Modular growth in seed plants

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Modular growth in seed plants may be analysed in terms of three architectural elements: the unit of morphogenesis, the module and the architectural model. Some of the salient features of these structures are reviewed, compared and contrasted. A variety of plant shapes and sizes may be derived schematically from them by two sorts of transformation, gigantism and repetition. The former is uncommon in seed plants, but repetition produces a wide array of constructions. Repetition of the architectural model, a process known as reiteration, leads to a colonial structure characteristic of the crowns of many mature trees. This is often an expression of the plant's opportunistic response to environmental variations in resource availability. The reiterated complexes formed as a result may show some characteristic ontogenetic and phylogenetic sequences to give an architectural continuum of construction.

1. Introduction

One of the salient architectural expressions of modular growth in seed plants is the serial repetition of plant organs by apical meristems. If derived from a single apical meristem these organs may form a monopodial axis, and if several meristems are involved the plant may be composed of a branched, sympodial series of axes. Although the idea of modular construction in plants is ancient (White 1979; Cusset 1982), its revival was cast in rather precise morphological terms, centred on the definition and recognition of a basic unit of construction, *l'article* (Prévost 1967; Hallé & Oldeman 1970), subsequently translated as module (Harper & White 1974).

In this paper the expression *modular growth* will be restricted to two different aspects of growth and form in seed plants; one refers to a group of architectural models, called *modular models* (Hallé *et al.* 1978); another refers to the process of repetition of the architectural model which occurs in most ageing trees, but less commonly in herbs, and has been termed *reiteration* (Oldeman 1977). Both involve modular growth and both lead to modular form, but there are significant differences between them, as I shall indicate.

2. Units of modular construction

The growth and form of the aerial part of seed plants may be analysed by considering three architectural elements; the unit of morphogenesis, the module, and the architectural model. A unit of morphogenesis is a length of vegetative shoot whose chronological limits are determined by a single period of continuous activity of the apical meristem (figure 1). This may be, but is not necessarily, the same as the unit of extension which is usually detectable on the shoots of trees and shrubs, either in tropical or extratropical climates, as the length of

vegetative shoot between two successive groups of bud scale scars (figure 1) (Hallé & Martin 1968).

The module is the leafy axis in which the entire sequence of aerial differentiation is carried out, from the initiation of the meristem that builds up the axis to the sexual differentiation of its apex (Hallé *et al.* 1978). At the base of the module, roots sometimes develop; more frequently they are not expressed but the module retains a rooting ability which can often be used for vegetative propagation (figure 2). Although some seed plants consist of only a single module according to this definition, most have an integrated complex of modules linked together sympodially.
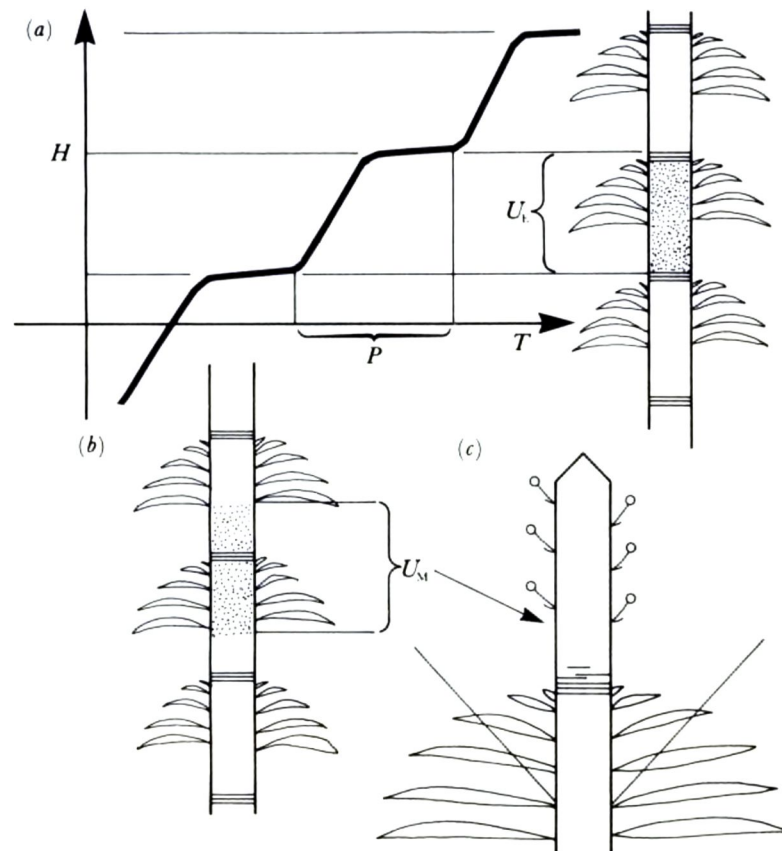

