

Growth and Architecture of two Altitudinal Populations of *Schima wallichii*

RAM BOOJH and P S RAMAKRISHNAN

Department of Botany, School of Life Sciences, North-Eastern Hill University,
Shillong 793014

(Received 20 April 1982)

Growth and architecture of two altitudinal populations of *Schima wallichii*, from lower (100 m) and higher (1600 m) altitudes in Meghalaya, north-eastern India were comparatively analysed. Both the populations conform to Rauh's model of architecture. Branch production which is normally through syllepsis was correlated with the rhythmic vigour of the populations. At higher altitude annual production of a single set of branches corresponded with a single peak of vigorous extension growth and two sets of branches at lower altitude were just the other facet of two similar peaks of extension. Lower altitude population showed more extension growth, longer growth period and lesser dormancy period compared to high altitude population. The turnover rate of leaves was faster at lower altitude compared to higher altitude.

Key Words: Tree growth pattern, Tree architecture, Tree adaptation, Leaf dynamics

Introduction

Earlier works on tropical tree growth were mostly general observations of major phenological events in many species (Holtum 1940, Koriba 1958), though in more recent years some intensive studies on shoot growth of tropical trees have been attempted (Hallé & Martin 1968, Gill & Tomlinson 1971). The work on architecture of tropical trees by Hallé and Oldeman (1970) and Hallé et al. (1978), though comprehensive is more of a qualitative nature. A few isolated studies on growth and architecture of tropical trees from an ecological viewpoint have also been done (Fisher 1978, Borchert & Slade 1981, Boojh & Ramakrishnan 1982 a, b).

Schima wallichii (DC) Korth (family Ternstroemiaceae) is a light demanding early

successional timber tree species in the north-eastern hill areas of India where it has a wide altitudinal range of distribution from 100-1600 m. This species comes up in the secondary successional fallows after slash and burn agriculture (*Jhum*, Ramakrishnan et al. 1981) through light wind-dispersed seeds. This species is also distributed throughout the Indo-Malayan region. In Jawa it is not a real pioneer but specializes in poor ruined soils far away from the rainforest (Hallé pers. comm.). Whitmore (1975) observed it locally colonizing man-made clearings in lowland and lower montane forests of Malaya.

The present study deals with a comparative morphometric and ecologic analysis of the growth pattern and architecture of *S. wallichii* from two altitudinal situations at Shillong

(25°34' N and 91°56' E, altitude 1600 m) and Burnihat (26°02' N and 91°52' E, altitude 100 m) in the Khasi Hills of Meghalaya in north-eastern India.

Climate

The climate at both the study sites is typically monsoonic. The year may be divided into four more or less well marked seasons; (i) the monsoon season of heavy rain during May to September due to the southwest monsoon; (ii) a transitional period of low rainfall due to the retreating monsoons during October to November; (iii) a winter season during December to February with scattered low rainfall; and (iv) a windy dry summer during March to April. The average annual rainfall during the study period was 1800mm at Shillong and 1550mm at Burnihat. The average maximum and minimum temperatures at Shillong during the monsoon were 24°C and 16°C, while during winter period these were 16°C and 6°C respectively. The temperature conditions at Burnihat were warmer with maximum and minimum temperatures of 32°C and 24°C during the monsoon and 25°C and 12°C during the winter (figure 1).

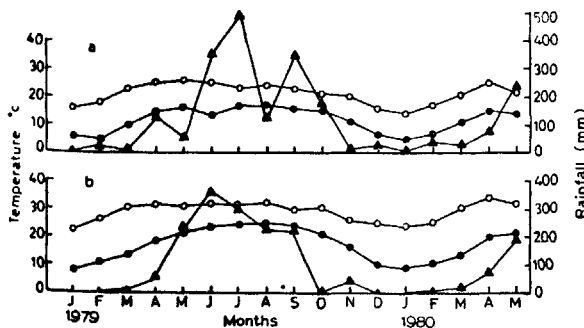


Figure 1 Ombrothermic diagram for the study sites at (a) Shillong and (b) Burnihat. (O), Mean maximum temperature; (●), Mean minimum temperature; and (▲), rainfall

