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Architecture and growth patterns of early versus late successional shrubs of sub-tropical moist forests of north-eastern India

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Abstract. Growth and architecture of early versus late successional shrubs are compared and contrasted to evaluate their leaf display characteristics. Early successional shrubs had a higher growth rate over an extended period of time compared to late successional shrubs. Inter-branch length and branch angle were greater for late successional species as compared to early successional ones. First- and second-order branch production over third-order branches was greater in late successional shrubs, whereas the reverse was the case for early successional ones. On the other hand, length contribution by all branch orders was higher for the early successional species. The bifurcation ratio was significantly higher for early successional species growing in the open as compared to late successional shrub species growing in shade. Early successional shrubs follow an exploitive strategy and make faster growth whereas late successionals have a conservative strategy for survival in shade.

Keywords. Plant strategies; shrub architecture; plant succession; light adaptation.

1. Introduction

It is only recently that morphometric analysis of tropical forest species in relation to environmental condition has started receiving attention, chiefly through our earlier studies on trees (Boojh and Ramakrishnan 1982a, b; Shukla and Ramakrishnan 1986; Tomlinson 1987). Architectural classification of tropical trees has, however, received much attention (Halle *et al* 1978). Unlike temperate tree species that offer limited diversity in growth and architecture, tropical species are more diverse. Studies on the architecture of the shrub strata in a forest has not received much attention. The only studies that we are aware of, on growth pattern and architecture of shrubs related to their environment are the studies done in broad-leaved forests of north-west America (Pickett and Kempf 1980; Kempf and Pickett 1981), where it was shown that branch length, inter-branch distance and branch angle are important display characters that differ over a successional gradient. Architectural features of shrubs are expected to be different from those of trees within the same forest community because of more restricted light availability in the shrub stratum, though plant architecture may also respond to differences in moisture availability in forest and open areas. In view of the paucity of information on growth characteristics of tropical shrub species, the present study was carried out at lower elevations of Meghalaya in north-eastern India, on two early successional species*, viz., *Melastoma malabathricum* L. and *Mussaenda frondosa* L., and two late successional ones, viz., *Litsaea khasiana* Meissn. and *Oxyspora vagans* Wall.

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*Subsequently referred to by the generic name only.

2. Study area

The present study was carried out at Lailad, about 70 km north of Shillong, Meghalaya (25°45′ latitude and 91°45′ longitude) at an elevation of about 296 m.

The climate of the area is typically monsoonal with 3 distinct seasons. The dry summer period extends from mid-February to April. The monsoon season is from May to September. The mild winter from November to February is relatively dry. Of the total annual rainfall of 2200 mm, about 80% falls during May–September. The mean monthly maximum and minimum temperatures during summer are 37 and 28°C and the corresponding values for winter are 26 and 11°C respectively.

2.1 *Architectural development*

The extension growth of all the branch systems of the two early successional species, (*Melastoma* and *Mussaenda*) and one of the late successional species (*Oxyspora*) is sympodial (figures 1, 2B). After the abortion of the apical bud of the current year, two (*Melastoma* and *Oxyspora*) or sometimes 3 (*Mussaenda*) axillary buds just below the apex are activated in the next growth season (prolepsis), of which one eventually takes over as the 0-order axis. Such a sympodial growth of the axis with seasonal dormancy in the case of all 3 species conforms to Koriba's model of Halle *et al* (1978); these species were aged, based on their growth pattern. However, these species differ from Halle's description of the model because the sympodial growth is through proleptically produced branches, although the normal

