# Architectural concepts for tropical trees

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Following Corner's ideas (1949, 1953, 1954) on the growth, form, and evolution of plants, the study of plant architecture became a discipline in its own right. The first syntheses were published by Hallé and Oldeman (1970), Oldeman (1974), and Hallé *et al.* (1978). Architectural studies started in tropical regions and were concerned with the aerial vegetative structure of trees. Architectural concepts, however, provided a powerful tool for studying plant form, and investigations quickly spread to temperate species, mostly herbs and lianas, and root systems were also investigated.

The architecture of a plant depends on the nature and relative arrangement of each of its parts; it is, at any given time, the expression of an equilibrium between endogenous growth processes and exogenous constraints exerted by the environment. The aim of architectural analysis is to identify these endogenous processes by means of observation (Edelin, 1984). Considering the plant as a whole, from germination to its death, architectural analysis is a global and dynamic analysis of plant development. For each species and each stage of development, observations are made on varying numbers of individuals, depending on the complexity of the architecture. The results are summarized in diagrams which symbolize successive growth stages. The validity of the diagrams is then checked by comparing them with reality, and they must apply to the architecture of any individual of the same species for the analysis to be considered complete. Architectural analysis depends on three major concepts: architectural model, architectural unit, and reiteration.

## The architectural model

For a tree, the growth pattern which determines the successive architectural phases is called its architectural model, (Hallé *et al.*, 1978).

The architectural model (Hallé and Oldeman, 1970) is an inherent growth strategy which defines both the manner in which the plant elaborates its form and the resulting architecture. It expresses the nature and the sequence of activity in the endogenous morphogenetic processes of

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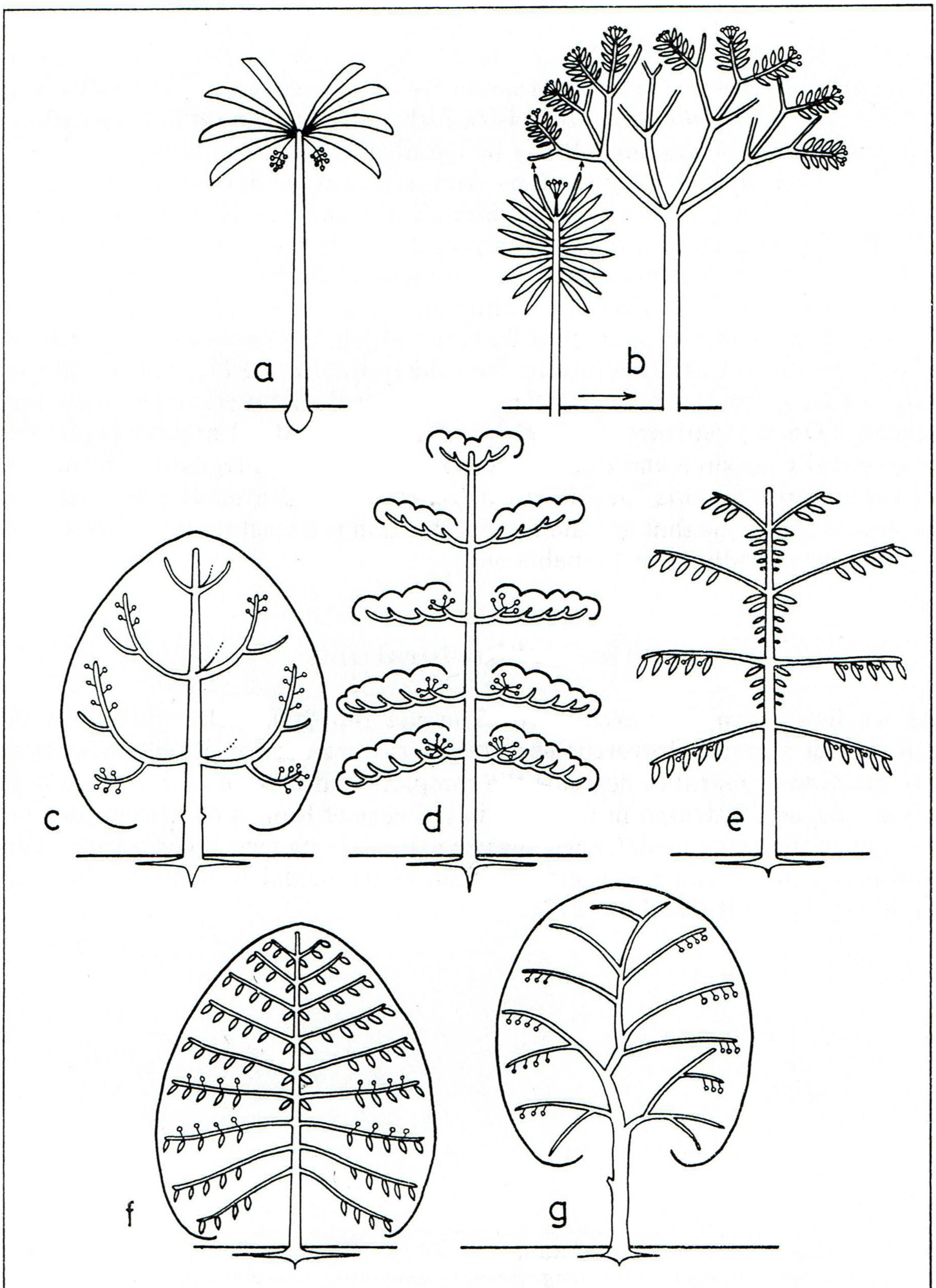
the organism and corresponds to the fundamental growth program on which the entire architecture is established. The identification of the architectural model of any given plant is based on the observation of four major groups of simple morphological features which are well documented (Hallé and Oldeman, 1970; Hallé *et al.*, 1978): (i) *the type of growth* (rhythmic or continuous growth); (ii) *the branching pattern* (presence or absence of vegetative branching, terminal or lateral branching, monopodial or sympodial branching, rhythmic, continuous, or diffuse branching); (iii) *the morphological differentiation of axes* (orthotropy or plagiotropy) and; (iv) *the position of sexuality* (terminal or lateral).

