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ARCHITECTURE AND GROWTH STRATEGIES OF TROPICAL TREES IN RELATION TO SUCCESSIONAL STATUS

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SUMMARY

(1) Crown architecture, growth and branch display were studied in two early-successional (*Anthocephalus cadamba* and *Duabanga sonneratioides*) and two late-successional (*Artocarpus chaplasha* and *Dillenia pentagyna*) tree species of subtropical humid forest in north-eastern India. While the early-successional species conform morphologically to Massart's model (*Duabanga sonneratioides*) or Roux's model (*Anthocephalus cadamba*), the late-successional species conform to Scarrone's model (*Dillenia pentagyna*) or Rauh's model (*Artocarpus chaplasha*) of tree architecture.

(2) While rhythmic extension growth of the leader axis has been identified on the basis of differences in leaf morphology and branch organization in the architectural models, this does not always agree with detailed growth analysis as, for example, in *Anthocephalus cadamba* and *Duabanga sonneratioides*.

(3) The extension and radial growth rates of early-successional species were very rapid compared with late-successional species.

(4) Faster growth over a longer annual-growth period results in the sparse branch arrangement in early-successional species which facilitates greater leaf exposure.

(5) The slower growth rate over a shorter growth period results in densely packed canopies with mutual shading of leaves of late-successional species.

(6) In the early-successional species the production and the contribution of first order branches to the total branch system was much higher than in the late-successional species, which had plasticity in the orientation and overall display of their branches in relation to irradiance.

INTRODUCTION

Most knowledge of tree growth is based upon temperate species (Cook 1941; Kozlowski 1964; Kramer & Kozlowski 1979). Recently, the canopy form of trees in relation to environmental conditions has received some attention (Brunig 1976; Nelson, Burk & Icebrands 1981) and several quantitative studies on branching pattern have been made (Whitney 1976; Fisher 1978, 1979; Steingraeber, Kasht & Frank 1979; Pickett & Kempf 1980; Borchert & Slade 1981). Temperate trees offer a limited diversity of pattern of architecture and growth and, although some studies on the growth pattern of tropical trees are available (Holdsworth 1963; Hallé & Martin 1968; Borchert 1969; Hallé & Oldeman 1970; Gill & Tomlinson 1971), the need for a deeper understanding of tree growth patterns in tropical forests was emphasized by Tomlinson & Gill (1973). The few studies on the pattern of growth of tree species in relation to their successional status suggest distinct strategies for early- and late-successional high-latitude species (Marks 1975) or high-altitude temperate species of India (Boojh & Ramakrishnan 1982a). No studies are

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available for tropical species except for a preliminary survey of twenty-two species which indicates a distinction between early-, mid- and late-successional species (Ramakrishnan & Shukla 1982). With the increasing emphasis on mixed-plantation forestry and agro-forestry systems, the identification of mutually compatible species mixtures has become important.

The objective of this paper is to analyse quantitatively the crown architectures and growth patterns of four tree species of different successional status in a subtropical humid forest.

STUDY AREA

The study area is located at Lailad (25°45'N, 91°45'E) which is about 70 km north of Shillong, Meghalaya in north-eastern India. It lies at an altitude of about 296 m. The Precambrian rocks are represented by gneiss, schists and granites, and the soil is a red sandy loam of lateritic origin. The climate (Shukla & Ramakrishnan 1982) is typically monsoonal with about 84% of the annual rainfall of 2200 mm falling during May–September; virtually no rain falls from November to March; April and October are intermediate. The monthly maximum and minimum temperatures during the winter are 26 °C and 11 °C, respectively. The hottest season is from mid-February to early April when there are strong winds and the monthly maximum and minimum temperatures are 37 °C and 21 °C, respectively.

The study site is part of a forest reserve which was clear-felled about 50 years ago. Outside the reserve are stands at different stages of early succession after slash and burn agriculture (Ramakrishnan & Toky 1978; Singh & Ramakrishnan 1982).

ARCHITECTURE AND GROWTH CHARACTERISTICS OF THE SPECIES

The architectural models described in this section are based on morphological characteristics (Hallé, Oldeman & Tomlinson 1978). These may not always agree with models based on morphometric growth analysis. Thus, rhythmicity is associated with such morphological features as: (i) axis articulation (pronounced segmentation), (ii) intermittent branch production, and (iii) regular change in leaf morphology. The absence of these characteristics is considered to indicate continuous growth. *Anthocephalus cadamba* and *Duabanga sonneratioides* do not conform to this (cf. next section).

The four species studied will now be described briefly. After their first mention, they will be referred to by their generic name only in the remainder of this paper. *Anthocephalus cadamba* and *Duabanga sonneratioides* are light demanders, *Dillenia pentagyna* is shade tolerant after establishment, while *Artocarpus chaplasha* can regenerate in the shade. The shade-intolerant species are described first.

Anthocephalus cadamba Miq. (*Rubiaceae*)

The heterogeneous axes with both an orthotropic leader axis and plagiotropic branches, acrotonic branching (branches not at the base but distal on the axis) without modular construction (leader axis distinct from the branches), monopodial trunk with a continuous pattern of growth (leaves with similar morphology and with regular branch production), and plagiotropic, monopodial, long-lived branches are features that assign this species to Roux's model.

The leader produces decussately arranged leaf pairs and branches. Branch dimorphism with an orthotropic trunk and plagiotropic branches is evident. First-order branches arise sylleptically (by the continued growth of lateral buds laid during the current year's growth) with a long first internode (hypopodium) before bearing foliage leaves. All the other branch orders arise proleptically (by the activation and growth of lateral buds laid during the previous year's growth). The decussate leaf arrangement on plagiotropic units shows dorsiventrality by secondary orientation of blades in a horizontal plane, exhibiting apparent discordancy with that of the trunk where the decussately arranged leaves may be oriented in several planes (Fig. 1).