FIGURE 1.(a) The growth curve of a shoot with rhythmic growth in *Hevea brasiliensis* (Euphorbiaceae) (rubber tree). H, shoot height; T, time; P, period of the rhythm; U_E, unit of extension, whose limits are two successive bud-scale scars. (b) The unit of morphogenesis (U_M) is a length of vegetative shoot whose chronological limits are determined by a single period of continuous activity of the apical meristem. (c) One isolated unit of morphogenesis, with leaves, axillary branching and lateral sexual structures.

The architectural model is the visible expression of the genetical programme of development of the plant, and represents the fully developed, complex plan of assembly of modules into a coherent construction (figure 2). In all but a relatively small number of seed plants it is multimodular. Of approximately 24 architectural models of trees so far described (Hallé *et al.* 1978), six are entirely modular, in the sense that the apical meristem of every module in the model completes the sequence of differentiation and eventually becomes sexual. These are architectural models known as Leeuwenberg, Chamberlain, Tomlinson, Koriba and Prévost (figure 3) in addition to the model of Holttum which consists, by definition, of a single module (Hallé *et al.* 1978).
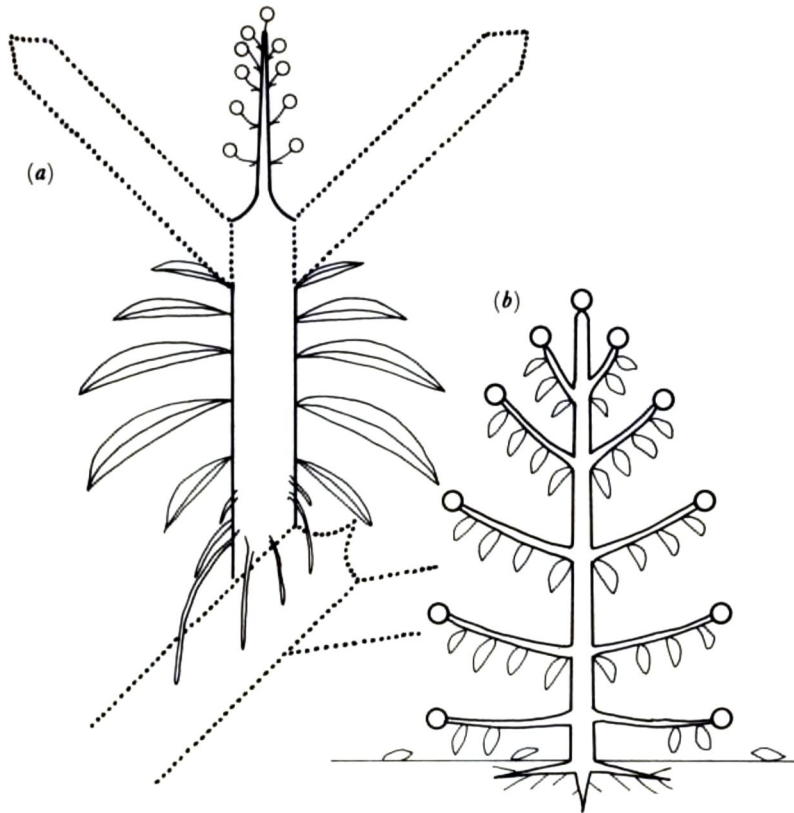
FIGURE 2.(a) A module. (b) an architectural model.

These three architectural levels constitute a hierarchy of elementary structures which have been found to be valuable for interpreting the processes of growth in any kind of seed plant, from small herbs to large trees. The three-dimensional arrangement of leafy axes within architectural models is regular, predictable and probably genetically controlled to a large extent. Models that are entirely modular (figure 3) are easily drawn by computer graphics, since their constructional rules are readily quantifiable (de Reffye 1979, 1983). But not all models are fully modular, insofar as the apical meristems of some shoots do not complete their differentiation and become sexual; in fact most architectural models show this phenomenon (Hallé et al. 1978). Some shoots grow upwards and overtop others to form a trunk, while others remain subordinate and produce leaves and flowers. This physiological and structural differentiation may also be seen in models that are entirely modular (for example, models of Koriba and Prévost: figure 3).