Each architectural model is defined by a particular combination of these morphological features and named after a well-known botanist. Although the theoretical number of combinations is high, there are apparently only 23 architectural models in nature. These models apply to arborescent or herbaceous plants from tropical or temperate regions of closely related or distant taxa.

In figure 1 some of these models are demonstrated. Each of them are represented by hundreds if not thousands of species. *Corner's model* (1a) concerns unbranched plants with lateral inflorescences, such as the commonly cultivated *Carica papaya*. *Leeuwenberg's model* (1b) consists of a sympodial succession of equivalent units called "modules" (Prevost, 1967, 1978; Hallé, 1986), each of which is orthotropic and determinate in its growth by virtue of its terminal inflorescence. Branching is three dimensional. Examples of this model are *Manihot esculenta* and *Ricinus communis*. *Rauh's model* (1c) is represented by numerous woody plants from both tropical (*e.g. Hevea brasiliensis*) and temperate areas (*e.g. Pinus spp.*). Growth and branching are rhythmic on all monopodial axes and sexuality is lateral. *Aubreville's model* (1d) is much less frequent than the previous ones and represented by *Terminalia catappa*. The trunk is monopodial and grows rhythmically bearing whorled branch tiers. Branches grow rhythmically but are modular, each of them being plagiotropic by apposition. *Massart's model* (1e) differs from the previous one only in that the branches are plagiotropic either by leaf arrangement or symmetry but never by apposition. Numerous trees exhibit this growth strategy in both temperate (many gymnosperms, *e.g. Abies, Araucaria*) and tropical areas (*e.g.* most species of Myristicaceae or Bombacaceae).

**Figure 1**. Seven of the 23 known architectural models: a - Corner's model, b - Leeuwenberg's model, c - Rauh's model, d - Aubreville's model, e - Massart's model, f - Roux's model, g - Troll's model. (From Hallé and Edelin, 1987; with permission).