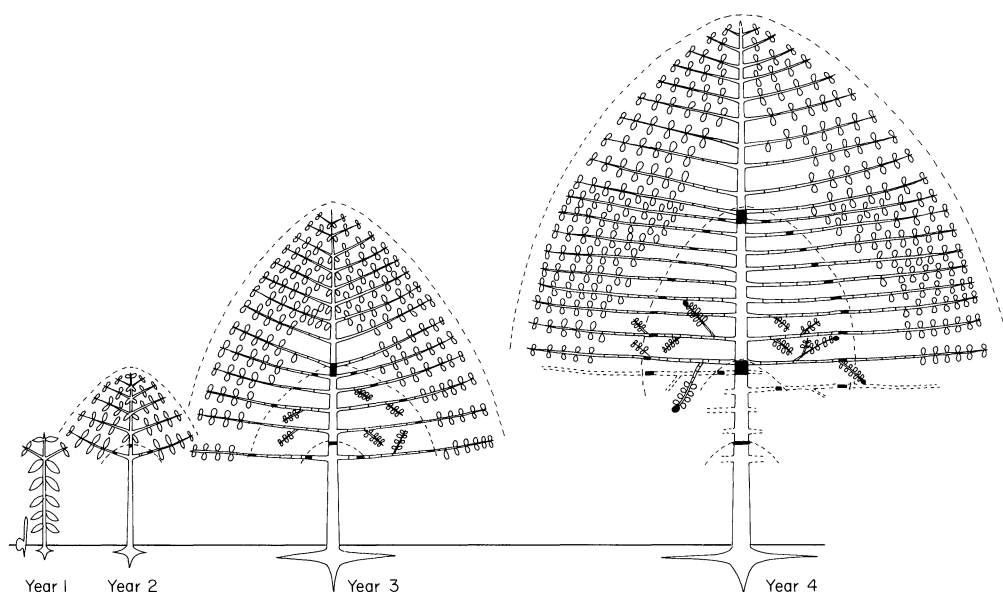


FIG. 1. Architectural development with excurrent crown form (Roux's model) of *Anthocephalus cadamba* in Meghalaya, north-eastern India during the first 4 years of growth (each demarcated by broken line). Short internode (articulation) shows cessation of annual growth.

Duabanga sonneratioides Ham. (*Sonneratiaceae*)

Morphologically this species conforms to Massart's model and shows many basic characteristics in common with Roux's model. The main difference is that the leader axis shows rhythmic growth (leaves with changing morphology and branches organized in tiers).

The radially symmetrical main axis produces spirally arranged leaves at short intervals and tiers of branches, each tier consisting of five branches. During the first year, only one branch tier is produced whereas in each subsequent year five tiers are formed. The orthotropic trunk bears plagiotropic branches. The first-order branches are extra-axillary and sylleptic and the higher-order branches are axillary and proleptic. The leaves are at long intervals on the branches and are dorsiventral. The growth units (branch tiers) are neither demarcated by scale leaves nor is there a rest period between successive tiers, unlike that reported by Hallé & Oldeman (1970) for this species from Malaysia (Fig. 2).

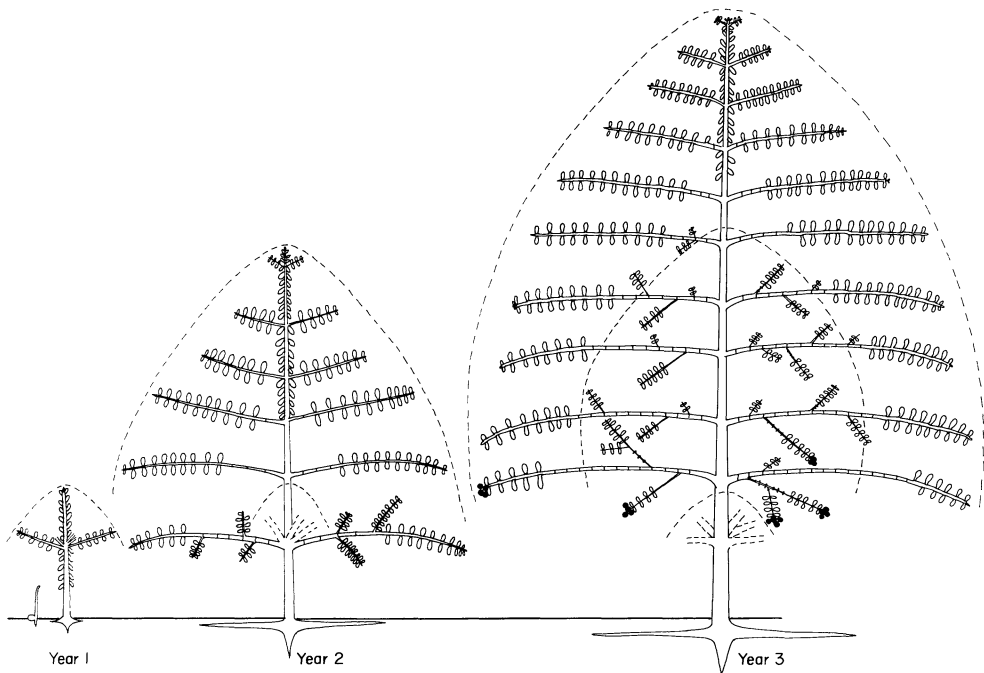


FIG. 2. Architectural development with excurrent crown form (Massart's model) of *Duabanga sonneratioides* in Meghalaya, north-eastern India during the first 3 years of growth (each demarcated by broken line). During the first year only one tier of branches is produced. In subsequent years five tiers of branches are produced per year. Only two of the five branches in each tier are shown.

Dillenia pentagyna Roxb. (*Dilleniaceae*)

The leader axis shows a rhythmic pattern of growth with a change in leaf morphology and the branches are arranged in loose tiers. The homogeneous axes are all orthotropic with terminal inflorescence resulting in sympodial branches at the periphery of the crown. This conforms to Scarrone's model.

All branches are produced proleptically only after the fall of axillant leaves (Fig. 3). The arrangement of leaves and branches is spiral. A 6-year-old tree produces about 3–5 first-order branches in a year. The branch growth is monopodial during the period of vegetative juvenility, but becomes sympodial after the onset of the terminal inflorescence. In older trees the lower branches may become pendulous.

Artocarpus chaplasha Roxb. (*Moraceae*)

The architectural model of this species differs from that of *Dillenia* in that the inflorescence is lateral and, therefore, the branches are monopodial. Hence, this species belongs to Rauh's model.