The three structural elements show some obvious differences, but they also show important similarities. As levels of a constructional hierarchy, they differ in that the highest level envelops the lower ones, as outlined above. This may be indicated schematically (figure 4).

On the other hand, they resemble each other: they represent whole sequences of differentiation, growth and organogenesis, photosynthesis, vascular construction, and are terminated by sexuality. They also have a capacity for individual enlargement (gigantism) and for repetition. These processes, especially the latter, are of great significance for the construction of large-scale organisms such as trees.
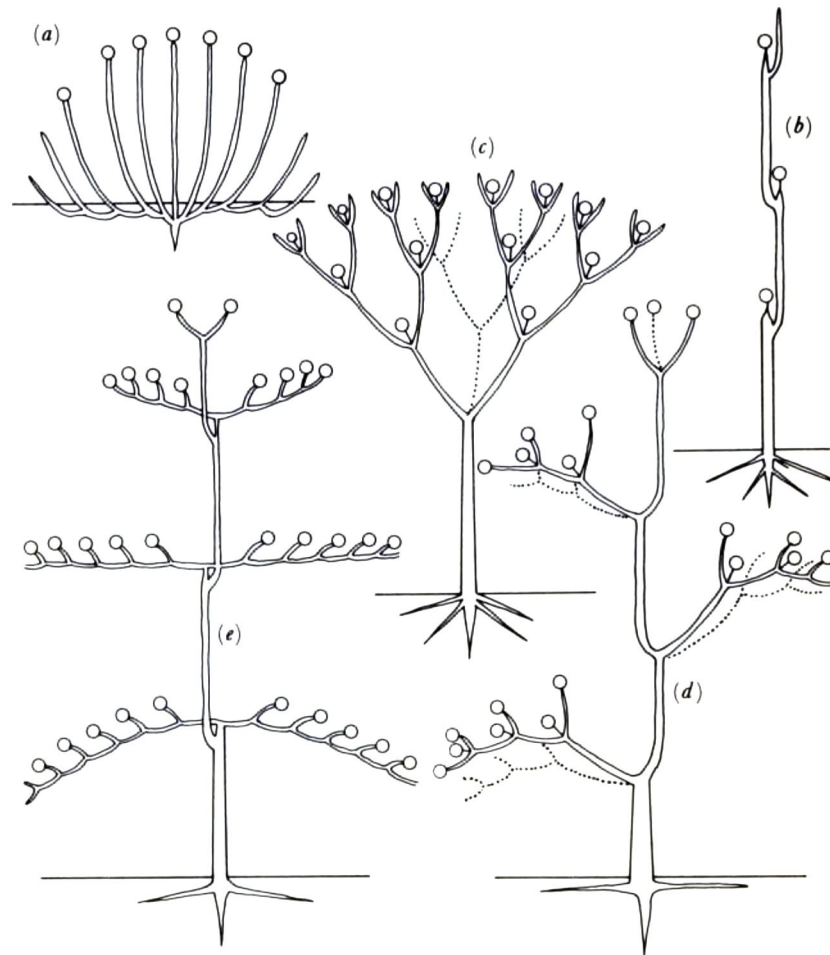
FIGURE 3. Modular architectural models, each drawn schematically. Some typical examples are listed. (a) Tomlinson's model: *Raphia* spp. (Arecaceae), *Musa* spp. (Musaceae), many grasses (Poaceae), a few dicotyledons, such as *Helleborus* sp., *Euphorbia* sp. and *Lobelia* sp. (b) Chamberlain's model: *Cycas* spp. (male plants) (Cycadaceae), *Philodendron* spp. (Arecaceae) and *Talisia* spp. (Sapindaceae). (c) Leeuwenberg's model: *Dracaena* spp. (Dracaenaceae), and a large number of dicotyledons, such as *Rauwolfia* sp., *Senecio* sp., *Croton* sp., *Anthocleista* sp. and *Solanum* sp. (d) Koriba's model: *Ochrosia* spp. (Apocynaceae), *Ochroma* spp. (Bombacaceae), *Homalanthus* and *Hura* spp. (Euphorbiaceae). (e) Prévost's model: *Excoecaria* sp. (Euphorbiaceae), *Cordia* spp. (Boraginaceae) and *Alstonia* spp. (Apocynaceae).
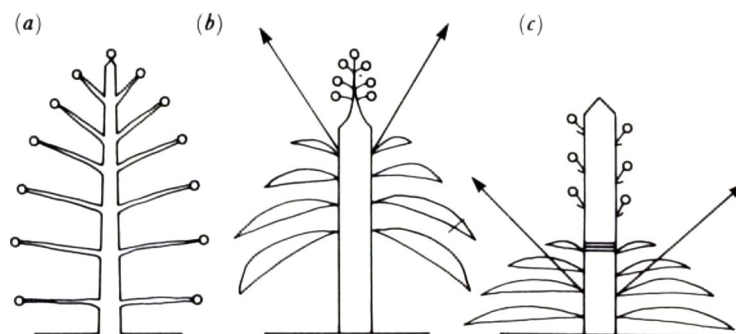

FIGURE 4. The architectural model (a), the module (b) and the unit of morphogenesis (c).