a
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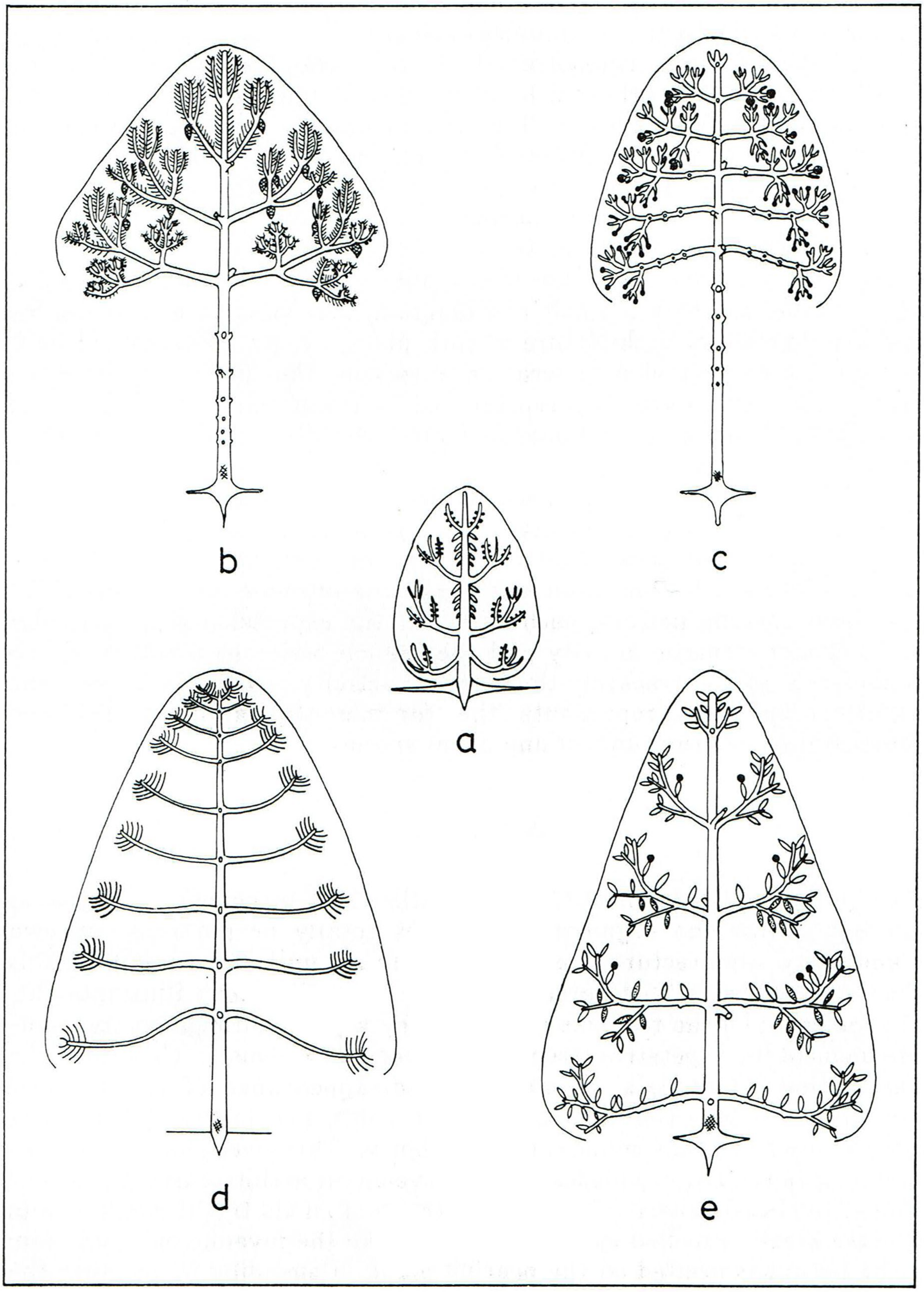
*Roux's model* (1f) is very close to Massart's model from which it differs only in the continuous or diffuse, not rhythmic, growth and branching of the trunk. This model is mainly represented by tropical species such as *Coffea arabica*. Finally, *Troll's model* (1g) which seems to be the most frequent in both tropical and temperate woody species. The axes are plagiotropic and the architecture is built by their continual superposition. Many examples of this model may be found in the Leguminosae.

