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MODULAR CONSTRUCTION AND ITS DISTRIBUTION IN TROPICAL WOODY PLANTS

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INTRODUCTION

The definition of module (a substitute for but not a translation of the French "article") has been given by Prévost (1967). The word seems to have a descriptive value and we can define modules as: simple morphogenetic shoot units of determinate growth constant in their expression, derived one from the other by a sympodial mechanism, the resulting sympodium being either linear, branched in one plane, or branched in three dimensions of space.

The important fact in this definition is the limitation of the apical activity of the module and consequently the sympodial construction which results from their proliferation. Determinate growth of each module may result from different causes.

1. Formation of a terminal flower, or an inflorescence as in, e.g. cassava, Manihot esculenta Crantz (Euphorbiaceae); Médard, 1973; castor-bean, Ricinus communis L. (Euphorbiaceae); frangipani, Plumieria spp. (Apocynaceae).
2. Formation of a terminal tendril, as in the woody climber Landolphia dulcis Pichon (Apocynaceae; Cremers, 1975).
3. Formation of a spine as in Carissa macrocarpa A.DC. (Apocynaceae; Brunaud, 1970).
4. Simple parenchymatization of the original apical meristem, as is frequent in many trees in the Apocynaceae during an initial vegetative phase of growth (Brunaud, 1971; Corner, 1952; Hallé & Oldeman, 1970; Prévost, 1967, 1972).

Modules may be orthotropic or plagiotropic in their orientation and morphology as an expression of endogenous activity, without obvious relation to external (ecological) factors. In this chapter, only branched trees are considered (cf. Hallé & Oldeman, 1970) although it is recognized that the same construction can occur in trees with a single sympodial trunk which is apparently unbranched (CHAMBERLAIN's model).

TYPES OF MODULAR CONSTRUCTION

The question asked here is "What is the place of modular construction within the architectural models recognized by Hallé & Oldeman (1970)?" Some trees exhibit this construction both in the trunk and the branches, we can call them fully modular models; others show the construction only in the trunk or in the branches, they are partially modular.

Fully modular models

Three models are included in this category, — LEEUWENBERG's, KORIBA's, and PREVOST's models.

In LEEUWENBERG's model the axes are all equivalent and orthotropic, as in cassava and frangipani, as already noted. The model is common in the Araliaceae (e.g. many species of Schefflera — see also Philipson, this volume). The epicotyl, i.e. the first module, the one produced by the plumular meristem, can exceed 10 m as in Didymopanax morototoni Decne. & Planch. (Araliaceae) from northern South America and Anthocleista nobilis G. Don. (Loganiaceae) from West Africa. This is important in making a tall tree possible.

In KORIBA's and PREVOST's models ^{two} types of axis are differentiated: on the one hand, orthotropic modules which collectively and successively give rise to the trunk ^{and} on the other hand, plagiotropic modules which collectively give rise to the branches. The mechanism of trunk formation differs in these two models. Essentially it is formed by secondary erection of successive orthotropic modules in KORIBA's model, but by primary orthotropic orientation in PREVOST's model. However, the topic is not dealt with further (see Hallé & Oldeman, 1970, p. 46-57 and Tomlinson, this volume).

The American balsa tree, Ochroma lagopus Swartz (Bombacaceae) and the African abale, Combretodendron africanum (Welw.) Exell. Lecythidaceae are good examples of KORIBA's model. The latter, a tall forest tree, demonstrates that modular trunk growth can produce tall single-trunked trees. The same is true of PREVOST's model, which may be exemplified by the emien, Alstonia boonei De Wild. (Apocynaceae), reaching a height of 50 m in the West African rain forest.

Partially modular models

In NOZERAN's model the trunk is developed by a succession of modules as is familiarly exemplified by cocoa, Theobroma cacao L. (Sterculiaceae), native to Amazonia. In this model the branches are plagiotropic, but not modular, since they are monopodial. The situation is reversed in FAGERLIND's and SCARRONE's models since the branches, but not the trunk, are modular. In FAGERLIND's model the branches are plagiotropic; this model is not frequent among familiar trees, but is shown by some Rubiaceae

(e.g. Randia fitzalanii F. Muell, see Fagerlind, 1943). In SCARRONE's model the branches are orthotropic as is evident in the familiar mango, Mangifera indica L. (Anacardiaceae).

It is of further interest to examine the distribution of modular models in some tropical families.

(A)

TAXONOMIC DISTRIBUTION OF MODULAR CONSTRUCTION

(B)

Family Level

The subject has been studied by Kahn (1975) whose results for the families Apocynaceae, Euphorbiaceae and Rubiaceae are summarized here.

(C)

Apocynaceae

The architectural model is known for about 50 species and in relation to the categorization already established, the following distribution is found:

<u>Model</u>	<u>No. of Species</u>
LEEUEWENBERG	17
KORIBA	7
PREVOST	8
SCARRONE	6
NOZERAN	1
[RAUH]	[2]
[Other Models]	[9]
TOTAL	50

From this it is clear that the Apocynaceae can be described as a "modular family" since 64% of known species (32 out of 50) represent a fully modular architecture, while only 22% (11 out of 50) belong to wholly "non-modular" models. This leaves a small percentage (14%) of partially modular examples.

