

GROWTH STRATEGY OF TREES RELATED TO SUCCESSIONAL STATUS I. ARCHITECTURE AND EXTENSION GROWTH

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ABSTRACT

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The architecture and growth pattern of early (*Alnus nepalensis* and *Schima khasiana*) and late (*Machilus kingii*, *Quercus dealbata* and *Q. griffithii*) successional tree species in a sub-tropical montane, humid, evergreen forest at Upper Shillong (1900 m) in north-east India were analyzed and related to their ecological strategy for niche occupancy in the forest ecosystem. In the early successional species the architectural development pattern and growth design are geared to maximize production under high light environments. These trees have an indeterminate pattern of shoot growth, a prolonged growth period with greater extension growth and rhythmicity (except for *A. nepalensis* with continuous growth) and branch mainly by syllepsis. These species emphasize vertical growth at the expense of lateral spread. In contrast, the late successional species make modest growth under a determinate scheme, the growth being confined to preformed bud primordia for a brief period of the growing season. There is less rhythmicity in growth and branch production is by prolepsis. These species emphasize lateral spread, as an adaptation to highly competitive environments. In forest situations these species have one determinate flush of shoot growth only but in open situations there were two such flushes. Bifurcation ratio values are found to vary in forest and open situations, suggesting the capacity of the species to adjust their architecture to changed light conditions.

INTRODUCTION

Much of our knowledge of the growth characteristics of tree species is based on their north temperate representatives (Kozlowski, 1964). Only recently has there been an attempt to understand the architecture and growth patterns of tropical and sub-tropical trees (Hallé et al., 1978). The ecological approach to studies on canopy structure and its relationship to light interception (Horn, 1971) and extension growth characteristics related to successional status of north temperate deciduous trees (Marks, 1975; P.S. Ramakrishnan, F.H. Bormann and T.G. Siccama, unpublished results, 1978) has resulted in a better understanding of growth strategies of developing forest communities. The present study considers growth strategies of trees from

these view-points. Such an approach is not only important for a better understanding of the production strategies of individual species and the community as a whole (Ramakrishnan, 1978) but could also contribute towards more rational forestry management (Stern and Roche, 1974).

The present study was done in a sub-tropical montane, humid, evergreen forest located at Upper Shillong ($25^{\circ} 34' \text{ N}$ and $91^{\circ} 56' \text{ E}$, altitude 1900 m) in the Khasi hills of Meghalaya in north-eastern India. The forest community is characterized by sub-tropical elements like *Schima khasiana*, *Machilus kingii*, *Manglitia insignis*, *Eugenia terragona* and *Ficus nemoralis*, along with a number of temperate species like *Quercus dealbata*, *Q. griffithii*, *Alnus nepalensis*, *Rhododendron arboreum* and *Betula alnoides*. For the present study two early (*A. nepalensis* Don. and *S. khasiana* Dyer) and three late (*Machilus kingii* Hook. F., *Q. dealbata* Hook F. & Thoms. and *Q. griffithii* (Hook. F. & Thoms.) successional tree species have been considered. The architecture and growth patterns of these two categories of trees are compared and related to their niche occupancy in the forest.

CLIMATE

The climate is monsoonal and the year may be divided into four more or less well marked seasons: (1) the monsoon season of heavy rains during May–September when over 80% of the total average annual rainfall (2350 mm) occurs; (2) a transitional period of low rainfall due to the retreating monsoons during October–November; (3) a winter season during December–February with scattered showers; and (4) a short, windy, dry summer period during

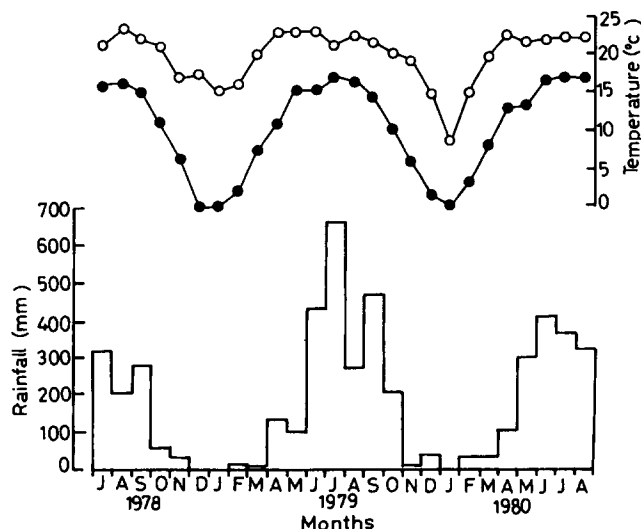


Fig. 1. Ombrothermic diagram for the study site. Open circles, mean maximum temperature; closed circles, mean minimum temperature; bars, monthly rainfall.

March–April. The average maximum and minimum temperatures were 22–16°C for the monsoon season and 16–2°C during the winter (Fig. 1).