Methods of Study

Five replicates of 5-year old trees were chosen randomly in forest openings at both the study sites. A stage was erected around the selected trees for making detailed observations on finer architectural changes. Measurements of extension growth pattern on the main leader and branches (5–10 branches for replicate tree) were made. The pattern of branch development was studied by marking the buds and shoots and following their fate on current increments of main leader and one-year old first order branches. The trees were divided into different sets of branches, one set per year at higher altitude and two sets per year at lower altitude representing the annual growth. Branch ordering was described using ordinal numbers, considering trunk of the tree as the starting point order zero and the branches of the first, second and third order respectively in chronological sequence (figure 2a) following Hallé et al. (1978). Architectural studies were based on a number of trees of different age classes available in the forest community.

Leaf census was made on each tree by tagging the previous leaves and constantly giving fresh tags to the newly recruited ones. Turnover rate (r) of leaves was calculated on the basis of a full year observation considering 30 day's month by recording birth and death rates. Leaf blade area was calculated by dividing the actual leaf area (planimeter-measured) of a sample of 100 leaves of each population by the calculated leaf area (length (L) \times width (W)). The leaf area (A) was subsequently calculated using the formula $A = CLW$, where C is a correction factor (Dolph 1977).

Leaf and branch angles were measured by a protractor. The most vertical aspect of individual leaf was measured as the degree inclination from the horizontal. Branch angles were measured as the orientation from the main trunk,

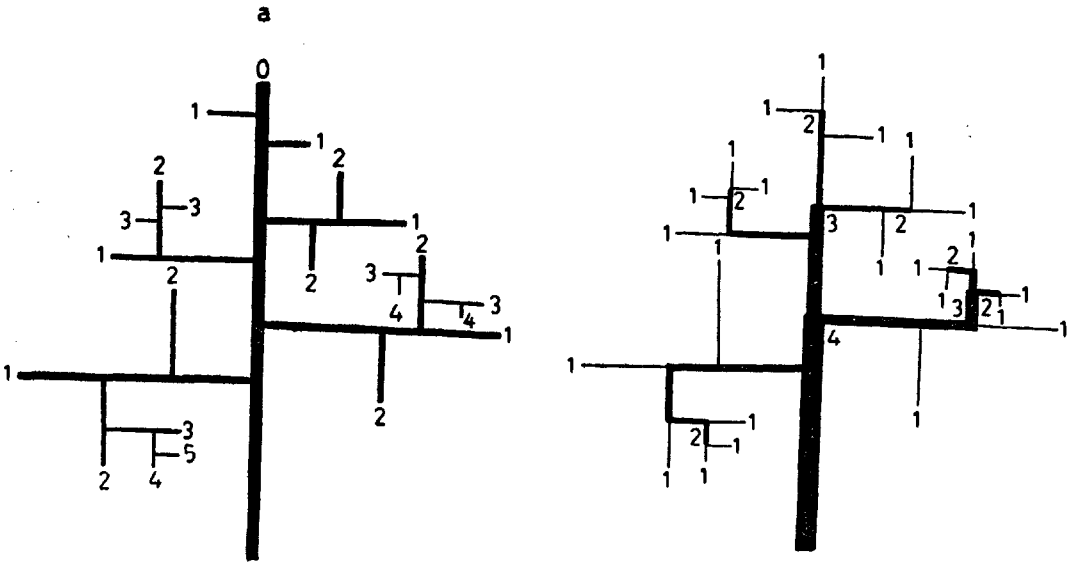


Figure 2 Diagrammatic representation of methods of branch ordering: a, ordering system of Halle et al; b, Strahler's ordering

For calculation of bifurcation ratio (*Rb*), branches were ordered according to Horton's (1945) rule, modified by Strahler (1957). In this method segments of branch system are ordered and a branching ratio was calculated which subsequently serves as an index of the degree of branching. Each ultimate branch is designated as the first order; at the meeting point of two first order branches the proximal segment is of the second order. A third order segment starts at the junction of two second order branches and so on down the system. Further, at the junction of branches of two unequal orders, the identity of the highest branch order is maintained. Thus the basal branch or trunk is of the highest order (figure 2 b). Bifurcation ratio was calculated by the formula :

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

where *N* is the total number of branches of all orders, *N_{max}* is the number of the branches of the highest order and *N₁* is the number of the branches of the first order

(Motomura 1947, Steingraeber et al. 1979). At each study site ten open growing and ten forest growing trees were ordered according to Strahler's method and the bifurcation ratio was calculated.