Axial conformity and the arrangement of leaves and branches in *Artocarpus* is similar to *Dillenia*. The trunk remains unbranched until the third or fourth year. Usually a single tier of proleptic first-order branches is produced each year, but occasionally two tiers may be produced through syllepsis. A single tier has 3–7 branches, depending upon the environmental conditions and the age of the tree, and separated from the next tier by a gap of 2–11 internodes (Fig. 4).

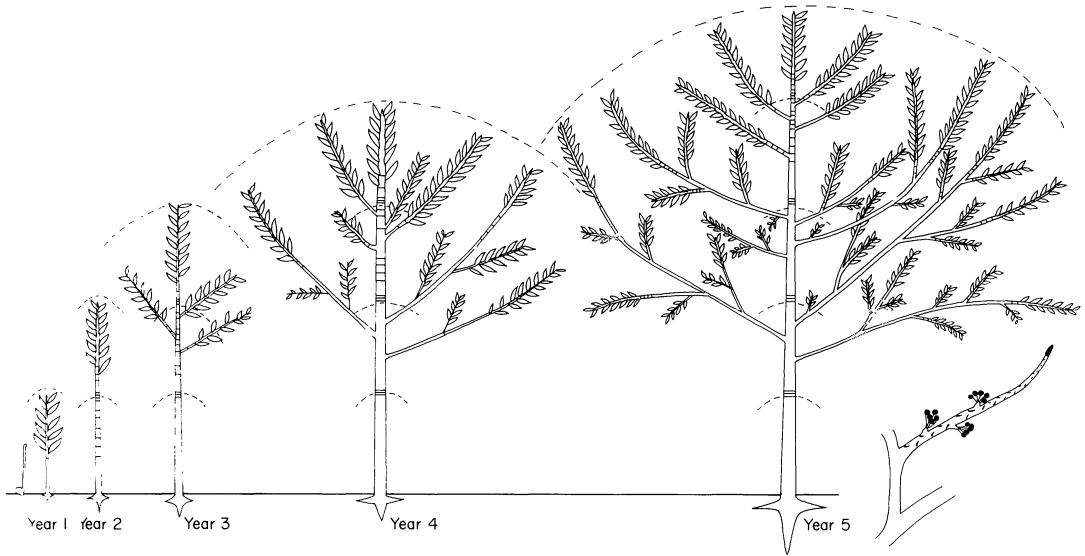


FIG. 3. Architectural development with decurrent crown form (Scarrone's model) of *Dillenia pentagyna* in Meghalaya, north-eastern India during the first 5 years of growth (each demarcated by broken line). Aggregation of nodes indicate cessation of annual growth. Terminal flowers on a third-order branch of an older tree is shown separately in the final drawing.

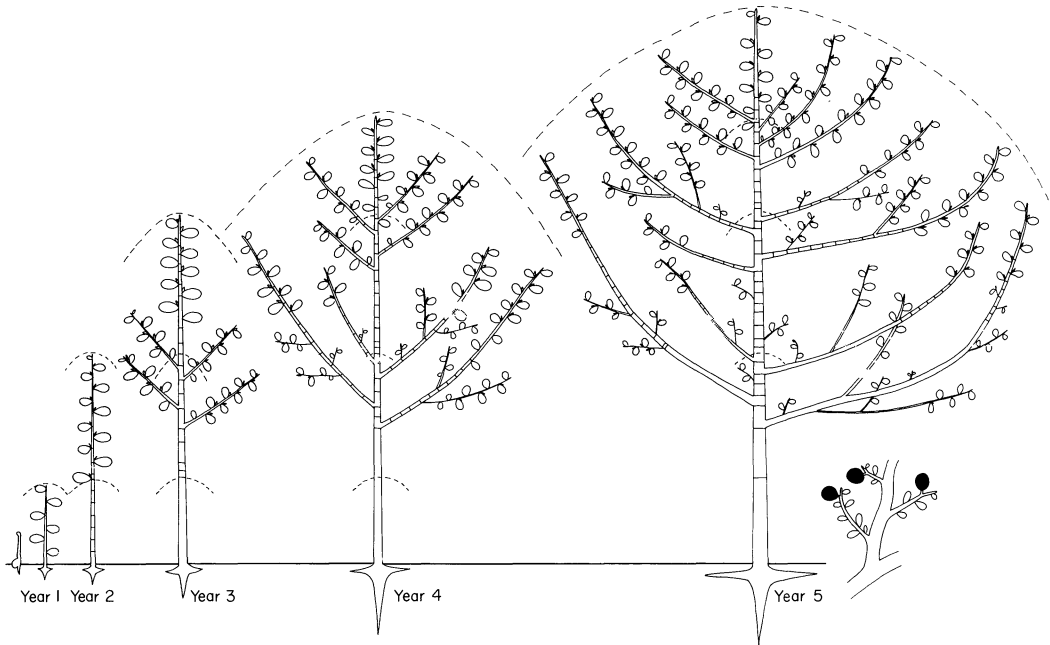


FIG. 4. Architectural development with decurrent crown form (Rauh's model) of *Artocarpus chaplasha* in Meghalaya, north-eastern India during the first 5 years of growth (each demarcated by broken line). One tier of 3-5 alternate branches with a long gap between tiers demarcates annual growth. Lateral position of flower on a third-order branch of an older tree is shown separately in the final drawing.

METHODS

For growth analysis, five 5-year-old trees of each of the four species were selected. These 'open-grown' trees were from different stages of early succession outside the forest reserve. Five trees of *Anthocephalus* and of *Artocarpus* of the same age, but growing in the forest, were also selected (trees of *Dillenia*, though growing in shade, could not be considered as they were of sprout origin). Unless otherwise stated, means of the five replicate trees were calculated.

Observations on growth characteristics commenced in January 1979 on the main axis (trunk) and actively growing branches of all the trees. The tree tops were approached from a wooden platform. Observations were made every 2 weeks on gbh (at 1.3 m above ground level) and the length of the main axis and individual branches. Branch orientation was measured by using a protractor and plumb bob and was expressed in degrees from the main axis.