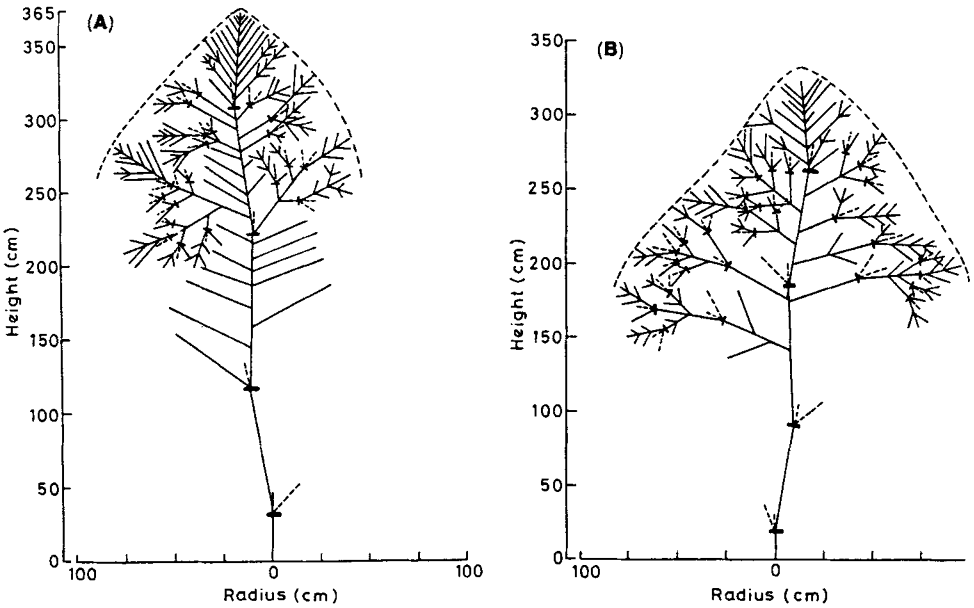

Figure 1. Architectural development with excurrent crown form (Koriba's model) of (**A**) *Melastoma malabathricum* (broken lines demarcates one year's growth) and (**B**) *Mussaenda frondosa* (sympodial branch formation with aborted tip represented by broken line demarcates one year's growth) in north-east India.

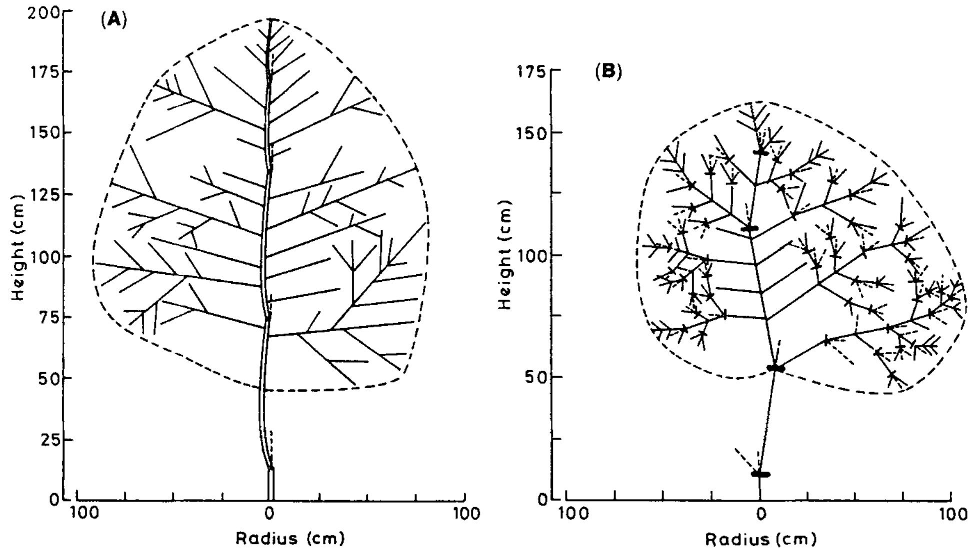

Figure 2. Architectural development of (A) *Litsaea khasiana* with decurrent crown form (with features of Koriba's model and Rauh's model) (articulation with many short internodes on the 0-order axis and sympodial branching with aborted tips represented by broken line demarcates one year's growth) and (B) *Oxyspora vagans* with decurrent crown form (Koriba's model) (sympodial branch formation with aborted tip represented by broken line demarcates one year's growth) in north-east India.