Growth patterns defined by architectural models are genetically determined. Only under extreme ecological conditions is their expression affected by the environment (Temple, 1975; Hallé, 1978; Barthélémy, 1986a). Different models can be represented by plants belonging to closely related species. Architectural analysis also shows that some plants frequently exhibit morphological features which are apparently related to two or three models (Hallé and Ng, 1981; Edelin, 1977, 1984). These intermediate forms prove that there is no real disjunction between the models. On the contrary, it must be considered that all architectures are theoretically possible and that there could be a gradual transition from one to the others. In this "architectural continuum," the models themselves represent the forms that are the most stable and the most frequent, that is to say the biologically most probable ones.

## The architectural unit

As we have seen, the architectural model represents the basic growth strategy of a plant. Nevertheless, the characters used in its identification are much too general to describe the complete and precise architecture of a plant. So, as illustrated in figure 2, in the case of Rauh's model, within the context of the same model, each species expresses its own architecture. For any given plant, the specific expression of its model has been called its architectural unit (Edelin, 1977).

**Figure 2.** Specific expression of Rauh's model (a) in four Gymnospermous species: b - *Pinus sylvestris*, c - *Cunninghamia lanceolata*, d - *Araucaria rulei*, e - *Metasequoia glyptostroboides* (From Edelin, 1977, with permission).



b
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The architecture of a plant can be seen as a hierarchical branched system in which the axes can be grouped into categories. The structure and function of each category is characteristic of its rank, and for each species, the number of axes categories is finite. The identification of the architectural unit is achieved by a complete diagnosis of the functional and morphological features of all its axes categories. For each of them the observation of all the architectural characteristics previously described is necessary, but the observations have to be as exhaustive as possible and may concern any kind of morphological feature including growth direction, phyllotaxis, syllepsis or prolepsis, form and size of foliar organs, and presence or absence of sexuality. The results may be summed up in a table and with the help of a diagram, they describe and define the specific elementary architecture of each plant, *i.e.* its architectural unit. Within the context of a general organization, the differences between architectural units are thus represented by the number of categories of axes, their functional and morphological features, and their relative positions.

This indicates that the architecture of a fully established branched system, whatever its complexity, can be summarized in terms of a very simple sequence of axes which represents its fundamental organization. In this sequence, leading from axis one to the ultimate axis following the specific branching pattern, each branch is the expression of a particular state of meristematic activity and the branch series as a whole can be considered to be tracking the overall activity. In this sense, the architectural unit represents the fundamental architectural and functional elementary unit of any given species.

## Reiteration

As defined by Oldeman (1974), reiteration is a morphogenetic process through which the organism duplicates totally or partially its own elementary architecture, *i.e.* its architectural unit. The result of this process is called a "reiterated complex". Two situations illustrate this phenomenon: (i) the traumas undergone by a plant throughout its whole life damage the vegetative structure more or less seriously. Generally, the destruction of an axis, involving the disappearance of its terminal meristem, allows the development of some previously dormant or suppressed meristems subjacent to the injury. This gives rise to branched systems, reiterated complexes, which develop an architecture identical to that of the bearing axis; (ii) within the crown of an old tree it is common to observe small branched systems that look like the juvenile one and seem to be naturally grafted on the bearing plant. Depending on whether the development of the reiterated complex is due to a trauma or not, one speaks respectively of "traumatic reiteration" or "adaptive reiteration".

As already noted, the development of a plant conforming to its model implies the notion of a sequence in the activity of the whole set of meristems; one speaks of a differentiation sequence. The occurrence of reiterated complexes in this sequence seems to be a move backwards within this sequence, a real dedifferentiation. A supernumerary trunk, resulting from the transformation of a growing branch (sylleptic reiteration) or from the development of a dormant meristem (proleptic reiteration), implies that the plant expresses all over again the juvenile growth pattern. This reversion in the growth pattern can be complete and thus involve again the total expression of the architectural unit leading from axis one to the ultimate branching order (complete reiteration), or it can be partial and duplicate only a part of the architecture of the plant (partial reiteration). This is well illustrated in cases of regeneration; when a trunk is cut, it produces sprouts identical to the bearing trees, whereas reiterated complexes that develop after a branch has been damaged have the same architecture as this branch.

In fact, reiteration encompasses several aspects including sprouts and root-suckers which have been known to botanists for a long time, but the fundamental interest of this concept is to regroup all these phenomena into a coherent whole to bring out a common morphogenetic event. Reiteration at first was considered as an opportunistic process. However, recent investigations (Edelin, 1984) have demonstrated that of adaptive reiteration is an automatic event that occurs after a definite threshold of differentiation during the normal development of a tree. This will be illustrated, in the context of complete reiteration by the following two examples.

