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Establishment of modular growth in a tropical tree: *Isertia coccinea* Vahl. (Rubiaceae)

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The developmental architecture of *Isertia coccinea* Vahl. (Rubiaceae) is described in terms of modular construction. In this paper a module is defined as a determinate shoot terminating in an inflorescence.

Isertia coccinea Vahl. is a small tree that conforms to Scarrone's architectural model. Before flowering, this tree is not modular and consists of an orthotropic trunk bearing rhythmic tiers of orthotropic branches. In a later stage, the lateral complexes branch sympodially as a result of terminal flowering, the whole tree displaying a partly modular stage. Later still, the trunk can terminate in an inflorescence, the tree's growth thus becoming entirely modular. The partly modular stage can be of long or short duration depending on the environmental conditions. In shaded conditions, this stage is long or indeterminate; in open conditions it can be very short, the entirely modular stage becoming dominant early in the life of the tree.

Introduction

Isertia coccinea Vahl. (Rubiaceae) is a small tree, characteristic of secondary forests. This pioneer has been studied in French Guiana, where it is quite common and abundant. Flowering is precocious, the orange-red tubular flowers being pollinated by hummingbirds. In the first section, the flowering process and architecture of individuals growing in sunny conditions are described. In the second, the influence of environmental conditions (especially light intensity) on the growth form and flowering process of this species is discussed.

Establishment of modular growth

Isertia coccinea Vahl. conforms to Scarrone's architectural model; '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' (Hallé *et al.* 1978) (figure 1).

In this section we refer only to the normal growth of this tree growing in open conditions in the secondary forest or at the margin of primary forest. In the following descriptions we shall use the terms 'modular growth' or 'module' in the sense of *article* (in French) defined by Prévost (1966) and Hallé (this symposium): a module consists of a determinate shoot terminating in an inflorescence (or otherwise aborting in some way). Thus a tree having a modular construction is made up of a series of equivalent morphological units repeated indefinitely. Most commonly, modules form sympodia.

Before flowering, the young tree is not modular, and conforms to Rauh's architectural model (Hallé & Oldeman 1975; Hallé *et al.* 1978) (see figure 1). The orthotropic trunk grows

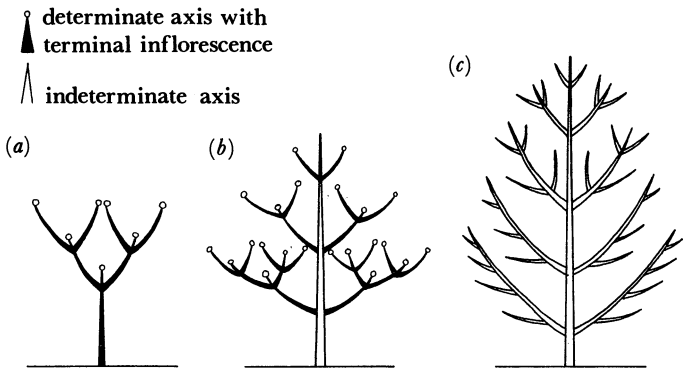

FIGURE 1. (*a*) Leeuwenberg's model; (*b*) Scarrone's model; (*c*) Rauh's model.

rhythmically and produces tiers of orthotropic branches. When the tree becomes older, the first lateral complexes produced can be shed without having flowered.

After a few years, the central axis of each lateral complex flowers terminally, the growth of the tree becoming partly modular (figure 3*d*).

In all the individuals observed in the above-mentioned environmental conditions, the trunk also bears a terminal inflorescence at an older stage, the whole tree thus displaying an entirely modular growth. The number of internodes produced by the trunk below the terminal inflorescence ranged from 65 to 80 in the individuals observed.

Concerning the proximal modules of each lateral complex, precise analysis of many individuals shows that, in general, the number of internodes produced below the terminal inflorescence of each axis is smaller for those inserted the higher on the trunk, than for the basal ones (figure 2*a*). Also their structure is simplified, the monopodial growth becoming shorter and shorter from the basal ones to those inserted at the top of the trunk. Correlated with this sequence, the proximal axis of the lower lateral complexes can carry branches on their monopodial growth as well as immediately below the terminal inflorescence, whereas on the proximal axes of the upper complexes, branching occurs only immediately below the terminal inflorescence, that is, in a subterminal position.

Similar sequences occur in the lateral complexes themselves. On large branch complexes, inserted on the lower part of the trunk, the distal units are simpler than the proximal ones, exhibiting a shorter monopodial growth and a smaller number of constitutive internodes (figure 2*d*).