3. GIGANTISM AND REPETITION

From the three architectural elements outlined in the previous section, a wide variety of shapes and sizes may be derived schematically by two sorts of transformation which will be referred to as gigantism and repetition. It is suggested that such transformations may have a phylogenetic significance, repetition being a more advanced transformation than gigantism (see figures 5 and 7 for comparison). Schematically one may consider three general developmental patterns in seed plants in which each of these three structural elements may:

(i) remain solitary; their dimensions remain small or may even become 'miniaturized' as herbs (Hallé *et al.* 1978);

(ii) remain solitary but grow increasingly large (gigantism), as in some trees;

(iii) retain their size within some narrow range, but increase in number (repetition) to give large organisms, such as most trees.
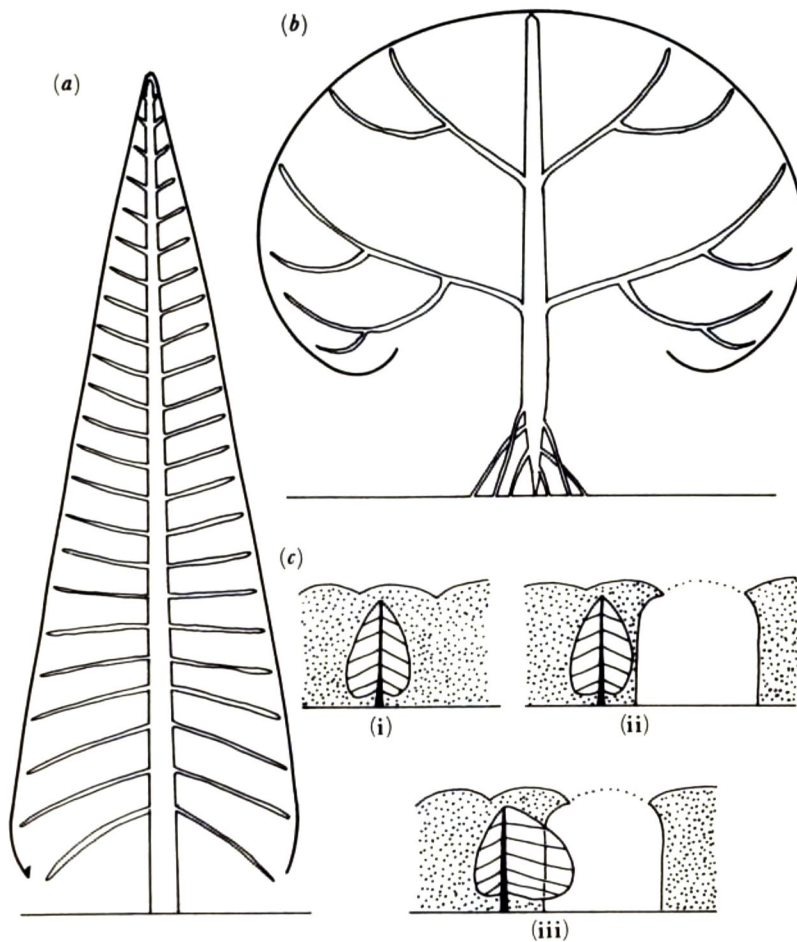

FIGURE 5. Gigantism of a single architectural model in *Araucaria columnaris* (*a*) and *Musanga cecropioides* (*b*). (*c*) The weak and incomplete opportunistic reaction of a mono-model tree to a variable environment. (i) The tree in a closed forest; (ii) the fall of a neighbouring tree creates a gap, giving sudden lateral illumination; (iii) the mono-model tree reacts by a deformation of its crown, but is unable to fill the gap and make full use of the available light.