Figure 3 shows the architectural sequence of *Shorea stenoptera* from South East Asia which conforms to Roux's model. Up to a height of one to two meters (3a) the trunk is not branched. Then (3b), the orthotropic trunk, a continuously branching monopodium, bears plagiotropic distichous branches. Each of these consists of a single second axis, rarely branched, which dies and self-prunes rapidly. Proleptic reiterated complexes grow out of some dormant buds borne on the trunk (3c), they branch rapidly and their plagiotropic branches are identical to those described above. This type of reiteration occurs although the tree is still in the understory shade most of the time. These reiterated complexes do not exceed 4-5 m before precociously dying and falling. When the tree reaches the forest canopy the same process goes on, but this time the reiterated complexes do not die (3d). On the contrary, they produce strong limbs (R). Within the crown of the adult tree (3e), new proleptic reiterated complexes (r) appear on the established infrastructure. There, the longer ones are formed on the upper side of the limbs. The others grow out from

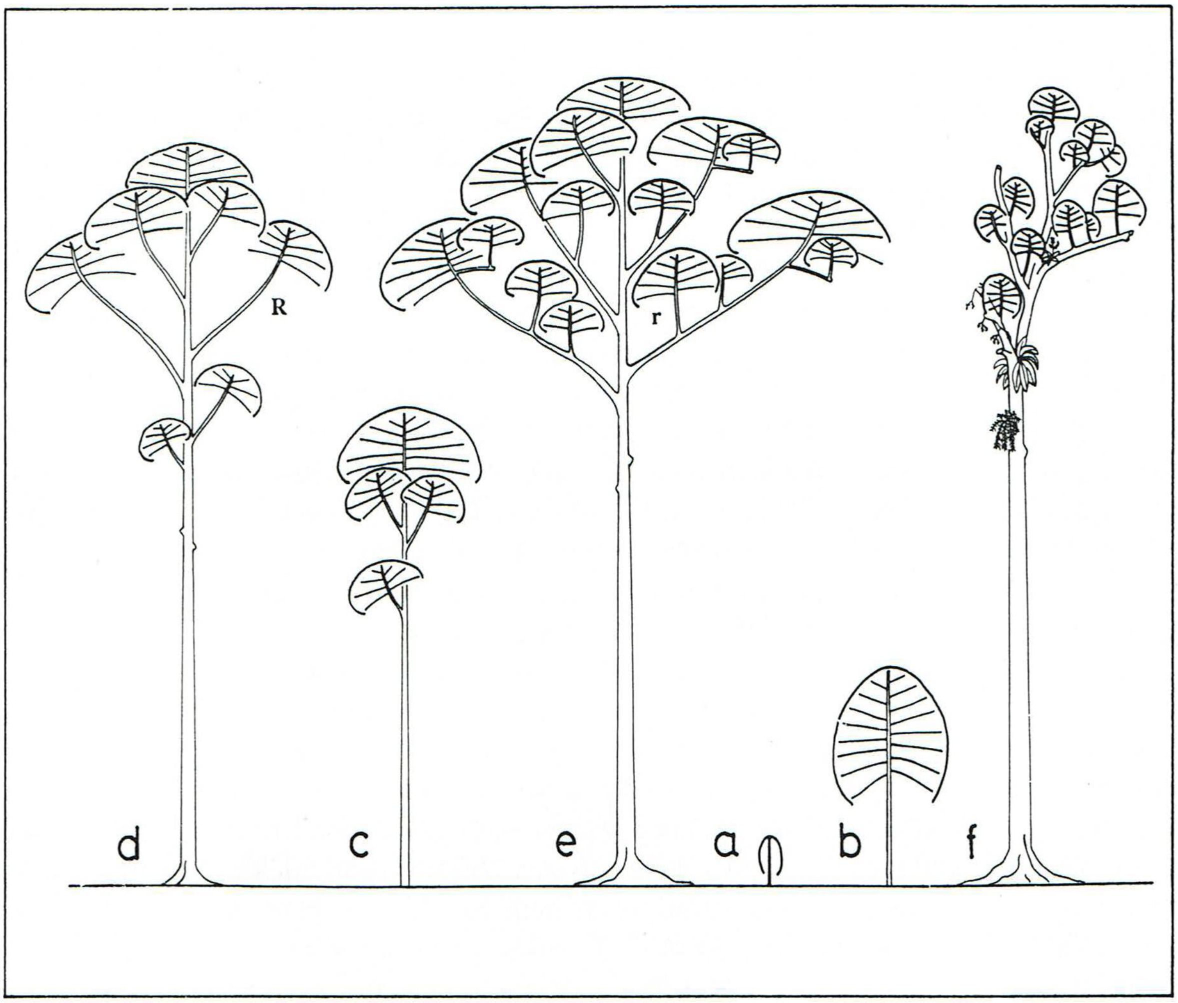


**Figure 3**. Diagrammatic representation of the developmental sequence of *Shorea stenoptera*. (From Edelin, 1984, with permission).

the branches and appear perpendicularly to them. The development and maintenance of the crown throughout the years is ensured by the constant renewal of these short-lived reiterated complexes. This process continues on the old tree which is marked by the death and gradual dislocation of the crown (3f).