Euphorbiaceae

In 36 species of known architecture, the following results have been obtained:

<u>Model</u>	<u>No. of Species</u>
LEEUVENBERG	6
KORIBA	8
PREVOST	2
SCARRONE	1
NOZERAN	4
[RAUH]	[15]
TOTAL	36

The family is appreciably modular, with 44% (16 out of 36) fully modular species, but only 14% (5 out of 36) partially modular species. One notes, however, the abundance of RAUH's model (42%, 15 out of 36) which is a non-modular type, exemplified in the family by Hevea brasiliensis Muell-Arg. This latter model is of interest in comparison with LEEUVENBERG's model since in both aerial shoots are equivalent and orthotropic. However, in the former construction is monopodial, with the growth segments developed successively as "units of extension", if one may so translate the term unité de croissance used by Hallé & Martin (1968) in their study of this species/.

In LEEUWENBERG's model the units are modules, and construction is sympodial. SCARRONE's model is intermediate, as we will see later.

Rubiaceae

In 45 species for which architecture is known, the following distribution appears:

<u>Model</u>	<u>No. of Species</u>
LEEUWENBERG	3
KORIBA	1
PREVOST	0
FAGERLIND	5
SCARRONE	1
NOZERAN	0
	<hr/>
TOTAL	10

It is clear that the Rubiaceae is not a modular family with only 22% (10 out of 45 modular). Of these only four species (9%) are fully modular.

Generic and Specific Level

At the generic level, we can speak of a polymorphic genus (Hallé, 1969) when it includes a variety of species exhibiting different architectural models. Some examples may be given. Alstonia (Apocynaceae) shows examples of the three fully modular models, Alstonia sericea Bl., from Malaysia (LEEUWENBERG), A. macrophylla Wall., from Malaysia (KORIBA) and A. boonei De Wild. from Tropical Africa (PREVOST). ~~It is also known that~~ all eight species of Alstonia whose architecture is known belong to one of these three

models (Corner, 1952; Hallé & Oldeman, 1970; Prevost, 1967; Veillon, 1976).

The genus Cordia (Boraginaceae) is somewhat comparable, with Cordia curassavica Lam., C. laevifrons Johnst. (PREVOST) and C. alliodora (FAGERLIND). All these species are from Africa, although the genus is widespread.

The genus Euphorbia (Euphorbiaceae) is the most diverse, with 11 models. In Madagascar alone, Cremers (1975) has observed ten of them.

At the specific level, the question may be asked whether in the development of a species two distinct architectural models can be accommodated within the same genetic framework, the variation being determined by ecological factors. In Fagara rhoifolia (Lam.) Engl. (Rutaceae) for example Hallé & Oldeman (1970) have described ontogenetic changes which allows one to relate this species initially to SCARRONE's but subsequently to KORIBA's model. When the tree is young the trunk grows rhythmically, producing periodically pseudo-whorls of orthotropic branch complexes with a modular construction. When the tree reaches a height of about 8 m the apical meristem of the trunk loses its vigor and is substituted by one or more relay axes which have a modular construction, but continue growth in height. In Pseudopanax crassifolium (Araliaceae) a similar loss of dominance is recorded by Philipson (this volume), with here a change from SCARRONE's to LEEUWENBERG's model. The phenomenon may be frequent in the family since Veillon (1976) finds it in three other genera (Dizygotheca, Myodocarpus, Tieghemopanax).

In the avocado (Persea gratissima, Lauraceae) Aubert & Lossois (1972) refer to a transition between ATTIM's and CHAMPAGNAT's model, but these models are not very similar and the interpretation seems wrong.

In a less tropical family, Temple (1975) recently recognized the same form of transition (between SCARRONE's and LEEUWENBERG's model) in two species of Erica (E. scoparia and E. cinerea). A tree member of this same family Arbutus unedo L. (strawberry tree) shows a similar change determined by the environment. In an open, well-lighted habitat the tree lacks a monopodial trunk and conforms to LEEUWENBERG's model, in a closed, shaded habitat a monopodial trunk is formed and SCARRONE's model is represented.

MODULES AND UNITS OF EXTENSION

Both types of growth unit are the result of rhythmic development of shoot systems, as has been established in the comparison of LEEUWENBERG's and RAUH's model. In the former the unit of growth (module) is established repeatedly by branching, these units are all equivalent in the architecture of the tree, with the activity of the apical meristem of each unit limited (determinate) and flowering is terminal. In the latter the unit of extension is determined by the indefinite (indeterminate) activity of a terminal meristem with rhythmically produced increments and flowering is laterally. However, axes are again all equivalent and orthotropic. Clearly there are significant parallels between these two models, although it should not be implied that there is any necessary continuity from one to the other. Where both models occur within a single genus, however, this continuity is suggested.