(a) Gigantism

When applied to a solitary unit of morphogenesis or to a solitary module, gigantism alone may give rise to large herbs or trees which are monocarpic (for example, *Agave*, *Puya*, *Metroxylon*), but this is relatively rare among seed plants. Gigantism of an architectural model involves the enlargement of the specific plan of construction characteristic of the model (figure 5). In such cases the process of repetition of modules or of units of morphogenesis occurs *within* the model, but the model itself remains solitary. Despite its apparent simplicity, this process is also rare among seed plants. It involves only a few old families, such as Myristicaceae, and several pioneer trees of the tropics: *Anthocephalus*, *Macaranga*, *Solanum*, *Cecropia*, *Musanga* or *Anthocleista*. At least two reasons may be suggested for this. Since only the younger parts of shoots carry leaves and the older parts support them structurally, the progressive enlargement of preexisting shoots without the addition of new (leafy) shoots (by repetition) would give rise to a well-illuminated crown, but one with inadequate photosynthate to support an increasing respiratory burden. On trees with long-lived leaves, such enlargement may be possible, as the architecture of some species of *Araucaria* suggests. Leaf longevity in *Araucaria* spp. may be up to 15 years (Molisch 1938). Another disadvantage of forming large structures by gigantism without repetition in a mono-model tree is the restriction placed on opportunistic growth from dormant apical meristems to exploit light, nutrients and other resources that the organism may encounter in a variable environment. This is depicted diagrammatically in figure 5.
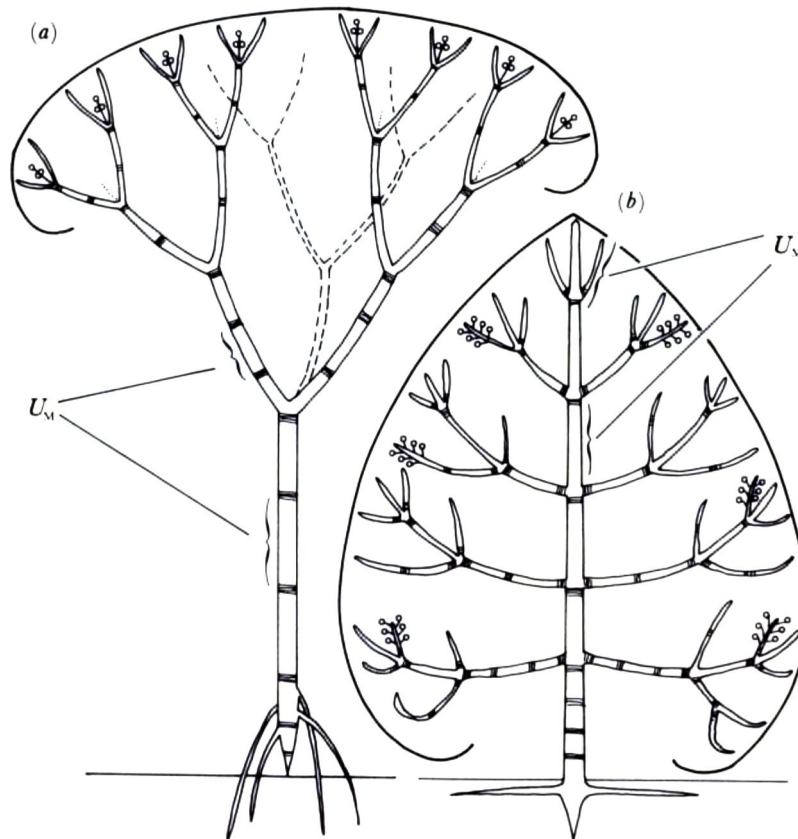

FIGURE 6. Repetition of the unit of morphogenesis (U_M) in *Schuurmansia heningsii* (Ochnaceae) (*a*) and *Pinus silvestris* (Pinaceae) (*b*).

(b) Repetition

Repetition of the unit of morphogenesis gives rise to a shoot with rhythmic growth, and usually with laterally borne reproductive structures. Such shoots are easy to observe in many tree species (figure 6).

Repetition of the module gives a modular architectural model (figure 3): the precise and regular arrangement of these modules is usually characteristic of a species in early life. When applied to the architectural model itself, repetition leads to a colonial structure characteristic of the crowns of many mature trees (figure 7). This particular repetition to give a multi-model tree is referred to as *reiteration* and usually starts with the activation of dormant meristems (Oldeman 1977).