Results

Architecture and Growth Pattern

Architectural model

S. wallichii follows the Rauh's model of architecture (figure 3, Hallé et al. 1978). The growth in the species starts with the flushing of new leaves after winter dormancy when rapid unfolding as well as expansion of pink coloured leaves occur. The leader axis, a monopodial trunk, is orthotropic with radial symmetry and spiral phyllotaxy. The lateral branches are morphogenetically equivalent to the leader axis as these are also orthotropic, radially symmetric and with spiral phyllotaxy. Branches are produced through syllepsis (Hallé et al. 1978), though in the present case a few proleptic branches may also be produced. Sylleptic branches arise from the

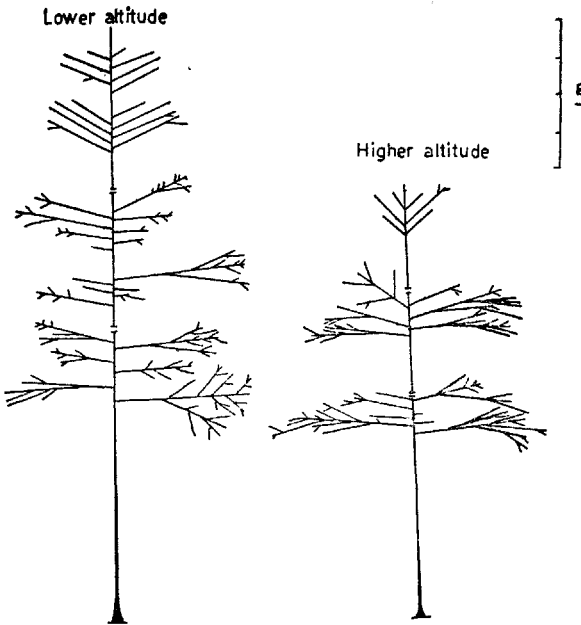


Figure 3 Architectural skeleton (Rauh's model) of *S. wallichii* drawn to the scale showing sets of branches in well separated tiers (demarcations on main axis represent the termination of annual growth delimited by the shortest internode of that growth year)

axillary buds without a dormant period and have an extended internode (hypododium). Development of these branches in *S. wallichii* is correlated with the rhythm of the main leader. At lower altitude, two sets of branches (7-8 branch per set) were produced corresponding to the two vigorous peaks of extension growth; while at higher altitude only one set of 5-6 branches was produced due to a single peak of extension. This conferred a tiered arrangement of laterals (rhythmic branching type of Hallé et al. 1978). Flowers being axillary did not affect the basic architecture of the tree.

In damaged trees resting buds were activated to proliferate into proleptic shoots (Hallé et al. 1978). In some cases a lateral branch adjacent to the damaged part started growing upward subsequently substituting as the main leader (Bayonet joint). In other

cases instead of one, two adjacent laterals substitute as equals making a forked trunk. In vigorous trees after damage to the trunk several stump sprouts arise. All these regenerative mechanisms did not affect the basic model of architecture (Rauh's model) but reiterated it. In mature trees several such reiterated complexes appear.

Extension growth

Table 1 summarizes some of the important growth characteristics of both the populations of *S. wallichii*. The height of the experimental trees was more at lower altitude than at higher altitude. The extension growth of the main leader was more at lower altitude while radial growth was more at higher altitude. Lower altitude population produced greater number of leaves and a larger leaf surface area than the higher altitude population.

The seasonal cumulative leader extension growth is shown in figure 4. There was a rapid extension growth during the early part of the season when more than 50% of extension growth was achieved. The growth continued up to November at higher altitude and up to December at lower altitude.