branch production is through syllepsis. This is because the leaves produced during the latter part of the growth season do not subtend any branches in the same year. Though branches in all the 3 species arise from the axiles of opposite decussate leaves, one of the branches may eventually abort. The basal node of each branch is usually somewhat longer (hypopodium). Flowering is terminal in all the 3 species. In *Melastoma*, flowering occurs in February on the apical shoot before it would abort at the time of initiation of the sympodial growth of the axis. However, flowering would occur only on branches that are at least 1-year old. In the other two species, flowering also occurs on the apical shoot but at the end of the growth period in August (*Mussaenda*) or September (*Oxyspora*) after the growth of the sympodially produced branch system is completed. In these two species, flowering occurs on all the branches irrespective of branch age.

With a sympodial axis, *Litsaea* also seems to conform to Koriba's model axis but with a major difference in that flowers are laterally placed (figure 2A). This species has many features in common with Rauh's model too, with respect to rhythmicity, branches that are morphogenetically identical with the trunk and lateral positions of flowers but without a monopodial trunk. The architecture, therefore, strictly does not conform to either of the two models.

3. Methods

The two early successional shrubs are shade-intolerant species, whereas the two late successional shrubs, are shade-tolerant species of older forests. Whilst *Oxyspora* is found in dense shade, *Litsaea* regenerates in the open and has the ability to withstand shade.

Monthly observations on the extension and radial growth of the leader axis and branches of different orders were made on five 4-year old individuals of each species. Radial growth was measured using a callipar at 10 cm above the ground level. The ordering of branches was done according to Halle *et al* (1978), using ordinal number, considering the leader axis of the plant as the starting point order 0, and the branches as the first-, second- and third-orders, respectively in chronological sequence. Branch angle was measured by using a protractor fitted with a plumb bob.

For calculation of the bifurcation ratio (R_b) (which strictly is 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 R_b of the branching system of the tree was derived on the basis of Mctomura's formula modified by Steingraeber *et al* (1979):

$$R_b = N - N_{\max}/N - N_1,$$

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. Statistical analysis using one-way ANOVA was done to detect differences between the two categories of species.

4. Results

The early successional species have more extension growth ($P<0\cdot01$), with greater diameter than late successional ones (table 1). With longer growth periods and the consequent shorter dormancy period, the early successional species had more extension and radial growth rates compared to late successional species. Open-grown *Litsaea* had significantly higher values for different parameters ($P<0\cdot01$) compared to forest-grown individuals, though not as high as for early successional species.

Table 1. Mean (±SE) growth characteristics of early and late successional shrub species in north-east India.

	Early successional		Late successional		
	Melastoma Open-grown	*Mussaenda* Open-grown	*Litsaea* Open-grown	*Litsaea* Forest-grown	*Oxyspora* Forest-grown
Height (cm)	357·9±10·5	326·4±9·3	254·3±6·5	196·0±7·5	169·0±5·4
Diameter (cm) at 10 cm above ground level	3·8±0·3	3·1±0·2	2·5±0·2	1·8±0·1	1·7±0·1
Growth period (days)	280·0±14	234·0±11	195·0±7·2	158·0±6·0	153·0±8·0
Extension growth per year (cm)	65·8±5·4	53·3±3·3	39·6±2·7	27·0±1·8	18·0±1·5
Dormancy period (days)	86·0±7·0	132·0±9·0	171·0±10·0	209·0±13·0	215·0±10·0
Radial growth per year (cm)	0·9±0·06	0·8±0·05	0·6±0·03	0·3±0·02	0·3±0·02

The differences between extension growth rates of early versus late successional species are significant ($P < 0·01$) only for the first and second-order branches but not for the third-order branches (table 2). The difference between open-versus forest-grown *Litsaea* was significant ($P < 0·01$) for the first-order branches only.