The last lateral complexes produced by the trunk are entirely modular and branch essentially as in Leeuwenberg's model (figure 1).

In the peripheral part of quite an old tree, all the modules are thus reduced in size. Indeed, at first glance they all seem to be of exactly the same structure. However, the analysis of such a crown shows that the number of internodes of these peripheral modules varies from 6 to 13 (most frequently from 6 to 10), and that these modules are of two kinds: Modules with 6, 7 or 8 internodes, are quite vigorous and composed of a single growth unit; modules of 9 to 13 internodes are slender, much less vigorous, and consist of short internodes. They show two flushes of growth and generally branch very little. Generally these modules, and the few axes they give rise to, soon die.

During the course of their growth, individuals of *Isertia coccinea* become more and more

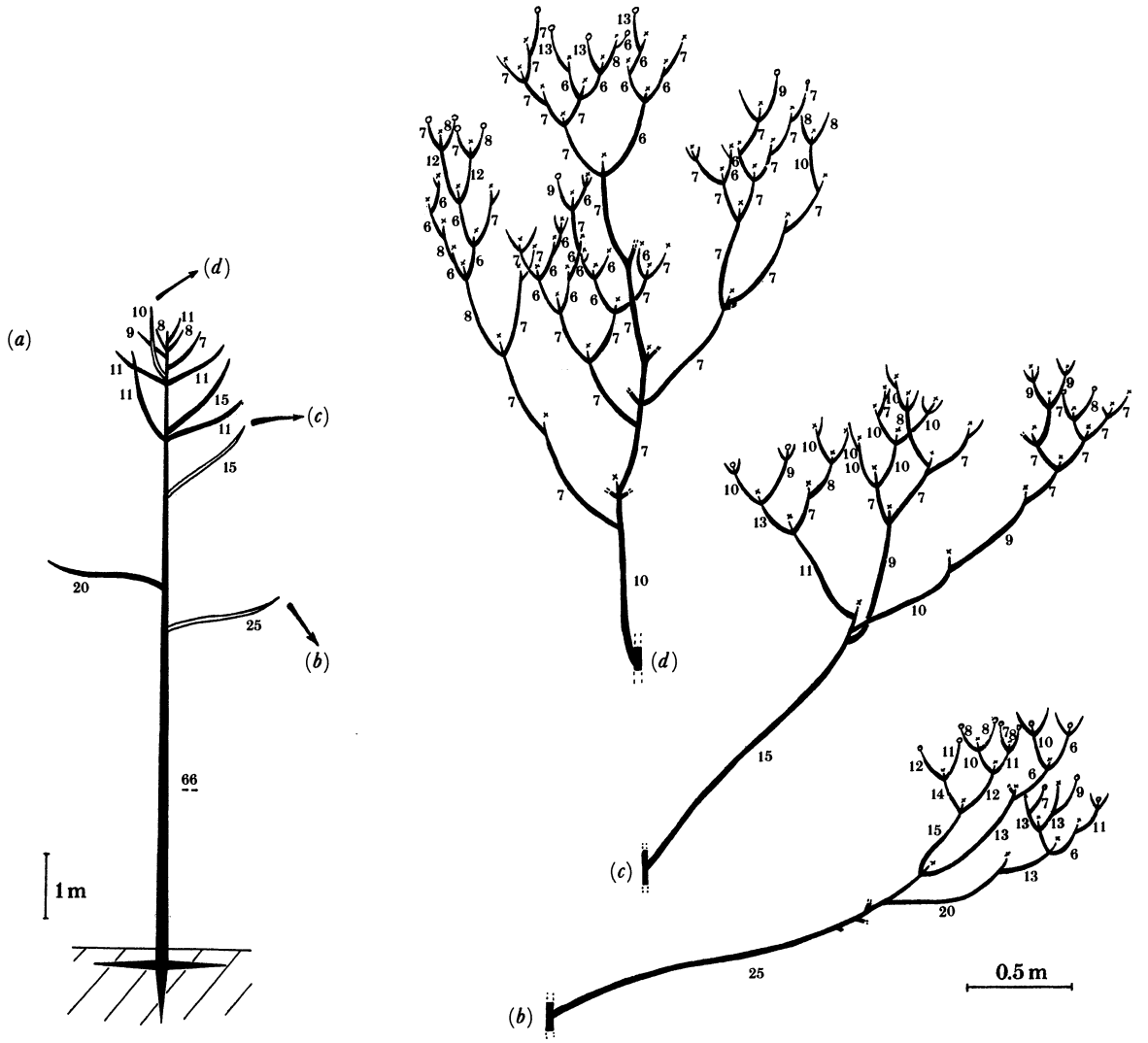

FIGURE 2. Natural individual of *Isertia coccinea* showing the development of modular growth in three lateral complexes (*b*, *c*, *d*) inserted at three different levels.