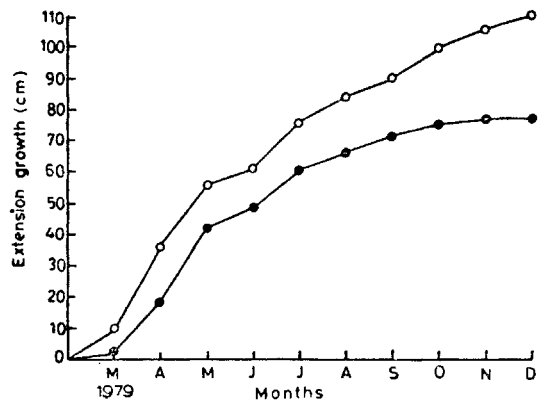


Figure 4 Seasonal pattern of cumulative extension growth in *S. wallichii* (O), Lower altitude population; (●), higher altitude population

Table 1 *Growth characteristics of Schima wallichii population from lower and higher altitudes*

Growth parameters	Lower altitude	Higher altitude
1. Dimensions of the experimental trees		
(a) Height (cm)	293	219
(b) diameter at 1.20 m. (cm)	1.80	1.94
2. Date of growth initiation	March 1	March 20
3. Date of onset of dormancy	December 25	November 25
5. Growth period (days)	300	250
5. Dormancy period (days)	65	115
6. Extension growth/yr (cm)	110	77
7. Radial growth/yr (cm)	0.63	0.79
8. Average internode number on main leader/yr	56	37
9. Average length of internodes/yr (cm)	1.96	2.08
10. No. of leaves produced/yr	1536	1029
11. Annual cumulative leaf area production ($10^3 \times \text{cm}^2$)	63	48

Extension growth of the leader as well as branches was greater for the lower altitude population compared to the higher altitude one. Both the populations showed strong correlative growth inhibition. Thus the main axis showed more extension than the branches which showed a sequence of first order > second order > third order and so on. Also the elongation of the current year's (terminal set) branches was maximum and decreased progressively down the system in the second, third and fourth year sets of branches (table 2).

Bud Dynamics

Figure 5 shows the dynamics of bud populations on the main axis and the one year old first order branches. On the main axis some of the axillary buds produced branches as soon as they were formed (syllipsis) in the same growth year, but a large number of them subsequently remained dormant forming reserve bud bank. To this extent it differs from the typical Rauh's model. At lower elevations branches proliferated twice; once in April and again in July (7-8 branches

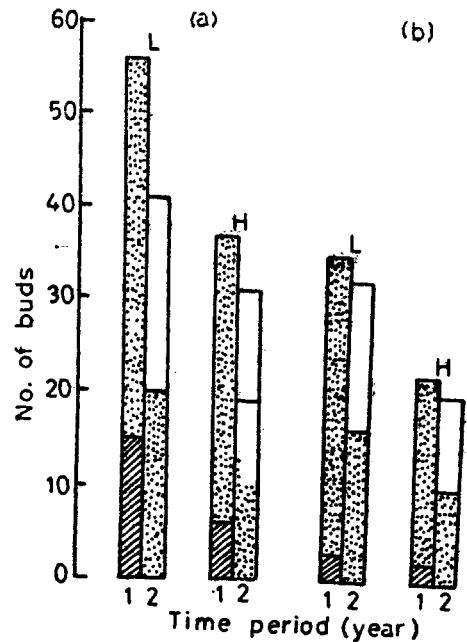


Figure 5 Dynamics of axillary bud populations on main axis (a) and one year old first order branches (b) of *S. wallichii* at lower altitude (L) and higher altitude (H). 1=buds present in first growing season and 2=their fate in the next growing season. (■), dormant buds; (▨), branches produced; and (□) buds died

Table 2 Pattern of shoot extension (cm/yr \pm S.E.) on different locations of *Schima wallichii* populations