Leaf area was calculated by a regression developed, for each species, between blade length, breadth and area. Since the leaves of *Artocarpus* were of two types, entire and lobed, and since the lobing characteristics varied with leaf size (Shukla & Ramakrishnan 1981), four regressions were developed, each based on a random sample of fifty leaves. For all studies, except for calculation of the bifurcation ratios, the branches were ordered using ordinal numbers, considering the trunk as the starting point, order zero, and the branches as first, second and third orders, respectively, in chronological sequence (Hallé, Oldeman & Tomlinson 1978). For calculation of the bifurcation ratio (*Rb*)—which is, strictly, a quotient—Strahler's (1951) method was followed in which the ultimate branch was designated as first order. Where two first-order branches come together the resulting proximal segment was the second order. Where two branches of unequal order meet, the resulting branch maintained the higher order. The bifurcation ratio of the branching system of the tree was derived on the basis of Motomura's formula modified by Steingraeber, Kasht & Frank (1979):

$$Rb = N - N_{\max} / N - N_1$$

where *N* is the total number of branches of all orders, *N*_{max} is the number of branches of the highest order, and *N*₁ is the number of branches of the first order.

Three open-grown 5-year-old trees of each species were harvested at the end of the growing season in November 1980, and the branches were divided into different orders and assigned to the length classes 0–10 cm, 10.1–20 cm, etc. The number of branches of each length class was then expressed as a percentage of the total number, with respect to first- and second-order branches.

RESULTS

Extension and radial growth

Morphologically, *Duabanga* had a rhythmic-growth pattern related to leaf morphology and branch organization (Massart's model), but the growth continued throughout the year though it slowed down during November and December. On the other hand, although *Anthocephalus* had a continuous-growth pattern from the point of view of leaf morphology and branch organization, it showed a dormant period during the winter. The other two species had a morphological rhythm and ceased growth during the winter. The length of winter dormancy in *Anthocephalus*, *Artocarpus* and *Dillenia* increased with age. For a

given species, depending upon age, the date of bud break was more variable than the date of the onset of bud dormancy. This pattern was more pronounced in *Anthocephalus*. In general, the late-successional species had shorter growth periods than the early-successional species (Fig. 5).

Rhythmic fluctuations in internode length (not presented here) and the area of the corresponding leaves along the main axis were found in all species (Fig. 6). This intrinsic rhythm was more conspicuous in early-successional than in late-successional species. The number of peaks and the number of nodes were fewer in the forest-grown trees of *Anthocephalus* and *Artocarpus* than in their open-grown counterparts.

Under open-grown conditions, the early-successional species had a more rapid and a longer period of extension growth than the late-successional ones. In the forest-grown

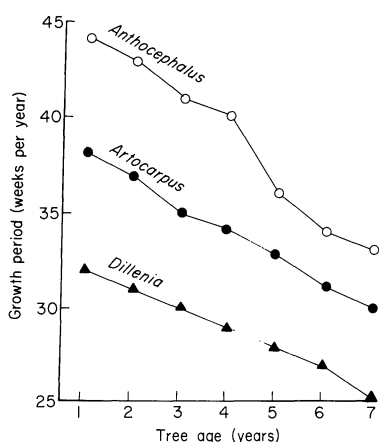


FIG. 5. The length of the growing period in relation to tree age for: (○), *Anthocephalus cadamba*; (●), *Artocarpus chaplasha*; and (▲), *Dillenia pentagyna* in Meghalaya, north-eastern India.

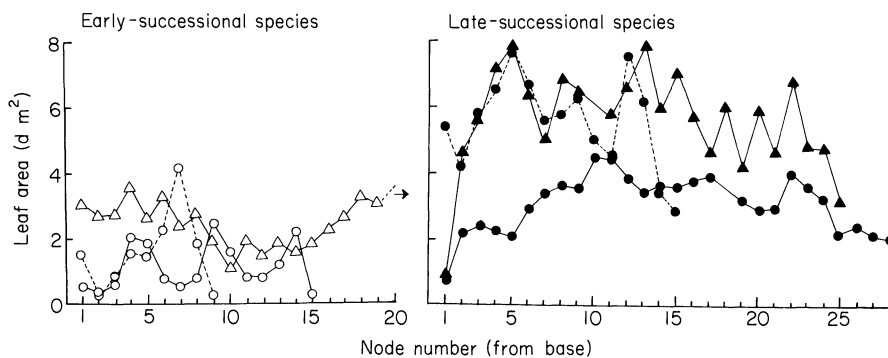


FIG. 6. Rhythmical changes in leaf area on the main axes of (—), open-grown; and (---), forest-grown trees of (○), *Anthocephalus cadamba*; (△), *Duabanga sonneratioides*; (●), *Artocarpus chaplasha*; and (▲), *Dillenia pentagyna*, in Meghalaya, north-eastern India. Only one tier of branches with a between-tier gap on the main axis are presented here for *Duabanga*. The arrow suggests that the rhythmicity continued for the other four tiers produced during the year in a similar way.

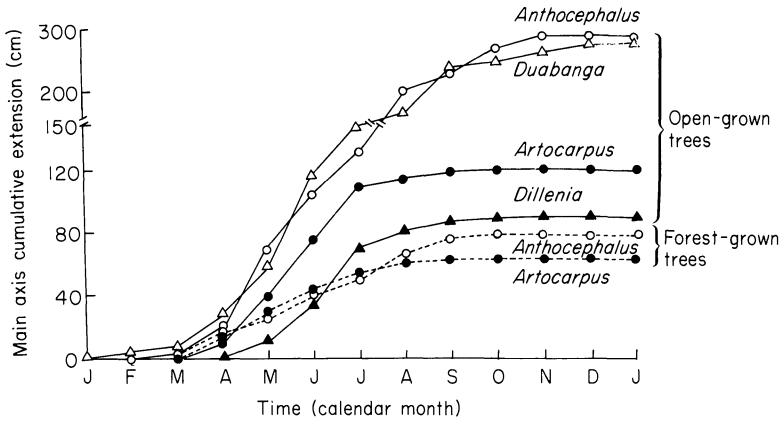


FIG. 7. Cumulative extension growth of the main axis of (—), open-grown; and (---), forest-grown trees of (O), *Anthocephalus cadamba*; (Δ), *Duabanga sonneratioides*; (\bullet), *Artocarpus chaplasha*; and (\blacktriangle), *Dillenia pentagyna* in Meghalaya, north-eastern India.

