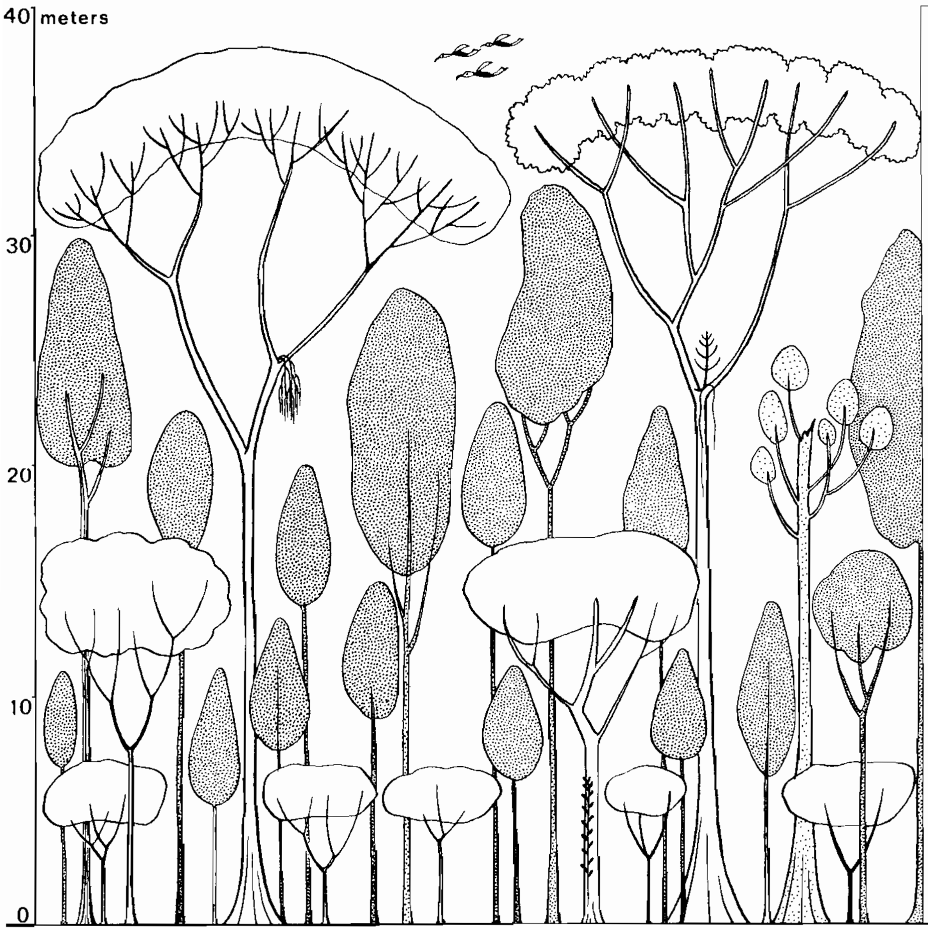
Trees drawn in outline in Figure 94 represent the set of the present. From their shape in comparison with Figures 74 and 92, it is clear that they are indeed trees of the present, expressing as many waves of reiteration as their size allows. Again we emphasize that size is not an absolute criterion for phase of development. On the figure, woody plants of 6 to 38 m height are included in this set. It is convenient to refer to anything woody in a tropical forest, less than 10 m high as a "shrub", without worrying about categories established by definition. This height limit is arbitrary because there is no fundamental architectural reason for so distinguishing shorter plants. In temperate forests, where proportions are smaller, we will put the height limit for shrubs at 5 m.

Proceeding upwards from the forest floor, one finds crowns concentrated at a few height levels. We stress again that these are not "strata", because they refer to only one set, containing trees of the present, and not the whole population. Within such a set we subdivide according to discrete height levels a number of *structural ensembles*; in Figure 94 there is a structural ensemble of "shrubs" with its height limit at about 6 m and two arborescent structural ensembles with height limits at 16 and 38 m. Of course, these limits are not of identical value for every plot with the same kind of architecture. Numerous factors determine these height levels: the heights and tree densities of ensembles above them, density of crown reiteration, configuration of leaves, presence or absence of lianes. Sometimes the presence of animals in the upper structural ensemble is significant. LESCURE (1974), describing the influence of nesting colonies of herons in the upper structural ensemble of *Avicennia* forests in the coastal zone of French Guiana commented on mechanical damage, accumulation of droppings below and reactions of underlying crowns to these factors.

For statistical recording of "strata" GODRON (1971) used normalized heights at 0.05, 0.10, 0.25, 0.5, 1.0, 2, 4, 8, 16, and 32 m. In our experience this corresponds to average levels around which oscillate the heights of successive structural ensembles in homeostatic forest plots with an amplitude of some 25% of each height. In the tropics one higher order exists, oscillating around a mean height of 64 m (see the profiles of plots from the Asian tropics in RICHARDS, 1952; ASHTON, 1964). The theoretical and ultimate order would oscillate between 96 and 160 m, with an average height of 128 m, only capable of being achieved in a homeostatic state by exceptionally tall extra-tropical trees like species of *Sequoia* and *Eucalyptus*.

To seek an explanation for the coexistence of structural ensembles at different heights in the set of the present, we must look beyond the behavior of its individual members, at their organized interac-

Fig. 94. Diagrammatic representation of the ▷ profile of a perfect homeostatic plot in the tropical forest, such as very seldom exists, in terms of its structural components as groups of trees representing sets of the present, future and past. Further explanation in the text, also compare Fig. 110



SET OF THE PRESENT	SET OF THE FUTURE	SET OF THE PAST	INFRASTRUCTURAL SET
arborescent structural ensemble II	empty layer		dense zone
	relatively densely populated layer		thin zone
		damaged trees	
arborescent structural ensemble I	less populated layer		dense zone
	relatively densely populated layer		thin zone
shrubby structural ensemble	less populated layer		dense zone
unobserved zone			dense zone

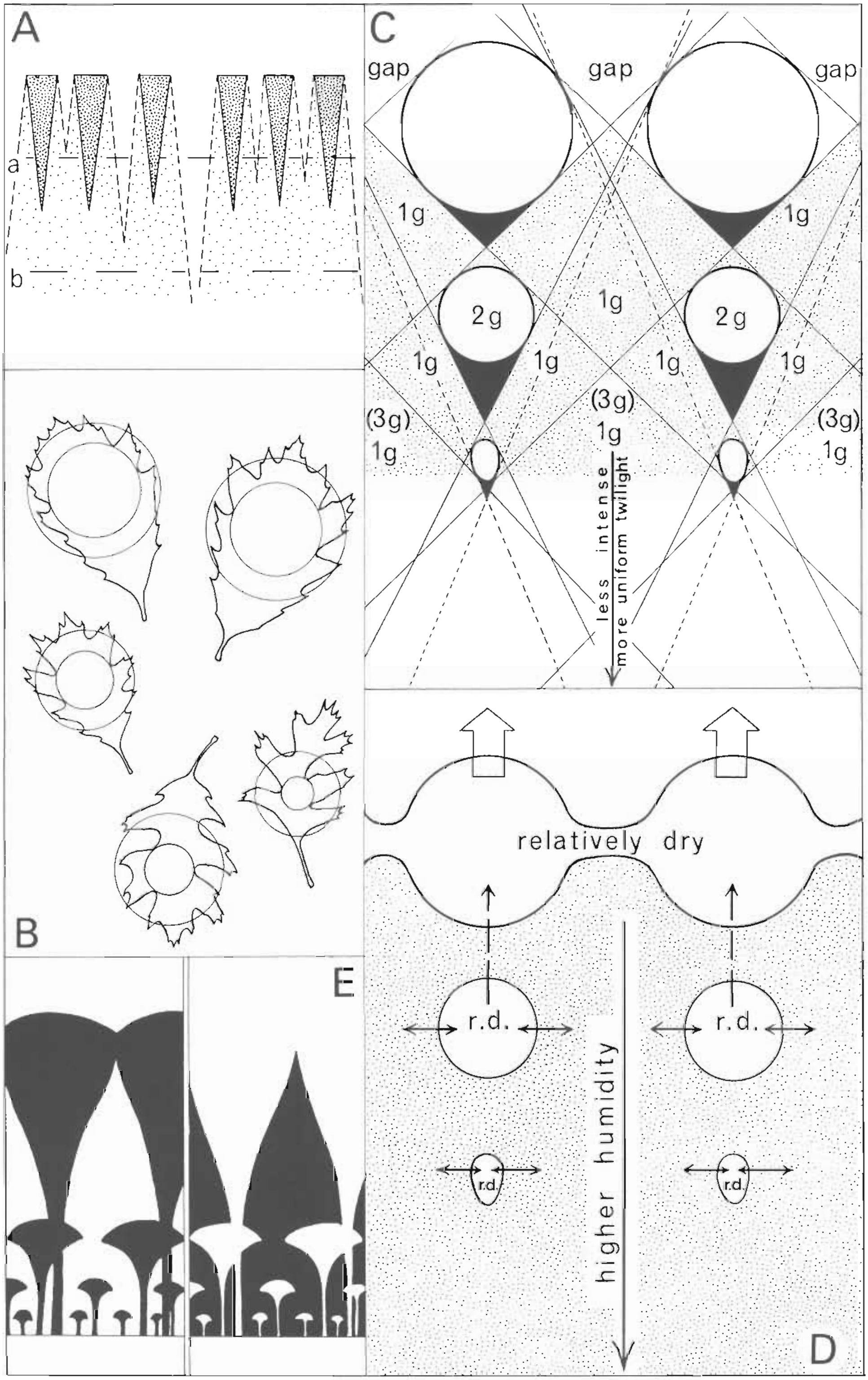
Root zone = imperfectly known _

tion. In a homeostatic forest plot the crowns of the set of the present intercept light in a way which we now analyze, disregarding for the moment the trees of other sets. In the vertically successive structural ensembles there is a mosaic of crowns shadowed by those above them. It is easy to estimate the amount of light absorbed by the highest structural ensemble, constituting the forest canopy, since it is simply the sum of the amount of light intercepted by each of its member trees. Under this canopy, however, individual influences are hard to recognize and a simple summation is inadequate.

Horn (1971) developed a geometrical model of shadow patterns under a layer of leaves, depending principally on the amount and direction of light penetrating through gaps between the leaves (Fig. 95A). It is possible to develop an analagous model for tree crowns separated by gaps. Figure 95C represents a very formalized forest in which the trees have opaque, globular crowns and form a single layer. Through the gap between two trees light enters and illuminates zones below, as shown. Immediately under each crown there is dense shade (in nature this would certainly receive some light penetrating through the crown). At some distance from the crowns there are atmospheric cells receiving light from one gap (1 g), two gaps (2 g) and three gaps (3 g). We may make this scheme correspond more closely to nature by adding a lower structural ensemble, which would reiterate under the 2 g conditions, and so we would find crowns at this appropriate level as another subdivision of the set of the present. The same principle would apply at a lower level with further small shadow cells where again light at a 2 g level is received. In this system there can be no cells with light from three gaps since interception by the crowns of lower structural ensembles always reduces the light intensity to 1 g. At greater depths in the forest the cells become so small as to dissolve into a uniform twilight with travelling sun flecks.

We must agree, however, that trees of the present do not have the uniform globular shapes we have allowed them in our model. A possible way of achieving a geometrical correction for representing tree models and reiteration patterns is suggested by the method Horn (1971) used to formalize complex and diverse leaf shapes. He represented leaf shape by drawing two circles (Fig. 95B), the first

Fig. 95A–E. Hypothetical forest construction ▷ on the basis of light and humidity gradients.
A Shadow of a leaf layer. (After Horn, 1971.) Leaves in the first layer would completely obscure the sun from parts of the leaves in a layer at *a*, but not from any part of a layer at *b*.
B Leaves of black oak (*Quercus velutina* Lam., Fagaceae) from a seedling and different parts of a tree, progressively more lobed at higher levels. In each leaf the small circle is the largest that can be inscribed within the outline of the leaf, the large circle has the same surface area as the leaf. (After Horn, 1971.)
C Diagram to show the distribution of decreasing light intensity below a canopy of tree crowns, represented by the circles, according to suggestions of Horn (1974, personal communication). The uneven distribution of shadows produces a pattern of light cells (some value of g, the fraction of light admitted by one average canopy gap). The distribution of these "cells" permits the development of tree crowns at lower heights below the canopy.
D Gradients of atmospheric relative humidity, as determined by the distribution of crowns established by the pattern in *E*.
E Schematic profile of the space occupied by the sets making up the forest; *left*, set of the present (*in black*) with some form of layering; *right*, space available for the set of the future (in black), without precise layering. (After Oldeman, 1974a.) Further explanation in the text


A
a
b
B
C
gap
gap
gap
1g
1g
2g
1g
2g
1g
1g
1g
1g
(3g)
1g
(3g)
1g
(3g)
1g
less intense
more uniform twilight
relatively dry
r.d.
r.d.
r.d.
r.d.
higher humidity
D
E

was the biggest circle that could be described within the limits of the leaf outline, the second was the circle that has the same surface area as the leaf. The ratio between the areas of these circles was used for making accurate predictions of the distance between succeeding leaf layers. The geometry of crown shape being more complex, similar formalization has not been attempted by us, but its application would allow us to correct the shadow cells in Figure 95 for real crown shape. This shape accounts among other things for the differences in the angle of incoming light and hence for the fluctuation in height in successive structural ensembles by elevating or lowering the level at which conditions favorable for reiteration could be found. When discussing vertical gradients, this fluctuation will be further specified.

The above approach to the problem of superposition of structural ensembles is a physical one. To this must be added the biological one, since it is clear that each ensemble possesses its own array of species, and sometimes even families (implied, for example, in the descriptions by OLDEMAN, 1974a; SCHULZ, 1960; HOLDRIDGE et al., 1971). This systematic segregation may be taken as an indication that different species can achieve maximum photosynthetic activity under different light regimes.

Sometimes epicormic reiterated complexes of taller trees can be observed to associate with lower structural ensembles (OLDEMAN, 1974a, Figs. 53, 63). This may be a method whereby some trees of the future, hidden in the darker shadow cells of the forest, extract photosynthetic energy out of lower and more privileged light cells. Other associates of the structural ensembles made by the trees are lianes and epiphytes, the latter becoming progressively more abundant in the higher parts of the canopy (cf. HLADIK, 1974).

Architecturally, the reiteration pattern gradually changes from the forest canopy towards the undergrowth, but there are no precise limits which allow a neat distinction between trees and shrubs. In the upper structural ensemble, there are very numerous waves of reiteration, the lower ones arborescent. These arborescent waves become rare in the underlying structural ensemble, and disappear altogether in the first ensemble under 10 m. From 10 to 2 m, reiteration first becomes mainly herbaceous, then progressively less common. Below the level of 2 m in the forest, reiteration plays an accessory role in forest architecture, but a very important one in model regeneration.

The set of the present, subdivided into structural ensembles, is the architectural backbone of the forest. In a homeostatic forest plot, the set of the future, next to be examined, is completely determined by this existing structural pattern.

2. *The Set of the Future*

In Figures 94 and 95, the set of the future is indicated by all those trees which are densely shaded. Again these trees are not recognized by size, but by the architectural criteria we have already established. Furthermore these trees cannot be referred to collectively as "young" trees, because they may be of the same chronological age as the trees of the present. That this does occur has been established by OLIVER (1975) in his demonstration of the uneven-size, even-age relationships for oak-maple forests in New England (Fig. 96). We cannot make any similar claim for a tropical forest because we cannot make statements about tree age on the basis of growth ring analysis. We suggest that tropical and temperate forests are similar in this respect because the same architectural principles apply in both of them. If the word "young" is applied to trees of the future this must refer to their *biological* age, i.e., their further growth potential.

No subdivision into structural height levels is possible for the set of the future. Its members are inserted into the space unoccupied by the set of the present and, in terms of the simplified diagram of Figure 95C, suppressed trees of the future occupy the least favorable shadow cells. Any layering is a passive phenomenon, determined by the activity of trees of the present and indicated by the space made available (Fig. 95E).

The collective behavior of the trees of the future has an impact on microclimate, principally on relative humidity of the atmosphere. The bioenergetic and energy exchange pattern of these trees has been discussed (p. 321, and OLDEMAN, 1974a) and it is suggested that transpiration is at a maximal level.

The very humid and shady microclimate of the set of the future provides an environment to which a group of epiphytes is peculiarly adapted. These are the "mobile plants" which grow vertically on tree-trunks and are represented by members of the Cyclanthaceae (e.g. *Carludovica, Dicranopygium*), Araceae (e.g., *Heteropsis, Philodendron*), Piperaceae (*Peperomia* spp.) and possibly some filmy ferns. As these plants grow upwards they die back basally so that the plant is gradually displaced vertically. Secondary root connection to the soil is possible and has been observed in *Carludovica* sp. (OLDEMAN, 1974a), together with expansion of their crowns when the plants reach a suitable light cell. During their creeping phase these plants are supplied with nutrients dissolved in rain water running down the host trunk. Often their leaves, however, are xerophyllous. This group of epiphytes therefore provides an example of adaptation to the microclimatic condition of the homeostatic forest.

As long as the homeostatic state of the forest plot is maintained the set of the future does not move and just survives.

3. The Set of the Past

It is scarcely possible to speak of a "set of the past", since trees of the past do not interact in any collective way. They are more likely to exist before homeostasis is established and so can be regarded as an influence lingering from an earlier disturbance of forest architecture. In a homeostatic plot the tree of the past is likely to be indicated by its remains on the forest floor. Only one example (lightly stippled) is shown in Figure 94.

The homeostatic forest plot can be thought of as a banquet at which three groups attempt to dine: the set of the present are successful but eat themselves to death on the abundant resources made available, the set of the future sit hungrily at the kitchen door hoping for a vacated place, the trees of the past are the elderly, decrepit, dying beggars chased away from every dish.

4. The Infrastructural Set: Meristems

When discussing strategies it has been remarked already that the most clear-cut elements of vegetation that the population biologist can count are neither individual plants, nor models, but meristems. In the forest two populations of meristems can be distinguished. The members of the first are functional, although they may be at rest between successive growth periods if their activity is rhythmic; they include branch meristems and germinating seeds. Meristems of the second group are latent, but available for mobilization when it is necessary for the plant to adjust to changing ecological conditions. In this second class both dormant branch meristems and seeds are included. The latter in most species have the shortest life span (NG, 1978).

The population of functioning meristems will be called here the *infrastructural set*. They are the ultimate source of productivity and are analogous to the industrial infrastructure of human society. The population of resting meristems will be called the *infrastructural complement.*

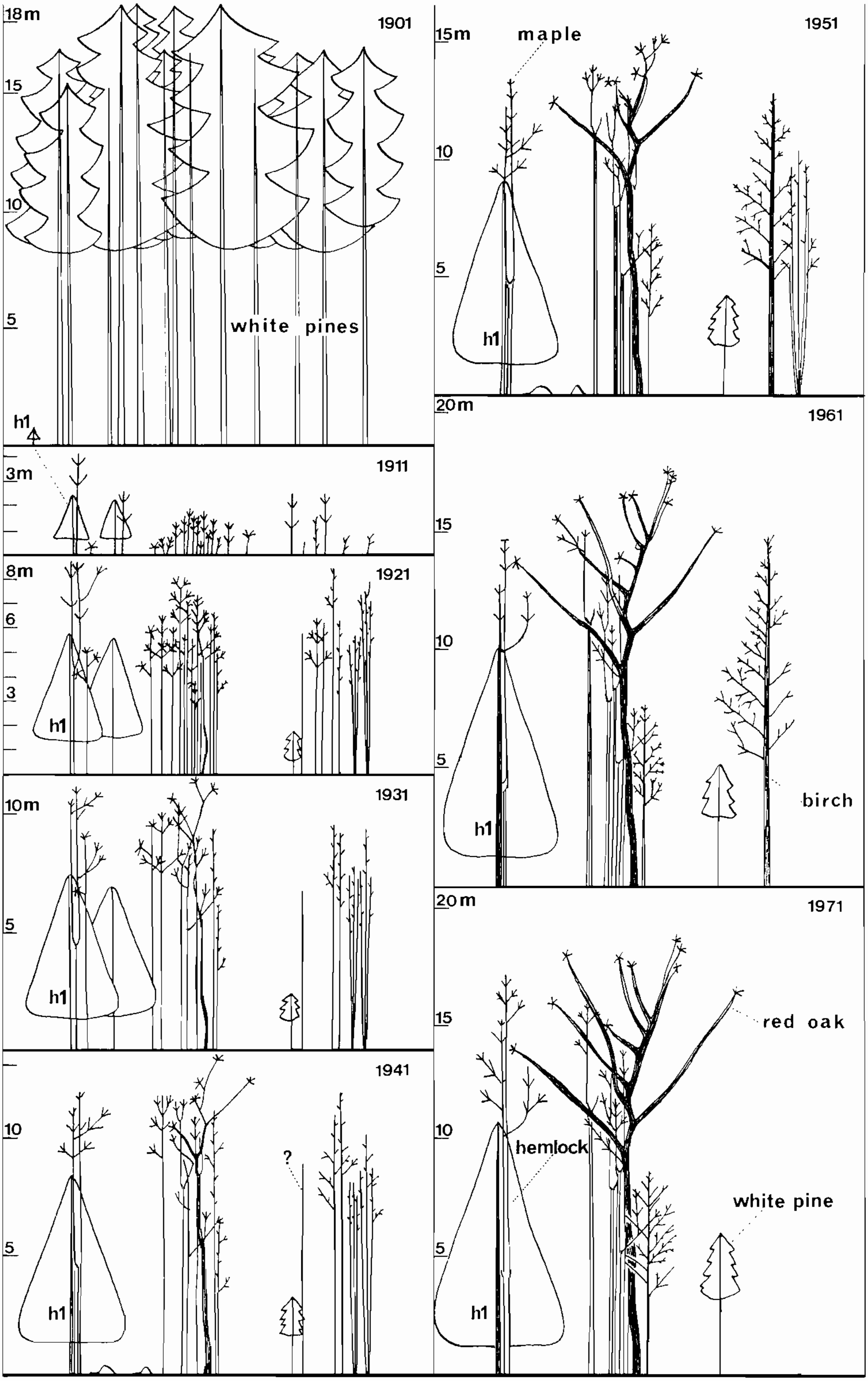
One can represent the infrastructural set in a homeostatic forest plot by Figure 97A which is derived from a schematic profile by putting a point, representing the apical meristem, at the end of each growing branch and omitting the contours of the trees. In the structural ensembles of the set of the present there are many reiterated complexes bearing many contemporaneously active meristems. In the set of the future, since reiteration is rare, there are fewer meristems. Towards the forest floor the density of meristems becomes more uniform while on the forest floor itself is a concentration of meristems of seedlings and herbs to which might be added the subterranean meristems of rhizomatous plants, e.g., Scitamineae, and the meristems at or below ground level in creeping plants, small Rubiaceae, Gesneriaceae, Melastomaceae. In well-established homeostatic forest the shade may be too dense for such meristems to be long active and they might well be included in the infrastructural complement as would, of course, all seeds. When activity occurs seasonally, these plants are cryptophytes in RAUNKIAER's sense (1934).