Tier** of branches	First Order*				Second Order				Third Order				Fourth Order			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Lower altitude	32.0 \pm 3.9	15.9 \pm 4.3	10.4 \pm 4.0	1.5 \pm 1.5	15.3 \pm 3.6	12.3 \pm 1.4	10.0 \pm 0.8	1.4 \pm 0.6	10.6 \pm 2.3	10.2 \pm 1.1	5.0 \pm 2.0	—	—	—	—	—
Higher altitude	24.4 \pm 3.5	17.0 \pm 2.7	11.0 \pm 5.3	6.0 \pm 0.8	10.0 \pm 0.0	14.2 \pm 1.9	10.7 \pm 1.5	6.7 \pm 1.6	13.5 \pm 0.9	10.2 \pm 1.3	5.0 \pm 1.1	4.5 \pm 1.1	—	—	—	—

*After Hallé et al. (1978)

**The 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

Table 3 Branch-angles (orientation from the main trunk) for *Schima wallichii*. The results are based on mean \pm S.E. of 20 branches from each canopy position of 5 replicate trees

	Open Grown Trees			Forest Grown Trees		
	Upper Canopy	Middle canopy	Lower canopy	Upper canopy	Middle canopy	Lower canopy
Lower altitude	56.33 ± 2.17	77.64 ± 1.79	80.30 ± 2.11	42.50 ± 3.18	60.50 ± 2.52	77.00 ± 3.18
Higher altitude	55.00 ± 2.44	70.00 ± 3.42	79.87 ± 2.50	45.00 ± 2.67	66.00 ± 3.06	72.50 ± 3.41

Table 4. Leaf angles (inclinations from horizontal) (\pm S.E.) in *Schima wallichii* at lower and higher altitudes. Results are based on a sample of 100 leaves from both sun and shade positions on each canopy levels of 5 replicate trees

	Sun Leaves			Shade Leaves		
	Upper canopy	Middle canopy	Lower canopy	Upper canopy	Middle canopy	Lower canopy
Lower altitude	85.00 ± 1.30	72.50 ± 3.22	71.50 ± 2.79	60.50 ± 2.88	55.10 ± 3.43	50.50 ± 2.84
Higher altitude	69.50 ± 1.53	62.92 ± 3.23	58.00 ± 2.81	49.50 ± 3.42	44.83 ± 3.19	40.77 ± 2.24

Table 5 Bifurcation ratio (*Rb*) values (\pm S.E.) for *Schima wallichii* populations.

	Open grown trees		Forest grown trees	
	Mean \pm S.E.	Range	Mean \pm S.E.	Range
Lower altitude	3.99 \pm 0.49	3.31 \pm 4.76	3.44 \pm 0.19	3.00 \pm 4.14
Higher altitude	3.85 \pm 0.20	3.00 \pm 4.20	3.40 \pm 0.14	3.00 \pm 3.95

each time) while at higher elevation branches were produced only once in the month of May (4–6 branches). This pattern of branch development was followed on the laterals too.

Branch and Leaf Orientation

The branch angles of open and forest grown trees are compared in table 3 which showed that the branches were more acutely placed in forest grown situations at all the canopy positions compared to those in the open grown trees. In general, branch angles increased from top to the base of the canopy along a vertical gradient.

Leaf display angles for both the populations were observed to be more acute in sun positions and was less so in the shade. This was more markedly seen for the low altitude population (table 4).

Bifurcation Ratio

The bifurcation ratio values given (table 5) for open and forest grown trees of the two populations suggest that the values under open grown situations though higher compared to the forest grown situations were not significantly different ($p > 0.05$). Further, there was no significant difference ($p > 0.05$) between the populations from the two altitudes.

Leaf Dynamics

Figure 6 shows the seasonal pattern of population flux of leaves for both the populations of *S. wallichii*, with time and the cumulative gains and losses that determine them. The low altitude population showed a more pronounced flux compared to the higher altitude one. The gain in leaf population was very sharp during early part of the growing season for both the populations, extending up to November at higher altitude and December at lower altitude. The losses became pronounced after October–November for both the populations, rate being faster at lower than at higher altitude. The net population size at lower altitude was maximum in September and at higher altitude it was maximum in October. Net population of leaves was always higher ($p < 0.01$) at lower altitude up to November compared to that at higher altitude, but afterwards it started to decline due to faster losses.