The number of vegetative internodes produced below the terminal inflorescence of each axis shows that the higher the axis is inserted on the trunk, the more modular the lateral branch complexes are, and the more precocious is the flowering process.

(*a*) Trunk and proximal axis of the lateral complexes. The number of internodes for each axis is noted.

(*b*) Basal lateral complex showing the structural development of the modules from the proximal to the distal part.

(*c*) Intermediate construction between the lateral complexes of (*b*) and (*d*).

(*d*) One of the highest lateral complexes displaying entirely modular growth.

modular. The peripheral part of an old tree is entirely modular and composed of modules which are quite similar in structure and which branch immediately below each terminal inflorescence, that is, in a subterminal position. The flowering process, closely related to this growth pattern, is more and more precocious. In the crown of an old tree, all the modules bear a terminal inflorescence, and the whole tree grows as in Leeuwenberg's model, exhibiting prolific flowering.

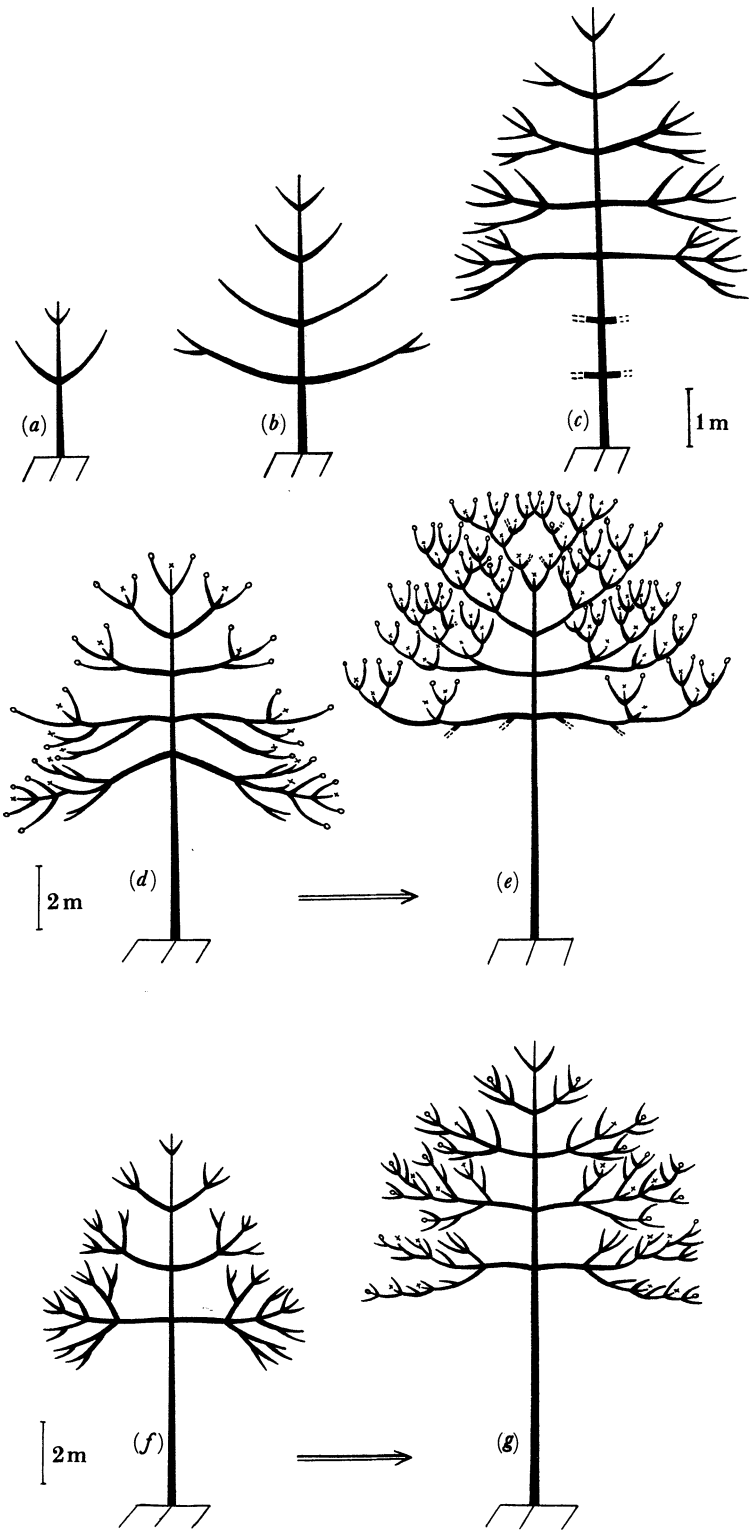

FIGURE 3. Schematic development of Scarrone's model in *Isertia coccinea* Vahl. in open conditions (*d*, *e*) and in shaded conditions (*f*, *g*). Before flowering this tree is not modular and consists of an orthotropic trunk rhythmically bearing tiers of orthotropic branches (*a*, *b*, *c*, *f*). In the following stage, the lateral complexes branch sympodially as a result of terminal flowering, the whole tree displaying a partly modular stage (*d*, *g*).

At an older stage the terminal meristem of the trunk can also flower terminally, the growth of the tree becoming entirely modular. The partly modular stage can be long or short, depending on the environmental conditions: in shaded conditions (*f*, *g*) this stage is long or indeterminate; in open conditions (*d*, *e*) this stage can be very short, the entirely modular stage becoming dominant early in the life of the tree.

The influence of environmental conditions

The vegetative architecture is a constant and stable characteristic of a plant. However, different environmental conditions can involve changes of form. These changes, whatever their importance, are quantitative and do not affect the basic architecture of the species (Hallé 1978).

The most important environmental factor is probably light intensity. The influence of incident light on the branching and flowering behaviour has already been reported for several trees and treelets (Nanda 1962; Kahn 1975; Temple 1975, 1977; Hallé 1978) and further investigations will no doubt provide many other examples. *Isertia coccinea* displays during its growth successively, non-modular, partly modular, and entirely modular architecture. In open conditions, the partly modular stage is short, as the trunk can bear a terminal inflorescence early in the course of its life, sometimes before it is ten years old. Thus in sunny conditions, the whole tree (when it is isolated) exhibits prolific flowering and branching in the course of a few years. Individuals of *Isertia coccinea*, however, can be found in shaded condition under the canopy of the primary forest or shaded by other pioneers such as *Cecropia* sp. (Moraceae). In this particular condition, the partly modular stage can be long or indeterminate, the growth of the trunk remaining monopodial for a long time and the tree displaying a pure Scarrone's model (figure 1).