*Dipterocarpus costulatus* (Fig. 4), another Dipterocarpaceae from South East Asia, conforms to Massart's model. It has an orthotropic monopodial trunk with spiral phyllotaxis and rhythmic growth. When juvenile, (4a) its branches are plagiotropic, distichous, and arranged in regular tiers. As it develops (4b), the trunk produces larger and more ramified branches. These features of development become more pronounced as the tree grows (4c). The appearance of a new branching order is followed by an architecturally stable period of variable duration that precedes and prepares the following stage of the development. As the tree grows, this process goes on and becomes more pronounced. The general production of 5th order branches (Fig. 4d-e) coincides with formation of sylleptic reiterated complexes, which represent the major limbs of the adult tree and on which sexuality occurs laterally among the ultimate axes. So, the development of *Dipterocarpus costulatus* is marked by a progressive transformation of its branches. From plagiotropic and poorly branched at the beginning, they become more and more orthotropic, and the adaptive reiteration represents a true "architectural metamorphosis" (Edelin, 1984).

Whether the limbs of the old tree are established by proleptic reiteration (*Shorea stenoptera*) or by sylleptic reiteration (*Dipterocarpus costulatus*), the crown of the old tree is a true colony of individuals of various sizes (Fig. 3e-f; Fig. 4e).