METHODS

Five-year-old trees of both the early and late successional species were identified at the study site. While the early successional species were studied under open situations only, as they do not grow in shade, the late successional species were studied both from open and forest situations. The detailed architectural analysis of trees was made by tagging buds and shoots and observing them at monthly intervals using a wooden platform erected around the tree to reach the top of the canopy. During the active growth period, however, the observations were made daily/weekly with a view to understanding the changes in finer architectural patterns. The branches were ordered according to Hallé et al. (1978) using ordinal numbers, considering the trunk of the tree as the starting point, order zero, and the branches as first, second and third orders, respectively, in chronological sequence. The patterns of branch development was studied by following the fate of buds on the current increment of the main leader and one-year-old first order branches. Extension growth of the main axis and individual branches, and radial growth of the main axis at breast height (1.20 m) were measured at monthly intervals. Branch angle was measured using a protractor and plumb bob and was expressed as degree orientation from the main trunk. Leaf display angle, i.e., deviation from the horizontal, was also measured using a protractor equipped with a plumb bob. The protractor was aligned with the midrib of the leaf and the angle was read. All measurements were made on randomly chosen sample branches. All observations are based on five replicates of trees.

For calculation of the bifurcation ratio alone the branches were classified according to their position in the crown using Horton's (1945) method as modified by Strahler (1957). The terminal branches are designated as first order. The juncture of two first order branches defines a segment of second order; the juncture of two second order branches makes a third order branch and so on through the system. The meeting point of branches of two unequal orders does not affect the classification of either. The bifurcation ratio (R_b) is calculated by Motomura's (1947) formula: $R_b = (N - N_{\max}) / (N - N_1)$, where N is the total number of the 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 (Steingraeber et al., 1979). The results are based on ten replicates. For branch angle and bifurcation ratio studies, a few forest-grown trees of *S. khasiana* which were mostly stump sprouts were also considered.

RESULTS

General growth pattern

For a precise description of the early and late successional tree species

under consideration, the determinate/indeterminate terminology used for temperate trees is adopted here, along with the broad categorization under rhythmic/continuous growth used by Hallé et al. (1978) with special reference to tropical tree species. Early successional species can be grouped under indeterminate type. In *S. khasiana* after a period of dormancy (from October to March) a flush of preformed new pink coloured leaves appear but growth is continued through neoformation during the growing season. The tree has characteristics of rhythmic growth expressed in rhythmic branches (in well separated tiers) and periodicity of internodal elongation and leaf area expansion (Fig. 2b). *A. nepalensis* showed continuous growth. In this species the growing terminal meristem consistently had a single leaf associated with a stipule and a branch primordium enclosed by the mature stipule of the unexpanded leaf to form a distinct bud which on expansion would simultaneously produce a leaf and a branch. In the unfavourable winter period growth is arrested.

The late successional species follow a determinate pattern of shoot growth where leaf and internode primordia are wholly preformed in the overwintering bud. However, plants growing under more favourable conditions in the open produce another flush of determinate shoots (lamina growth) from the dormant bud laid down during the quiescence period. This pattern can be placed under rhythmic growth as discussed by Hallé et al. (1978).

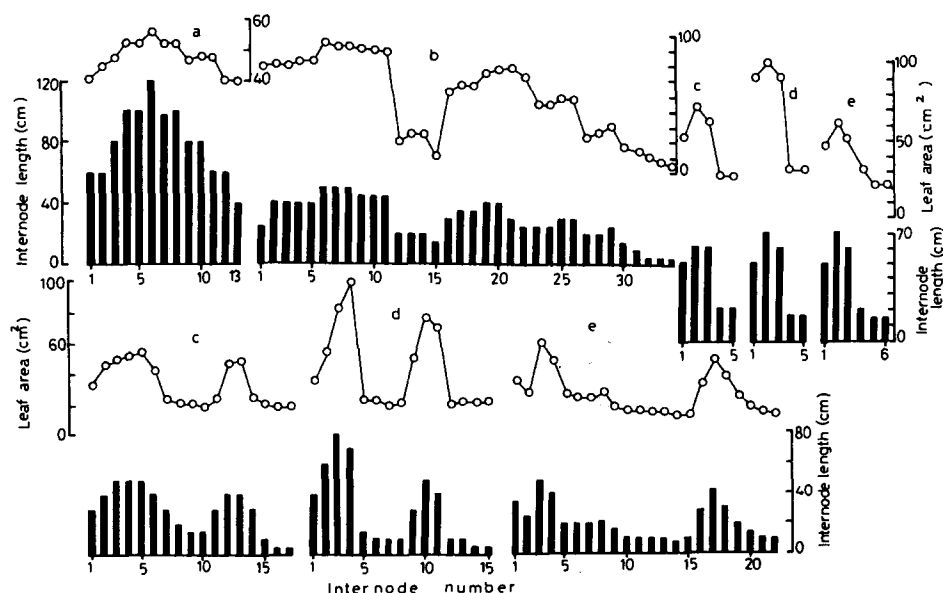


Fig. 2. Annual growth rhythms in internodal elongation (bars) and leaf area changes (open circles) on the leader axis of: (a) *A. nepalensis*; (b) *S. khasiana*; (c) *Q. dealbata*; (d) *Q. griffithii*; and (e) *M. kingii*. Inset figure is for forest grown individuals.