In individuals shaded by dominant trees, a longer period of monopodial growth is also found throughout the lateral complexes which are sparsely branched compared with individuals freely exposed to bright sunlight. Flowering behaviour is also modified considerably in trees growing under the shade of other trees, and flowering is sparse throughout the whole tree; it is also much less precocious than in open conditions.

The developmental sequence of growth pattern for *Isertia coccinea* in open and shaded conditions is shown in figure 3 in diagrammatic form.

The influence of light intensity on the growth and flowering behaviour of plants is unlikely to be restricted to *Isertia coccinea*, and the current studies of many other species (unpublished data) indicates the same behaviour in many plants. Previous studies (Nanda 1962; Kahn 1975; Temple 1977) also show similar processes in various species, and the reduction of the vegetative stage in individuals of a species growing in open conditions compared with individuals of the same species growing in shaded conditions seems to be a general rule.

Conclusion

Isertia coccinea Vahl. shows clearly the establishment of modular growth in a tree exhibiting orthotropic axes and terminal inflorescences. This establishment of modular growth in Scarrone's model seems to be a frequent process for a number of species ranging from small treelets (unpublished data) to large trees (Nanda 1962).

This example also shows the close relationship that can exist between different architectural models such as Leeuwenberg's model, Scarrone's model and Rauh's model.

In *Isertia coccinea* Vahl. the modular growth is closely related to flowering and in the entirely modular crown of an old individual exposed to bright sunlight flowering and branching is profuse. By comparison, when the tree is smaller and younger, flowering is sparse and in the lower part of the tree some lateral branch complexes can be shed before they have flowered. This is more obvious in individuals growing shaded by other trees; in this situation the

monopodial vegetative growth phase is much longer and flowering remains sparse, sometimes for most, if not all, of the life of the tree.

Flowering in this species is probably related to the intensity of light and is much more precocious and profuse for the individuals exposed to bright sunlight than for individuals shaded by other trees. This has very important consequences for the form of the tree as the inflorescences are terminal. The more precocious the flowering is, the earlier modular growth will occur.

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