The infrastructural set and the infrastructural complement summarize the functional characteristics of the forest. We will find it useful to consider coherent populations of meristems when examining them in the context of successional processes in the chapter dealing with sylvigenesis.

5. *Geometry of Homeostatic Forests with Their Vertical Gradients*

Figure 95E represents a schematic transect of space occupied in a homeostatic forest plot by the sets of the present (left) and future (right), shaded like positive and negative images. These diagrams can be compared to the configuration of shadow cells (Fig. 95C) and humidity cells (Fig. 95D). Figure 95E represents the biological pattern which results from the physical patterns of scattered light and diffusion gradients of water vapor; but with the contours considerably more regularized than occurs in nature. Another image is possible, which in some respects is the counterpart of the first: in a canopy with very heterogeneous crowns i.e., with very heterogeneous gaps, shadow cells could even each other out and the result would be the existence of microclimatic layers with distinct average characteristics, between succeeding structural ensembles. In truth, the situation lies somewhere between complete differentiation into mi-

Fig. 96. Development of an even-aged oak-maple forest in New England (USA) after clear-cutting of a white pine stand in 1901. (After OLIVER, 1975.) Between 1931 and 1941 a hurricane wrought havoc in the region; this explains the disappearance of several trees. Note sinuous growth of trunk in the oak (reiteration). The author has drawn this series of diagrams after counting growth rings in all branches and trunks of still existing trees in 1971, and analyzing the traces which were preserved in the soil to discover the existence, form and age of trees which died between 1901 and 1971. This figure is to be compared with Figure 110, which represents tropical sylvigenesis as appreciated following totally distinct, architectural, criteria ▷


18m
1901
15
10
5
white pines
h1
3m
1911
8m
1921
6
3
h1
10m
1931
5
h1
1941
10
5
?
h1
15m
maple
1951
10
5
h1
20m
1961
15
10
5
birch
h1
20m
1971
red oak
15
10
hemlock
white pine
5
h1

croclimatic cells, and the existence of different layers with constant average conditions. This last state can be described by graphs representing light intensity and relative humidity plotted against height within the forest, in which the points have average values for a plot (Fig. 97C).

WHITTAKER (1970, Fig. 2.1) has already estimated that the shape of the light intensity curve should be modulated and neither linear nor uniform. His presumption is based on the premise that the forest possesses layers of tree crowns (but not layers of functional sets in our sense) between which there would be empty spaces without light interception. This treats all crowns as equal, but our previous discussion suggests that it is closer to the real circumstances to think of maximal light interception in the structural ensembles and a diminished interception in the small suppressed crowns of trees of the future.

OLDEMAN (1974a) made estimates of this differential light interception. He measured the projection of the crown of each tree on to the forest floor by placing a number of observers vertically under the tips of the outermost branches. These observers provided map reference points. The process was repeated for all trees. By planimetry the surface of these projections for each of the structural ensembles was mapped. There are as alternatives simple optical devices for measuring vertical crown projections in the absence of observers (e.g., JACKSON and PETTY, 1973). KIO (1971) suggested a method using ground photography. Still, the practical difficulties in accurately observing distant branches among other branches, by other means than the human eye, should not be underrated.

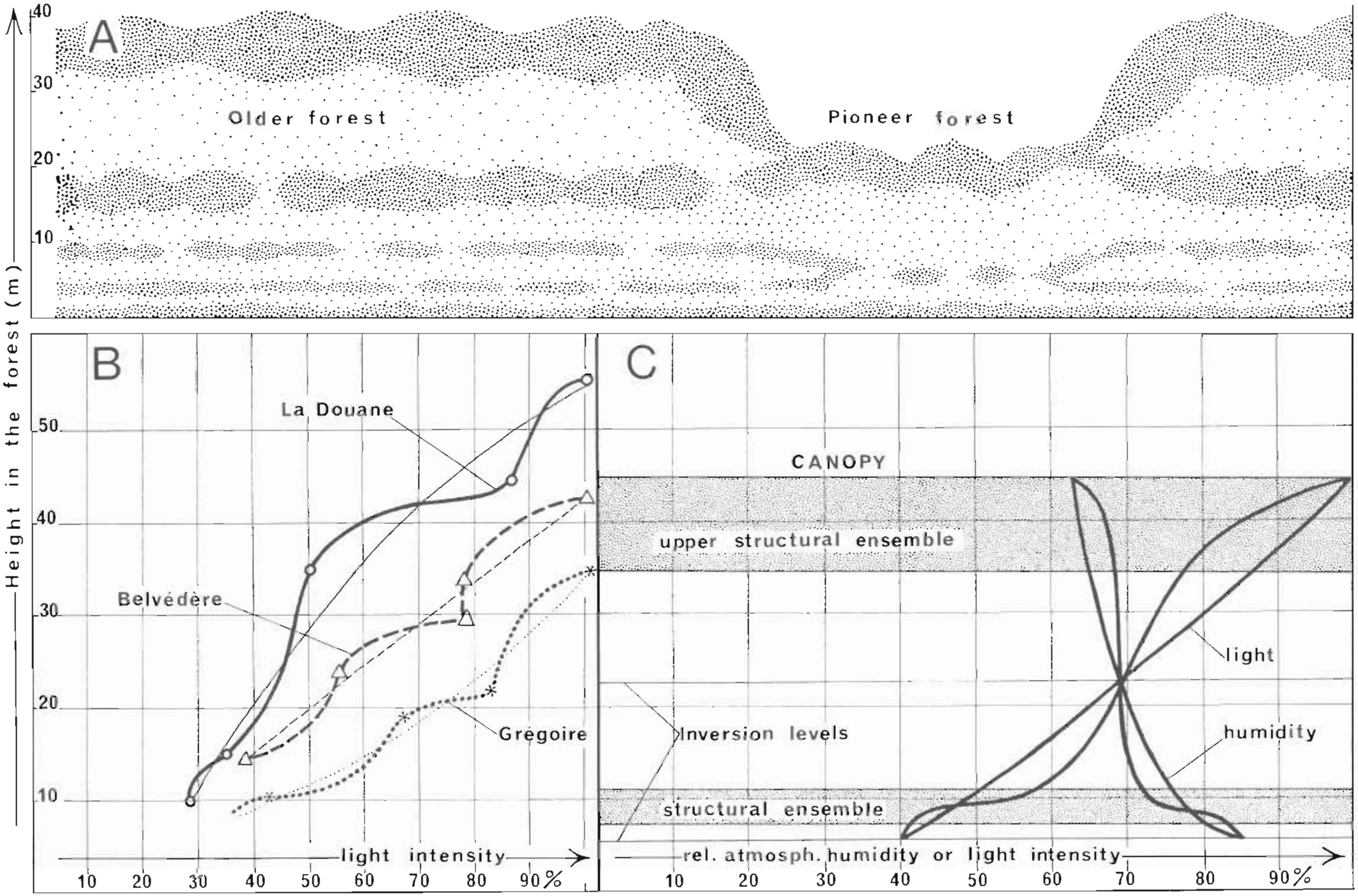
Results for three forest plots are shown in Figure 97B, confirming the general shape of the vertical light gradient predicted by WHITTAKER. The curves are drawn at a relative scale as a percentage of the total light intensity outside the forest. These values are calculated on the assumption that each crown lets through about 10% of the incoming light. This rough and preliminary figure is obtained from light measurements using an ordinary photographic exposure meter under the dense crowns of cultivated trees. Our curve is the modulation of a regression line drawn free-hand and giving the *average* light extinction between canopy and forest floor whereas the modulated line, passing through all calculated points, gives the *real* extinction. The form of the regression curves is a function of forest density; the straight line indicates an aver-

Fig. 97A–C ▷

A Population of functioning meristems (each represented by a dot) or infrastructural set in two kinds of forest (pioneer and older). The layering represents concentrations of meristems determined by the structural ensembles.

B Gradient of light intensity as a function of height determined for three plots on the basis of canopy density above each height, established by planimetric methods (see text). The actual profiles (Douane, Crique Grégoire, Belvédère) are presented and discussed in Chapters 3, 4, and 5 in OLDEMAN (1974a). See also Figures 100 and 103. In each set of figures the values oscillate about a uniformly decreasing value (represented by the less prominent line) which is determined essentially by the set of the future, its shape relating to tree density. (*Note:* The height scale for the Mont Belvédère hill-side forest is horizontal, not parallel to slope; this accounts for the different starting point. In Crique Grégoire, all trees of more than 6 – not 10 m – high have been measured.)

C Principal ecological gradients with their major modulation and their relation to forest architecture as determined by structural ensembles. The gradients are determined from different sources (but see especially CACHAN and DUVAL, 1963) and remain to be determined accurately for a single forest plot. They are intended to show how the ecological inversion surfaces are related to modulation of microclimatic conditions


A
B
C
Height in the forest (m)
40
30
20
10
Older forest
Pioneer forest
La Douane
Belvédère
Grégoire
50
light intensity
10 20 30 40 50 60 70 80 90%
CANOPY
upper structural ensemble
light
Inversion levels
humidity
structural ensemble
rel. atmosph. humidity or light intensity

age tree density, the line with its convex side up a low tree density and the line with its convex side down a high tree density. The form of the modulated curves, oscillating around the regression line, translates the effects of forest architecture on light extinction: direct measures of light intensities at different heights in Guianese rain-forest by BONHOMME (1973) confirmed the modulated vertical light gradient. Other examples and models are discussed by MILLER (1969).

Data on the vertical gradient of relative humidity are rare, but are provided in the classic work of CACHAN and DUVAL (1963) on the Ivory Coast. There is some modulation of a kind which is interpretable in terms of humidity cells of the kind but not necessarily of the form we have represented diagrammatically in Figure 95D, with a concentration around the set of the future. This is our interpretation, made possible because CACHAN and DUVAL gave a profile diagram of the forest plot in which their meterological tower was located. A comparison of this profile with a Guianese one, published by OLDEMAN (1974a, plots at Forêt du Banco and at Crique Grégoire) shows that architecturally the American and the African plots are similar, although, of course, floristically they are quite different. However, this has allowed the construction of an artificial diagram (Fig. 97C) in which vertical gradients of humidity (measured directly) and light intensity (estimated indirectly) are combined. This figure is useful in discussing ecological inversions and accords well with our understanding of the metabolism of trees of the present and future and with the geometrical configuration of shadow and humidity cells.

So far we have constructed little more than a paper forest. Our theoretical exploration will now be balanced with examples of actual plots of forest in a homeostatic phase, the observation of which preceded, of course, the elaboration of theory during our research.

III. Examples of Forest Plots

1. A Forest at Montagne La Fumée, Saül, French Guiana

Figures 98 and 99A represent the profile diagram and the plan of crown projections on the forest floor which provide the basic elements for a discussion of a forest plot. Features which are initially measured are total height and height to the largest forks of a few selected trees of different height. These then serve as vertical measuring sticks to evaluate the heights of all other trees. The circumference of the trunk above the roots was measured for all trees. The position of these trunks in the plot was then measured and drawn. Crown projections were estimated, as we have said, by placing an observer perpendicularly under peripheral branch tips and mapping his successive positions. The method is more precise than it seems and eminently practical in the rain-forest.

Trees are drawn out semi-diagrammatically on the profile diagram (Fig. 98) on the basis of field sketches which show the main branching pattern. Errors of perspective are corrected by referring to the field measurements. In this profile the undergrowth was too crowded for clear rep-

Fig. 98. Profile of a forest plot 20×30 m at Montagne La Fumée, Eperon Sud, Saül, French Guiana, prepared by the methods described in the text. Trees of the present: *in outline*; trees of the future: *densely stippled*. No trees of the past were present in this plot. The dense understorey of trees below 10 m is not included, except for the single *Astrocaryum* to the left. *Scale:* see man and tapir. Further explanation in the text. (After OLDEMAN, 1974a) >


Lecythis
Qualea (Vochys.)
45
45
Pithecellobium (Leg.)
40
Laurac.
Sapot.
35
35
Anac.
30
Sapind.?
Annonaceæ
Sapot.
Leg.
Sapot.
25
25
Sapot.
Gustavia
Laurac.
Swartzia?
Lecyth.
Sapind.
Sapind.
Rub.
Sapind.
15
Leg.
?
Leg.
Bombac.
Sapot.
Rosac.
Annon.
Myrist.
Leg.
Leg.
Astrocaryum
Eu
Lecyth.
5
Sapot.
Bombac.
Apoc.
Bombac.
Myrist.
Sapot.
Annon.
Myrist.
Guttif.
Sapot.
Myrist.
Lecyth.
Laurac.
Guttif.
Bombac.
Apoc.
Myrist.
0
5
1,0
1,5
2,0
2,5
30

resentation so that all trees of the future between 10 and 20 m high were left out of one half of the diagram. Where one tree stands directly behind another from the point of view of the observer it is drawn slightly to one side of its real position. On the crown projection map (Fig. 99) this displacement has not been made. Such voluntary errors have been introduced only after a careful check with the original basic drawing so that the analysis has not been influenced.

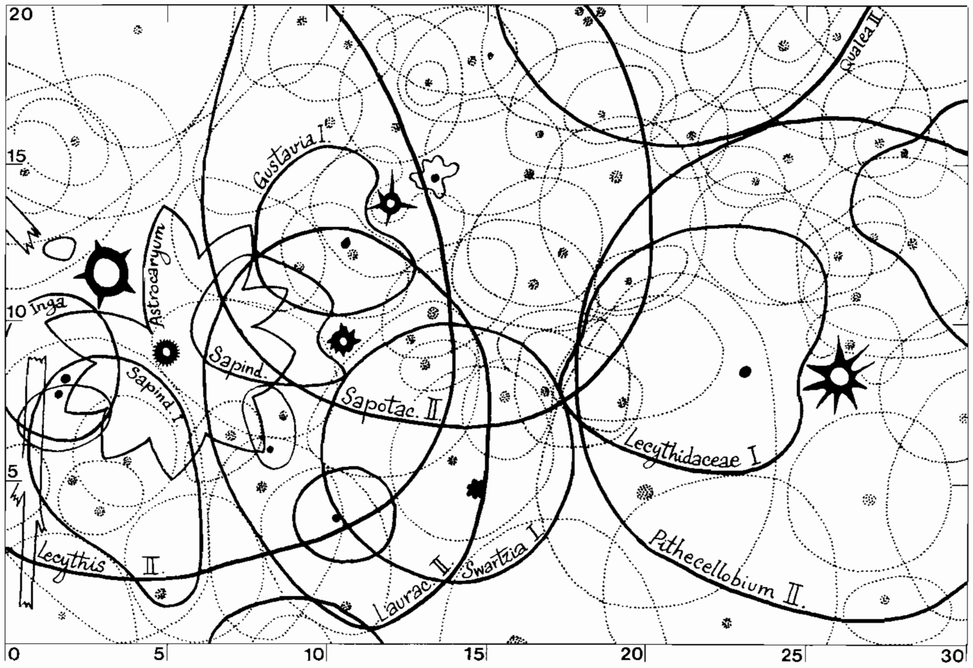
The forest from which the plots were drawn was situated on a saddle between two hills each about 400 m high and in a zone of volcanic matrix material on which a deep, rich soil had developed. This soil had a good structure and texture with high organic matter content down to 50 cm, a horizon enriched with clay between 60 and 80 cm, and below this a higher content of both coarse and fine clays. Fertility was higher and acidity lower than normal in tropical soils (the pH varied from 4.5 to 5.4 in the first 200 cm of soil). Permeability was high in the horizons above the clay layer which, however, was not completely impermeable. These characteristics portray an excellent forest soil in which no limits to root growth can be expected.

The shallow depression in the middle of the canopy of this plot (Fig. 98) reveals that some much earlier disturbance has been almost overcome. Other factors support this. The presence of the anacardiaceous tree (at mark 20) representing a transition from the set of the future to that of the present (but here drawn as a tree of the future because its growth potential is not yet exhausted) is quite symptomatic. Another piece of evidence is the distribution of the first major forks (morphological inversion points) in the set of the present. At the margins of the plot these points are in the upper half of each of the trees of the present, indicating a first step towards senility. Near the center of the plot these points are at or below the middle height which indicates a continuing vigorous growth phase which will end (Anacardiaceae sp.) or is ending (Sapotaceae sp.) by establishment of the crown in the forest canopy. The trees of the lower structural ensemble show an analogous distribution of their morphological inversion points.

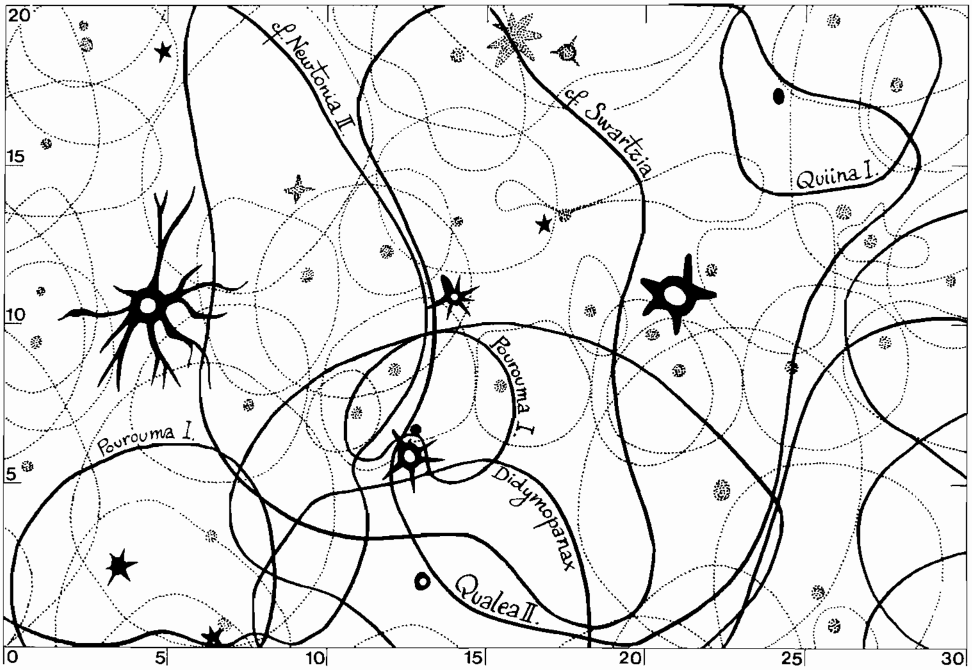
The highest structural tree ensemble can be clearly distinguished, with its crowns lying principally between 25 and 45 m, whereas a lower but discontinuous structural tree ensemble has its crowns between a height of 14 and 22 m. At and below 9 m there was a structural ensemble of mature palms (*Astrocaryum paramacca*) but only one of these has been drawn because they were at levels excluded from this inventory. Such sets of palms in the lower reaches of the forest are often survivors from an earlier phase of forest reconstitution following a disturbance.