TABLE 1. Annual extension growth (cm) of the main axis and of first- and second-order branches in three positions in the canopy of open-grown trees of four species in Meghalaya, north-eastern India. The growth rates for forest-grown individuals, which were available for two species only are given in parentheses. Values are means \pm 1 S.D. $n = 5$.

Order of shoot and canopy position	<i>Anthocephalus cadamba</i>	<i>Duabanga sonneratioides</i>	<i>Artocarpus chaplasha</i>	<i>Dillenia pentagyna</i>
Zero (main axis)	286 \pm 36.4 (79.5 \pm 10.2)	298.2 \pm 32.2	123.0 \pm 28.1 (66.5 \pm 8.64)	102.2 \pm 13.7
First				
Top canopy	262 \pm 24.6 (122.0 \pm 16.0)	259.4 \pm 32.8	104.2 \pm 32.6 (74.0 \pm 17.8)	35.7 \pm 14.0
Middle canopy	208.6 \pm 28.4 (86.0 \pm 0.4)	174.1 \pm 34.3	86.0 \pm 29.6 (48.4 \pm 6.4)	31.7 \pm 11.5
Bottom canopy	127.4 \pm 28.8 (42.4 \pm 8.6)	44.4 \pm 16.5	54.6 \pm 18.6 (29.0 \pm 17.2)	22.2 \pm 12.9
Second				
Top canopy			43.2 \pm 20.2 (27.5 \pm 5.9)	6.3 \pm 7.02
Middle canopy	34.6 \pm 13.2	53.8 \pm 21.6	65.2 \pm 20.8 (47.5 \pm 13.1)	6.93 \pm 3.3
Bottom canopy	45.2 \pm 14.5	23.0 \pm 9.7	23.7 \pm 16.2 (12.6 \pm 8.5)	2.3 \pm 1.4

trees, extension growth was reduced much more in the early-successional species (Fig. 7). Radial growth followed a similar pattern and is not presented here.

A comparison of the main axis with first and second order branches (Table 1) suggests that there is a general decrease of extension growth with increase in the order of branching and at lower canopy positions. However, in early-successional species the decrease in extension growth with increase in branch order was more marked at lower canopy levels than that for late-successional species.

Branching pattern

Under open-grown conditions the seasonal pattern of first- and second-order branch production of early-successional species was spread over many months, whereas it was

confined to a short period for late-successional species (Fig. 8, where only the first-order branches are shown). In *Artocarpus*, maximum production was about a month earlier in forest-grown than in open-grown trees.

In all species studied, the branch angle increased significantly from the top of the canopy to its base (Table 2); P (t -tests) < 0.001 for all species except open-grown *Artocarpus* where $P < 0.05$. In general, early-successional species had branch angles in the range of $68\text{--}90^\circ$ and late-successional species of $50\text{--}65^\circ$. The branches of forest-grown *Anthocephalus* were less erect than those of the open-grown ones ($P < 0.05$); there were no significant differences for the late-successional species.

The total length of all the branch systems and the contribution by the first-order branches were more for early-successional species than for late-successional ones (t -tests, in all cases $P < 0.001$) (Table 3). Conversely, the contribution of second-order branches was significantly higher in two late-successional species compared to the early-successional ones. Third-order branch production was present in *Artocarpus* only.

The length classes of first-order branches of early-successional species had wider range and a larger number of branches of greater length-class than did the late-successional species which were all below 200 cm long (Fig. 9). However, the length of the second-order branches of both early- and late-successional species were very similar to each other and are not presented here.

The bifurcation ratio for open-grown early-successional species was significantly higher than that for the late-successional species in all cases (t -tests) $P < 0.05$. (Table 4); only

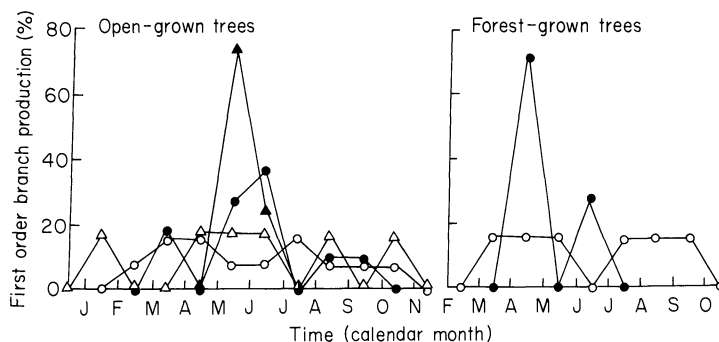


FIG. 8. Monthly production (%) of first-order branches of (○), *Anthocephalus cadamba*; (△) *Duabanga sonneratioides*; (●), *Artocarpus chaplasha*; and (▲) *Dillenia pentagyna* growing in open- and forest-grown conditions, in Meghalaya, north-eastern India.

TABLE 2. Branch angles ($^\circ$ from main axis from the apex) of first-order branches at two canopy positions of open-grown and forest-grown trees of four species in Meghalaya, north-eastern India. Values are means ± 1 S.D. $n = 5$.

Canopy position	Open-grown trees		Forest-grown trees	
	Top	Bottom	Top	Bottom
<i>Anthocephalus cadamba</i>	68.2 \pm 2.4	86.3 \pm 1.8	72.4 \pm 3.4	89.5 \pm 1.4
<i>Duabanga sonneratioides</i>	72.2 \pm 1.5	88.6 \pm 2.4		
<i>Artocarpus chaplasha</i>	55.0 \pm 2.7	60.4 \pm 2.6	54.2 \pm 2.0	64.6 \pm 2.7
<i>Dillenia pentagyna</i> *	51.0 \pm 1.8	63.8 \pm 3.1	50.6 \pm 1.7	62.2 \pm 2.5

* Includes some trees of sprout origin.