The reiteration process is also a manifestation of modular growth, but of a different kind from that previously outlined. Whereas the architectural model appears to be a standard growth response to a narrow range of conditions (for example, trees in the forest understory), the reiterated complex of architectural models represents a more opportunistic response to a greater diversity of conditions. This is shown diagrammatically in figure 7.
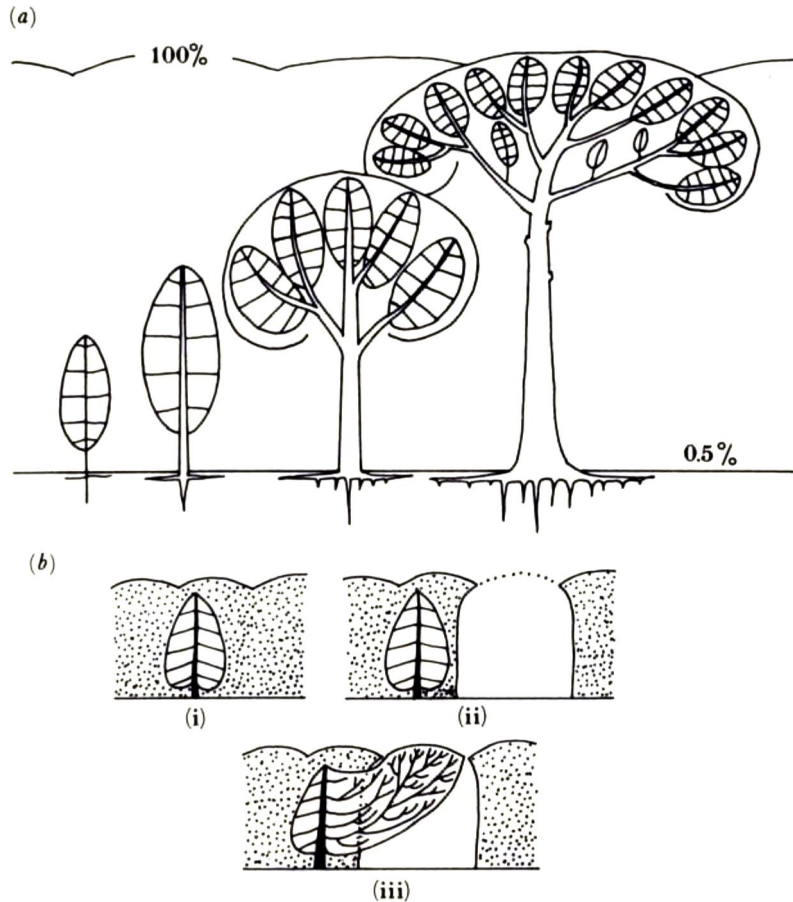