The set of the future was dense, as we have mentioned, indicative of a high survival rate consequent on limited natural thinning and the persistence of very tolerant species (Leguminosae, Sapindaceae, Sapotaceae). No trees of the past were recognized. A few trees which were included in the set of the future because they conform to their initial model or show very little reiteration, such as the

Fig. 99A and B. Plans of crown projections of > the forest plots represented in Figures 98 and 101.
A Montagne la Fumée.
B Trois Sauts.
Crowns of the present in *heavy lines, Roman numbers* indicate the structural ensemble they belong to. Crowns and trunks of the future: *stippled.* Elements of the past: *thin lines.* The contours were determined in the field by an observer taking a position vertically under the extremities of branches (see text)


20
15
10
5
0
5
10
15
20
25
30
Qualea II.
Gustavia I.
Astrocaryum
Inga
Sapind.
Sapind. I.
Sapotac. II.
Lecythidaceae I.
Lecythis II.
Laurac. II.
Swartzia I.
Pithecellobium II.

A


20
15
10
5
0
5
10
15
20
25
30
cf. Newtonia II.
cf. Swartzia
Quiina I.
Pourouma I.
Pourouma I.
Didymopanax
Qualea II.

B

two myristicaceous genera (*Iryanthera*, *Virola*) and the annonaceous tree 35 m in height and with a diameter of 35 cm at the left of the profile may better be considered as sciaphilous nomads. When trees of this kind are frequent this provides evidence for rather early successional forest (OLDEMAN, 1974b). The size of the annonaceous nomad and the rather low frequency and low average stature of the two Myristaceae suggest a much older successional sere. The low frequency of climbers emphasizes this. It is from these general data about the forest that we can ascribe the anacardiaceous tree to the set of the future, whereas this fact would be doubtful if the tree were considered alone (p. 321).

Figure 100D–F provides three further kinds of data which characterize this plot at Montagne la Fumée. Figure 100E is the H/d curve for all the trees on the plot, with a distinction made between trees conforming to their model (M), having their model regenerated more or less successfully (R), showing profuse reiteration (+) or of doubtful architecture (neither R or +) but pertaining to the set of the future (×). The situation of these points with respect to the line $H = 100\,d$ (i.e., that characterizing the model) conforms to findings in monospecific populations (Fig. 84). The distribution of the cloud of points shows the heights of structural ensembles by virtue of its bulges to the right as well as the set of the future filling the intervening space.

Figure 100F gives the estimated light extinction curve determined according to the planimetric method described on p. 344. This curve is modulated, as is the general rule in homeostatic forest, and the regression curve, bulging upwards on a linear scale, indicates the high overall density of the forest (Crown Area Index, CAI ≈ 3.00)[16]. Figure 100D represents the forest as a population of tree models at differing heights. In order to obtain this curve, a count at successive levels has been made of all *trunks*, whether initial or reiterated, whether large or small. The structural ensembles then stand out as zones with numerous reiterated trunks. This graph should be compared with the classical height frequency curve, in which whole trees, each of which may represent a number of reiterated models, are counted as members of the population. As we have established (p. 334), this classical approach is of limited value in demonstrating or refuting layers in the forest.

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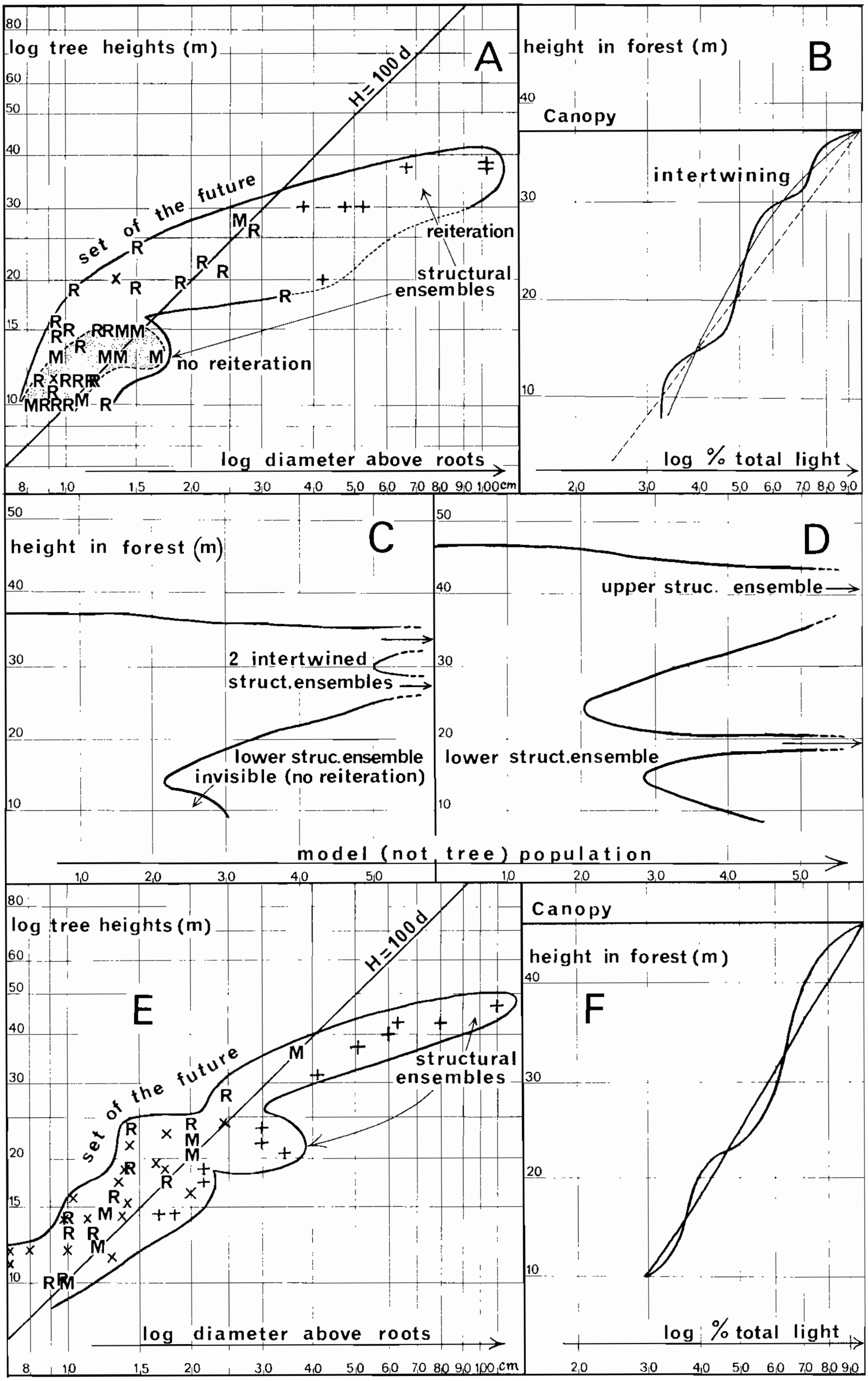
[16] Crown area index as leaf area index in which surface of leaf is replaced by surface of crown projection. CAI allows a more generalized approach than LAI.

Fig. 100A–F. Quantitative information from ▷ profile diagrams of Figures 98 and 101.

A Trois Sauts and *E* Montagne la Fumée. Log tree height against log trunk diameter above roots. M: tree conforming to its model; R: tree regenerated by reiteration; +: tree showing profuse adjusting reiteration; x: tree of the future of uncertain architectural status.

B Trois Sauts and *F* Montagne la Fumée. Estimated modulation in relative light intensity (*above canopy* = 100%) with height, on the basis of total planimetered canopy above each level (cf. Fig. 97*B*, *C*).

C Trois Sauts and *D* Montagne la Fumée. Total number of model trunks (not tree trunks) against height in the forest. This represents a measure of the amount of reiteration and indicates the presence of "layers" corresponding to structural ensembles. *Open-ended parts of the graph:* models herbaceous, too small and too numerous to be counted


A
log tree heights (m)
H=100d
set of the future
reiteration
structural ensembles
no reiteration
log diameter above roots
8 1,0 1,5 2,0 3,0 4,0 5,0 6,0 7,0 8,0 9,0 1,00cm
80 60 50 40 30 20 15 10
B
height in forest (m)
Canopy
intertwining
log % total light
2,0 3,0 4,0 5,0 6,0 7,0 8,0 9,0
40 30 20 10
C
height in forest (m)
2 intertwined struct.ensembles
lower struc.ensemble invisible (no reiteration)
50 40 30 20 10
D
upper struc. ensemble
lower struct.ensemble
50 40 30 20 10
model (not tree) population
1,0 2,0 3,0 4,0 5,0
1,0 2,0 3,0 4,0 5,0
E
log tree heights (m)
H=100d
set of the future
structural ensembles
log diameter above roots
8 1,0 1,5 2,0 3,0 4,0 5,0 6,0 7,0 8,0 9,0 1,00 cm
80 60 50 40 30 20 15 10
F
Canopy
height in forest (m)
log % total light
2,0 3,0 4,0 5,0 6,0 7,0 8,0 9,0
40 30 20 10

2. A Forest at Trois Sauts, Oyapock River, French Guiana

This forest is situated 2 km from the Wayap̃i Indian village of Trois Sauts. The profile diagram (Fig. 101) and plan (Fig. 99B) are drawn by the same methods as the preceding example. The soil is a red sandy loam, derived from a granitic matrix, and covers a region with little relief. No soil analyses were made but conditions in such soils are usually less favorable to development of an undisturbed forest root system than in the previous example because of the existence of hardpans which decrease permeability.

The forest cover is younger than that at Montagne la Fumée and is best considered a late successional sere. There are architectural reasons for this statement but the floristics and autoecology of the trees present support it. Large Mimosaceae and Vochysiaceae as well as the smaller *Pourouma minor* (Moraceae), although they characterize mature, stable stands are not the last word in forest succession (cf. Fig. 110).

The architecture of this plot is fairly homogeneous. The structural ensembles need to be considered first. The upper structural ensemble forms a regular forest canopy at a height of about 37 m, but below it is not homogeneous horizontally. The large mimosaceous tree (cf. *Newtonia suaveolens*) at the left-hand side of the plot, with its lace-like foliage lets through appreciable amounts of light sufficient to explain the presence under its crown of one early successional tree (*Didymopanax morototoni*, Araliaceae) in the foreground of the plot where it touches a recently disturbed area. In addition there are two trees of analogous stature belonging to genera often found in imperfectly closed canopies (*Swartzia* sp. – Caesalpinioideae and *Licania* sp. – Chrysobalanaceae). All are trees of the present. The vigorous development of the set of the future in this part of the plot also shows the effect of relatively low light interception by the canopy. The trees of *Pourouma minor* in the lower structural ensemble conform to their model (Rauh's model); they represent a genus that is generally light-loving. The round crowns of *Protium* sp. (Burseraceae, Rauh's model) at the right of the plot are included in the set of the future, but the expansion of their crowns and the low inversion point indicating actual vigor should be noted. According to our Indian guides this species does grow into a high tree, but it is possible that they were mistaken and that it represents a light-loving species of limited stature, in which case it would be more appropriate to include it in the same structural ensemble as *Pourouma minor*. All crowns of these trees are at a height of 13 to 15 m. Whether one includes *Protium* or not, this ensemble is not continuous (cf. plan, Fig. 99B). The lack of prolific reiteration in these trees shows that this property is not always inherent to a structural ensemble (cf. p. 340).

At a height of approximately 8 m there was a dense and neat structural ensemble of shrubs. This architectural plan demonstrates that the set of the present by no means always shows a simple layered pattern. A pattern is there, however, and notwithstanding complicated (e.g., *Didymopanax, Licania, Swartzia*) or doubtful (e.g., *Protium*) examples, the pattern remains completely understandable according to the principles we have established.

The set of the future fills in the space between the trees of the present, and we have already mentioned its vigorous development on the left of the plot. The tree of *Qualea* cf. *rosea* (Vochysiaceae), 28 m high and 27 cm in diameter at the base deserves notice. It conforms to Massart's model and it may be compared to

Fig. 101. Profile of a forest plot 20 × 30 m at Trois Sauts, French Guiana prepared by the methods described in the text. Trees of the present: *in outline*; trees of the future: *densely stippled*. *Scale:* man with "catouri" backpack. The understorey, below 8 m, not represented

a tree of the same species belonging to the set of the present, situated at mark 20. These two provide a very clear example of the developmental stages in forest trees. In the set of the future there are many vigorously growing trees with the lowest living branch inserted below the middle of their total height, several less vigorous trees with the lowest branch inserted at a higher level on the trunk, together with some dead trees serving as props for climbers and mobile epiphytes. This indicates that homeostasis is just becoming established. The low inversion point of the large specimen of *Newtonia* (tree of the present) also supports this.

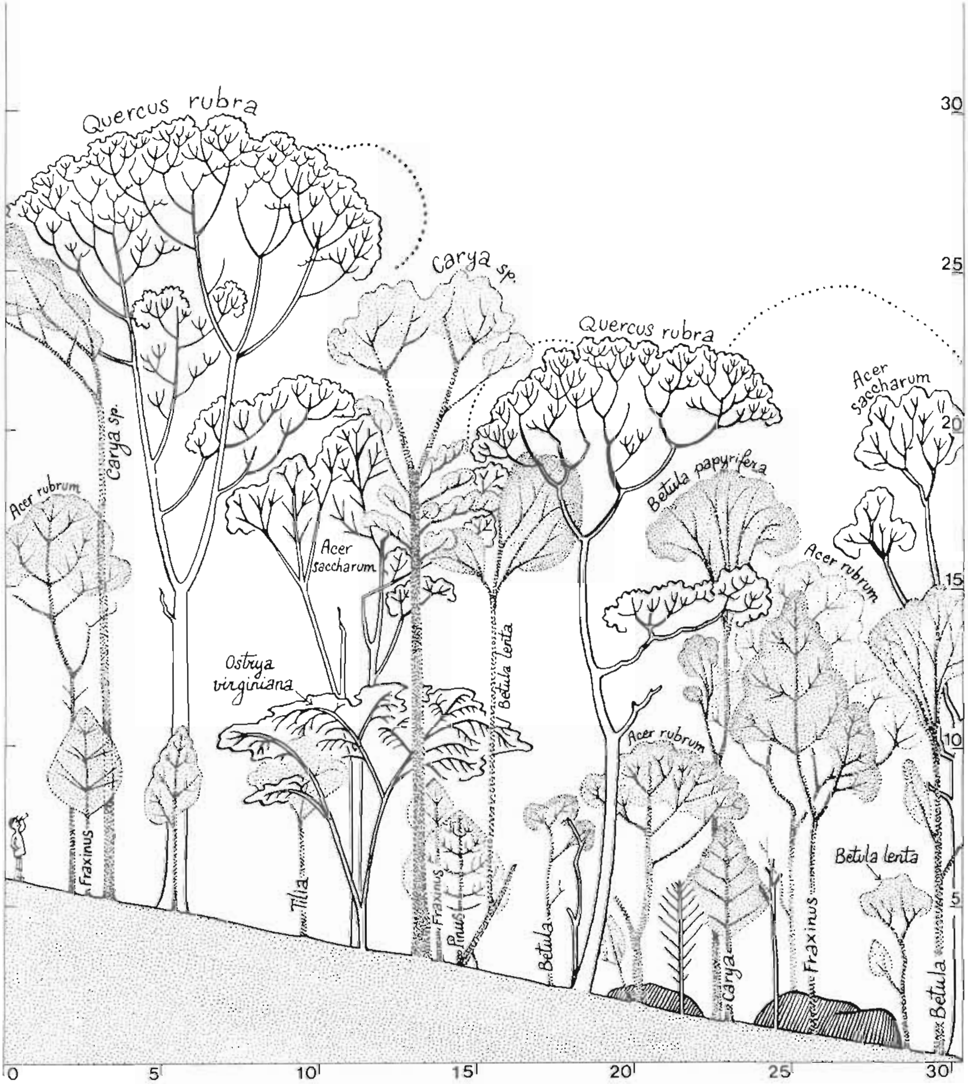
Figure 100A–C represents the same supplementary information about this forest plot as provided for Montagne la Fumée. On the H/d curve trees conforming to their model approximate closely to the relationship $H = 100\,d$. The cloud of points shows the upper structural ensemble, but not the lower one wherein trees conform to their model (Fig. 100A). This phenomenon has been noted elsewhere (e.g., in the analysis of the forest at Crique Douille, French Guiana presented by OLDEMAN, 1974a). The vertical light intensity gradient is again modulated, and its regression curve bulges upward, but this bulge is probably accentuated because the interception by the big mimosaceous tree on the left-hand side of the profile diagram has been overestimated; the CAI equals 2.9 in these conditions (Fig. 100B). Finally, Figure 100C shows the population of tree models in which the thick upper structural ensemble is due to the lower trees of the present intertwined with the imperfectly closed canopy. The discreteness of the lower structural tree ensemble is a consequence of its members still conforming to their model, so that the number of trunks equals that of individuals and is not reinforced by reiterated trunks.

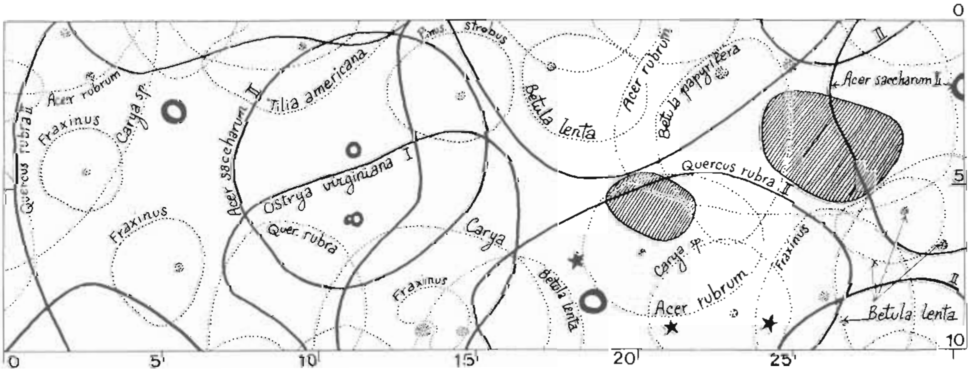
3. *A Forest at Tom Swamp, Harvard Forest, Massachusetts*

The same principles of forest architecture demonstrated in the tropics apply also to temperate forests. Figure 102 gives the profile diagram and plan of a 110-year-old tract in red oak-maple forest which is characteristic of much of New England. This tract escaped a devastating hurricane in 1938 (cf. Fig. 96) and so had time to establish homeostasis. The soil is rocky but seemingly presents no generally unfavorable conditions for root development. According to OLIVER (1975) trees are even-aged, although this does not mean that all originated from seed, since many may be stump sprouts. The hickories (*Carya* cf. *glabra*) may have come in later, some 30 years after the oak/maple forest started growth in height.

In order to adapt the scale of analysis to its smaller size this forest has been studied to a level 5 m from the forest floor and on a surface 30 × 10 m. The upper structural ensemble shows two distinct crown levels, both horizontal. The profile shows their imbrication, like overlapping roof-tiles, characteristic of structural ensembles on slopes, an adaptation of the canopy to this type of topography. At the point of imbrication a tree of *Acer saccharum* (at 12 m from mark 0), representing the set of the present but not more than 15.5 m high, acts as a "relay-tree" between the two canopies of different

Fig. 102. Upper: Profile diagram of a temperate > red oak–maple forest at Tom Swamp, Harvard Forest, Massachusetts, prepared by the methods described in the text. Trees of the present: *in outline*; trees of the future: *densely stipled.* The understorey, below 5 m, not represented. *Scale:* man. *Lower:* Plan of the crowns of all trees on the plot. *Shadowed by lines:* rocks


Quercus rubra
Carya sp.
Quercus rubra
Acer saccharum
Carya sp.
Acer rubrum
Acer saccharum
Betula papyrifera
Acer rubrum
Ostrya virginiana
Betula lenta
Acer rubrum
Fraxinus
Tilia
Fraxinus
Pinus
Betula
Carya
Fraxinus
Betula lenta
Betula
30
25
20
15
10
5
0
5
10
15
20
25
30


0
Pinus strobus
Tilia americana
Acer rubrum
Acer rubrum
Fraxinus
Carya sp.
Quercus rubra II
Acer saccharum II
Ostrya virginiana I
Quer. rubra
Fraxinus
Carya
Fraxinus
Betula lenta
Acer rubrum
Betula papyrifera
Acer saccharum II
II
Quercus rubra II
Carya sp.
Fraxinus
Acer rubrum
Betula lenta
Betula lenta
II
5
10
0
5
10
15
20
25

height, making it appear that the lower canopy emerges from below the upper one. At this place there is the suggestion of a lower structural ensemble, but represented only by a single tree of *Ostrya virginiana*.