Considering the cohort of leaves produced in 1979, leaf area production reached its peak in September–October for both the populations with maximum values attained at lower altitude. In the subsequent months leaf area started decreasing sharply due to leaf fall and all the leaves of that cohort were shed by February in case of low altitude population and by March–April in the case of high altitude population (figure 7).

Figure 6 Flux of leaf populations in *S. wallichii* at lower (solid lines) and higher (broken lines) altitudes. (O) cumulative gains; (●), cumulative losses; and (▲) net population size

Figure 7 Leaf area dynamics (monthly pattern of change in total leaf area) for *S. wallichii* at lower (O) and higher (●) altitudes

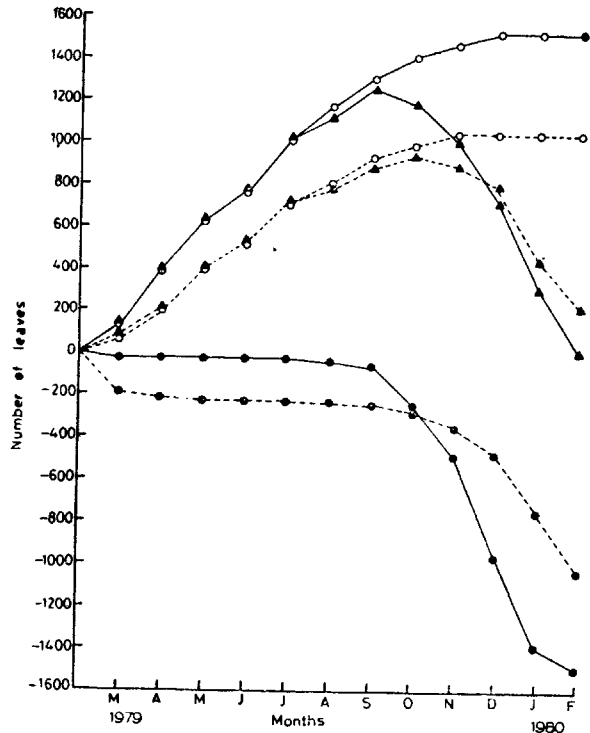


Fig. 6

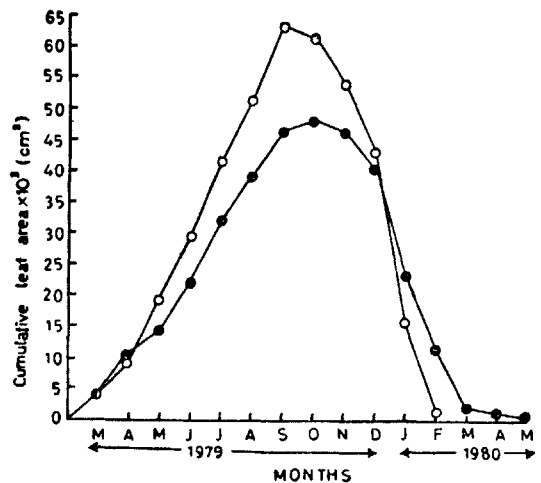


Fig. 7

Table 6 Seasonal pattern of turnover rate (r) of leaves of *Schima wallichii* at lower and higher elevations

Months	Birth rate		Death rate		Turnover rate	
	Lower altitude	Higher altitude	Lower altitude	Higher altitude	Lower altitude	Higher altitude
1979						
March	4.2	2.2	0.7	6.3	3.5	-4.1
April	8.8	4.5	0	0.7	8.8	3.8
May	7.7	7.2	0	0.3	7.7	6.9
June	4.8	3.8	0	0	4.8	3.8
July	8.2	6.2	0	0	8.2	6.2
August	4.4	3.7	0.3	0.2	4.1	3.5
September	5.2	3.5	1.0	0.5	4.2	3.0
October	3.5	2.0	5.9	1.2	-2.4	0.8
November	2.8	1.2	8.3	2.2	-5.5	-1.0
December	1.5	0	11.5	4.2	-10.0	-4.2
1980						
January	0	0	13.9	10.9	-13.9	-10.9
February	0	0	9.7	7.5	-9.7	-7.5

Table 6 shows the seasonal pattern of birth, death and turnover rates of leaves. At lower altitude both the birth and death rates were higher. Consequently the turnover rate of leaves was more rapid at lower altitude compared to at that higher altitude.

