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Modular construction and its distribution in tropical woody plants

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The definition of module (a free 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 linear, branched in one plane, or branched in three dimensions. The important fact in this definition is the limitation of the apical activity of modules and consequently the sympodial construction that 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 cassava, *Manihot esculenta* Crantz (Euphorbiaceae: Médard, 1973); castor bean, *Ricinus communis* L. (Euphorbiaceae); and frangipani, *Plumeria* 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 common in many trees in the Apocynaceae during an initial vegetative phase of growth (Corner, 1952; Prévost, 1967, 1972; Hallé & Oldeman, 1970; Brunaud, 1971).

Modules may be orthotropic or plagiotropic in their orientation and morphology as an expression of endogenous activity, without obvious relation to external (ecologic) factors. In this chapter, only

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Present address: ORSTOM, B. P. 165, 97301 Cayenne Cedex, French Guiana branched trees are considered (see Hallé & Oldeman, 1970), although it is recognized that the same construction can occur in trees with a single sympodial trunk that 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 in both trunk and branches; we can call them "fully modular models." Others show the construction only in the trunk or only in the branches; they are "partially modular."

Fully modular models

Three models are included in this category: Leeuwenberg's, Koriba's, and Prévost's.

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 Chap. 12). 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 Prévost's models two types of axes are differentiated: (1) orthotropic modules, which collectively and successively give rise to the trunk, and (2) plagiotropic modules, which collectively give rise to 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 Prévost's model. However, the topic is not dealt with further here (see Hallé & Oldeman, 1970, pp. 46–57; Chap. 7).

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 Prévost'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; a familiar example is cocoa, *Theobroma cacao* L. (Sterculiaceae), native to the Amazon region. In this model the branches are plagiotropic, but not modular, as they are monopodial. The situation is reversed in Fagerlind's and Scarrone's models: The branches, but not the trunk, are modular. In Fagerlind's model the branches are plagiotropic; this model is not common among familiar trees, but is shown by some Rubiaceae (e.g., *Randia fitzalani* F. Müll.; see Fagerlind, 1943). In Scarrone's model the branches are orthotropic, as in the familiar mango, *Mangifera indica* L. (Anacardiaceae).

Taxonomic distribution of modular construction

Family level

The distribution of modular construction in some tropical families has been studied by Kahn (1975). His findings for the Apocynaceae, Euphorbiaceae, and Rubiaceae are summarized in Table 9.1.

Table 9.1. *Distribution of modular construction in Apocynaceae, Euphorbiaceae, and Rubiaceae*

Family	Model	No. of species
Apocynaceae	Leeuwenberg[a]	17
	Koriba[a]	7
	Prévost[a]	8
	Scarrone[b]	6
	Nozeran[b]	1
	Rauh[c]	2
	Other[c]	c.9
	Total	50
Euphorbiaceae	Leeuwenberg[a]	6
	Koriba[a]	8
	Prévost[a]	2
	Scarrone[b]	1
	Nozeran[b]	4
	Rauh[c]	15
	Total	36
Rubiaceae	Leeuwenberg[a]	3
	Koriba[a]	1
	Prévost[a]	0
	Fagerlind[b]	5
	Scarrone[b]	1
	Nozeran[b]	0
	Total	10

a, fully modular models; *b*, partially modular models; *c*, nonmodular models.

The architectural model is known for about 50 species of Apocynaceae, and on the basis of the distribution shown in Table 9.1, it is clear that this can be described as a modular family; 64% of known species (32 out of 50) represent a fully modular architecture, and only 22% (11 out of 50) belong to wholly nonmodular models. This leaves a small proportion (14%) of partially modular examples.

The distribution of the 36 species of Euphorbiaceae whose architecture is known shows that the family is appreciably modular, with 44% (16 out of 36) fully modular species, but only 14% (5 out of 36) partially modular species. Note, however, the abundance of species that conform to Rauh's model (42%, 15 out of 36), which is a nonmodular type, exemplified in the family by *Hevea brasiliensis* Müll.-Arg. Rauh's model is of interest in comparison with Leeuwenberg's because 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 shall see later.

The Rubiaceae is not a modular family. Of its 45 species with known architecture, only 10 (22%) are modular. Of these, only 4 species (9%) are fully modular.