On the left of the profile diagram the set of the future mostly contains trees with little vigor and consequently with the lowest living branch inserted high on the trunk. On the right, where the main canopy is interrupted, some of the more vigorous trees of the future have started to reiterate more profusely. We believe that root development is here impeded by a concentration of rocks in the substrate and so causes this architectural imperfection, i.e., in this spot the canopy is never maximally closed. In such locations trees of the future with a smaller root system acquire an architecture resembling that of trees of the present but with less reiteration. In the shadow of these small trees are several which have been suppressed to the point of extinction.

Two other features of this set of the future are of interest. The first is the presence of two hickories (*Carya* cf. *glabra*) which penetrate the canopy. This species is capable of producing taller individuals than red oak (*Quercus rubra*) and it seems significant that the best structured tree is located at the downhill limit of the upper canopy on this slope. *Carya* is near the limit of its range in this part of Massachusetts. Further south where *Carya* is more common its crowns overtop the lower ones of the structural ensemble of oaks and may replace it.

Figure 103A shows the H/d curve for this plot. The principles evident in this graph are the same as in the tropical examples, but the cluster of points is displaced to the right, i.e., there is a tendency for temperate trees to grow proportionately bigger in diameter than tropical trees. In temperate trees, even where the $H = 100\,d$ relationship is expressed precisely, reiteration will have taken place. Four examples appear in the graph, shown by small letters m, instead of capitals. Otherwise there must be a general tendency for regenerative reiteration on rather massive trunks which become broken (see profile). This is true also of trees of the future. Heights of trees in the upper structural ensemble of the set of the present are not equal, of course, because the ensemble is not parallel to the ground. The *Carya* specimen in the imbrication zone shows proportions intermediate between a tree of the future and of the present.

Light interception, counting from the canopy down and discounting the topographical slope, shows a modulated vertical gradient, as in tropical forests (Fig. 103B). Its regression line bulges upwards, the CAI being 2.3, denoting a high overall crown density for temperate forest. The model population versus height (Fig. 103C) has been counted twice, along the geocentric vertical (left) and at right angles to the slope (right). In both cases the upper structural ensemble appears, but only in the population counted along the vertical are details of its configuration evident. The contrasted curves demonstrate how classic height-frequency curves on slopes mask rather than reveal structural phenomena, since height classes are averaged out.

IV. Morphological and Ecological Inversion Surfaces

We have earlier established the concept of a morphological inversion point, corresponding to the level of insertion of major trunk forks (p. 325). Since only trees of the present determine forest architecture, their inversion points become important markers in forest analysis, and we need

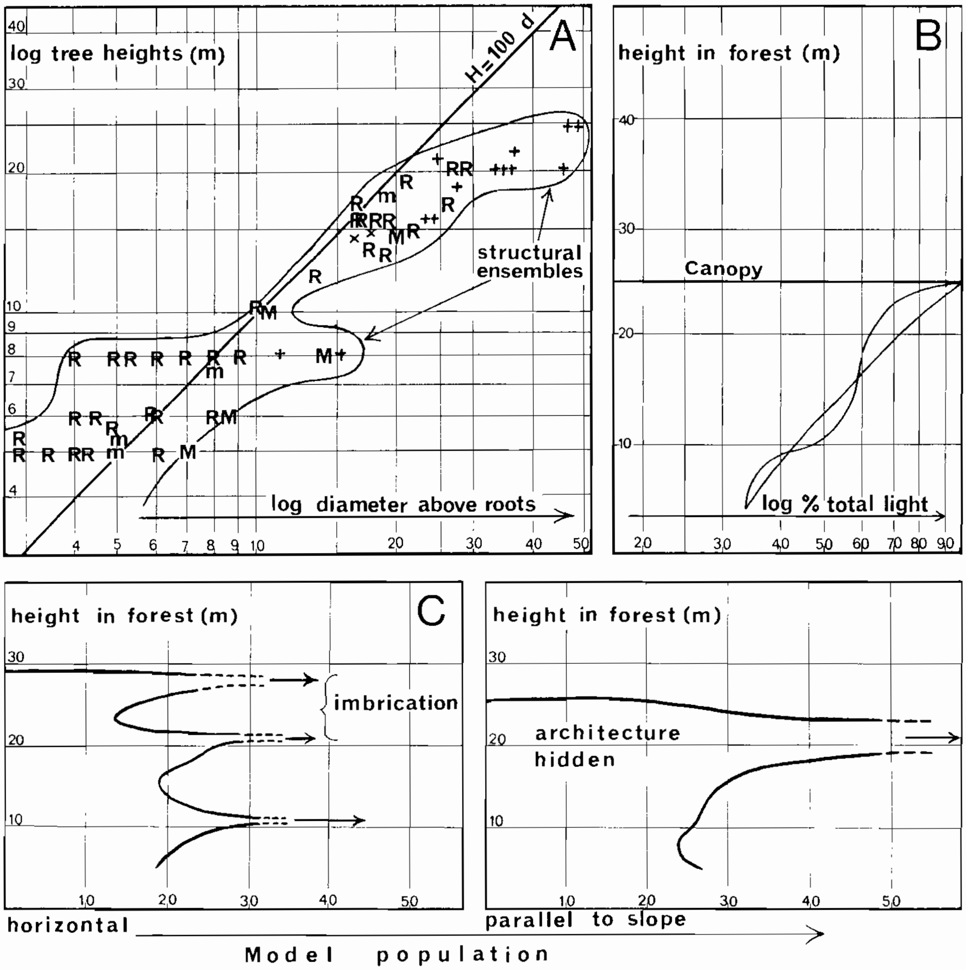


Fig. 103A C. Information relating to Figure 102 (Tom Swamp) graphed in the standard way used earlier (cf. Fig. 100).

A Height–diameter relationships of all trees plotted on a log/log scale. M: Model-conforming trees, R: trees regenerated by reiteration; +: profusely reiterated trees; m: see text.

B Modulation of light intensity determined by the canopy above a particular level at different heights, established by a planimetric method after the plan (Fig. 102, lower half).

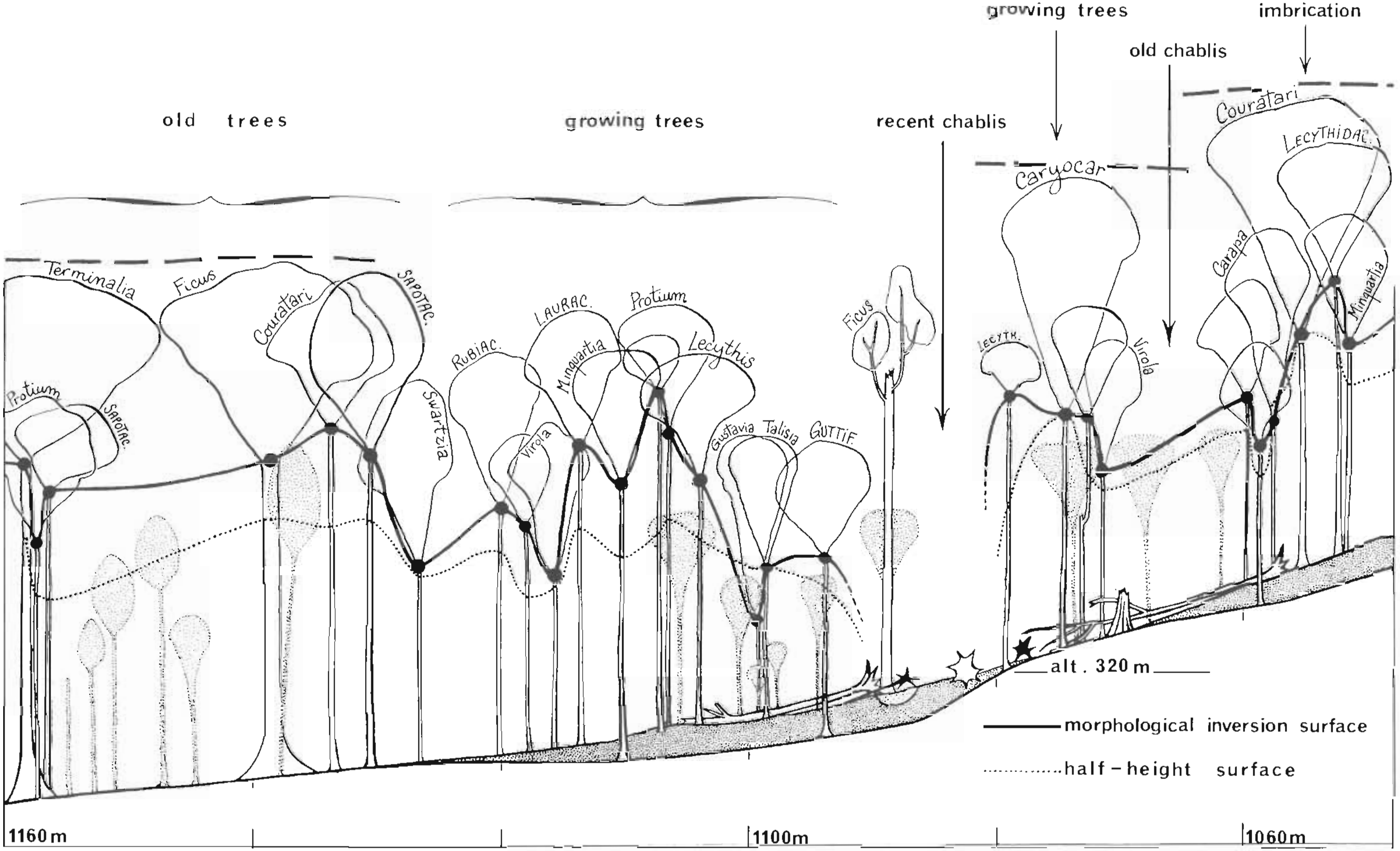
C Plot of total model trunks at different heights in two different directions, *left*, along an absolute vertical; *right*, along a line at right angles to the contours of the slope. The second method of plotting obscures the (horizontal) architecture. Further explanation in the text only concern ourselves with trees of the upper structural ensemble (but to some extent with the next lowest) because the canopy is the master regulator of the forest. We can consider these inversion points collectively as lying in an undulating surface, the *morphological inversion surface*. This surface gives a topographic indication of the distribution of either vigorous, or recently established or senescent canopy trees. It establishes the homeostatic, dynamic or disrupted state of the forest (Fig. 104), as a sort of graphic summary of the forest architecture. Quite evidently the morphological inversion surface is easy to establish, and when added to the standard elements of forestry inventory (total tree height, height of the tree trunk, diameter or circumference at breast height) gives a biological dimension to the record.

Evidently the position and nature of the morphological inversion surface has a bearing on microclimatic regulation within the forest. This can be demonstrated by crown depth diagrams of the type established in Thailand forests by OGAWA et al. (1965) which may be compared to a graph containing similar information from the plot at Montagne la Fumée (Fig. 105). The elements given in the publication by OGAWA et al. (crown projection map; plot surface; height of tree, overtopped and twice overtopped crowns) are interpreted by us to show that this plot did not possess a homogenous intact homeostatic architecture (see OLDEMAN, 1974b).

The oscillation around their average regression curves, in function of height, which defines the modulated nature of vertical light and humidity gradients in the forest, is caused by the vertical discontinuity of structural ensembles. Modulation is effected for light and for humidity, in the manner that we have seen (p. 342ff.). The first modulation counting from the canopy down (Fig. 97C) is due to the upper structural ensemble. The location of this modulation depends on the architecture of the canopy, which we have shown to be represented by the position of the morphological inversion surface. Where the modulated curves (Figs. 100B, F and 103B) cross their regression lines there are points representing a microclimatic "inversion" from less to more light than average extinction would account for and from more to less than average humidity build-up (Fig. 97C). The collected points in the forest where this inversion takes place can be thought of as forming an *ecological inversion surface* which undulates through the forest touching the ground at each hole in the canopy ("chablis", see p. 368) and reaching its maximum height under crowns of the trees of the present which are on the point of decline. In homeostatic plots it may become stabilized for a long lapse of time around mid-height of the forest.

However, the effort should be made to relate the morphological to the ecological inversion surface, because if a constant relationship exists between them, determination of the one, which is a relatively simple matter, would give information

Fig. 104. Inversion surfaces exemplified by a ▷ section of a corridor transect of 1160 × 20 m at Mt. Galbao, Saül, French Guiana, marks below corresponding to the position in the transect. The morphological inversion surface unites the points where organ complexes, from larger (trunk) become smaller (reiteration); the surface at half-height is tentatively equated to the ecological inversion surface (cf. Fig. 97*C*). Note near-horizontal position above half-height of the morphological inversion surface in old, well-structured forest, and wavyness in growing or disturbed forest. As the corridor is 20 m wide, there is a lateral variation of the inversion surfaces, which of course is obscured in the present type of diagram


old trees
growing trees
recent chablis
growing trees
old chablis
imbrication
Terminalia
Ficus
Couratari
SAPOTAC.
Protium
SAPOTAC.
Swartzia
RUBIAC.
LAURAC.
Protium
Minquartia
Lecythis
Virola
Gustavia
Talisia
GUTTIF.
Ficus
LECYTH.
Caryocar
Virola
Couratari
LECYTHIDAC.
Carapa
Minquartia
alt. 320 m
morphological inversion surface
half-height surface
1160 m
1100 m
1060 m

about the other without recourse to expensive micrometeorological techniques.

As we have seen (Fig. 92) the morphological inversion point changes its position in successive developmental phases of the individual tree. This implies changes of form and level of the morphological inversion surface during sylvigenesis (Fig. 111), a dynamic aspect of the forest to be treated in detail later (p. 375ff.).

V. Variations in Homeostatic Architecture

The pattern of horizontal structural ensembles in forest architecture permits several variations determined by adaptive or topographic factors. Some are standard responses to frequently occurring ecological situations and may be surveyed briefly now (Fig. 107).

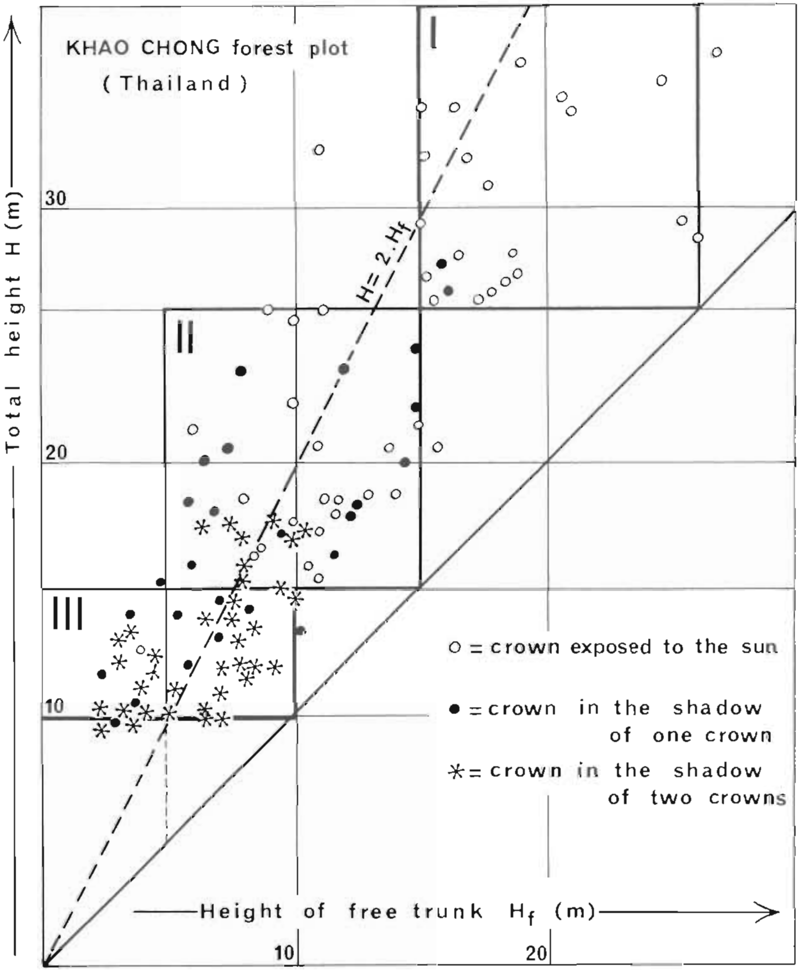
1. Forest Imbrication on Slopes

An imbricated pattern of the canopy surface on slopes, which may be likened to overlapping series of roofing-tiles, was mentioned briefly in the description of the forest plot at Tom Swamp (Fig. 102). This imbrication is common in forests on slopes, since we have observed it in regions as widely distant as Germany, Ecuador (Fig. 106), French Guiana, and New England. The general architecture of imbricated forest is shown in Figure 107A.

Canopies on slopes harbor trees of different heights, and since potential tree height is a characteristic of each species, a larger number of species can be accommodated in one canopy on a slope, compared with a canopy on horizontal ground, since a greater range of height potential can be included. Trees of lower height potential can become established in the canopy on the uphill side of the slope without being overtopped. This partly explains the floristic richness of slopes as observed by collectors, e.g., in French Guiana.

The "tiles" or zones of imbrication, i.e., along the contours, when they are intact, show two features worthy of attention. The trees at the downhill edge of a canopy zone often show a marked river-bank effect with asymmetric crown development toward the abundant light coming in laterally over the uphill edge of the next lowest "tile". In addition, the lower canopy can often be followed back under the upper canopy as a lower structural ensemble of the uphill part of the forest (cf. Tom Swamp, Fig. 102). In general the transition from the one region to the other is not quite horizontal since the upper part of one ensemble, where it becomes shaded by the canopy of the next "tile", is depressed somewhat. This represents a degree of variation in the adjustment to shadow where one ensemble

Fig. 105. Relation between total height (H) and free trunk height (H_f) in a plot of 40 × 40 m in Thailand (after OGAWA et al., 1965: his information concerning the zone under 10 m has been left out since it could not be compared) and in the plot at Montagne la Fumée (Figs. 98, 100). In the well-structured forest at la Fumée there are 2 points on or at the left of the line $H = 2.H_f$ (half-height) for 20 to the right; in Khao Chong, as in heterogeneous Guianese forest (OLDEMAN, 1974b) this rate is much higher than 2/20. The distribution of crowns which are either exposed to the sun, or once, or twice shadowed in Khao Chong also indicates a disturbed architecture. A comparison with Figure 104 shows how close our approach is to that of OGAWA et al., but also that these authors do not mean the same, when mentioning "strata" (*roman numbers*), as our structural ensembles. The numbered layers of these authors might correspond to sylvigenetic phases (see Fig. 110) ▷


KHAO CHONG forest plot
(Thailand)
I
II
III
H= 2.Hf
30
20
10
10
20
Total height H (m)
Height of free trunk H_f (m)
○ = crown exposed to the sun
● = crown in the shadow of one crown
✳ = crown in the shadow of two crowns

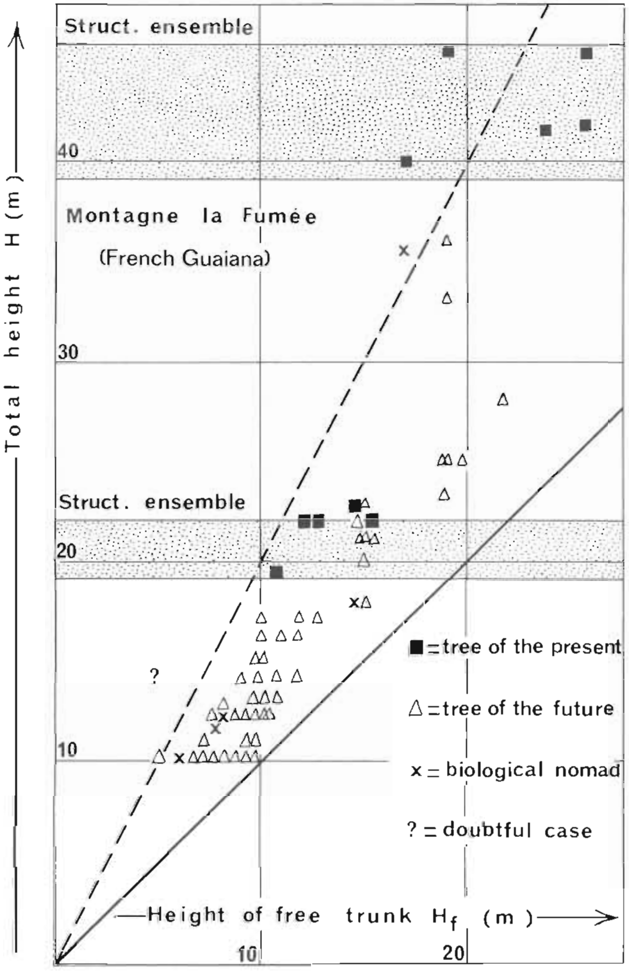

Struct. ensemble
Montagne la Fumée
(French Guaiana)
Struct. ensemble
40
30
20
10
10
20
Total height H (m)
Height of free trunk H_f (m)
■ = tree of the present
△ = tree of the future
x = biological nomad
? = doubtful case

Fig. 106. Imbrication of forest canopies on a steep slope in the Ecuadorian Andes (c. 1800 m). Imbrication produces a roof-tile arrangement with holes where big trees have fallen. It can only exceptionally be seen directly because of its erratic distribution on slopes. (See OLDEMAN, 1974a)

Fig. 107A–D. Variation in homeostatic forest structure.