For all the species cumulative extension growth was sharper up to July and levelled off subsequently. Peak growth rate for all the species occurred in June (figure 3) but with sharper peaking for late successional species compared to early

Table 2. Mean (± SE) extension (cm) of first-, second- and third-order branches of early and late successional shrub species in north-east India.

	Early successional		Late successional		
	Melastoma	*Mussaenda*	*Litsaea*		*Oxyspora*
Order of shoot	Open-grown	Open-grown	Open-grown	Forest-grown	Forest-grown
First-order	36·2 ± 1·8	29·9 ± 1·9	20·4 ± 1·6	16·2 ± 1·2	15·7 ± 0·6
Second-order	22·2 ± 1·4	16·3 ± 0·9	12·6 ± 0·6	11·5 ± 0·5	9·4 ± 0·4
Third-order	10·0 ± 0·7	9·5 ± 0·6	8·2 ± 0·5	8·0 ± 0·5	7·9 ± 0·2

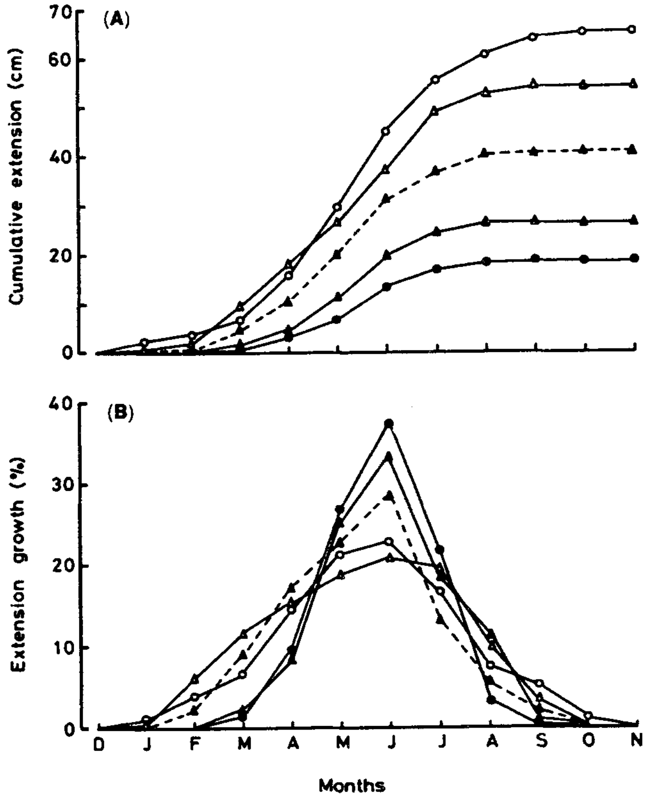

Figure 3. Cumulative extension growth (**A**) and monthly percentage (**B**) of the main axis of open-grown early successional *Melastoma malabathricum* (○) and *Mussaenda frondosa* (△), and forest-grown late successional *Litsaea khasiana* (▲) and *Oxyspora vagans* (●), in north-eastern India. Open-grown *Litsaea khasiana* is represented by broken lines.

successional ones. Early successional species had relatively more uniform growth rates in different months compared to late successional species. Later initiation and early termination of extension growth occurred in late successional species unlike the early successional ones. Open-grown *Litsaea* had significantly higher extension growth rates ($P < 0{\cdot}01$) compared to forest-grown individuals.

Radial growth rate followed a similar pattern as extension growth (hence data not presented), except that radial growth was generally initiated earlier and terminated later, than the extension growth.