FIGURE 7. (a) The process of repetition applied to the architectural model: reiteration. Relative levels of illumination inside and outside the forest canopy are indicated. (b) The efficient opportunistic reaction of a multi-model tree to a variable environment. (i) The tree in a closed forest; (ii) the fall of a neighbouring tree creates a gap, giving sudden lateral illumination; (iii) the colonial tree reacts by reiteration to fill the gap completely and use all available light.
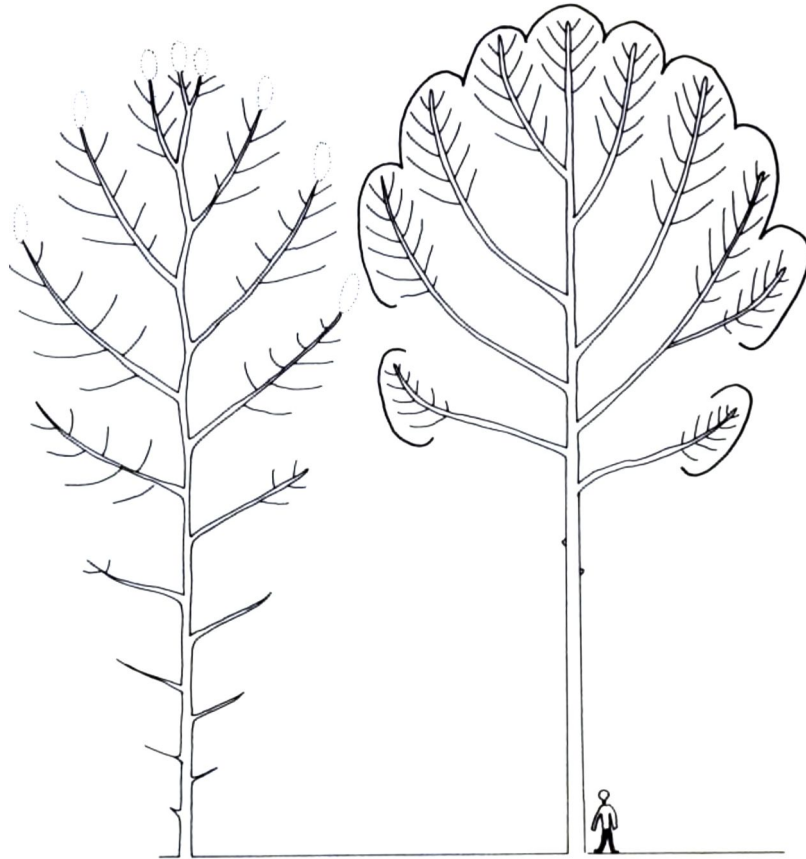
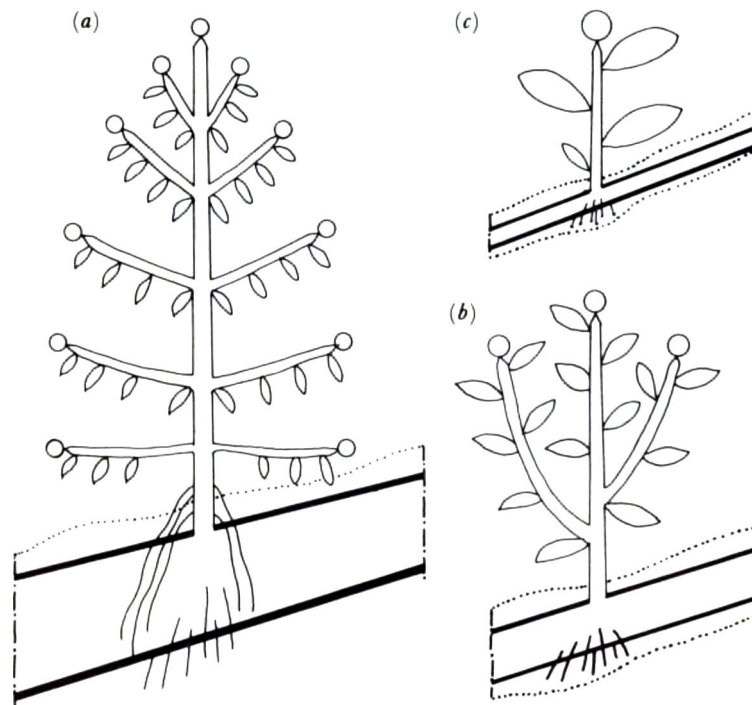FIGURE 8. Architectural metamorphosis in two species of Dipterocarpaceae.

FIGURE 9. Diminished vegetative growth of successive reiterated complexes in the tree crown during ontogenesis. Canopy roots (Nadkarni 1981) are often easy to observe when the mantle of epiphytic plants wrapping the supporting branch (dotted lines) are removed. (*a*) Reiterated complexes borne on the trunk or on thickened branches develop like small trees. The architectural mollé, including its root system, is fully expressed. (*b*) After several episodes of reiteration, the complexes are smaller and frutescent (shrub-like), and the architectural model is only partly expressed. (*c*) The smaller axes of the crown support herbaceous reiterations which are neotenic.

In contrast to the rather precise arrangement of modules within architectural models, the spatial distribution of reiterated complexes is neither regular nor predictable. They may appear early in life on an isolated tree, but may be inhibited by the dark forest undergrowth until a tree reaches a height of 20–30 m. In the absence of precise rules for their three-dimensional arrangement, it has so far been difficult to model reiterated complexes with computer graphics, although some promising attempts have been made recently (P. de Reffye, personal communication).

The spatial distribution of reiterated complexes to form a crown shows, none the less, a gradient of predictability. The positions of large reiterated complexes, whose formation and expansion are governed by illumination of the exposed canopy, are impossible to predict morphologically. Their precise extent depends on the levels of interference among themselves. Such interference may be very evident in some trees (for example, *Pinus pinea*, *Nothofagus* sp., *Leptospermum* sp. and many members of the Dipterocarpaceae and Vochysiaceae): the term 'crown shyness' (French *timidité*) has been used to describe this phenomenon (Ng 1977; Hallé 1979; Hallé & Ng 1981).

Reiterated complexes may become organized in a somewhat more predictable manner. This is evident in some dipterocarps whose architectural dynamics have been described by Edelin (1984). Metamorphosis (Edelin 1984) is the process by which the plagiotropic branches characteristic of the sapling (with their limited ability to develop secondary thickening) are abruptly replaced by orthotropic branches imitating the trunk. By acquiring the same orientation of growth and the same thickening ability as the trunk itself, the branches undergoing metamorphosis become adventitious trunks, that is, reiterated complexes (figure 8). Architectural metamorphosis is a fundamental process in the growth and development of most tree species (Edelin 1984).