Architectural development

The architectural development pattern of *A. nepalensis* (Fig. 3a) follows Attim's model (Hallé et al., 1978). In this species the continuous activity of the formative meristem results in a continuous branching pattern which becomes intermittent during the winter due to suppression. This helps in determining the age of the tree. The continuous activity of the meristem is expressed in the more or less constant bud composition and little variation in leaf shapes and sizes along the axis. However, the growth rate is not uniform as is clear from the rhythmicity of internode length and leaf area pattern on the main axis (Fig. 2a) as well as the temporary suspension of growth during the winter. Branches are produced through syllepsis (Hallé et al., 1978). They are inherently orthotropic with spiral phyllotaxy and radial symmetry, but may subsequently become horizontal, with leaves arranged in one plane through twisting of the petioles (secondary orientation). The inherent orthotropy of such a branch is revealed in damaged trees where the leader is readily replaced by an adjacent lateral which conforms to the original architecture.

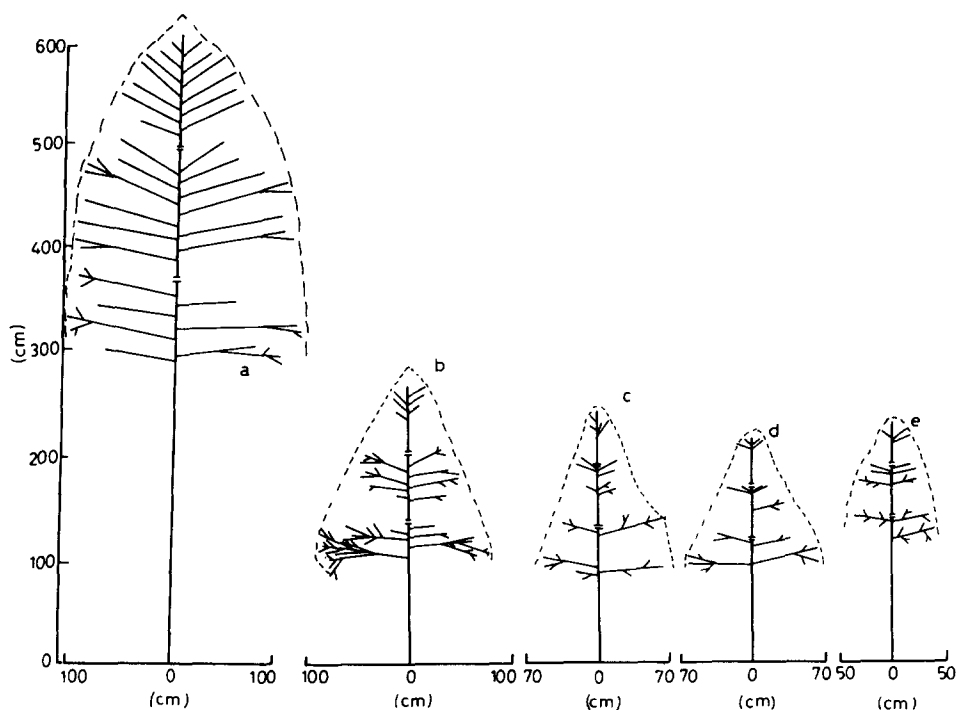


Fig. 3. Architectural skeleton and branching pattern in open grown trees of: (a) *A. nepalensis*; (b) *S. khasiana*; (c) *Q. dealbata*; (d) *Q. griffithii*; and (e) *M. kingii*. Demarcations on main axis represent the termination of annual growth delimited by the shortest internode of that growing season.

All the other species follow Rauh's model of architecture (Fig. 3b, c, d and e) as defined by Hallé et al. (1978). The early successional *S. khasiana* which follows this model showed more rhythms of internodal elongation and leaf area production than the late successional species (Fig. 2b, c, d and e). *S. khasiana* produces branches through syllepsis whereas all late successional species branch through prolepsis (Hallé et al., 1978). The rhythmicity in growth of the leader axis with branches in tiers helps to determine the age of these species.

Reiteration of the architectural model (Oldeman, 1974) occurs after damage to the aerial parts in all the species. In early successional species reiterated complexes generally show more vigorous growth with a prolonged growth period. In late successional species such reiterated complexes exhibit an indeterminate growth pattern instead of the typical determinate growth. In *A. nepalensis* reiteration always occurs through the substitution process, by a lateral branch adjacent to the damaged part. In all other species it may be achieved either through the activation of a dormant lateral meristem, substitution or coppicing.

Bud dynamics

Fig. 4 shows the dynamics of bud populations for both early and late successional species. On the main axis (Fig. 4A) early successional species, though sylleptic in nature, had some dormant buds. The proportion of dormant to non-dormant buds was very high in *S. khasiana* compared with *A. nepalensis*. In the next growth year some of these dormant buds died and the remaining ones formed the reserve bud banks; in *A. nepalensis* their number was fewer. In late successional species, though dormant buds