TABLE 3. Contribution of first- and second-order branches to the total length of the branch system of open-grown trees of four species in Meghalaya, north-eastern India. Values are lengths and as a proportion of the total length of all branch systems. $n = 3$.

Branch order	First		Second		Total length of all branch systems (cm)
	Length (cm)	Proportion (%)	Length (cm)	Proportion (%)	
<i>Anthocephalus cadamba</i>	4619	69	2042	31	6661
<i>Duabanga sonneratioides</i>	5006	81	1208	19	6214
<i>Artocarpus chaplasha</i>	1441	57*	1015	39*	2625
<i>Dillenia pentagyna</i>	1269	52	1149	48	2418

* 4% were third-order branches.

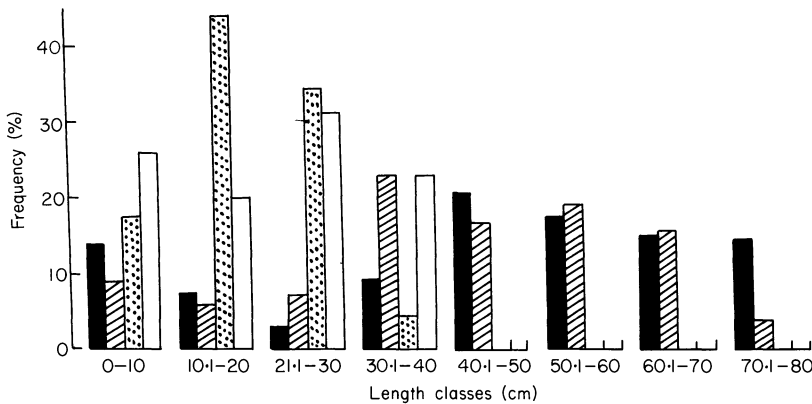


FIG. 9. Percentage distribution of first-order branches of open-grown trees of different length classes in Meghalaya, north-eastern India. Symbols: ■ *Duabanga sonneratioides*; ▨ *Anthocephalus cadamba*; ▩ *Dillenia pentagyna*; □ *Artocarpus chaplasha*.

TABLE 4. Bifurcation ratio (R_b) for open-grown and forest-grown trees of four species in Meghalaya, north-eastern India. Values are means \pm 1 S.D. $n = 5$.

Species	Open-grown trees	Forest-grown trees
<i>Anthocephalus cadamba</i>	8.7 \pm 2.1	3.3 \pm 0.4
<i>Duabanga sonneratioides</i>	9.3 \pm 2.0	
<i>Artocarpus chaplasha</i>	5.8 \pm 0.9	4.8 \pm 0.6
<i>Dillenia pentagyna</i> *	6.3 \pm 0.6	5.5 \pm 0.8

* Includes some trees of sprout origin.

Anthocephalus showed a significantly lower ratio under forest-grown conditions ($P < 0.001$) compared to open-grown ones.

DISCUSSION

Of the four species studied here, *Anthocephalus cadamba* and *Duabanga sonneratioides* are considered shade-intolerant, early-successional species while the other two, *Artocarpus chaplasha* and *Dillenia pentagyna*, are shade-tolerant, late-successional species. However, since *Dillenia* regenerates chiefly in the open but can tolerate shade

only after establishment, we consider it to be an earlier element in the succession than *Artocarpus*, which regenerates well even in shade.

Architecture

The four species belong to the four architectural models of Hallé, Oldeman & Tomlinson (1978) but, on the basis of the present study, it is difficult to relate these models to the ecological niche which the species occupy in the succession. Similarly, studies on a subtropical montane forest at Shillong (north-eastern India) at an altitude of 1900 m (Ramakrishnan, Shukla & Boojh 1982) suggested that there is no relationship between the architectural models and the successional status of the tree species and that quantitative differences in tree architecture are more significant ecologically than qualitative differences represented by these models. Further, a dynamic approach to growth analysis is essential in order to understand the architecture and growth strategies of trees. The phenomenon of continuous vs. rhythmic growth is an example which illustrates this. The species which show a morphological rhythm, such as *Duabanga*, in reality have no seasonal bud dormancy in north-eastern India; unlike the same species studied in Malaysia by Hallé, Oldeman & Tomlinson (1978). On the other hand, species considered to have continuous growth on the basis of morphology (e.g. *Anthocephalus*) in reality have a distinct period of seasonal bud dormancy.

Reiteration due to damage to the trunk observed in older trees was more frequent in late-successional species than in early-successional ones, and such a substitution growth would result in a bayonet-like joint (Hallé, Oldeman & Tomlinson 1978).

Growth pattern

The date of bud break in temperate tree species is relatively constant, whereas that of growth cessation is usually more variable (Kramer 1943). In the present study the time of bud break showed more variation. For example, in *Anthocephalus*, it occurred between late January (winter) and late March (a warmer period), suggesting that temperature has less control of bud break in this species than endogenous factors which may be related to age. In contrast, *Duabanga* had continuous growth throughout the year.

In the three species where dormancy is evident, growth initiation occurred during the drier period (January–May) and this agrees with the observations on other tropical tree species (Longman & Jenik 1974). Contraction of the growth period by the gradual bringing forward of dormancy and postponement of growth initiation with age is interesting and, obviously, is related to intrinsic factors rather than external causes. The decrease in photosynthetic biomass in relation to non-photosynthetic biomass (Shukla & Ramakrishnan 1984a) with age resulting in reduced vigour (source: sink ratio) could be a possible explanation. This needs to be tested further.

The early-successional species had extension growth over a longer period than the late-successional species. Moreover, the early-successional species showed continuous radial growth throughout the year whereas in the late-successional species and in forest-grown *Anthocephalus*, this ceased for about 2 months during the winter. These observations suggest that extension and radial growth need not always be related to one another (Hummel 1946) and that they are probably controlled by environmental factors.

All four species showed rhythmic fluctuations in internodal length and leaf area within a growth period. Obviously, this rhythmic fluctuation is intrinsic. More rhythmic fluctuations of this kind occurred in early-successional species compared to late-successional ones, and in open-grown compared to forest-grown trees of the same species,

suggesting that the rhythm frequency is dependent upon the rate and duration of growth of the individual concerned.