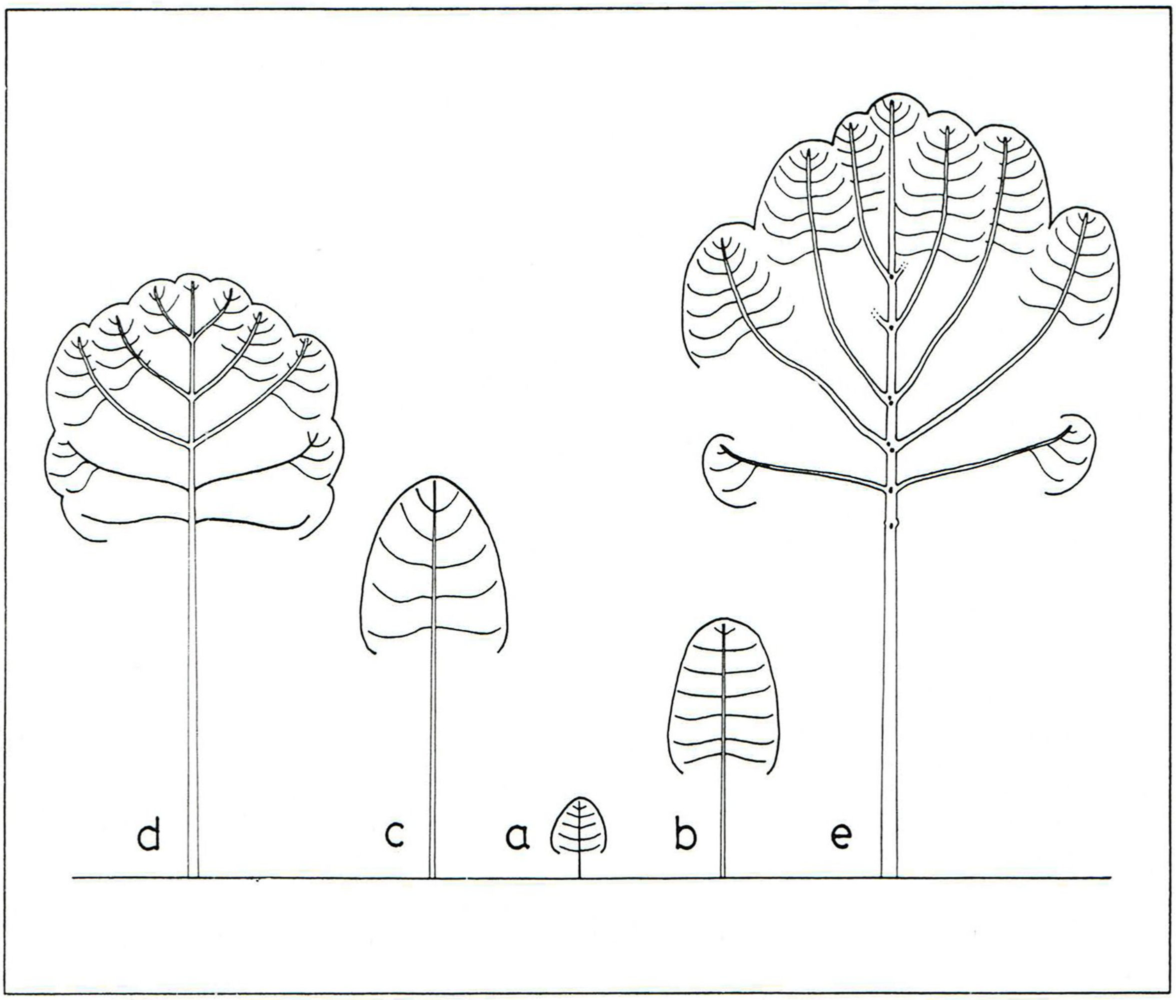


**Figure 4**. Diagrammatic representation of the developmental sequence of *Dipterocarpus costulatus*. Ultimate axes are not represented. (From Edelin, 1984, with permission).

The reiterated complexes, naturally "grafted" together as it were, are relatively independent and exert a strong selective competition on each other (Torquebiau, 1979). Following a progressive and precise sequence of events, each species expresses its own "reiterative strategy" (Edelin, 1986). However, these events are incorporated into a more general cycle which leads the "colonial tree" from germination to death.

The life of a forest tree is thus marked by three major architectural stages (Oldeman, 1974): (i) the tree of the future, corresponds to growth in the understory, and possesses an architecture that strictly conforms to the architectural unit. The tree expresses its architectural unit from axis one to the ultimate axis which is the threshold of reiteration; (ii) the tree of the present has reached the forest canopy and has developed a large crown by means of adaptive and traumatic reiteration. It is composed of the juxtaposition of increasingly smaller reiterated complexes, which are termed arborescent, frutescent, and herbaceous; (iii) the tree of the past is marked by death and gradual dislocation of the crown. The limbs start breaking, leaving stumps on the trunk on which populations of epiphytes become established. The crown progressively breaks up heralding the death and the fall of the tree.

## Conclusion

The discovery of the concepts of architectural model, architectural unit, and reiteration has provided botanists with a powerful tool for studying plant form and structure. More than 150 families have undergone architectural analysis, and these observations concern herbaceous as well as woody plants from both temperate and tropical regions.

Architectural analysis has proved to be probably one of the most efficient means that we presently possess for the study of the organization of arborescent plants, and architectural concepts appear to be of particular interest for the understanding of crown construction in trees. Nevertheless, numerous problems are still unsolved. At the present time, architectural studies of crown construction in trees continue, but research has also spread to the understanding of the flowering process in tropical plants (Barthélémy, 1986b) and to the architectural analysis of root systems (Kahn, 1983; Atger, 1986). On the other hand, the quantitative knowledge of plant architecture linked with mathematical approaches has also led to the development of a mathematical model for computer simulation of every kind of tree architecture known at the present time and their evolution during tree growth (Reffye *et al.*, 1986).

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