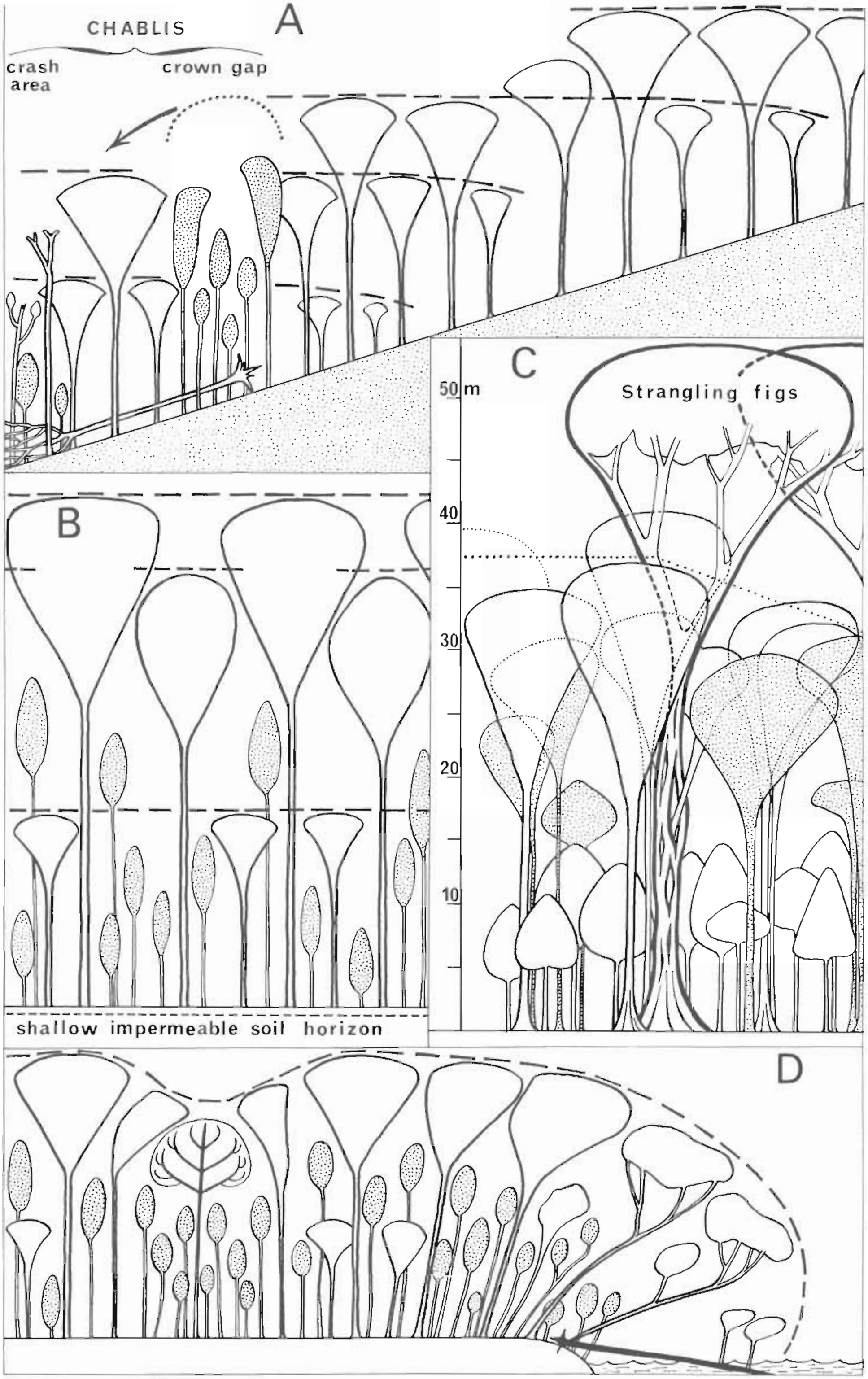
A Forest imbrication on slopes, or roof-tiled succession of canopies, due to the lack of species high enough to build a horizontal continuing canopy downhill. Note riverside behavior of crowns at the downhill side of "tiles", where there also is increased risk of chablis. Every canopy "emerges" from under the shadow of a higher one, so that it is not completely horizontal uphill from the imbrication zone.

B Intertwining of canopies, when, often on shallow soil which causes stunted root growth, the highest trees cannot close the canopy completely, so a second, somewhat lower one grows into the intervals.

C Under strangling figs, as observed at Saut Maripa (French Guiana), the upper canopy of surrounding forest is lowered. Compare with the imbrication zones in *A*. Note the still visible host of the *Ficus* in the center, which was an *Eperua* sp. (Caesalpinioideae).

D Where the forest is interrupted, as on riverside, the whole canopy is constructed by asymmetrical crowns and curves down to the river (or road). Note the old chablis on the left, with two asymmetric crowns at the side: essentially this is the same "riverside behavior"

▷


A
CHABLIS
crash area
crown gap
B
shallow impermeable soil horizon
C
50 m
40
30
20
10
Strangling figs
D

is superposed over another (also see Fig. 100 D).

However, the zones of imbrication are often not intact since the very height which the uphill forest canopy reaches induces a maximum of instability (Figs. 106 and 107). This is because such places can be occupied only by giant trees which are exposed. Asymmetric crown development reduces the mechanical stability of a tree. All these factors become exaggerated the greater is the steepness of the slope and the closer together are the imbrication zones. The figure in SCHNELL (1971, p. 692) illustrates a steep slope with numerous canopy gaps. When steepness exceeds a certain critical angle (probably of the order of 25 to 35°) homeostasis is improbable and a continuous turnover of trees is experienced (OLDEMAN, higher parts of the Mt. Galbao corridor, of which a small section is represented in Fig. 104).

2. *Intertwining of Structural Ensembles* (Fig. 107B)

Many conditions can lead to the imperfect closing of or to diminished light interception by crowns in the highest structural ensemble. Two factors which are important are wind breakage and leaf fall and they have been emphasized in the literature because they are frequent in temperate regions. They are also important in the tropics, but other factors may predominate. This diversity of disturbing factors will be discussed later; only those needed to understand a particular case will be discussed here.

In the tropics leaf shedding may occur in seasonally flooded valleys, apparently as a result of reduced root respiration. Shallow impermeable layers which reduce the root volume result in stunted trees. Seasonal flooding, which is common on such soils, will augment this handicap. On hillsides impermeable layers of constant depth can inhibit root development and reduce efficiency in the taller trees, i.e., those which grow in imbricating zones. Large rocks or rock outcrops may have the same effect. In New England OLIVER (1975) found that that the crowns of red oaks (*Quercus rubra*) swaying in the wind mutually shear off peripheral branches, so that crowns become separated by empty "interaction zones" through which light penetrates into the forest. Tree species (e.g., members of the Mimosoideae; *Newtonia*, Fig. 101) with delicate, lacy foliage permit the passage of more light than broader-leaved trees.

All these effects produce spaces under the upper forest canopy in which slightly smaller trees of the present can become established. The result is two intertwined structural ensembles, neither one complete in itself, the one some meters higher than the other (Figs. 100C and 107B). The phenomenon either may be localized as in the plot at Trois Sauts (Fig. 101), or extended over larger areas, e.g., plateaus on hills with shallow lateritic pans. Intertwining is less easily recognized than imbrication when examining a profile diagram since at first sight it appears as a lack of organization of the canopy. Closer examination reveals the intertwining. Published forest profiles from Ivory Coast, Gabon, French Guiana, and Malawi (East Africa), discussed and interpreted in OLDEMAN (1974a), show intertwined structural ensembles, the first three resulting from impermeable soil layers and the last one probably resulting from seasonal leaf shedding.

Canopy configuration or peculiarities of individual species should be assessed in this particular context. An example would be the heliophilous character of lower structural ensembles in the plots at

Trois Sauts (Fig. 101) or in the profile at Crique Douille published by OLDEMAN (1974a). The growth and reproduction of *Jacquinia pungens* (Theophrastaceae), an understorey tree in Costa Rica, shows a periodicity which coincides with the seasonal *leafless* condition of the upper canopy, a strategy discussed by JANZEN (1970a).

3. The Riverside Effect in Whole Canopies (Fig. 107C)

The "river-bank effect" in individual tree crowns was discussed earlier referring to the lateral crown growth in the direction of light in forest trees fringing water courses. The structure of the whole vegetation is affected by the tilting or bending of trees. This movement, which OLDEMAN (1972) compared to a continually closing fan is due to erosion and undercutting of concave banks along river meanders causing partial or total uprooting of trees. Soil instability is further accentuated in the wet season and brings to work the potential momentum of the tree towards the river which already exists because of an asymmetric crown.

The river-bank forest one sees when travelling by boat along tropical rivers therefore has a high proportion of horizontal axes (Fig. 107C), representing both orthotropic axes which have fallen from an upright position as well as an excess of axes with primarily or secondarily acquired dorsiventrality. Since light interception still takes place according to the same principles as in the canopy of an inland forest, the riverbank may be considered to have a tilted canopy. Precisely similar circumstances govern the behavior of trees which find themselves at the margin of other openings in the forest. The two circumstances differ, however, since above the water a tilted canopy is continually maintained and lacks a set of the future. Around a chablis, on the other hand, the hollowed-out canopy grows towards a vertical light source and with the participation of nomads and trees of the future, a horizontal canopy is gradually restored.

4. Architecture of Forests with Strangling Figs (Fig. 107D)

Established strangling figs of the genus *Ficus* are referred to because of their unusual method of crown-trunk development. Their frequency in homeostatic forest is much less than one might expect, but when present they induce distinctive architectural features. However, they are common in secondary forest as seems to be the situation with *F. anguina* in French Guiana, suggesting that if such trees are established on small host trees, their future development is limited because they can be overtopped easily without the benefit of starting development at a high vantage point (Fig. 1D).

Figure 107D represents, very schematically, a plot near Saut Maripa (Oyapock River, French Guiana) with almost $^2/_3$ of its surface beneath the crowns of two giant *Ficus* trees, each 55 m high. The canopy level is at an average level of 37 m on the left of the diagram; on the right and under the figs it is depressed to an average height of about 30 m. This effect recalls the imbrication of canopies on slopes. In addition there is a lower structural ensemble at 12–14 m of trees conforming to Massart's model (mainly a species of *Iryanthera*, Myristicaceae). This may be caused by intertwining of trees of the present, as in Trois Sauts (Fig. 101) but equally likely could be ascribed to the presence of a *Terminalia* species (*T.* cf. *pamea*) which is a seasonal leaf-shed-der, represented by several individuals in the highest structural ensemble under the *Ficus*.

The *Ficus* tree in the center of the plot probably germinated on its still visible host, somewhere near 20 m above the ground. Consequently its inversion point should be measured from this level and not the ground. This then accounts for the rather free-standing architecture of the upper part of its crown and the visible state of vigor of the tree.

B. Sylvigenesis

Sylvigenesis refers to the processes by which forest architecture is built—the process of forest-making, as morphogenesis refers to the establishment of the form of the individual plant. Sylvigenesis includes a range of phenomena, for instance, the processes which lead from a recently established, though architecturally still unstable forest, to the mature homeostatic forest which may include the same species, in the same proportions, but not at the same developmental stage. In order to establish this concept of sylvigenesis, several of the events which characterize it need to be described.

I. Disturbances of Existing, Functioning Forests

At one end of the spectrum of possibilities, sylvigenesis starts from unoccupied ground, at the other end it can start repeatedly in openings in existing forest. Our estimates based on experience in French Guiana suggest that some three to five percent of the total natural forest in regions not subjected to major climatological or geological catastrophe may be occupied by recent disturbances recognizable in the form of chablis. A larger area (about 10–20%) is under a recently grown tangle of low secondary forest, indicating more or less complete clearance during the last twenty years. When one views these figures against any extended time scale one is amazed that mature homeostatic forest can be recognized at all, especially as the frequency of natural chablis is probably currently underestimated (cf. VAN STEENIS, 1956a, b; BUDOWSKI, 1961; LONGMAN and JENÍK, 1974). As visitors from a temperate country who have spent some years in tropical forest, we are impressed by the rapidity with which creeks and small rivers become obstructed by fallen trees, since these impede river travel and induce frequent diversions along any forest trail. The crash of trees falling in the adjacent forest will frequently wake the camper from his hammock at night. Apparently, havoc is wrought continually in the forest. Why is this so?

An opinion frequently found in the literature is voiced by LONGMAN and JENÍK (1974, p. 41): "Except where other powerful mechanical factors such as elephants are at work, only wind interferes profoundly with the forest equilibrium, changing at a stroke the conditions for regeneration, growth and reproduction in the lower layers." The dominant role of hurricanes or cyclones in regions like the West Indies and Australasia where they are common is certainly clear and has been discussed by WHITMORE (1975, 1978). In other parts of the tropics, like Amazonia and Central Africa, other factors predominate. COUSENS (1965), though emphasizing the importance of various disturbances in the rain-forest, still stresses the dominant role of the wind.

In tropical rain-forests water works together with wind as a major factor in plant demolition. In French Guiana, there is a marked increase in tree fall during the wet season (OLDEMAN, 1972), mainly because the soaked soil loses its cohesiveness. Root anchorage of trees may then become precarious. In addition, surface run-off erodes the soil around roots while subsurface run-off tends to loosen superficial soil horizons above shallow impermeable clays or lateritic pans. Subterranean erosion is probably responsible for the long persistence of pits initially caused by the uprooting of a tree, since sediments are annually scoured out of the pit to a depth of 50 cm. This kind of pit is so common in French Guiana that is possesses a specific Creole name ("dyougoung-pété", BLANCANEAUX, 1971).

In these unstable conditions numerous trees with asymmetric crowns topple over, particularly on slopes and river-banks. Small gusts of wind, such as those in the tropics which generally precede heavy showers, now become the accomplices of soil instability because they are capable of throwing over trees with exposed and asymmetric crowns, i.e., emergents and trees at the edge of imbrication zones. One can, in fact, estimate the potential destructiveness to the forest of such processes. In a corridor, a fragment of which is shown in Figure 104, with a total surface of 1160 × 20 m, there are 16 asymmetric and 26 exposed crowns between 20 and 40 m high, representing 42 potential chablis each with an average area of 10 × 30 m. This total area of future chablis, 12,600 m^2 is more than half the total area (23,200 m^2) of the corridor. In addition, 34 incompletely decomposed uprooted trees and 17 dead tree stumps between 2 and 10 m high were observed in the same corridor. The stumps are evidence for occasional direct wind breakage of trees. Taking into account that the effects of these 51 examples of destruction do not necessarily fall wholly within the corridor, the numbers of present (51) and future (42) chablis are close. This picture is by no means unusual and a similar, but not always quantified impression is given by forest in the Ivory Coast (NIERSTRASZ, 1975), Ecuador (OLDEMAN, 1978), and Brazil.

Additional quantitative information is, however, provided by POORE (1968) in Malaysian rain-forest (Jengka Forest Reserve). On a plot of 122,400 m^2 in which homeostatic sites occur with an intact upper structural ensemble between 45 and 50 m high, as can be seen in his published profile diagram, he found approximately 10% of the area occupied by "gaps", (our chablis). Moreover, he counted 75 fallen trees, 90 dead but not yet decayed trunks, and 40 to 50 standing dead trees all with a girth of over 91 cm. The largest chablis he found measured 20 × 30 m. From this maximum value and the size of the biggest trees in his profile diagram it can be estimated that the average surface area of a chablis is 400 m^2 ($^2/_3$ of the maximum). Consequently the 165 trees which he estimated to have fallen during a period of twelve years would occupy an area of 66,000 m^2, or a little over half of the total surface. These figures correspond closely to those we have established in French Guiana. The relative absence of dead standing trees in the Galbao corridor (partly on Fig. 104) contrasts with their abundance (20% of all dead trees) in Malaysia. POORE mentions that a considerable number of fallen trees made small gaps in the canopy which could be repaired by neighboring trees without successional phenomena. He estimates that recent chablis occupy 22,800 m^2 out of a total chablis area of 66,000 m^2 and that it takes twelve years for a dead trunk to decay. His further estimate of a recent chablis remaining visible as a canopy gap for four years also seems reasonable to us. POORE gives no evaluation of causes of tree fall in this Reserve, a deficiency made good by WHITMORE'S (1975, p. 67) discussion of the subject. He emphasizes lightning as a cause of tree destruction.

Despite this scale of forest destruction, which is related to soil phenomena and hydrology, the subterranean part of the biotope and accumulated organic matter on the forest floor remain intact. This is also true for hurricane-damaged forest even when destruction occurs over very large areas. Biotic impact on the forest is frequently destructive in various ways: elephants toppling a series of trees, termite attack, root undermining by armadillo holes, rot by fungi and bacteria, overweight of water-saturated epiphytes in the wet season – all induce forest openings. The impact of man is often quite similar, as when he selectively and by hand fells commercial timber trees, clears an area under the big trees to make a gold mine, or removes *Aniba rosaeodora* (rose wood) to supply a mobile distillery. Nevertheless, these effects tend to leave the floor of the forest relatively unmodified.

In contrast, man-made disturbances using fire and machinery over large areas produce changes which are paralleled in nature only by landslides and earthquakes, since the substrate is modified and even more or less sterilized. This process of destruction is summarized by the aphorism "La forêt précède l'homme, le désert le suit." Destruction on this scale is causing concern among ecologists (e.g., AUBRÉVILLE, 1947; BUDOWSKI, 1961; GOMEZ-POMPA et al., 1972; WHITMORE, 1975). It allows us here to consider questions of scale and degree of disturbance in determining the starting point of sylvigenesis. When deforestation also destroys the upper soil horizons further sylvigenesis is retarded or may even become impossible. The establishment of pauperized herbaceous vegetation on such sites has been reviewed on a pantropical scale by BUDOWSKI. The original forest may never reappear, or only specialized forest facies may survive the onslaught. Teak provides the classic example of a species able to establish itself in areas which are yearly burned, because its seedlings are fire-resistant and it has a root system developed at a depth sufficient to escape the heat of the fire.

Temporary human activity produces disturbances on a smaller scale, as when the supply of timber or firewood is exhausted in the immediate environment of a village or when shifting cultivators abandon their fields because of soil exhaustion and weeds. Forest, of a sort, will develop and sylvigenesis occurs without a long prior phase of herbaceous vegetation. The more usual small fields in forest regions settled by peasants with high mobility are rather more directly comparable to chablis as far as the first stages of sylvigenesis are concerned, since a completely intact infrastructural complement is left (HAXAIRE, 1977). The chablis itself is, however, the most significant natural disturbance and needs to be examined in further detail.

II. The Chablis

The word "chablis" we have adopted from the medieval vocabulary of French foresters, who indicated with the term both the toppling of a tree, for whatever reason, as well as the fallen tree itself, the resulting hole in the canopy and accumulated debris. In alternative terminology "windthrow" is limited to a specific influence and "gap" denotes the result only; chablis is useful in both senses.

In a medium-sized or large chablis a process of forest rejuvenation takes place (the "building phase" of WHITMORE, 1975, 1978), starting from a level which is determined by the remnants in the chablis, together with individual trees which are able to recover from damage by reiteration. Trees which are unable to survive this injury become trees of the past in the newly developed forest. On the forest floor there may be an existing seed mixture to which are added newly imported seeds. Cryptophytes and geophytes are to be found here, together with root suckers. All these available meristems and seeds represent a new infrastructural complement which is rapidly mobilized. A fresh chablis at this stage is represented schematically in Figure 109 (top), with, at the same level, its infrastructural ensemble. This phase, or only a little older, is represented also on Figure 108.