Monthly branch production pattern (figure 4) was studied with respect to all the branch orders but that with respect to first- and second-order alone are presented, as the third-order branches had a similar pattern to second-order ones. First-order branch production for early successional species was more uniformly distributed without any distinct peaking, unlike late successional species which had a sharp peaking in June and a sharper decline on either side; branch production in late successional species was confined to a very short duration between April and July. On the other hand, second- and third-order branch production showed peaks

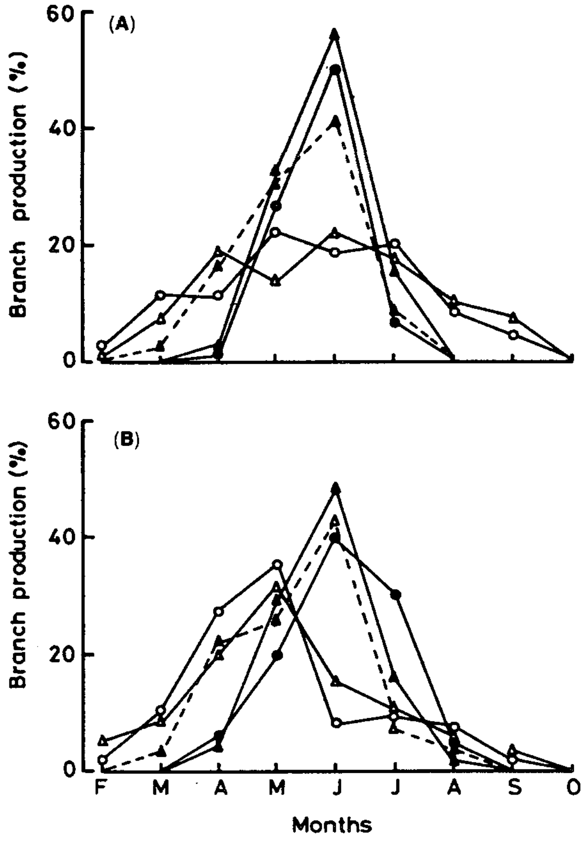

Figure 4. Monthly production (%) of first-order (A) and second-order (B) branches of open-grown early successional *Melastoma malabathricum* (○) and *Mussaenda frondosa* (△), and forest-grown late successional *Litsaea khasiana* (▲) and *Oxyspora vagans* (●). Broken line represents open-grown *Litsaea khasiana*.

for both early and late successional species with an early peak in May for early successional species and a delayed and sharper peaking in June for late successional ones.

Distances between two consecutive branches on the axis with respect to first-, second- and third-order branches (table 3) shows that the differences are significant ($P < 0{\cdot}05$) between open-grown early successional species and forest-grown late successional species. Open- and forest-grown *Litsaea* did not differ significantly ($P > 0{\cdot}05$) (table 1).

The branch angle of late successional species was generally more ($P < 0{\cdot}01$) than that of early successional ones (table 4). Further, branch angle increased significantly ($P < 0{\cdot}01$) at lower canopy positions, as compared with upper canopy positions, though this increase was less pronounced in higher order branches. Forest-grown individuals of *Litsaea* did not differ significantly ($P > 0{\cdot}05$) from the open-grown individuals.

First- and second-order branch production as a percentage of the total was markedly higher for late successional species compared to early successional ones, whereas the reverse was the case for third-order branch production (table 5). No significant differences ($P > 0{\cdot}05$) were observed between open- and forest-grown *Litsaea*.

The bifurcation ratio for early successional open-grown species (*Melastoma*, 5·7 ± 0·43; *Mussaenda*, 4·3 ± 0·36) was significantly higher ($P < 0{\cdot}05$) compared to late successional species (*Litsaea*-open-grown 3·7 ± 0·29; *Litsaea*-forest-grown, 2·9 ± 0·14; *Oxyspora*-forest-grown, 2·7 ± 0·23). Open-grown *Litsaea* had higher values ($P < 0{\cdot}05$) compared to forest-grown individuals.

Table 3. Mean (±SE) inter branch length (cm) of the first-, second- and third-order branches of early and late successional shrubs in north-east India.