During the course of evolution as the reiterated complexes become smaller and simpler, their spatial location can be more accurately predicted. During ontogenesis, the successive complexes may become miniaturized and morphologically indistinguishable from a module (figure 9).

4. ARCHITECTURAL CONTINUUM

Modules and reiterated complexes both result from the repetition of a genetic programme of ontogenesis and differentiation. But there appears to be a gradient of predictability in their levels of organization. The architectures of mature trees may be interpreted, with such distinctions in mind, as stages of an architectural continuum. This may be illustrated by some general of tropical woody plants such as *Alstonia* (Prévost 1967), *Solanum* (Prévost 1978), *Cordia* (Edelin & Hallé 1985) and *Tabebuia* (Borchert & Tomlinson 1984), where a complete range of intermediary states between reiterated complexes and modules can be observed (shown schematically in figure 10). The last stage in this continuum is represented by the model of Prévost.
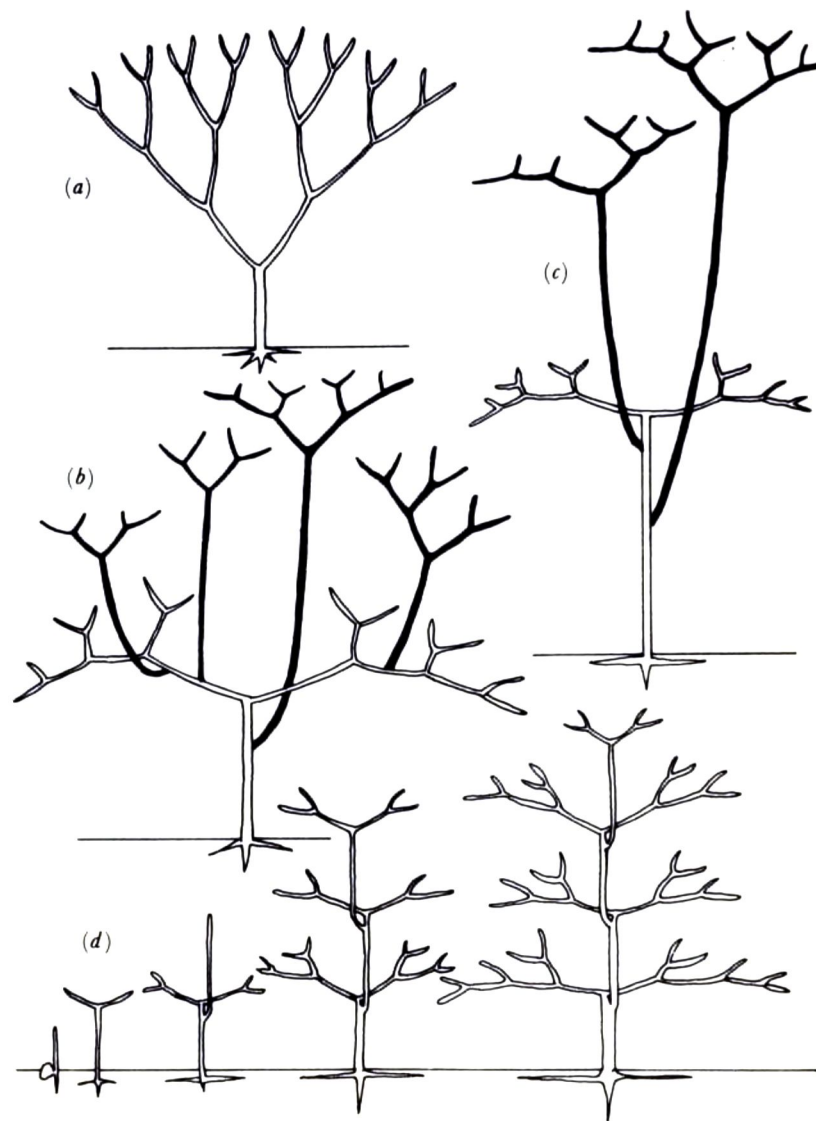
FIGURE 10. Architectural continuum of models and reiterated complexes. (a) Leeuwenberg's model, without reiteration. (b) Diffuse reiteration in Leeuwenberg's model. (c) Concentration of reiterated complexes in the apical part of the trunk module. (d) Ontogenesis of Prévost's model. This architectural continuum occurs in genera such as *Solanum* (Solanaceae), *Cordia* (Boraginaceae), *Tabebuia* (Bignoniaceae) and *Alstonia* (Apocynaceae).

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