Transitions and Intermediate Models

Where one model combines characters of two others, or is transitional in some features we can refer to an "intermediate model", but must recognize that this is an artificial concept derived from the parameters used in model recognition. In this sense, SCARRONE's model, in which the trunk consists of units of extension, but the branches of modules, stands intermediate between LEEUWENBERG's model (trunk and branches all modular) and RAUH's model (trunk and branches all units of extension). If there were any genetic continuity, one might expect to find similar numbers of representatives in a single family but the above figures (p. 00) show that in the Apocynaceae the disproportionate representation of LEEUWENBERG's (17 out of 50 species), SCARRONE's (6 out of 50) compared with RAUH's model (2 out of 50) species. RAUH's model in this family is known so far only for Couma guianensis Aubl. (Hallé & Oldeman, 1970), and Alyxia clusiophylla Guill. (Veillon, 1976).

Similarly in the Euphorbiaceae, there is only one recorded example known (out of 40 species investigated) which conforms to SCARRONE's model, although six conform to LEEUWENBERG's and 15 to RAUH's as already indicated (p. 00). The "intermediate model" is, therefore, exceptional in the Euphorbiaceae, even though this family is architecturally rich (Hallé, 1971).

It is not surprising that it is even more difficult to find contrasts within one genus, but they exist in Guttiferae and Loganiaceae. In Montrouzeria (Guttiferae) endemic to New Caledonia, Veillon (1976) finds M. sphaeroidea Planch. and M. verticillata Planch. represent LEEUWENBERG's model, but M. cauliflora Planch. represents RAUH's model.

In Loganiaceae, two genera illustrate the point. In Anthocleista, A. procera Leprieur and A. nobilis G. Don. are both African species representing LEEUWENBERG's model; but A. amplexicaulis Baker, from Madagascar represents SCARRONE's model. The genus Fagraea is quite polymorphic, and includes examples of modular models, F. schlechteri Gilg et Ben. (KORIBA) endemic to New Caledonia; F. crenulata Clarke, (FAGERLIND) from Malaysia, as well as non-modular models, like F. fragrans Clarke (AUBREVILLE) from Malaysia and F. racemosa Jack. (ROUX) from Australia and New Guinea. It should be remarked that in AUBREVILLE's model although construction of the branches is sympodial, the units are not of determinate growth. Flowering is lateral and growth of each unit continues indefinitely (albeit slowly) in the orthotropic position.

EXPERIMENTAL APPROACHES

It is of interest to know if the natural distinction between modules and units of extension, which seems to depend on endogenous control, can be so influenced either ecologically or experimentally that one can be converted into another.

Natural transformation

The continuous activity of the terminal meristem of Hevea, otherwise naturally rhythmic, is observed in the so-called "lamp-brush" form, described by Hallé & Martin (1968). Fox-tailing of Pinus has been reported repeatedly (e.g. Kozłowski and Greathouse, 1970) and was noted as long ago as 1935 by Guinier in Abies.

The complete transformation of unit of extension into module has been recorded by Dupuy & Guédès (1969) in Pinus pinaster Ait. ssp. maritima since the female cones are abnormally terminal.

Experimental transformation

A synthetic creation of the lamp-brush form in Hevea was managed by Hallé & Martin (1968) by cutting off the median leaflet of all leaves, i.e. by reducing the leaf area. In a similar experiment on cocoa Vogel (1975) produced shoots with continued activity of the apical meristem by repeatedly pruning away all leaves before they reached a length of 4 cm. In Impatiens balsamina L., Nanda & Purohit (1966) claim to have produced determinate shoots with terminal flowers, instead of the normal indeterminate shoots with lateral flowers, by successively removing the axillary floral buds. In the reverse process, Médard (pers. comm.) working with cassava has been able to produce shoots whose growth is not determinate by flowering but can become rhythmic with successive units of extension.

These few examples are sufficient to show that there is a degree of plasticity in the functioning of meristems, either limited in modules, or unlimited in units of extension, so that a degree of manipulation is possible.

CONCLUSIONS

This brief discussion serves to show the architectural possibilities inherent within trees constructed of modular units. These modules may be

orthotropic or plagiotropic and are capable of producing tall rain forest trees. Some families are predominantly modular in their construction, as far as present observations indicate, notably Apocynaceae but also Loganiaceae and Boraginaceae. We may contrast them with "amodular" families of which Moraceae is a good example. ^{In this family,} of 14 studied species, examples from six architectural models have been observed, i.e. ATTIM's, AUBREVILLE's, COOK's, RAUH's, ROUX's and TROLL's, none of them with modular construction.

The other main growth unit of tropical trees has been termed a "unit of extension" and the fundamental difference in the activity of the terminal meristem has been indicated. Normally the two types of unit are distinct; one exception is Schuurmansia heningis K.Schum., as observed by Hallé (1974) in New Guinea. It is organizationally typically of LEEUWENBERG's model, except that each module is developed by a series of successive units of extension.

This serves to emphasize what should always be borne in mind in making use of architectural categorizations, that there is considerable developmental plasticity of shoot organization in tropical trees. The experimental interruption of rhythms, or their imposition emphasizes this. Nevertheless, in natural conditions quite clearly contrasted patterns of construction remain evident and this is of obvious ecological significance.

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