Various terms such as intermittent (Koriba 1958), episodic (Romberberger 1963), articulate (Tomlinson & Gill 1973) and rhythmic (Hallé, Oldeman & Tomlinson 1978) have been used for discontinuous growth of tropical trees and have caused considerable confusion. Basically, the four species considered here have 'indeterminate growth' of two types: (i) evergrowing—with no dormant phase (*Duabanga*), and (ii) periodic—with a dormant phase (*Anthocephalus*, *Dillenia* and *Artocarpus*). Leaf production (Shukla & Ramakrishnan 1984b) and extension growth in all these species is continuous throughout the growth period although the rate may fluctuate. Other late-successional tropical trees may show 'determinate growth' with leaf production and extension growth restricted to pre-determined leaves from an earlier dormant-bud phase. Such species may have only one flush per year, as in *Engelhardia spicata*, *Mesua ferrea* and *Myristica linifolia*, two flushes, as in *Actinodaphne augustifolia*, three flushes, as in *Castonopsis indica*, or even four, as in *Chikrasia tubularis* (Ramakrishnan & Shukla 1982).

Branching pattern

The early successional species, with their sylleptic first-order branch production, have a rapid extension of their plagiotropic branches which results in multilayered canopy with little overlapping of leaves. In this way they are able to capitalize upon the light resource, before it becomes limiting. Further, the hypopodium (Hallé, Oldeman & Tomlinson 1978) of sylleptic branches helps to extend the branch to avoid the shade of the parent shoot leaves (White 1979).

Shoot tip damage or considerable tip abortion in second-order branches, which checks growth in early-successional species, also results in less shading of leaves in the interior of the canopy. Greater shoot tip abortion in second- compared with first-order branches of the early-successional species alone may be indicative of shade intolerance of the early-successional species, as the second- and third-order branches are often further in the canopy and under greater shade.

Self-pruning of the first-order branches is better developed in early- than late-successional species (Shukla & Ramakrishnan 1984a) perhaps due to shading, as suggested by Kramer (1958), resulting in a faster upward growth shift of the canopy. This, together with the greater extension of the first-order branches of the early-successional species, when compared with the second-order branches, results in an excurrent crown form. By comparison, the production of proleptic first- and second-order branches in late-successional species over a brief period of time, characterized by increased production and extension of second-order branches, results in the development of a broader tree crown (decurent crown form) where the leaves are placed more peripherally. Thus, they are able to increase their photosynthetic potential under the shade of the forest canopy.

The overall geometry of a living tree, which depends partly upon branch orientation, is a manifestation of its adaptive strategy (Honda & Fisher 1978; Fisher 1979). In open-grown trees of early-successional species, first-order branch angle increased markedly at lower canopy positions compared with late-successional species where the differences at different canopy levels are often not statistically significant. When open- and forest-grown trees are compared, such a difference between early- and late-successional species is again obvious. In a multi-layered leaf organization, as in early-successional species, an increase in the branch angle under low irradiance would help to open up the canopy for more efficient light capture. On the contrary, in late-successional species with a decurent crown form

and where the leaves are peripherally placed, the branch angle may not make much difference to the arrangement of leaves and the efficiency of light capture.

Early-successional species exhibited long and comparatively less forked axes leading to multi-layered canopies, whereas late-successional species produced more forked axes leading to a denser peripheral arrangement of the leaves (Horn 1971). According to Whitney (1976), the early-successional species should have a higher bifurcation ratio in view of the reduced forking of their axes. This is in agreement with the present results. The lower bifurcation ratio of forest-grown individuals in comparison with open-grown ones is consistent with the observations of Steingraeber, Kasht & Frank (1979). However, Borchert & Slade (1981) found that bifurcation ratios were highly variable. Results from trees at higher altitudes in Meghalaya (Boojh & Ramakrishnan 1982b; Ramakrishnan, Shukla & Boojh 1982) suggest that the bifurcation ratio may not always be an ecologically reliable criterion. Further, the biological significance of ordering branches by methods that ignore their morphological equivalence is questionable. More work is needed to understand its significance.

It may be concluded that early-successional species, like *Anthocephalus* and *Duabanga*, show an exploitive growth strategy (Bormann & Likens 1979) with the maximization of vertical growth due to rapid extension over a longer growing season, but during a short life period when light is not limiting. Late-successional species, like *Artocarpus* and *Dillenia*, have a conservative growth strategy with slow growth even under shade and thus can survive until they are able to grow more rapidly either through gap formation or after their emergence above the general canopy. A mixture of early- and late-successional species with diverse strategies should be compatible for exploiting the diverse light regimes available at different canopy positions in mixed-plantation forestry. In addition, native early-successional tree species could form the basis for agro-forestry programmes using native early-successional tree species.

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REFERENCES

- Boojh, R. & Ramakrishnan, P. S. (1982a). Growth strategy of trees related to successional status. I. Architecture and extension growth. *Forest Ecology and Management*, **4**, 359–374.
- Boojh, R. & Ramakrishnan, P. S. (1982b). On bifurcation ratio in *Schima* species. *Current Science*, **51**, 436–437.
- Borchert, R. (1969). Unusual shoot growth in a tropical tree, *Oreopanax* (Araliaceae). *American Journal of Botany*, **56**, 1033–1041.
- Borchert, R. & Slade, N. A. (1981). Bifurcation ratios and the adaptive geometry of trees. *Botanical Gazette*, **142**, 394–401.
- Bormann, F. H. & Likens, G. E. (1979). *Pattern and Process in a Forested Ecosystem*. Springer, New York.
- Brunig, E. F. (1976). Tree forms in relation to environmental conditions: an ecological view point. *Tree Physiology and Yield Improvement* (Ed. by M. G. R. Cannell & F. T. Last), pp. 139–156. Academic Press, New York.
- Cook, D. B. (1941). The period of growth in some northeastern trees. *Journal of Forestry*, **39**, 957–959.
- Fisher, J. B. (1978). A quantitative study of *Terminalia* branching. *Tropical Trees as Living Systems* (Ed. by P. B. Tomlinson & M. H. Zimmermann), pp. 285–320. Cambridge University Press, New York.
- Fisher, J. B. (1979). Branch geometry and effective leaf area: a study of *Terminalia* branching pattern. 2. Survey of real trees. *American Journal of Botany*, **66**, 645–655.