Generic and specific levels

We can speak of a genus as polymorphic (Hallé, 1969) when it includes a variety of species exhibiting different architectural models. *Alstonia* (Apocynaceae) possesses examples of the three fully modular models: *A. sericea* Bl., from Malaysia (Leeuwenberg); *A. macrophylla* Wall., from Malaysia (Koriba); and *A. boonei* De Wild., from tropical Africa (Prévost). All eight species of *Alstonia* whose architecture is known belong to one of these three models (Corner, 1952; Prévost, 1967; Hallé & Oldeman, 1970; Veillon, 1976). The genus *Cordia* (Boraginaceae) is somewhat comparable: *C. curassavica* Lam. and *C. laevifrons* Johnst. display Prévost's model and *C. alliodora* follows Fagerlind's model. All these species are from Africa, although the genus is widespread. The genus *Euphorbia* (Euphorbiaceae) is the most diverse, with examples representing 11 models. In Madagascar alone, Cremers (1975) has observed 10 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 ecologic factors. In *Fagara rhoifolia* (Lam.) Engl. (Rutaceae), for example, Hallé & Oldeman (1970) have described ontogenetic changes that allow this species to be assigned initially to

Scarrone's, but subsequently to Koriba's, model. When the tree is young the trunk grows rhythmically, producing periodically pseudowhorls 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 for by one or more relay axes that have a modular construction, but continue growth in height. In *Pseudopanax crassifolium* (Araliaceae) a similar loss of dominance has been recorded by Philipson (Chap. 12), with a change from Scarrone's to Leeuwenberg's model. The phenomenon may be common in the family, as Veillon (1976) found it in three other genera (*Dizygotheca*, *Myodocarpus*, and *Tieghemopanax*).

In the avocado, *Persea gratissima* (Lauraceae), Aubert & Lossois (1972) refer to a transition betwen Attims'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 models) 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 units are the result of rhythmic development of shoot systems, as has been established in the comparison of Leeuwenberg's and Rauh's models. 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 determinate and flowering terminal. In the latter, the unit of extension is determined by the indeterminate activity of a terminal meristem, with rhythmically produced increments and lateral flowering. 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

When one model combines characteristics of two others or is transitional in some features, we can refer to it as an "intermediate model," but we 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 figures in Table 9.1 show in the Apocynaceae a disproportionate representation of Leeuwenberg's (17 out of 50 species) and Scarrone's (6 out of 50) models compared with Rauh's (2 out of 50 species) model. 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 1 recorded example (out of 40 species investigated) that conforms to Scarrone's model, although 6 conform to Leeuwenberg's and 15 to Rauh's (Table 9.1). The intermediate model is, therefore, exceptional in the Euphorbiaceae, even though this family is architecturally rich (Hallé, 1971).

Not surprisingly, it is even more difficult to find contrasts within one genus, but they exist in the Guttiferae and the Loganiaceae. In *Montrouzeria* (Guttiferae), endemic to New Caledonia, Veillon (1976) found *M. sphaeroidea* Planch. and *M. verticillata* Planch. to represent Leeuwenberg's model, but *M. cauliflora* Planch. to represent Rauh's model.

In the 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. & Ben. (Koriba), endemic to New Caledonia, and *F. crenulata* Clarke (Fagerlind), from Malaysia – as well as nonmodular models – *F. fragrans* Clarke (Aubréville), from Malaysia, and *F. racemosa* Jack. (Roux), from Australia and New Guinea. It should be mentioned that in Aubréville'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 influenced either ecologically or experimentally so that one can be converted into another.

Natural transformation

Continuous activity of the terminal meristem of *Hevea*, otherwise naturally rhythmic, is observed in the so-called lampbrush form, described by Hallé & Martin (1968). Foxtailing of *Pinus* has been reported repeatedly (e.g., Kozlowski & 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,* where the female cones are abnormally terminal.

Experimental transformation

The lampbrush form in *Hevea* was obtained experimentally 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 induce nondeterminate (i.e., nonflowering) shoots, but growth 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 shows 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 the Moraceae is a good example. In this family, of 14 studied species, examples from six architectural models have been observed – Attims's, Aubréville'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 units are distinct; one exception is *Schuurmansia heningsii* K. Schum., as observed by Hallé (1974) in New Guinea. It is organizationally typical 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: 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 ecologic significance.

General discussion

Tomlinson: Have you any information about the cause of parenchymatization of apices of those modules that are determinate for this reason?
Prévost: We can imagine that the volume of the meristematic zone becomes too large.
Tomlinson: Do you have evidence that the shoot apex does increase during development of the individual module?
Prévost: No.
Oldeman: In several species of *Cordia* in French Guiana there are, at the apex of the trunk modules, all transitions between a functional inflorescence and a parenchymatization. It may be that for some physiologic reason the meristem is too small or too young to make a flower and ends up as parenchyma.
Philipson: In the development of inflorescences, where the lateral branches become great in size compared with the apex and are adjacent to it, the apex is, as it were, entirely used up in the production of laterals.
Hallé: In my opinion parenchymatization is due to the very rapid growth of the selected branches around the dying apex. In other words, branching precedes parenchymatization.
Nozeran: Parenchymatization of the apical growing point is probably due in large measure to the influence of the leaves proximal to the meristem. In *Pinus* the parenchymatization of the apices of brachyblasts is similar. These short shoots do normally not continue to grow. If leaves are removed at a very early stage, apical growth continues (see Chap. 18).

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