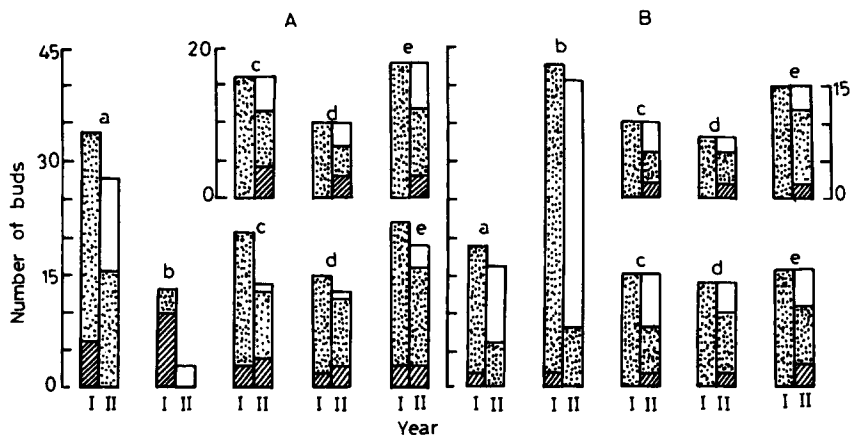


Fig. 4. Dynamics of axillary bud populations on the leader axis (A) and the first order shoot of the previous year (B) of: (a) *S. khasiana*; (b) *A. nepalensis*; (c) *Q. dealbata*; (d) *Q. griffithii*; and (e) *M. kingii*. Inset bar diagrams are for forest grown trees. Hatched bars, branched produced; stippled bars, dormant buds; open bars, dead buds.

TABLE I

Growth characteristics (\pm standard error) of early and late successional species; all measurements are based on five replicate individuals

Growth characteristics	Early successional		Late successional		<i>Q. griffithii</i>		<i>M. kingii</i>	
	<i>A. nepalensis</i>	<i>S. khasiana</i>	<i>Q. dealbata</i>					
	Open	Open	Open					
Dimensions of the experimental trees								
height (m)	5.05 ± 0.68	2.03 ± 0.39	1.96 ± 0.75	1.54 ± 0.90	1.74 ± 0.35	1.25 ± 0.60	1.85 ± 0.25	1.37 ± 0.26
dbh ^a (cm)	3.55 ± 0.35	1.28 ± 0.34	1.14 ± 0.29	0.73 ± 0.29	1.05 ± 0.29	0.68 ± 0.30	1.14 ± 0.30	0.74 ± 0.30
Growth period (days)	334.00 ± 10.50	190.00 ± 9.18	73.00 ± 1.88	35.00 ± 0.69	63.00 ± 2.00	30.00 ± 1.35	72.00 ± 4.63	33.00 ± 1.00
Dormancy period (days)	31.00 ± 10.50	175.00 ± 9.18	292.00 ± 1.88	330.00 ± 0.69	302.00 ± 1.99	335.00 ± 1.35	293.00 ± 4.63	332.00 ± 1.00
Extension growth per year (cm)	104.00 ± 6.50	64.00 ± 3.09	49.00 ± 2.50	21.00 ± 1.90	46.00 ± 1.60	21.00 ± 1.60	44.00 ± 2.30	23.00 ± 2.35
Radial growth per year (cm)	0.95 ± 0.09	0.57 ± 0.15	0.55 ± 0.06	0.27 ± 0.03	0.42 ± 0.05	0.25 ± 0.05	0.49 ± 1.12	0.20 ± 0.02
Total height to crown width ratio	3.12 ± 0.22	2.75 ± 0.12	1.71 ± 0.04	1.56 ± 0.06	1.98 ± 0.20	1.62 ± 0.02	1.78 ± 0.09	1.62 ± 0.02
Ratio of total height to height at lowest branch	2.56 ± 0.16	2.63 ± 0.24	4.32 ± 0.74	5.66 ± 0.22	3.61 ± 0.28	5.25 ± 0.23	3.02 ± 0.30	4.86 ± 0.36

^a Diameter at breast height (1.20 m in the present case).

generally produced branches in the next growth season only, under open grown situations some of them proliferated into lamma shoots due to a second flush in the same growing season. The pattern of branch production on the main axis was also repeated on the first order branches (Fig. 4B). However, because of syllepsis in the early successional species and prolepsis in the late successional species, the second order branching patterns are different.

Extension and radial growth

The important growth characteristics of early and late successional tree species are summarized in Table I. The former had a prolonged growth period, a shorter dormancy period, and more extension and radial growth than the latter. The tree height/crown width ratio was higher in early successional species, while the ratio of the total height to the height up to the lowest branch was higher for the late successional species.

Extension growth in *A. nepalensis* started in February and continued until December with one month of dormancy in January, whereas that in *S. khasiana* started in April and continued until September with dormancy for the rest of the year. Both species showed maximum extension growth in May. On the other hand, the open-grown late successional species all had two brief extension growth periods with dormancy in June–July, and