- Gill, A. M. & Tomlinson, P. B. (1971). Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica*, **3**, 109–124.
- Hallé, H. & Martin, R. (1968). Study of the growth rhythm in *Hevea brassiliensis* (Euphorbiaceae-Crotonoidae). *Adansonia*, **8**, 475–503.
- Hallé, F. & Oldeman, R. A. A. (1970). *Essai sur l'Architecture et la Dynamique de Croissance des Arbres Tropicaux*. Masson, Paris.
- Hallé, F., Oldeman, R. A. A. & Tomlinson, P. B. (1978). *Tropical Trees and Forests: an Architectural Analysis*. Springer, New York.
- Holdsworth, N. (1963). Intermittent growth of the mango tree. *Journal of West African Science Association*, **7**, 163–171.
- Honda, H. & Fisher, J. B. (1978). Tree branch angle-maximizing effective leaf area. *Science, New York*, **199**, 888–890.
- Horn, H. S. (1971). *The Adaptive Geometry of Trees*. Princeton University Press, Princeton.
- Hummel, F. C. (1946). The formation of growth rings in *Entandrophragma macrophyllum* A. Chev. and *Khaya grandifolia* DC. *Empire Forestry Review*, **25**, 103–107.
- Koriba, K. (1958). On the productivity of tree growth in the tropics with reference to the mode of branching, the leaf fall and the formation of the resting bud. *Gardens' Bulletin, Singapore*, **17**, 11–81.
- Kozlowski, T. T. (1964). Shoot growth in weedy plants. *Botanical Review*, **30**, 335–392.
- Kramer, P. J. (1943). Amount and duration of shoot growth in tree seedlings. *Plant Physiology*, **19**, 239–257.
- Kramer, P. J. (1958). Photosynthesis of trees as affected by their environment. *The Physiology of Forest Trees* (Ed. by K. V. Thimann), pp. 157–186. Ronald, New York.
- Kramer, P. J. & Kozlowski, T. T. (1979). *Physiology of Woody Plants*. Academic Press, New York.
- Longman, K. A. & Jenik, J. (1974). *Tropical Forest and its Environment*. Longman, London.
- Marks, P. L. (1975). On the relation between extension growth and successional status of deciduous trees of the north-eastern United States. *Bulletin of Torrey Botanical Club*, **102**, 172–177.
- Nelson, N. D., Burk, J. & Icebrands, J. G. (1981). Crown architecture of short-rotation, intensively cultured *Populus*. I. Effects of close spacing on first order branch characteristics. *Canadian Journal of Forest Research*, **11**, 73–81.
- Pickett, S. T. A. & Kempf, J. S. (1980). Branching patterns in forest shrubs and understory trees in relation to habitat. *New Phytologist*, **86**, 210–228.
- Ramakrishnan, P. S. & Shukla, R. P. (1982). On the relation among growth strategies, allocation pattern, productivity and successional status of trees of a subtropical forest community. *Improvement of Forest Biomass* (Ed. by P. K. Khosla), pp. 403–412. Indian Society of Tree Scientists, Solan, India.
- Ramakrishnan, P. S., Shukla, R. P. & Boojh, R. (1982). Growth strategies of trees and their application to forest management. *Current Science*, **51**, 448–455.
- Ramakrishnan, P. S. & Toky, O. P. (1978). Preliminary observations on the impact of Jhum (shifting agriculture) on the forested ecosystem. *Resources, Development and Environment in the Himalayan Region*, pp. 343–354. Department of Science and Technology, Government of India, New Delhi.
- Romberger, J. A. (1963). *Meristems, growth and development in woody plants*. United States Department of Agriculture, Forest Service Technical Bulletin 1293.
- Shukla, R. P. & Ramakrishnan, P. S. (1981). The nature and ecological significance of heterophylly in *Artocarpus chaplasha* Roxb. *Proceedings of the Indian National Science Academy*, **B47**, 551–555.
- Shukla, R. P. & Ramakrishnan, P. S. (1982). Phenology of trees in a sub-tropical humid forest in north-eastern India. *Vegetatio*, **49**, 103–109.
- Shukla, R. P. & Ramakrishnan, P. S. (1984a). Biomass allocation strategies and productivity of tropical trees related to successional status. *Forest Ecology and Management*, **6**, 315–324.
- Shukla, R. P. & Ramakrishnan, P. S. (1984b). Leaf dynamics of tropical trees related to successional status. *New Phytologist*, **97**, 697–706.
- Singh, J. & Ramakrishnan, P. S. (1982). Structure and function of a subtropical humid forest of Meghalaya. I. Vegetation biomass and its nutrients. *Proceedings of the Indian Academy of Sciences, Plant Sciences*, **91**, 241–253.
- Strahler, A. M. (1951). Quantitative analysis of watershed geomorphology. *Transactions of American Geophysical Union*, **38**, 913–920.
- Streingraeber, D. A., Kasht, L. J. & Frank, D. H. (1979). Variation of shoot morphology and bifurcation ratio in sugar maple (*Acer saccharum*) seedlings. *American Journal of Botany*, **66**, 441–445.
- Toky, O. P. & Ramakrishnan, P. S. (1983). Secondary succession following slash and burn agriculture in north-eastern India. I. Biomass, litterfall and productivity. *Journal of Ecology*, **71**, 735–745.
- Tomlinson, P. B. & Gill, A. M. (1973). Growth habits of tropical trees: some guiding principles. *Tropical Forest Ecosystem in Africa and South America: A Comparative Review* (Ed. by B. J. Meggers, E. S. Ayansu & W. D. Duckworth), pp. 129–143. Smithsonian Institution, Washington, D.C.
- White, J. (1979). The plant as a metapopulation. *Annual Review of Ecology and Systematics*, **10**, 109–145.
- Whitney, C. G. (1976). The bifurcation ratio as an indicator of adaptive strategy in weedy plant species. *Bulletin of Torrey Botanical Club*, **103**, 67–72.

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