The new recruits to this ensemble are the meristems of heliophilous species which cannot live in a homeostatic forest. These "heliophilous nomads" (p. 380) enrich the area floristically if the existing flora has not been reduced by the chablis. Once the new infrastructural set is established by mobilization of part of the infrastructural complement, a phase of vigorous growth begins. As none of the trees has yet reached the status of a tree of the present, there are no structural ensembles and there is no architectural layering when regrowth starts (Fig. 109). As expansion of the crowns in fierce competition elevates meristems they reach a level where shading progressively suppresses the lower part of the developing canopy. Dominance of certain crowns is eventually established. These crowns at the border of the opening may be those of previous trees of the future which survived the chablis intact, whereas in the center there are one or more light-loving biological nomads. Trees of the first category expand their crowns by reiteration, in the second the model contains fast-growing meristems with a large capacity for energy conversion. In the tropics this establishment of a first upper structural ensemble may be very rapid; it can be said to be homeostatic over a short period (Fig. 109). For example, it has been observed that a mixture of *Cecropia* species planted in the botanical garden of the ORSTOM Center in Cayennne needed about four years for the establishment of a continuous but diffuse canopy. In temperate forests canopy closure takes longer and the canopy is denser. Figure 96 shows the process as represented by Oliver (1975) for *Quercus/Acer* forest in Connecticut. In these examples the pioneer species (*Cecropia* and *Quercus*) both represent Rauh's model, but there are significant differences in the way in which the model is expressed. In *Cecropia* it is a tree conforming closely to its model which develops the canopy since large meristems building few axes at a high energetic level are involved. In red oak, on the contrary, the crown develops as the result of a vigorous reiteration pattern, a circumstance which is usual in temperate trees. Strategically *Cecropia* has a rigid, standardized pattern of growth, but the pattern in *Quercus* is elusive, flexible and adaptable, as can be seen in the shape of its trunk.

The forest canopy produced by *Cecropia* is sufficiently light-admitting for growth of other species to be facilitated. This initial canopy has a limited life span, estimated at some 20 years (Budowski, 1961). This has to be contrasted with *Quercus* which can form a dense canopy casting shade for over a century and inhibiting the growth of other species (*Acer*, *Betula*). In the tropical inland forest *Cecropia* forest is certainly not a final phase, but it may become so in inundated areas ("pri-pri"), whereas the initial oak-maple forest can often become permanent, e.g., in hurricane regions. Although the time scales for these contrasted types of forest are so very different, the initial sylvigenetic processes within them mark a dynamic period during which a steady state is prepared. This allows us usefully at this point to consider in further detail this concept of "homeostasis", which we have already used quite widely.

III. Homeostasis in the Forest

Thermodynamically, a closed system is called homeostatic when no "useful" energy remains, i.e., when a final equilibrium is reached. Biological systems are open and retain an energy exchange with their environment. In these systems homeostasis is judged to be attained when energy flow into the system equals that going out. For this reason, WADDINGTON (1939 in THOM, 1968, Appendix) has suggested the term homeorrhesis when speaking of living systems. No confusion is likely, however, in using homeostasis ecologically to refer to a stable state, even though the application lacks thermodynamic rigor.

The term used in this way applies well to two of the forests examined in Figure 109 in which there is very constant production or energy exchange rate. The situation is the very opposite of that which prevails in the chablis, where energy uptake considerably exceeds energy return to the environment, i.e., net increase of biomass is rapid. The homeostatic phase is a static one, the chablis phase a dynamic one. As we have seen, forest architecture is a marker for these phases, with a well-layered forest reflecting the homeostatic condition.

Homeostasis in plant ecology has been mainly associated with "climax communities" or "mature stages", terms which are meant to indicate the ultimate stage of succession, as discussed by DRURY and NISBET (1973).

Four statements from the literature indicate changes in meaning of the term homeostasis, the first being closest to our usage.

1. WHITTAKER (1970, p. 73): "The end point of succession is a climax community of relatively stable species composition and steady-state function, adapted to its habitat and essentially permanent in its habitat if undisturbed."

2. ODUM (1971, p. 262): "In a word, the 'strategy' of succession as a short-term process is basically the same as the 'strategy' of long-term evolutionary development of the biosphere – namely increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations." Protection from environmental stress has been added in this definition.

3. PIANKA (1974, pp. 16–17): "Because any individual organism has a finite energy budget, it must also have a limited capacity for regulation of homeostasis (which is the ability to re-establish a normal state after being disturbed)."

4. VAN DER PIJL (1969, p. 89, Table 2): "Secondary forest: unstable, more open to pests; climax rain forest: homeostatic, more immune to pests."

In these last statements protection from the action of environmental factors is a dominant consideration.

In order to understand how self-protection came to be associated with homeostasis, we have to go back to the thermodynamic concept in closed physical systems. Here, all differences between the elements (particles) of the system have been evened out during a period of energy exchange from higher to lower levels and the result-

Fig. 108. Chablis, illustrated in the Guianese ▷ rain-forest, a dynamic early stage in sylvigenesis, unstructured with competing trees

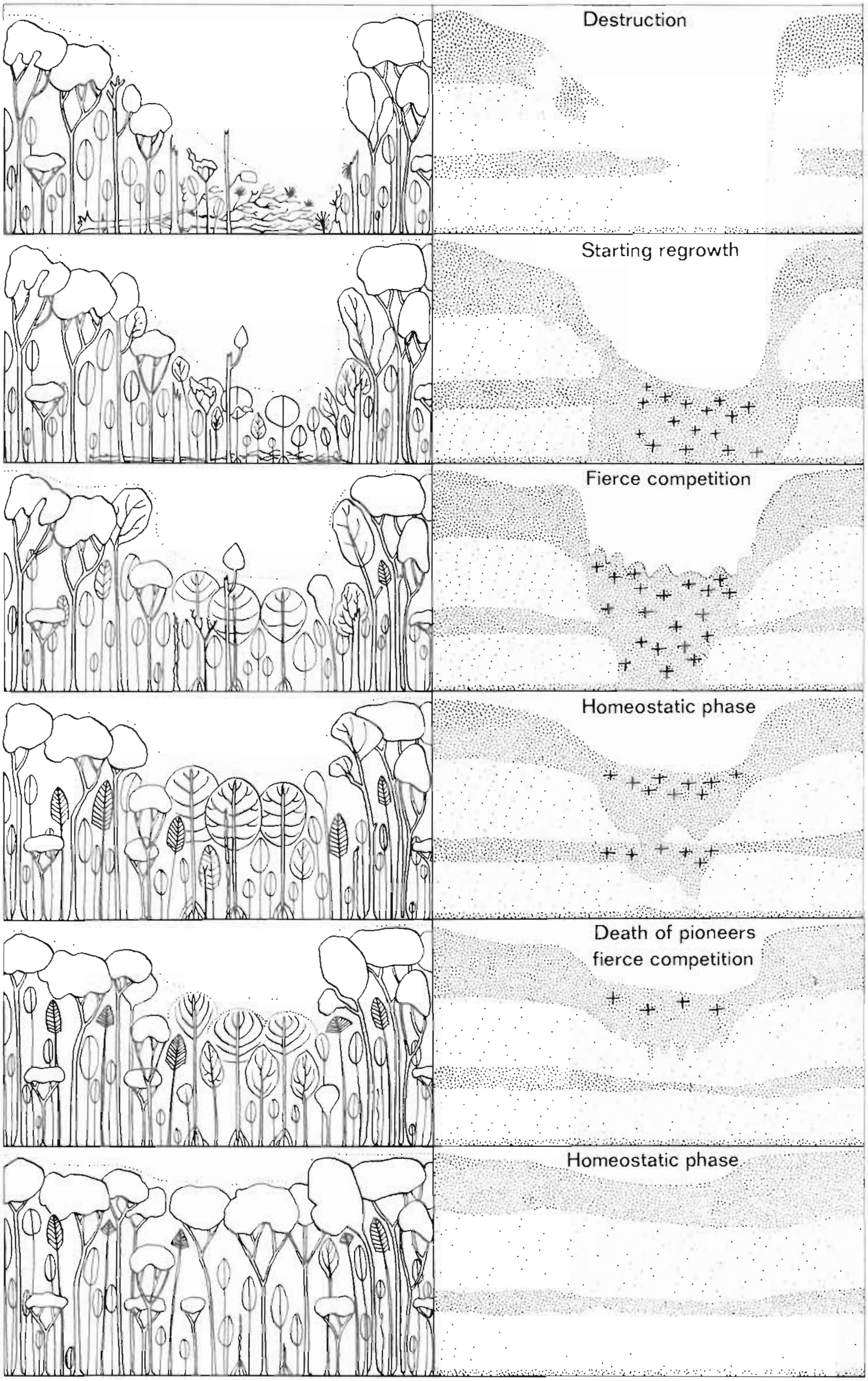
ing situation admits no more change because there are no more differences in potential. Energy which remains stored in the particles cannot escape and is useless or entropic. The situation is well characterized by saying that it lacks differentiation or organization. If the system is abruptly opened and some energy drained from particles near the opening before it is closed again, energy interchange occurs and becomes generally stabilized at a lower homeostatic level. Is this return to complete dedifferentiation – the "same state", but at another energy level – to be identified with biological return to a previous state of higher organization? If the answer is yes, then self-protection or regeneration can also be identified as aspects of homeostasis.

We have already seen in the example of the tree of the present and of the homeostatic forest that the final state of both these biological systems is the most highly organized they achieve. The tree of the present *cannot* regenerate itself; a new tree has to grow to replace it, for a damaged tree of the present becomes a tree of the past. At the scale of the forest, the same phenomenon occurs: the first sylvigenetic phase in a chablis gives rise to *another* forest, transitory though it may be. With respect to drastic disturbance both systems are extremely vulnerable and not resistant to extreme stress. Why, then, should such systems be termed homeostatic?

Two facts argue in favor of this term. On the one hand there is the accumulation of an enormous amount of dead biomass, mainly the heartwood of the trees in which biochemical energy is tied up without the immediate possibility of redistribution. This matter is comparable to the particles of a closed physical system. The majority of biomass in mature trees in established homeostatic forests is in this state. Living biomass and energy flow, in contrast, remain at minimal levels compatible with survival. On the other hand, minimal energy flows and senescent architectures exercise a rigid internal control on the physiological level within the tree and the microclimatological environment in the forest; these suggest a comparison with the uniform level of energy in a physical homeostatic system. We can regard the opening of the forest and its rapid closing, by analogy with the physical system, as represented by some event like the fall of a large branch from a tree of the present, the death of a tree in a lower structural ensemble, or gradual death of a standing canopy tree. The relative scarcity of living biomass in homeostatic forest is suggested by several observations.

LESCURE (personal communication) has commented upon the sparse populations of frogs and toads, represented by few species, in well-developed high forest in French Guiana. These animals largely depend on insect populations for food supply. The traveler knows that in a camp under high forest one can sleep without mosquito netting, ticks and other parasites are common only in places where the canopy is low or imperfectly closed.

Fig. 109. The chablis, its sylvigenetic destiny, ▷ and the dynamics of the infrastructural set (meristems) which accompany these early stages in sylvigenesis. *Destruction:* the infrastructural set is disrupted; *starting regrowth:* out of the infrastructural complement, latent meristems are mobilized (seeds, others); *fierce competition:* the forest is without structure, composed of competiting pioneers, and the infrastructural set extends throughout vertically; *homeostatic phase:* pioneers are maximally expanded trees of the present, infrastructural set a variant of Figure 97*A*; *death of pioneers:* competition among more shade-tolerant trees of the future underneath; *homeostatic phase:* new structural ensembles made and maintained by this second group of trees. +: pioneer meristem. Further explanation see text


Destruction
Starting regrowth
Fierce competition
Homeostatic phase
Death of pioneers
fierce competition
Homeostatic phase

According to JAGO (1973, p. 187) for grasshoppers in West Africa "forest speciation and adaptation are to be considered an evolutionary dead end and the forest ecosystem a 'species sink'." For birds, AMADON (1973) refers to 19 African species of heron along Congolese rivers, but only one around small creeks in the forest. He also comments upon the numerous other species of birds which live in forest clearings and asks the question: where did they live before man cleared so much forest, giving his own answer (p. 271): "they must have evolved and lived in the *scattered* natural clearings resulting from *windfalls,* brush along streams, etc., but in *smaller numbers* than at present (our italics)." Birds, however, are mobile so that a better example may be provided by small rodents which in French Guiana are few in high forest, whereas in chablis and especially fields of shifting cultivation they are numerous (DUBOST, personal communication). Terrestrial mammals, represented by Ungulates, show similar differences. BOURLIÈRE (1973, Table 5) records in Africa 27 species from the forest and 68 from savanna biomes; in tropical America the respective numbers are nine and six. This last anomaly can be accounted for in part because several orders of savanna ungulates are absent from the neotropics (Equoidae, Rhinoceratoideae). The only group in tropical America for which direct comparison is available, the Cercoideae (deer), has five savanna species and four forest species. For forest habitats, numbers of mammals are comparable on both continents: in Africa three species of Proboscidae and Hippopotamidae, in America three species of Tapiroideae; both continents harbor two species of forest hogs (Suoidae), but one must contrast the 22 species of forest Ungulatae in Africa (Bovoideae, Giraffoideae, Traguloidae) with the four species of New World Cervoideae. The size and mobility of forest mammals are such, however, that they can avoid high homeostatic forest and feed in chablis, clearings, or along rivers.

In contrast to terrestrial animals, the canopy contains a concentration of birds, amphibians, and mammals (primates, flying squirrels). Figures for primates are given by HLADIK and HLADIK (1969). For insects the situation is probably similar, although we have no precise figures. As one climbs a ladder which had been constructed in a relatively undisturbed patch of forest in Saül, French Guiana, flying insects become most noticeable at a height of 10 to 20 m. Colonies of cockroaches are most common in the rosettes of epiphytic Bromeliads in the forest canopy. Nests of ants and termites are again more common on higher branches. It is important, as zoologists are well aware, to be cognisant not only of this vertical layering of faunas, but also of the patchiness of forests which produces a horizontal mosaic.

These zoological considerations emphasize the points made about the homeostatic forest phase. They reflect the concentration of accumulated living biomass in the upper structural ensembles which we have compared elsewhere (p. 279) to herbaceous vegetation borne by the old trunks. Animals, and perhaps also fungi, do produce more or less regular disturbances in the upper, reiterated "herbaceous" canopy of the homeostatic forest, but these disturbances are readily corrected with little loss of vigor.

The argument has thus been made that we should maintain the term homeostasis for the condition of biologically old and well-structured forest in view of the relatively low rate of energy exchange, the constant level of biochemical energy immobilized in dead biomass and the low uniform useful energy level (or vigor) of all trees. We refrain from undue emphasis on aspects of system-repair given by PIANKA and VAN DER PIJL, even though this may more directly convey a cybernetic meaning.

To conclude this section two examples of small disturbances followed by reestablishment of the forest are given from New England (HORN, 1975; OLIVER, 1975). These are interpreted by their authors as successional processes although alternative explanations are possible. The term "self-replacement" used by HORN is a useful concept, although he applies it in a floristic sense, whereas we use it here for the architecture of the forest canopy. OLIVER (1975) showed that in places where the forest canopy of oak-maple forest had been thinned by a hurricane in 1938, trees of what he terms the "B-stratum" and we term set of the future, were released and restored the canopy. In places where the forest had been wholly destroyed a new forest of the same character as the old one grew up, suggesting that here it is difficult to draw the line between small and large disturbances. In this respect the oak-maple forest of New England is more directly comparable to secondary tropical forests than to later phases of primary tropical forest. OLIVER illustrates (1975, Fig. 5.1) a tree which in 1938 had a height of 38 ft (13 m), became released by hurricane damage to surrounding trees and added 4 m of height in the following ten years, even though the canopy tree overtopping it survived. This provides an example of the mechanism of canopy repair without the formation of a chablis.

Horn's mathematical treatment of sylvigenesis in similar forests, on the basis of replacement of dead individuals by seedlings from a selection of species, shows how a pattern of constant species distribution results. Deviation between theoretical predictions and observed conditions may, in our opinion, be ascribed to the fact that the replacement process is stepwise, since some individuals persist in the set of the future so that the forest is repaired, rather than subjected wholly to successional processes. Horn's mathematical model postulates elimination of isolated individuals but can be applied to groups of trees.

In the absence of any statement about the nature of damage done to the forest canopy, i.e., whether by chablis, or by breaking of major branches or by death of standing trees, one cannot comment upon the class of subsequent growth phenomena which these authors describe. These examples are nevertheless particularly instructive because they establish the format for questions about sylvigenesis and fluctuations in homeostatic forests.

IV. Sylvigenetic Cycles and Phases

Sylvigenesis within the first three or four years of a chablis involves a change from a dynamic architecturally undetermined phase to a static phase with a pronounced architecture. Stasis has to be judged at the appropriate time-scale, just as forest architecture has to be considered at the appropriate geometric scale (p. 332). The biological measure for the time-scale in forest growth phases is the potential life-span of its most important members. *Cecropia* includes many species in which the individual life-span is about 20 years. It requires only three or four years for them to establish a form which they then retain for the remaining four-fifths of their life. This ultimate but protracted state is thus homeostatic.

With this in mind we return to sylvigenesis in the chablis. A detailed (but non-architectural) account of what happens on abandoned fields of shifting cultivation in Costa Rica and Panama, together with a review of studies on tropical secondary forest is provided by BUDOWSKI (1961) in a work which is unfortunately not readily available. This author states (p. 51): "Re-establishment of the climax is most rapid when the disturbed area is small and a seed source is close by. Under favourable conditions the number of seral stages is relatively small." Architecturally the first homeostatic forest built on a chablis is a phase (seral stage) whose longevity depends on the floristic content of the infrastructural complement out of which it is recruited. If *Cecropia* is the main constituent of the forest canopy, the life-span of the phase is about 20 years. For other species the formation of the first upper structural ensemble may be much longer. The absence of datable growth rings in tropical trees prevents quantification of this statement. In the Guianas, species alternative to *Cecropia* which provide a longer phase include among others: *Schefflera* (*Didymopanax*) *morototoni, Schefflera paraensis* (Araliaceae), *Spondias mombin, Tapirira guianensis* (Anacardiaceae), *Astrocaryum paramacca, Oenocarpus oligocarpa* (Palmae), *Hymenaea courbaril* (Caesalpinioidae), *Jacaranda copaia, Tabebuia* spp. (Bignoniaceae), *Apeiba* spp. (Tiliaceae), *Sloanea* spp. (Elaeocarpaceae). In "climax forests" of Central America with recent sporadic felling, BUDOWSKI (1961) frequently mentions the same genera and sometimes species; where they occur they constitute in our opinion evidence of sylvigenetic processes having originated in chablis several decades earlier.