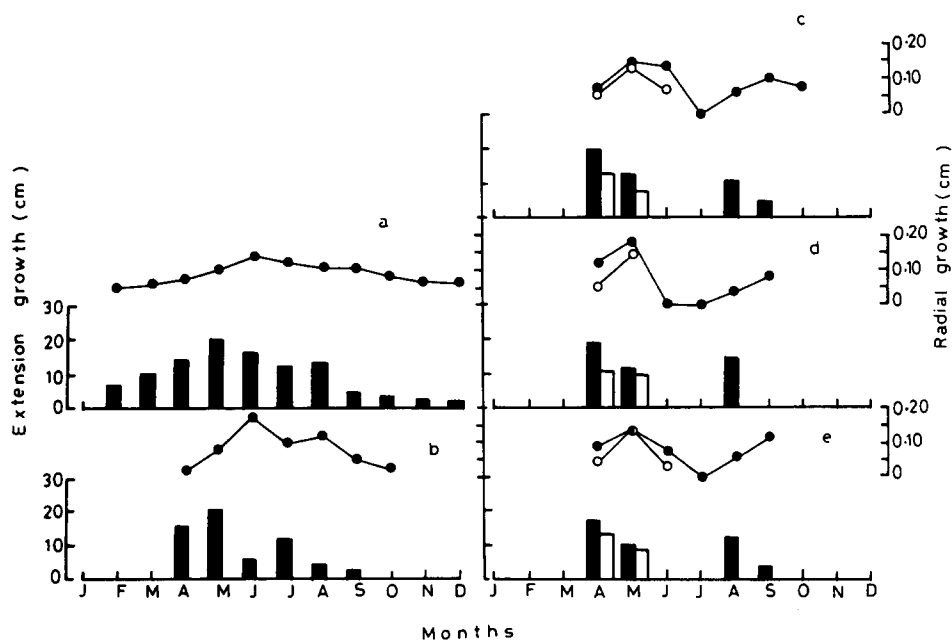


Fig. 5. Extension (bar diagram) and radial (open and closed circles) growth in: (a) *A. nepalensis*; (b) *S. khasiana*; (c) *Q. dealbata*; (d) *Q. griffithii*; and (e) *M. kingii*. Open bars and circles represent forest grown trees.

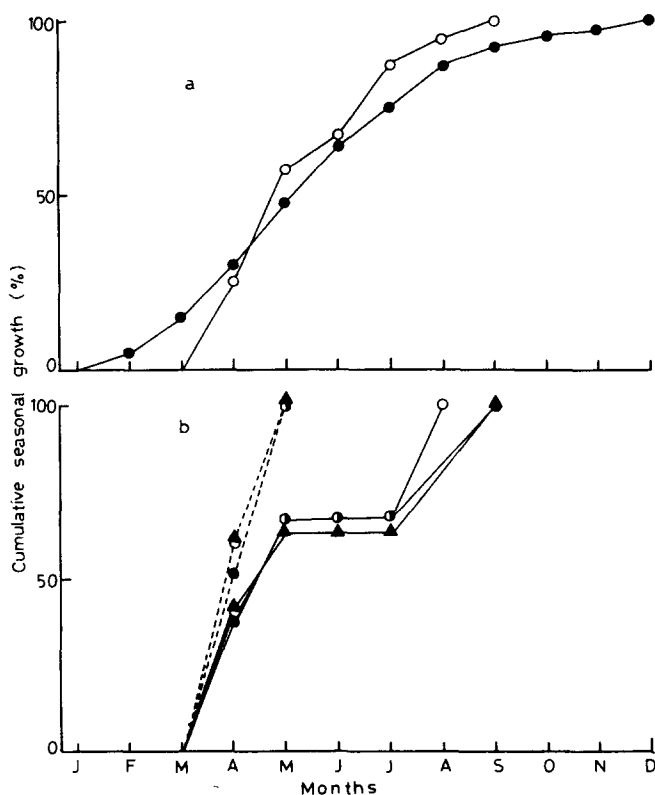


Fig. 6. Cumulative percentage of extension growth completed during the growing season at various dates: (a) early successional species: *A. nepalensis* (closed circles) and *S. khasiana* (open circles); (b) late successional species: *Q. dealbata* (closed circles), *Q. griffithii* (open circles) and *M. kingii* (closed triangles); dotted lines: forest grown trees.

October–March. Shade-grown late successional, however, had only one flush of extension growth (Fig. 5). More than 50% of the extension growth of early successional species was completed by May–June while that of open-grown late successional species was made in the first flush in April–May. Forest-grown late successional, however, complete 100% extension in one short flush only (Fig. 6). Monthly radial growth also showed a similar pattern to extension growth except that growth initiation as well as peaking was postponed by a month.

Table II presents the extension growth pattern at different positions on the trees of different species. Main leader extension was greater than that of the first order branches followed by second and third order branches. Extension growth was maximal in the terminal tier and declined progressively down the tree. In general, early successional species showed greater extension growth than did the late successional ones.

TABLE II

Variation in shoot extension (cm/year \pm standard error) on different positions of early and late successional tree species

	First tier ^a		Second tier		Third tier		
	Branch order ^b						
	0	1	1	2	1	2	3
Early successional							
<i>A. nepalensis</i>	104.0 ± 10.6	50.0 ± 5.7	33.6 ± 2.9	30.0 ± 3.8	15.3 ± 2.4	13.9 ± 3.1	12.5 ± 1.9
<i>S. khasiana</i>	64.0 ± 3.1	23.5 ± 1.6	16.2 ± 2.6	15.4 ± 1.7	13.7 ± 3.9	7.9 ± 1.1	15.3 ± 1.8
Late successional							
<i>Q. dealbata</i>	49.0 ± 3.5	16.2 ± 3.1	10.0 ± 3.5	9.2 ± 1.7	7.3 ± 2.7	4.2 ± 1.0	4.0 ± 1.0
<i>Q. griffithii</i>	46.0 ± 3.6	13.2 ± 2.4	10.0 ± 1.0	8.2 ± 4.3	9.2 ± 2.7	7.2 ± 1.4	7.1 ± 1.5
<i>M. kingii</i>	44.0 ± 3.3	18.5 ± 0.6	11.3 ± 2.0	6.4 ± 1.2	10.4 ± 1.5	5.1 ± 0.6	4.7 ± 2.2

^a A set of branches produced in one year constitutes a tier. The first tier consists of current year's branches, the second tier of the previous year's and so on down the system.