	Early successional		Late successional		
	Melastoma Open-grown	*Mussaenda* Open-grown	*Litsaea* Open-grown	Forest-grown	*Oxyspora* Forest-grown
First-order	3·8 ± 0·2	4·2 ± 0·5	5·4 ± 0·4	6·2 ± 0·2	6·6 ± 0·6
Second-order	2·6 ± 0·3	3·3 ± 0·3	4·2 ± 0·4	5·8 ± 0·3	6·2 ± 0·3
Third-order	1·9 ± 0·1	2·1 ± 0·1	2·4 ± 0·1	2·7 ± 0·2	2·6 ± 0·2

Table 4. Mean (±SE) branch angle of early and late successional shrub species of north-east India.

		Early successional		Late successional		
Order of shoot	Canopy position	*Melastoma* Open-grown	*Mussaenda* Forest-grown	*Litsaea* Open-grown	Forest-grown	*Oxyspora* Forest-grown
First-order	Upper	36·2 ± 2·8	41·6 ± 3·3	43·6 ± 3·3	45·6 ± 3·6	44·5 ± 2·9
	Lower	60·5 ± 3·6	65·4 ± 4·5	75·6 ± 4·3	83·5 ± 5·2	72·2 ± 4·2
Second-order	Upper	31·4 ± 1·9	36·4 ± 2·8	39·1 ± 3·5	40·7 ± 4·0	42·4 ± 2·6
	Lower	40·3 ± 2·4	45·3 ± 4·0	53·2 ± 4·4	58·6 ± 4·7	50·5 ± 3·3
Third-order	Upper	29·8 ± 2·6	34·8 ± 2·9	35·6 ± 2·9	36·6 ± 3·2	38·2 ± 2·3
	Lower	35·6 ± 3·3	42·2 ± 3·2	42·9 ± 3·8	43·5 ± 2·7	45·4 ± 3·5

Table 5. Number of branches (expressed as % of the total) of different categories of early and late successional shrub species (mean ± SE).

	Early successional		Late successional		
Order of shoot	*Melastoma*	*Mussaenda*	*Litsaea*		*Oxysporus*
	Open-grown	Open-grown	Open-grown	Forest-grown	Forest-grown
First-order	4·2(11·83)	5·0(12·92)	14·3(22·22)	15·9(23·50)	15·9(23·50)
	652 ± 14	419 ± 12	163 ± 10	82 ± 6	63 ± 5
Second-order	29·5(32·90)	32·5(34·76)	67·6(55·30)	64·5(53·43)	56·5(48·73)
	2908 ± 150	1483 ± 65	479 ± 57	230 ± 15	132 ± 9
Third-order	66·5(54·63)	62·6(52·30)	18·2(25·25)	19·8(26·42)	28·3(32·14)
	2970 ± 190	1672 ± 92	83 ± 7	49 ± 4	63 ± 5

Numbers in parentheses indicate total length (cm) of different branches.

5. Discussion

5.1 *Architecture*

Of the 4 species under consideration here, *Melastoma*, *Mussaenda* and *Oxyspora* confirm to Koriba's model, but with significant departures from the typical. In *Melastoma* flowering is initiated in the terminal axis that is about to abort. Further, flowering does not occur in branches that are less than 1-year old. This is a marked departure from the other two species where flowering occurred later in the growing season. While resembling Rauh's model in many features, *Litsaea* is significantly different from it becauseof its sympodial growth which it shares with Koriba's model. Further, *Litsaea khasiana* considered here does not conform to Massart's model either, to which Halle *et al* (1978) refer another species of this genus, viz., *Litsaea sebifera*. Thus, it becomes evident that the classification of models of Halle based on qualitative morphology can at best be considered only as a useful set of reference points with many intergrading forms; even ontogenetic change from one architectural model to another could occur during the life cycle of the same species (Halle and Ng 1981; Borchert and Tomlinson 1984).