In larger clearings which have been burned at least once, sylvigenesis in tropical America starts with *Cecropia* (in Africa it is usually *Musanga* and in tropical Asia, *Macaranga*; in Malesia a complete list of such light-demanding species would be large and include representatives in *Commersonia, Trema, Mallotus, Campnosperma, Anthocephalus, Gmelina, Octomeles*, ... etc.). Within 20 years *Cecropia* trees become senescent and gradually die off. Under the light canopy developed by these pioneers a set of the future, rich in lianes, has developed but remained more or less stagnant. It is possible that the tangle of lianes here plays an important role in regulation of light and humidity, analogous to the role of lower structural ensembles by trees in older forests. When *Cecropia* dies out other trees of the suppressed layer start a phase of expansion (Figs. 109 and 110), resulting in a deformation of the layering in the infrastructural ensemble. The same process is then repeated, with a set of trees of the future developed and entering into competition with each other. Those individuals with an optimal combination of vigor

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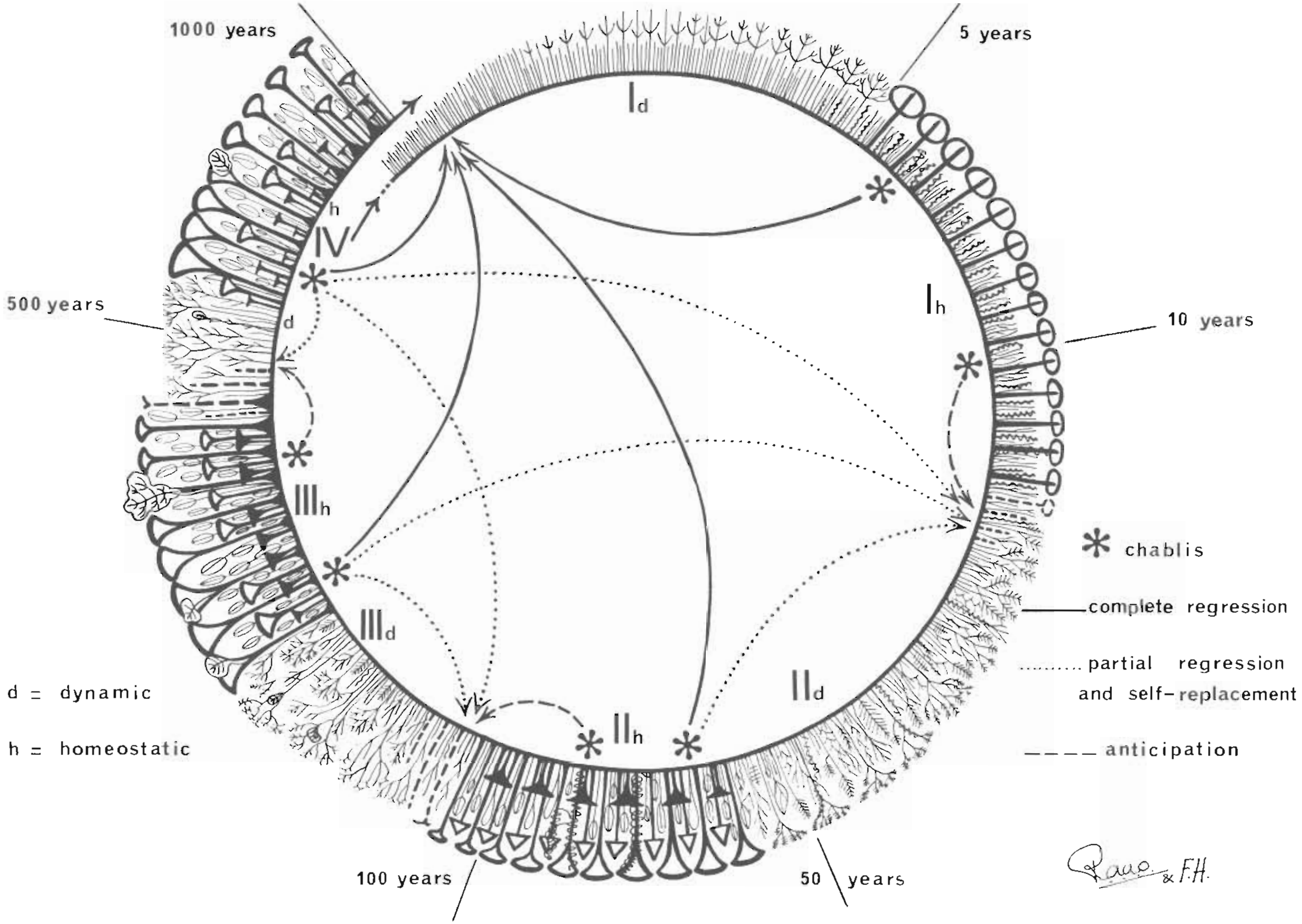
Fig. 110. Sylvigenetic cycles. The process of sylvigenesis can be divided into successive phases, each of which shows a dynamic, growing stage (I_d, II_d etc.) and a homeostatic, steady stage with minimal growth (I_h, II_h etc.). The cycle starts with the first arborescent, pioneer phase and does not take into account possible herbaceous forerunners. Chronology is rather well known for pioneers (BUDOWSKI, 1961), estimated by sylvicultural practices for the second phase, and completely hypothetical for the following ones (in the tropics). Time on logarithmic scale. Note growth phases of forest trees (cf. Fig. 92), and installation of stranglers in Phases III and IV. *Stars* represent chablis. From a chablis regression can be complete to pioneer phase (*full arrows*); partial to some earlier but not pioneer or to its own dynamic phase – self-replacement – *dotted arrows*); or there may be anticipation of a further phase, depending on the presence of suitable trees of the future and the extent of damage (*dashed arrows*). Which pathway is followed depends on size and degree of destruction of the chablis. Sylvigenesis includes all these pathways, and hence is more than a simple succession or regeneration ▷


1000 years
5 years
500 years
10 years
100 years
50 years
I_d
I_h
II_d
II_h
III_d
III_h
IV
h
d
* chablis
complete regression
.... partial regression and self-replacement
– – – – anticipation
d = dynamic
h = homeostatic
Raoo & F.H.

and architectural strategy end up by building a new forest canopy, a structural ensemble which is somewhat denser than the dead one which preceded it. Some longer-living species found in the first phase may be present and may even occur in the upper structural ensemble if their meristems exist in sufficient numbers. The second longer-lasting homeostatic phase is now established. Its constituent species show biological properties cited by BUDOWSKI (1961): shade-tolerance in earlier stages of development, heliophily in later stages, rapid growth rates and rather soft wood. Such trees possess a certain capacity to survive for a short time in a suppressed state in the set of the future, whether it is recent, as under early pioneers, or old and regularly renewed as under later homeostatic phases. The upper structural ensemble they form is often not very dense and permits the installation of those trees we have named sciaphilous nomads. Frequently a relatively dense structural ensemble of dicotyledonous shrubs, to about 8 m high, can be found in this homeostatic phase. The general configuration of this second phase is represented by Figure 110.

These same sylvigenetic processes repeat themselves, i.e., a third homeostatic phase replaces the second one after a dynamic interlude without precise architecture. The third phase is likely to include species which are still more shade-tolerant and can survive for a long time in the set of the future in their early stages of development. In this way recruitment is not necessarily from seedlings, since the third homeostatic phase may be constituted by even-aged trees which germinate at the same time as the initial *Cecropia* population. The "lag" is the result of growth slower and more often interrupted than that of the preceding forest canopy members—often their capacity for reiteration is more important than model performance. Sciaphilous nomads disappear from this forest and discontinuous lower structural ensembles may be found between 12 and 20 m (average 16 m) and between 6 and 10 m (average 8 m).

From this analysis it should be clear that sylvigenetic processes of two kinds are always at work in the forest, transition between dynamic and homeostatic phases and repair mechanisms in homeostatic phases. Both are distinct from forest succession, which can be regarded as the sequence of stages within each of which the above processes take place. This can be illustrated by means of Figure 110 in which the *Cecropia* phase is taken as an arbitrary starting point, i.e., it can be preceded by a herbaceous sere. *Sylvigenetic cycles* occur when a homeostatic patch of forest is damaged. Slight damage, which is represented by dotted arrows in the figure, means that the set of the future in the same or an earlier phase is mobilized, but never that of the pioneer phase; essentially such partial regression is a more or less extensive repair program. More extensive damage (in the tropics this is usually chablis) means a return to the pioneer phase, of course at its dynamic stage (full arrows in the figure). The figure includes the possibility of successive phases V, VI, VII etc. It is clear, however, that the more phases there are, the more complex the situation becomes, since the number of possible cycles increases with the rank order of the phase. There is an inherent limit in phase number, because the risk of destruction by chablis increases with age. If, for instance this risk becomes 100%, or a certitude, in Phase V, sylvigenesis ends there; destruction is inevitable. Cycles might be expected to include the same species association in the same site at longer or shorter intervals, but there seems no way of testing this chronologically in the absence of reliable methods of age determination.

The time span within these phases may be as short as 10–30 years for Phase I, to several centuries for the homeostatic part Phase IV, this spacing being achieved by death of standing trees in the upper structural ensemble. COUSENS (1965), for example, estimates a maximum life expectancy of 1400 years or more for the Malaysian "late-seral component" which includes *Balanocarpus heimii* (Dipterocarpaceae). An "early successional component" like *Shorea leprosula* is estimated to live for 300 years. But these are only estimates, based on maximum growth rate figures for the first forty years compared with largest recorded sizes.

Return to an earlier phase need not be complete, since within a chablis there can be anticipation of the next phase if the damage does not destroy those elements of the future needed to build the next phase (dashed arrows in Fig. 110). An example of this is the establishment of oak–maple forest after clear cutting of pine forest in New England (OLIVER, 1975; our Fig. 96).

If we admit four sylvigenetic phases, then there are fifteen different possible events when homeostasis is interrupted, four involve self-replacement or repair, four involve anticipation of later phases and seven involve rejuvenation, i.e., a return to a younger phase. Repair is facilitated when homeostasis has not been established too long and may become more difficult the longer the homeostatic phase has persisted. BUDOWSKI (1961) mentions the lack of "regeneration" of constituent canopy species in late successional and climax forest. Similarly anticipation of a later phase is most probable after homeostasis has been long established, one can see that this is likely because of the accumulation of appropriate trees of the future. Rejuvenation, however, is always possible because dormant seeds of pioneer species persist or are regularly introduced by birds (see OLDEMAN, 1974a).

Self-replacement, or repair, of the existing homeostatic condition when disturbed may rate high in the strategy of some forest trees. One of the most efficient ways to achieve self-replacement is root-suckering, the initiation of a reiterative complex at soil level. Examples include *Musanga cecropioides* (tropical Africa), *Eucalyptus* species e.g., *E. globulus* (Australia), *Cecropia* species (New World tropics), *Artocarpus incisa* (Asian tropics, Oceania). It is common in certain genera like *Diospyros* and *Drypetes*. In temperate regions of North America examples include species of *Fagus, Liquidambar, Populus, Rhus, Sequoia*. Root suckers indeed provide a means of avoiding the impasse which otherwise produces trees of the past (p. 352) since the reserves left in trunk and roots and which otherwise are lost, can be used to develop clonally a new set of the future. HORN (1975) in his observations on the American beech (*Fagus grandifolia*) suggests that not only is root suckering a repair mechanism in homeostatic stands but also an aggressive device for infiltration into the set of the future in neighboring stands. In some ways the bamboos provide a tropical analogue; though "suckering" from the rhizome is a feature of the architectural model and not a reiterative process. Rhizomatous herbs, derived from Tomlinsons's model, provide herbaceous examples.

From these considerations we can now adjust our view of the unchanging image of the forest with a standard physiognomy to one in which, given a sufficient time scale, change becomes the essential feature, with the only permanent feature being the *processes* of sylvigenesis. From this modified viewpoint we may now look at the concept of "niche".

V. Tree Ecotopes

The separation between ecological *niche* as the "role of the species in the community" and habitat as the "response of the species to the factors of community environment" cannot be applied to plants. Here we use the term *ecotope* in the sense of niche plus habitat, originally proposed by WHITTAKER et al. (1973), as a single concept applicable to plants. Niche and habitat should be distinguished for animals, which are mobile. Trees are usually fixed at the point of germination so that interaction of environment and plant and regulation of microclimate by vegetation is much more intimate (OLDEMAN, 1974b). Exceptions can probably be made for those rhizomatous plants with "vegetative mobility", as exemplified by BELL (1974), or our description of certain tropical epiphytes (Araceae, Cyclanthaceae). Trees change in size during their continuing development, and so does their influence. Animals in contrast can be represented, at the scale of a forest, simply as moving points, and their interactions need not be localized.

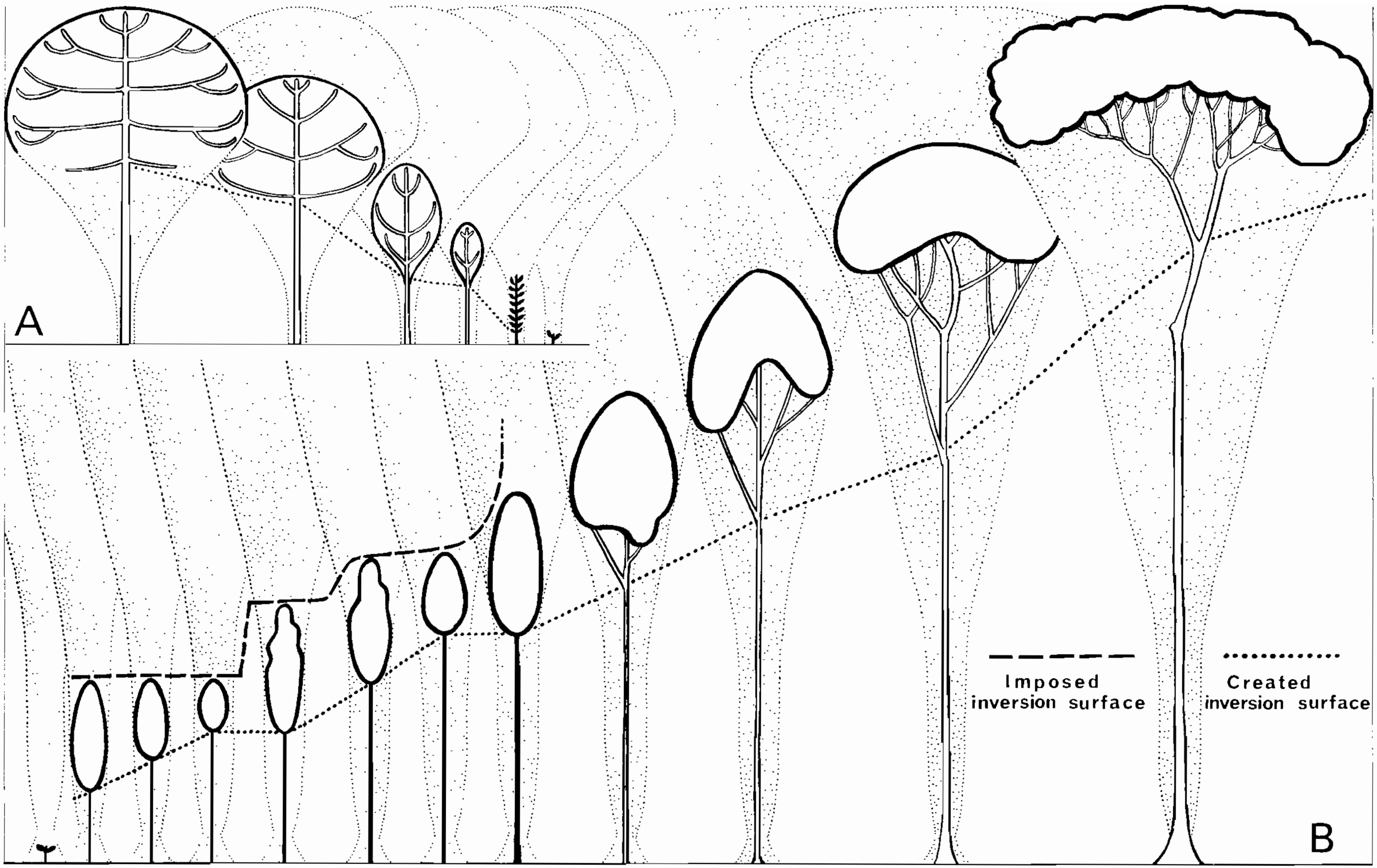
Because of the fixed position of trees and the predictable character of their architecture we can sketch the outline of the space they occupy during various developmental stages. The energetic conditions prevailing during each stage can be indicated by the ecological inversion surface made by the tree and its neighbors. These outlines are represented, both geometrically and energetically in Figure 111 where they show the ecotopes of two very different kinds of tree. The first is a biological "nomad" or pioneer, the second is a biological "dryad" or high forest tree (to use the terms suggested by VAN STEENIS, 1956a). The reader is cautioned that the final volume does not represent some goal towards which the tree is growing, but a set of conditions that a certain proportion of the members of the species partially encounter and partially create, in order to survive. Where there is no suitable ecotope no specifically adapted tree can occupy it, this is why there are no palms in temperate forests. Our illustrations at this point represent qualitatively observed processes which remain to be measured – the morphological inversion surface has been substituted for the ecological one for this reason. Despite the lack of quantitative data Figure 111 serves to show the architectural approach to the problem of the ecotope, which uses the form of the tree as a measure of ecological conditions. It is hoped that meteorological and mathematical refinement of instruments will eventually allow accurate measurement.

Figure 111A shows a biological nomad (p. 383) growing in the open and uninfluenced by overlying ecological inversions. Very early, however, it begins to create its own inversion point. The large leaf blades characteristic of such species suggest that even in the monocaul stage there is slight inversion of trends in light and humidity gradients. These trends are reinforced when the tree starts to branch and they reach a maximum when the branches are fully deployed as the largest

Fig. 111A and B. The ecotope (=niche+habitat) of the immobile organisms that are trees, is a qualified space, in which energetic conditions change as indicated by the inversion surfaces. If a tree does not find a suitable ecotope (i.e., the correct pulsations of energy from outside) it dies; if it survives it creates in its turn ecotopes. >

A *From right to left:* ecotope occupation and creation by a pioneer, growing up in the macroclimate and leaving "behind" it a still discretely regulated microclimate.

B *From left to right:* same for a big forest species growing up in successive ecotopes created by its predecessors and creating a strongly regulated microclimate


A
B
Imposed inversion surface
Created inversion surface

possible crown. Biological nomads (e.g., *Trema, Macaranga*) have a limited ability to reiterate the model and this is probably one reason why their crowns, when seen from below, are more light-admitting than those of large forest trees. We may say therefore that ecological inversions, even in the homeostatic stage of development, remain moderate. Sciaphilous nomads, growing in later homeostatic forests under canopies which remain fairly open, may eventually penetrate the canopy and may be compared to heliophilous nomads of earlier phases. They are tolerant of moderate shade induced by a higher canopy because their meristems can function at lower energy inputs.

Another example can be provided by a potentially tall forest tree which after a short period of vigorous growth becomes suppressed by an existing ("imposed") ecological inversion, indicating that above this level energetic conditions are too low to sustain its growth. The tree then functions as a suppressed tree of the future and remains so until a modification in the overlying forest heightens the imposed inversion level, which may happen at the onset of one of the sylvigenetic cycles illustrated in Figure 110. More advanced trees then impose a new inversion level which permits limited growth before suppression. Suppression is promoted because high forest trees grow slowly (BUDOWSKI, 1961). By repetition of this process such a species gradually gains the canopy, creating during the process another ecological inversion under its own crown. The meristems of such slow-growing trees are organs of low productivity, so that the model itself cannot absorb large quantities of energy without mobilization of reserve meristems. Consequently a high capacity for reiteration marks such trees and it is only the existence of a large number of reiterating meristems which ensures that the early high shade tolerance of the suppressed tree is followed by equal efficiency as a canopy tree which now has to adapt to the macroclimatic environment.

We thus have the beginnings of an understanding in bioenergetic terms of the difference between leptocaulous and pachycaulous species, to use the terms proposed by CORNER (1949) for thin-twigged and thick-twigged species respectively. Many small meristems, individually with low energy consumption, can easily be replaced; large meristems with individually high energy consumption are less readily replaced. A pachycaulous tree consequently always reveals reiterative processes as being individually more costly in energetic terms. A damaged *Cecropia* tree of the present shows by ugly scars and axis deformations the places where broken branches have regenerated, whereas such substitution is more subtle in oak. Similar rules may be applicable to trees limited by factors other than shade.

A series of examples from the American tropics will illustrate the architectural relation between shoot diameter and reiteration. *Cecropia*, highly intolerant of shade, has been mentioned already. *Iryanthera* species conform closely to their model but branch profusely by means of rather slender axes, are somewhat shade tolerant and may be described as sciaphilous nomads. *Voucapoua americana* is quite tolerant of shade when young, but where it penetrates into the canopy around the edges of a chablis, it develops more slender branches and shows profuse reiteration. In *Lecythis* cf. *davisii* the branches are thin, as in most temperate trees, and reiterative processes are promoted. The analogy with temperate trees should not be made too closely, since in the tropical rain-forest the environment is regulated more obviously by biotic factors than by macroclimate.

From the point of view of life form in relation to the dynamics of architecture and growth of trees, and during sylvigenesis, the ecotopes can be seen as qualified spaces, unceasingly expanded and destroyed, like a series of children's balloons inflated by a series of puffs (but of light energy, not air) and finally bursting and disappearing after having displayed a particular form. The dynamism is here different from the dynamics of zoological niches; because of the mobility of animals the analogy is no longer apt, since abstract, nongeometrical aspects are dominant. It is the biotope as a whole, more than individual ecotopes which determines the livable space for animals, a statement which the concept of territoriality might qualify.

VI. Biological Nomads and Towering Trees

In the preceding chapters, the concept of biological "nomads" has been frequently used, and towering trees or emergents have been mentioned. These terms need discussing to indicate their meaning. Biological nomads (VAN STEENIS, 1956a, b) refer to sun-loving trees with a short life-span which appear irregularly in the forest. They have also been referred to both as "scar species", symptomatic of the way they appear to heal "wounds" in the forest (MANGENOT, 1955), and as pioneer species (WHITMORE, 1975), appearing in open spaces before others. Clearly such trees are readily recognizable as a biological entity. Regardless of their name we have found that architecturally they reiterate little, if at all within their crowns when subject to increased energy levels. Reiteration more frequently occurs at the base of their trunks, as in *Casearia* spp., *Trema occidentalis, Myrcia bracteata* from the Guianas, or from root suckers. Their growth is very fast and their meristems can transform high amounts of energy. Dry matter so produced is used to produce bulky organs, since these trees are characterized by hollow axes and soft wood (e.g., *Apeiba tibourbou,* corkwood or "bois-bouchon"; *Ochroma lagopus,* balsawood). Combined with prolific and early flowering and fruiting (BUDOWSKI, 1961) these characteristics recall oversized herbs. The term "weed trees" given them by CORNER (1952) seems equally appropriate. As elements in the forest they constitute a unique architectural set.