^b After Hallé et al. (1978), see text for explanation.

TABLE III

Orientation of branches (degrees) with respect to main axis (trunk) for early and late successional tree species; the results are the mean \pm standard error of 20 branches from each canopy positions of five replicate trees

	Open grown trees			Forest grown trees		
	Upper canopy	Middle canopy	Lower canopy	Upper canopy	Middle canopy	Lower canopy
Early successional						
<i>A. nepalensis</i>	52.2 ± 3.7	64.7 ± 2.4	79.1 ± 2.1	—	—	—
<i>S. khasiana</i>	46.4 ± 1.4	58.6 ± 2.1	87.1 ± 1.5	34.3 ± 2.0	56.4 ± 3.2	59.4 ± 2.7
Late successional						
<i>Q. dealbata</i>	60.0 ± 3.2	77.0 ± 2.3	84.0 ± 2.7	78.0 ± 2.2	87.5 ± 0.9	89.3 ± 2.4
<i>Q. griffithii</i>	58.4 ± 3.0	73.8 ± 1.4	81.7 ± 3.3	62.2 ± 3.0	78.9 ± 4.4	92.7 ± 3.0
<i>M. kingii</i>	57.7 ± 3.2	72.2 ± 2.1	84.0 ± 1.9	67.6 ± 1.7	79.2 ± 2.1	88.8 ± 1.0

TABLE IV

Leaf display angles (\pm standard error) with respect to horizontal for early and late successional tree species (values in parentheses are for forest grown situations); the results are based on 100 leaves from each canopy position for both sun and shade leaves on five replicate trees

	Peripheral (sun) leaves			Inner crown (shade) leaves		
	Upper canopy	Middle canopy	Lower canopy	Upper canopy	Middle canopy	Lower canopy
Early successional						
<i>A. nepalensis</i>	62.2 \pm 1.9	27.3 \pm 2.0	10.7 \pm 1.5	7.2 \pm 1.6	4.6 \pm 0.8	3.5 \pm 0.6
<i>S. khasiana</i>	75.0 \pm 1.3	61.5 \pm 2.5	50.0 \pm 2.0	31.8 \pm 1.5	27.0 \pm 4.3	17.5 \pm 3.2
Late successional						
<i>Q. dealbata</i>	52.3 \pm 2.4 (40.8 \pm 2.2)	47.3 \pm 1.3 (39.5 \pm 1.6)	43.5 \pm 1.9 (35.1 \pm 1.9)	37.1 \pm 2.2 (35.0 \pm 1.2)	30.9 \pm 1.4 (27.3 \pm 1.1)	28.6 \pm 1.6 (16.8 \pm 1.1)
<i>Q. griffithii</i>	50.9 \pm 2.9 (44.1 \pm 1.1)	43.7 \pm 3.5 (39.0 \pm 1.0)	47.7 \pm 2.0 (30.3 \pm 0.9)	30.6 \pm 1.3 (26.1 \pm 2.8)	24.1 \pm 0.8 (22.2 \pm 1.5)	14.6 \pm 0.9 (12.5 \pm 0.9)
<i>M. kingii</i>	49.7 \pm 3.5 (39.5 \pm 1.4)	43.3 \pm 1.5 (33.6 \pm 0.9)	31.3 \pm 1.7 (29.2 \pm 1.1)	44.1 \pm 1.2 (29.7 \pm 1.1)	24.4 \pm 1.0 (23.1 \pm 0.7)	19.1 \pm 1.2 (14.5 \pm 1.0)

Branch and leaf orientation

Branch angles increased from the top to the base of the canopy for both early and late successional species, but with the branches more acutely placed for the former than for the latter at all canopy positions. Branch angles of forest-grown trees of *S. khasiana* were very acute whereas the late successional species had more horizontal branches in forest than in open situations (Table III).

At all canopy levels, the peripherally placed leaves were more acute than the inner crown leaves. Further, in open conditions, the early successional species had more acutely placed leaves than the late successional species. However, in *A. nepalensis* the large megaphylls (except for upper canopy peripheral leaves) were placed near to horizontal and in one plane due to secondary orientation. Generally, the leaves of forest-grown individuals were placed more horizontally than those of open-grown ones (Table IV).

Bifurcation ratio

The bifurcation ratio values were much higher for *A. nepalensis* than for all the other species under open conditions. Open-grown trees of *S. khasiana* and the late successional species had a significantly higher ratio than did forest-grown ones. Besides, open-grown early successional had a higher R_b value than did forest-grown late successional species (Table V).