5.2 *Growth pattern*

The faster extension growth of early successional shrubs as compared to late successional ones is due to longer growth period for this category and partly due to the higher growth rate being maintained over an extended period, with variation in the start and end of the growth period, a pattern unlike that in late successional shrubs. Whilst these observations agree with those made for tropical tree species (Shukla and Ramakrishnan 1986), they contrast with those of temperate species where the date of bud break is relatively constant and growth cessation is usually more variable (Kramer 1943). Marks (1975) suggests that early successional species have a more oppertunistic indeterminate growth pattern allowing them to take advantage of a longer growing season. Apart from probable intrinsic factors, availability of light would seem to play an important role in bud break initiation, since open-grown *Litsaea* initiated growth a month earlier than forest-grown individuals.

Branch production and extension growth are concentrated in jhum in late successional species. This is due to favourable climatic conditions at that time of the year. The faster extension growth of early successional shrubs compared to late successional ones (Boojh and Ramakrishnan 1982a, b; Shukla and Ramakrishnan 1986) was significant up to second-order branches only. Further, the decline in the rate of extension growth of branch systems with increasing branch order was more marked in early successional species than in late successional ones. Such a differential trend in extension growth between early versus late successional shrubs may contribute to a multilayered leaf display in early successional shrubs of higher light regime and to a mono-layered peripheral leaf display in late successional shrubs growing in shade. The leaf population display was loosely organized and multilayered early successional shrubs. It could be further enhanced because of the larger proportions of third-order branches compared to first- and second-order branches, in contrast to a larger proportions of second- and first-order branch number of late successional species.

Fewer numbers of first- and second-order branches, which have a higher extension growth rate compared to third-order branches in early successional shrubs, would result in a narrow (excurrent) crown form in this category of species (Shukla and Ramakrishnan 1986). This crown form is advantageous in early succession because it allows them to gain the canopy. On the other hand, more numbers of first- and second-order branches as compared with third-order branches and a lesser decline in extension growth with increasing branch order in late successional shrubs would result in a broader (decurrent) crown form, thereby increasing leaf display under shade. Increased inter-branch length and branch angle at first- and second-order levels for late successional shrubs would further help in avoiding overlap of leaves (Pickett and Kempf 1980; Kempf and Pickett 1981) under reduced light environments. Thus, the overall geometry depends upon the orientation of branches and is an expression of its adaptive strategy (Honda and Fisher 1978) for optimizing photosynthesis through effective leaf display under a given light regime.

In agreement with the earlier observations that the early successional species should have a higher branching ratio in view of reduced forking of their axis (Whitney 1976) and in agreement with our earlier observations on tropical trees (Shukla and Ramakrishnan 1986), these early successional shrubs have a higher R_b and so too the open-grown *Litsaea* as compared with forest-grown individuals of the same species (Steingraeber *et al* 1979). A higher bifurcation ratio because of less forking of the axis would result in a multi-layered canopy in early successional shrubs, whereas more forking of the axis would enable organization of a denser peripheral arrangement of leaves (Horn 1971). However, the usefulness of this ratio for evaluating the adaptive strategy of species is suspect (Pickett and Kempf 1980; Borchert and Slade 1982; Boojh and Ramakrishnan 1982b) because this ratio does not follow a set pattern in all cases.

Conforming to our earlier conclusions with respect to adaptive strategies of early versus late successional trees (Boojh and Ramakrishnan 1982a; Shukla and Ramakrishnan 1986) the shrub species too show two distinct strategies over a successional gradient: an 'exploitative strategy' for capitalizing upon a higher light regime in an early successional environment and a 'conservative strategy' for survival under shade in a late successional environment, though with a slower growth rate. With light availability being more restricted for the early successionals at the shrub stratum and with deeper shade in the late successional forests, as compared with the tree stratum, the differences between the two categories of shrubs are more pronounced than for trees.

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