In contrast to biological nomads it seems possible to recognize a class of tree for which the term "sciaphilous nomad" seems appropriate. These depart little from their model and have a distribution which bears little relation to existing forest sets. Examples of such trees in French Guiana include species of *Duguetia* (Annonaceae), *Virola* and *Iryanthera* (Myristicaceae). *Lacmellea aculeata* (Apocynaceae) is a similar occupant of the undergrowth. Sometimes, however, these species appear with some regularity in the canopy (e.g., *Virola surinamensis*). Reiteration then may occur, and is striking because of the otherwise precise regularity of the tree. In West African forests the myristaceous tree *Pycnanthus angolensis* is comparable, though less abundant. Growth of these sciaphilous nomads is relatively fast (*Virola surinamensis* is exploited in Surinam with a 40-year rotation). Their wood is relatively light and they start flowering rather early; fruit production within the model is abundant. Sciaphilous nomad is an appropriate name because one may encounter these trees anywhere in the forest, provided the upper canopy is not too dense. Whenever they themselves form closed forest canopies, as *Virola* and *Iryanthera* often do in marshy regions of Central America (BUDOWSKI, 1961), Ecuador and the

Guianas, the regular character of this canopy is closely comparable to that in forests formed by heliophilous nomads like *Musanga* and *Cecropia*.

Weed trees represent one extreme of a range of possibilities, the other extreme of which is represented by towering giants of the forest. Size alone, however, is not necessarily a reliable indication of advanced sylvigenetic phases. COUSENS (1965) cites among his "early-seral components" in Malaya very big trees in the genus *Shorea* (Dipterocarpaceae). BUDOWSKI (1961) pointed out that some high forest trees belong to species with a very large geographic distribution and a wide ecological tolerance which grow relatively fast and have rather soft wood. Examples include *Terminalia amazonia* (Combretaceae), *Ceiba pentandra* (Bombacaceae), *Goupia glabra* (Celastraceae), together with commercially important genera of the Meliaceae from both West Africa and the Americas (*Entandophragma, Khaya, Swietenia*), all of which can surpass heights of 50 m. Others with harder to very hard wood and slower growth are sparsely though regularly distributed in the rain-forest and include species of *Lecythis* (e.g., *L.* cf. *davisii*), *Couratari* (Lecythidaceae), *Aspidosperma* (e.g., *A. megalocarpon,* Apocynaceae) and probably some African Sapotaceae.

The giant *Ceiba* spp. (Bombacaceae) of the western lowlands of Ecuador are straightforward pioneer species with the same crown shape whether they grow in the open or not. In French Guiana the highest tree of *C. pentandra* we observed (approaching 60 m) grew in openings in forest in periodically inundated valleys. *Hura crepitans* (Euphorbiaceae) is a tree which reaches sizes up to 55 m in similar valleys in the forest, but forms a low spherical typically free-standing crown in open places along the coast. *Terminalia amazonia,* as a tree of the future, is present in secondary thickets in the surroundings of Saül (French Guiana). In one place (Mt. Boeuf Mort) it forms a close structural ensemble over 50 m high above a second structural ensemble about 30 m high dominated by Burseraceae and a third about 10 m high dominated by *Quararibaea turbinata* (Bombacaceae). A diffuse set of the future is present, containing mainly the same trees and occupying the space left open by the structural ensembles. According to the villagers, this forest may be about fifty years old, confirming that it probably constitutes Phase II in a sylvigenetic cycle which began with *Cecropia* (Figs. 109 and 110).

On the upper Approuague in the same country we observed patches of seemingly much older forest with an upper structural ensemble of an undetermined *Aspidosperma* species (Apocynaceae – "bois-anguille") of comparable height but with hard wood. Giant *Couratari* (cf. *C. stellata,* Lecythidaceae) formed similar patches of high forest near Saül, whereas another unidentified species of the same genus occurred as the highest tree in imbrication zones on the slopes of Mt. Galboa. *Lecythis* cf. *davisii* is represented by isolated individuals with the same general height as the upper canopies of which they are members, but sometimes they tower above the surrounding forest at levels up to 55 m, when they have the crown physiognomy of a forest tree and not a free-standing tree.

Without more detailed knowledge of the autecology of giant species it is difficult to generalize about their role and status. However, trees towering above the forest by no means can be considered simply as having "pierced the closed canopy" to emerge from the underlying structural ensemble and having continued to grow to an enormous height, as is suggested by the word "emergent" which is so often used to describe them. Some certainly do this, but others represent relicts of high forest canopy with surrounding trees fallen by chablis. It is an unfortunate handicap that ages of tropical trees cannot be assessed precisely so that one cannot distinguish between even-aged and uneven-aged sylvigenesis. This means that the time scale of our phases remains hypothetical. It seems certain, however, that in many instances isolated tall trees are relicts and not emergents in the primary sense of the word.

Concluding Remarks

If it is polite to lead the reader into a book by way of an introduction, this person should then not be forgotten at the end, even if it is only because the authors insist on having the last word.

We wrote the book in order to present to English-speaking readers, a new method of analyzing trees by considering momentary architectural stages in the dynamic context of a growth model. We came to suspect that all living systems are capable of being analyzed in this way. For trees it has allowed us to proceed from a consideration of organ morphology to tree architecture, seen as the expression of the growth model. Multiple expression of growth model in one tree was recognized as the manifestation of a phenomenon we have termed reiteration. From the model tree in an optimal environment we moved to the reiterated tree in forest sites and from the architecture and growth of forest sites an easy step took us to forests and the architecture of successional mosaics. This enlargement of scale by modest steps allowed us to proceed from one geometrical model to another geometrical model but keeping very close to Nature itself. Our approach has been unashamedly qualitative, indeed we have deliberately avoided the dimensions of a higher order than four, three-dimensional space plus time, in much of our analysis of tree form, in order to produce a book that can be used without extensive mathematical equipment or technologically advanced instruments. In this way we have tried to produce something readable and recognize that others, better equipped, having shared our collective experience will extract those concepts they find useful and improve upon them. We particularly hope that the book will be universally useful to all those who are interested in plants and vegetation and will be used as a means of furthering understanding of trees as a renewable resource. We ask our reader not to forget that the represented viewpoints are of tropical rather than temperate origin so as not to be deceived when finding that in a particular environment some of the elements we refer to are lacking. We hope that the tropical reader does not find that the elements once so readily available in immensely rich diversity have been destroyed forever, when seeking to satisfy a curiosity we hope we have aroused (GÓMEZ-POMPA et al., 1972).

Glossary

Terms as used in this book; if definitions are due to other authors, these are not cited here but generally in the text.

absolute branch order, see branch order, absolute.

actinomorphic, radially symmetrical.

anemochores, plants with wind-dispersed propagules.

apparent branch order, see branch order, apparent.

apposition growth, see growth, apposition.

architectural tree model, see model.

architecture, the visible, morphological, expression of the genetic blueprint of organic growth and development.

articulated growth, rhythmic growth which results in shoot units separated by morphological discontinuities, e.g., bud-scale scars; hence, articulated shoots (cf. *continuous growth*).

articulated shoot, shoot produced by articulated growth, usually with distinct bud-scale scars.

axis, supporting part of an organ or complex, e.g., leaf axis, stem.

bamboo, a member of the subfamily Bambusoideae, Gramineae.

bamboo habit, distinctive architecture as exemplified by a bamboo (cf. McClure's model, p. 139).

bayonet-joint, articulation, usually in orthotropic shoots, where substitution growth has occurred; may be the result of sequential branching (in the model) or reiteration (after damage).

biomass, dry or wet weight of organic matter produced by growth of an organism.

biotope, the living space occupied by an organism.

branch order, the numerical sequence of an axis; hence *absolute* branch order, the morphological order of a branch as determined by primary development.

apparent, relative or *visible* branch order, the actual branch order determined by secondary changes and available for simple analysis.

branching, sequential, the sequence of appearance of branches as determined by the architectural model; hence *reiterative* branching, or *branching by reiteration,* the appearance of branches not determined by the architectural model, e.g., in damaged trees.

bud, (in this book) the shoot apical meristem and its immediate derivatives (leaf primordia, bud scales).

bud complex, a group of closely juxtaposed buds; may be either *primary,* e.g., a series of buds all of the same branch order developed within a single leaf axil, or *secondary,* the products of repeated branching producing an aggregate of buds belonging to several branch orders.

bud-scale, a modified leaf or other organ enveloping and protecting a resting bud.

cauliflory, production of flowers on the trunk.

chablis, a gap in the forest produced by the fall of a tree; the fall of the tree itself and the resulting forest damage (from the French).

colleter, secretory, usually nonvasculated organ (gland or multicellular hair) associated with a bud.

continuous growth, growth without visible rhythm producing shoots without distinct articulations (cf. articulated growth).

Corner's rules, axiomatic rules governing branching frequency and axis-appendage correlations in relation to axis size (see p. 81).

crown area index (CAI), total projected crown area above unit area of ground surface: a measure of canopy density.

cryptocotylar germination, see hypogeal germination.

cryptogeal germination, germination in which the plumule is buried by late extension of the cotyledonary axes.

cyclophysis, the organizational status of a meristem in a tree determined by its age.

decussate (leaf) arrangement, in pairs, the successive pairs at right angles.

dedifferentiation (of axes), change from one level of differentiation to a previous, "younger", level—often as an ecological response expressed by the apical meristem (=rejuvenation), e.g., from plagiotropy to orthotropy if the model sequence goes from orthotropy to plagiotropy.

dendrochronology, determination of historical events on the basis of annual growth increments in tree trunks.

diaspore, a unit of dispersal.

differentiation (of axes), morphological specialization either as sequential expression of meristematic specialization or growth correlation (e.g., from orthotropic to plagiotropic shoots).

distichous (leaf) arrangement, alternate, but restricted to a single plane.

dryad, a high forest tree occupying a precise ecotope.

ecological inversion point, see inversion point, ecological.

ecological inversion surface, see inversion surface, ecological.

ecotope, combination of niche and habitat occupied by a plant.

emergent, an isolated tree standing above the average forest canopy, but which did not necessarily emerge.

energy flow, transfer of energy within the tree or between the tree and its environment (p. 284).

ensemble, see set.

epicormic, originating from the trunk, as in an *epicormic shoot* developing from a latent meristem.

epicotyledonary axis, stem immediately above the cotyledonary node.

epigeal germination, in which the cotyledon(s) escape from the seed coat and usually appear above ground as photosynthetic organs (= phanerocotylar germination).

epinasty, the effect of one branch on another which determines their final orientation.

episodic growth, rhythmic growth.

epitrophy, generalized response leading to the formation of erect axes.

establishment growth, post-seedling growth of plants, usually without secondary thickening meristems (cambiums), resulting in gradual development of massive primary axes (e.g., monocotyledons).

flush, rapid primary shoot expansion and elongation, usually in contrast to existing foliage.

growth, apposition, resulting in branching by displacement of a continued active terminal meristem by a more vigorous lateral, i.e., no meristem abortion involved, cf. *growth, substitution,* resulting in branching by replacement of a terminal meristem which is determinate either by abortion or, most usually, by becoming a flower or inflorescence (see also plagiotropy by apposition or substitution).

growth-habit, the ultimate form of a plant as expressed in its physiognomy, i.e., growth-habit is not defined by a precise differentiation sequence, but more or less by an overall appearance.

habit, see growth habit.

habitat, the community environment.

hapaxanthy, development of an axis which is determinate by terminal flowering, hence *hapaxanthic shoot,* a shoot which flowers terminally (cf. *pleonanthy*).

heliophilous nomad, see nomad, heliophilous.

heteroblastic, with a morphological difference between juvenile and adult (e.g., in leaf shape and size).

homeostasis, in an ecological sense, a community in a steady state, with minimal free energy (see p. 370).

homeostatic forest, a forest in a condition with minimum free energy.

hypogeal germination, in which the cotyledon(s) remain within the seed coat and usually do not appear above ground as photosynthetic organs, e.g., palms (=cryptocotylar germination).

hypopodium, the part of a branch which is localized between its origin and its first leaf; usually long in sylleptic branches, it remains very short in proleptic ones.

infrastructural complement, the population of latent meristems in a forest, representing potential growth.

infrastructural set, the population of functioning meristems in a forest, representing actual growth.

initial complex, the visible complex of axes and active meristems produced by a tree when growing precisely according to its model (i.e., without reiteration).

intermittent growth, noncontinuous growth without the predictable regularity of rhythmic growth; hence *intermittent branching.*

inversion point, ecological, the point in the forest where real vertical microclimatic gradients (e.g., of humidity and light intensity) cross the average vertical gradient (regression curve).

inversion point, morphological, the insertion of the lowest major limb of a tree above which all branch or reiterative complexes are progressively smaller.

inversion surface, ecological, collective microclimatic inversion points, as of light intensity and humidity.

inversion surface, morphological, collective inversion points of individual trees in a forest, indicative of that forest's status.

K selection, selective conditions which favor longevity of individuals at expense of reproductive capacity.

K strategist, a species adapted to maximum survival of individuals at expense of reproductive capacity.

lammas shoot, late season flush of growth in a temperate tree which normally flushes annually.

leaf area index (LAI), cumulative projection of leaf area above unit ground area, a measure of leaf density.

leptocaul, a thin-twigged and usually much-branched tree.

linear sympodium, a single stem made up of successive, usually determinate, monoaxial units.

long shoot, where there is shoot dimorphism, an extended shoot contributing to the architecture of a tree.

marcottage, artificial propagation by stimulation of aerial root formation in a woody axis.

model (botanical), short for *architectural tree model,* generalized growth program which determines successive architectural phases of a tree.

modular construction, way of building trees or branch complexes out of modules.

modulation (of humidity and light gradients), progressive but nonuniform change in microclimatic conditions throughout the forest canopy.

module (=article in French), shoot unit with determinate growth, either by apical abortion or conversion of apex to an inflorescence.

monocaul, with a single trunk.

monolayer, with leaves spread in a single horizontal layer, i.e., without overlap; hence:- *multilayer,* with leaves distributed vertically and some degree of overlap.

monopodium, an axis established by a single indeterminate meristem, i.e., branches remain subordinate; hence *monopodial growth,* growth by continued activity of a single meristem.

morphological inversion point, see inversion point, morphological.

morphological inversion surface, see inversion surface, morphological.

multilayer, see monolayer.

naked bud, a resting meristem without obvious morphologically specialized protective organs.

neoformation, formation of an organ or part of a shoot system immediately prior to its expansion (cf. preformation).

neoteny, precocious sexuality in animals or plants; botanically it often implies loss of several preceding vegetative steps of the differentiation sequence; it may be an ontogenetic or a phylogenetic process.

niche, the energetic position of a species in a community.

nomad, biological, a pioneer tree on a disturbed site (synonyms: scar species, weed tree).

nomad, heliophilous, frequently occurring but-short-living tree species favoring regions of high light intensity in a forest community, and generally without reiteration.

nomad, sciaphilous, frequently occurring somewhat longer-living tree species tolerant of low light intensity in a forest community, and generally without reiteration.

nonarticulated growth, continuous growth, resulting in a *nonarticulated shoot.*

organ complex, the total interacting complex of organs forming an individual tree or part of a tree, such as a branch system (e.g., plagiotropic complex).

orthostichy, vertical series of leaves or leaf scars.

orthotropy, gravitational response which produces a vertical axis, hence *orthotropic shoot* with the complex of characters resulting from this response, i.e., radial symmetry and vertical orientation (cf. plagiotropy).

pachycaul, a thick-twigged, little-branched tree.

paedomorphism, persistence and/or elaboration of juvenile characters (may be ontogenetic or phylogenetic).

pagoda habit, tree physiognomy with regular tiers of horizontal branches, the tiers progressively shorter distally, and the end of each branch upright.

parastichy, regular oblique series of leaves or leaf scars.

pauperization, reduction of vigor and size such that architecture is minimally expressed; may also result in dedifferentiation and reiteration.

periphysis, the organizational status of a tree meristem influenced by environment.

phanerocotylar germination, see epigeal germination.

phyllomorphic branch, determinate short-lived and strongly plagiotropic branch axis with some or many of the biological characters of a compound leaf.

pipe model theory, theory which relates units of crown structure to vascular units, or "pipes", in the axes supporting them (cf. unit pipe).

plagiotropic complex, set of interacting meristems forming an extended plagiotropic branch system, from not necessarily plagiotropic axial components.

plagiotropy, gravitational response which produces an oblique or horizontal axis, hence *plagiotropic shoot* with the complex of characters resulting from this response i.e., dorsiventral symmetry and horizontal orientation (cf. orthotropy).

plagiotropy by apposition, character of a plagiotropic complex determined by apposition growth.

plagiotropy by substitution, character of a plagiotropic complex determined by substitution growth.

plastochrone, time interval between two successive similar events, as in leaf development, often used in a descriptive sense for its morphological result.

pleonanthy, development of an axis which is not determinate by flowering, i.e., flowers or inflorescences are lateral; hence *pleonanthic shoot*, a shoot with lateral flowers.

plot, in vegetational analysis, the smallest sample representative of a sylvigenetic phase.

pneumatophore, aerating organ, usually an aerial root, best known in woody swamp or mangrove plants.

preformation, formation of the whole of an unexpanded shoot system prior to its subsequent complete expansion (cf. neoformation).

prolepsis, development of a lateral branch only after a period of dormancy as a lateral bud; hence *proleptic branch*, a branch developed by prolepsis.

pseudowhorl, a close set series produced morphogenetically in sequence but simulating a whorl.

ramiflory, production of flowers on older branches.

reiteration, development of shoots outside the normal expression of the architectural model of a tree, as a specialized environmental response.

reiterative complex, the complex of meristems produced by reiteration.

rejuvenation, see dedifferentiation.

relative branch order, see branch order, relative.

relay axis, an axis taking over growth in a tree, either according to the model or as a result of reiteration.

rhythmic branching, production of branches in a regular sequence associated with rhythmic growth.

rhythmic growth (=episodic growth), growth of an axis determined by a rhythm which results in periodic shoot extension alternating with dormancy.

river-bank effect, growth response of trees unevenly illuminated, as on a river-bank.

r selection, selective conditions which favor high reproductive rates at expense of individual vegetative longevity.

r strategist, a species adapted to high rates of sexual reproduction at expense of individual longevity.

sciaphilous nomad, see nomad, sciaphilous.

semi-hypogeal germination, in which the hypocotyl elongates during germination, e.g., durian.

sequential branching, see branching, sequential.

set (or *ensemble*), group of trees within a forest with equivalent developmental potential (e.g., set of future, present and past).

sexuality, in higher plants the transposition of the individual or an axis to the flowering condition.

short shoot, where there is shoot dimorphism, an unextended, often specialized axis bearing leaves and usually flowers, not contributing to the overall architecture of the tree.

spiral (leaf) arrangement, alternate, but radially arranged, i.e., forming a helix.

spirodistichous (leaf) arrangement, alternate, two-ranked, but the ranks each describing a helix.

strategy, the mechanisms by which an organism's genotype is preserved (cf. *r*-strategist, *K*-strategist).

structural ensemble, a subdivision of the set of the present according to height.

substitution growth, see growth, substitution.

syconium, the inflorescence and subsequent infructescence of a fig.

syllepsis, development of a lateral branch without a period of dormancy, i.e., contemporaneous with its parent axis; hence *sylleptic branch*, a branch developed by syllepsis.

sylvigenesis, the process of forest formation.

sylvigenetic cycle, one of the repeating processes in sylvigenesis.

sylvigenetic model, the analogue of a tree model in the development of a forest.

sylvigenetic phase, a subdivision of a sylvigenetic cycle, not necessarily repeated.

sympodium, a single axis formed by a series of lateral meristems in sequence; *sympodial growth*, growth from successive lateral meristems.

tier, a group of closely inserted branches or branch complexes (whorled or pseudowhorled) widely separated from other groups of branches.

topophysis, the organizational status of a meristem in a plant body determined by its position and stable through vegetative propagation.

tree (botanical), a tall, usually woody plant with a single trunk.

tree (mathematical), a series of interconnected lines without loops, i.e., only one possible pathway between any two points in the tree.

tree of the future, tree with potential for future expansion within the forest mosaic.

tree of the past, over-mature, decaying or damaged tree in process of elimination from the forest mosaic.

tree of the present, dominant tree which codetermines forest architecture, but without further capability for expansion.

treelet, a small tree.

unit of extension, a morphologically discrete growth increment.

unit of morphogenesis, a unit of growth determined by a single cycle of mitotic activity of the apical meristem.

unit pipe, the unit supporting and supplying one crown unit in the pipe model theory.

verticillate or *whorled (leaf) arrangement,* several appendages inserted at precisely the same level.

vigor, excess of growth rate over death rate in a tissue, organ or plant.

visible branch order, see branch order, visible.

whorled, see verticillate.

woody, with a high proportion of lignified tissue.

zygomorphic, bilaterally symmetrical.

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