TABLE V

Bifurcation ratio values (\pm standard error) for early and late successional trees

	Open grown			Forest grown	
	Mean	Range	t-value	Mean	Range
Early successional					
<i>A. nepalensis</i>	6.18 ± 0.20	5.50–7.41	—	—	—
<i>S. khasiana</i>	3.91 ± 0.14	3.38–4.75	4.06**	3.24 ± 0.09	3.00–3.59
Late successional					
<i>Q. dealbata</i>	4.72 ± 0.22	3.75–5.45	7.27**	2.91 ± 0.12	2.35–3.64
<i>Q. griffithii</i>	4.62 ± 0.49	3.64–7.00	2.77*	3.62 ± 0.14	3.20–4.67
<i>M. kingii</i>	4.02 ± 0.34	3.50–4.40	5.84**	3.23 ± 0.08	2.93–3.71

**Significant at 1% and *significant at 5% level of significance.

DISCUSSION

The patterns of growth and architectural development of early and late successional species are well suited to their strategy of niche occupancy in the forest ecosystem. The shade-intolerant early successional species, chiefly through an indeterminate pattern of growth and leaf production, achieve more extension growth than the late successional ones, which are determinate and have a brief growth period. Such a strategy helps the former to gain in height and exploit a high light regime in the forest. However, the two determinate flushes in the open-grown late successional tress and only one in the forest-grown trees are indicative of their ability to adjust their growth strategy, at least to some degree, depending upon light availability. Thus, though the late successional species are adapted to grow under low light regimes where resources are often limiting, they also have the ability to adjust their growth pattern favourably under open situations such as openings in the forest canopy.

Attim's architectural model, of which *A. nepalensis* is an example, is particularly geared to achieve fast and efficient growth through continued activity of the apical meristems. Ideally, meristematic activity should be continuous; this species has a brief dormancy period of about a month during winter, which, however, is often not obvious. The early successional *S. khasiana* and all the late successional species follow the same architectural model (Rauh's), but with quantitative differences in growth as expressed in the rhythmicity in extension which was less in late successional species. Early successional species produce branches sylleptically and the late successional branch by prolepsis. It is suggested that the switch from a 'lower' state which determines prolepsis of a lateral meristem to another 'higher' state which determines syllepsis is conditioned by a 'threshold' which in turn is determined by the growth vigour of the parent shoot (Tomlinson and Gill, 1973). Such a sylleptic branch production in early successional species, it seems, is intended to make quick growth under fast diminishing light resources in a developing community as also reported in *Schima wallichii* (R. Boojh and P.S. Ramakrishnan, unpublished results, 1982). The growth of a hypopodium in sylleptic branches is presumably a mechanism by which the leaves are put outside the shade created by the leaves of the parent shoot (Wheat, 1980).

The reiteration which helps the tree to adjust its architecture to environmental modifications and disturbances may be advantageous for early successional species which may adjust to changing light environments. Each wave of reiteration in these species enables the tree to activate dormant meristems to grow more vigorously. Likewise, for late successional species, this process may often be triggered in response to canopy openings. Thus, reiteration allows the tree to exploit the changes in the environmental energy level. The trees utilize the larger quantity of incoming energy which results from environmental changes or disturbances by increasing the numbers or sizes of the producing organs. Branching and reiteration in the tree crown are ex-

amples of this process. Thus, branching within the model is a standard solution to the bio-energetic relationship, whereas reiteration allows for ecological opportunism (Hallé et al., 1978).

Bud dynamics, which takes into account the number and longevity of meristems, their positions, time and potential of development leads directly to the dynamic concept of architecture (Hallé et al., 1978) and allows plant growth to be interpreted in terms of an organized flux of constructional units. While in the early successional species proliferation from the axillary buds occurs synchronously with terminal bud growth, late successional species proliferate after a dormant period for the bud, and the activity depends upon the resources of the environment. Thus, the branches proliferate continuously in *A. nepalensis* due to continuous meristem activity, while in *S. khasiana* branching is rhythmic due to rhythmic activity of the terminal leader. This allows the two early successional species to deploy an extensive branching system through syllepsis by utilizing the current year's energy. The lesser number of reserve buds and their high mortality or inability to proliferate in the following year also suggests that all resources are directed exclusively toward the current year's growth and branch production. The late successional species in open situations are able to make some bud proliferation during the current year through lamma shoot formation in the second flush; shade-grown trees, however, produce branches in the next year only. This may be due to the limiting light conditions that exist in late successional environments.

The early successional species, though they make about 50% of their annual extension growth in the beginning of the growing season by April–May, continue growth almost all through the favourable growth season. This pattern allows them to use more effectively temporary conditions of increased resource availability and reduced competition in early successional environments. The modest extension growth of the late successional species may be an adaptation to the relatively predictable and highly competitive environments of closed forests. Radial growth started and terminated later than the extension growth for all the species, and similar results are reported for many temperate trees (Kozlowski, 1971) and also for some tropical trees (Chowdhury, 1957).

Differential elongation of different axes usually determines the form of woody plants. The excurrent crown form which was more pronounced in early successional species is achieved through stronger correlative growth inhibition with apical control over the growth of the branches beneath (Brown et al., 1967) than is found in late successional species. The aspect of stem architecture documented by various ratios between stem and crown shows that early successional species tend to maintain a higher, narrower crown than the late successional which have lower, wider and deeper crowns. The former species tend to emphasize height growth in order to attain a superior competitive position. Late successional species, on the other hand, have more lateral crown growth. Hence, early successional are able to exploit

a high light regime while late successional species are able to put out a larger leaf surface area to exploit low light intensity.

The orientation of branches and leaves in space and time usually shapes the geometry of the tree crown and this has been related to its adaptive strategy for light interception (Horn, 1971; Brunig, 1976; Honda and Fisher, 1978). The increase in branch angles down the tree along the vertical gradient of sunlight results in a greater increase in the gap between the two first order branch complexes. The highly acute branch angles of early successional *S. khasiana* under forested situations show its inability to tolerate shade, while the reverse situation for late successional species under forest situations increases the spread of the crown to provide the maximum possible effective leaf surface area. The leaf display angles in the late successional species are nearer to horizontal for both sun and shade leaves than in the early successional species which have the sun leaves placed vertically and shade leaves placed near horizontal. Such a light interception strategy, as also reported by Pickett and Kempf (1980), enhances photosynthesis of leaves of late successional species and shade leaves of early successional ones under limited light conditions and promotes cooling of the sun leaves during high solar radiation (McMillan and McClendon, 1979).

Open-grown early successional species had a higher bifurcation ratio compared to forest-grown late successional species. Thus, while the former tend to produce long, unbranched stems which lead to the more open, more layered canopies (multilayer of Horn, 1971), the latter produce frequently forked leaf supports which lead to a more regular arrangement of leaves (monolayer) and this is consistent with the findings of Whitney (1976). The lower bifurcation ratio of forest-grown trees compared to open-grown ones supports the view of Steingraeber et al. (1979) and Pickett and Kempf (1980), that this ratio could vary with changes in light environments, suggesting that the trees have a plasticity with respect to leaf displacement and light interception depending upon stand structure.

Thus early successional species with rapid and prolonged growth follow an exploitive strategy in the fast changing environments where they grow, whereas the late successional species with determinate growth and consequent predictable shading of leaves and with more lateral crown growth are adapted to a conservative strategy in late successional environments (Bormann and Likens, 1979).

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REFERENCES

- Bormann, F.H. and Likens, G.E., 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, Berlin/New-York, 253 pp.
- Brown, C.C., McAlpine, R.G. and Kormanick, P.P., 1967. Apical dominance and form in woody plants: a reappraisal. *Am. J. Bot.*, 54: 153–162.
- Brunig, E.F., 1976. Tree forms in relation to environmental conditions: an ecological viewpoint. In: M.G.R. Cannell and F.T. Last (Editors), *Tree Physiology and Yield Improvement*. Academic Press, New York, NY, pp. 139–156.
- Chowdhury, K.A., 1957. Extension and radial growth in tropical perennial plants. *Mod. Develop. Plant Physiol., Proc. Delhi Univ. Semin.*, 1957, pp. 138–139.
- Hallé, F., Oldeman, R.A.A. and Tomlinson, P.B., 1978. *Tropical Trees and Forests: An Architectural Analysis*. Springer-Verlag, Berlin, 441 pp.
- Honda, H. and Fisher, J.B., 1978. Tree branch angle — maximizing effective leaf area. *Science*, 199: 888–890.
- Horn, H.S., 1971. *The Adaptive Geometry of Trees*. Princeton University Press, NJ, 144 pp.
- Horton, R.E., 1945. Erosional development of streams and their drainage basins: hydro-physical approach to quantitative morphology. *Bull. Geol. Soc. Am.*, 56: 275–370.
- Kozłowski, T.T., 1964. Shoot growth in woody plants. *Bot. Rev.*, 30: 335–392.
- Kozłowski, T.T., 1971. *Growth and Development of Trees. Vol. I, Seed Germination, Ontogeny and Shoot Growth*. Academic Press, New York, NY, 444 pp.
- Marks, P.L., 1975. On the relation between extension growth and successional status of deciduous trees of the north-eastern United States. *Bull. Torrey Bot. Club.*, 102: 172–177.
- McMillan, G.G. and McClendon, J.H., 1979. Leaf angle: an adaptive feature of sun and shade leaves. *Bot. Gaz.*, 140: 437–442.
- Motomura, I., 1947. Further notes on the law of geometric progression of the population density in animal association. *Physiol. Ecol.*, 1: 55–60.
- Oldeman, R.A.A., 1974. *L'Architecture de la Forêt Guyanaise*. Mémoires Forêt Orstom, 73, Paris.
- Pickett, S.T.A. and Kempf, J.S., 1980. Branching pattern in forest shrubs and understorey trees in relation to habitat. *New Phytol.*, 86: 219–228.
- Ramakrishnan, P.S., 1978. Observations on biological aspects of productivity of forest ecosystems. In: J.S. Singh and B. Gopal (Editors), *Glimpses of Ecology (Professor R. Misra Commemoration Volume)*. International Scientific Publications, Jaipur, India, pp. 194–199.
- Steingraeber, D.A., Kascht, L.J. and Franck, D.H., 1979. Variation of shoot morphology and bifurcation ratio in sugar maple (*Acer saccharum*) saplings. *Am. J. Bot.*, 66: 441–445.
- Stern, K. and Roche, L., 1974. *Genetics of Forest Ecosystems*. Chapman & Hall, London, 330 pp.
- Strahler, A.M., 1957. Quantitative analysis of watershed geomorphology. *Trans. Am. Geophys. Union*, 38: 913–920.
- Tomlinson, P.B. and Gill, A.M., 1973. Growth habits of tropical trees: Some guiding principles. In: B.J. Meggers, E.S. Ayensu and W.D. Duckworth (Editors), *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Institution Press, Washington, DC, pp. 129–143.
- Wheat, D., 1980. Sylleptic branching in *Myrsine floridana* (Myrsinaceae). *Am. J. Bot.*, 67: 490–499.
- Whitney, G.G., 1976. The bifurcation ratio as an indicator of adaptive strategy in woody plant species. *Bull. Torrey Bot. Club*, 103: 67–72.