Discussion

The architectural models of trees are based on morphological expression of growth which can be basically similar for the same species under different environmental situations or for different species of varied ecological status in the community, but there may be quantitative and developmental differences in growth expression. In the present case, the quantitative differences in growth were expressed in greater extension, longer growth period and more branch and leaf production for lower altitude population compared to the higher altitude population of

S. wallichii. This could be attributed to the duration of favourable growth period which was more at lower altitude. Intrinsic factors have also been implicated for such differential growth expressions (Kozłowski 1971, Kramer & Kozłowski 1979), but this is a possibility due to population differences which needs to be further investigated.

The correlation of rhythmicity in branch production and growth vigour of the parent shoot as was documented in the present case, has also been reported by others (Champagnat 1965, Borchert & Slade 1981). Branch production through syllepsis also suggests a high vigour of the trees. Tomlinson and Gill (1973) have proposed that the switch from a lower state of prolepsis to a higher state of syllepsis is conditioned by a threshold which in turn is determined by the growth vigour of the parent shoot. Thus, at lower altitude *S. wallichii* due to a higher growth vigour

deploys an extensive branch system and at higher altitude it has less vigour and therefore with lesser branch production. Hallé (pers. comm.) has reported branch production through prolepsis in the Indonesian population of this species. This is a case of intraspecific variation and may be due to its adaptation to nutrient poor ruined soils and sub-optimal growth conditions. The growth of a longer internode (hypopodium) in sylleptic branches may be a mechanism helping extension of branch to avoid shade created by the parent shoot (Wheat 1980).

The entire growth pattern in the species is regulated by the apical meristem which may grow repeating the same pattern throughout its life. But in case of a damage to it reiteration (Oldeman 1974) of the initial architecture model occurs. In *S. wallichii* due to the morphogenetic equivalence of the axes reiteration is readily achieved without affecting the original architecture. The mode of development may differ only when a dormant bud proliferates through prolepsis. Each wave of reiteration helps the adjustment of tree architecture to environmental changes and increases chances of survival for the species.

The geometry of tree crown is maintained through the differential elongation as well as orientation of branches in space and time and this has been related to the adaptation for light interception (Horn 1971, Brunig 1976, Honda & Fisher 1978). The relative growth processes which determine differential branch extension depend on the growth vigour of populations, being more pronounced at lower altitude, than at higher altitude. The progressive increase in branch angle down the tree as in the present case may be in response to its adjustment to space and may be caused due to increased branch weight and active bending caused by reaction wood.

The differential display of sun and shade leaves as seen from the present study have

also been reported by others and such a light interception strategy is meant to enhance photosynthesis of shade leaves under limited light conditions and to promote leaf cooling during high solar radiation in sun leaves (McMillan & McClendon 1979).

The bifurcation ratio values are not significantly different between open and forest grown trees of *S. wallichii*. This supports the views of Oohata and Shidei (1971) and Whitney (1976) who concluded that these values approach a species specific constant and are indicative of the adaptive geometry of trees. However, more extensive studies of ours, on this aspect have shown that bifurcation ratio is quite variable depending upon the species and environment and therefore it cannot be used as a reliable criterion for ecological generalizations (Boojh & Ramakrishnan 1982a, c). Similarly, Steingraeber et al. (1979), Pickett and Kempf (1980) and Borchert and Slade (1981) also have observed the variable nature of bifurcation ratios.

The dynamics of leaf populations show that the gain and loss as well as the resultant flux are faster for the lower altitude population compared to the higher altitude one. Also, the turnover rate was faster at lower altitude. This may to some extent be attributed to altitudinal differences especially temperature which affect leaf expansion (Longman & Jenik 1974, Mithorpe 1976). It may be noted that the faster growth of early successional species as the present one lies in their capacity for unrestricted leaf production rather than efficient energy conversion (Combe 1960, Combe & Hadfield 1962). The pattern of leaf change reported here suggests that the flushing in the species is a result of drought induced shedding of older leaves. Borchert (1980) has suggested that the timing of bud break will result from the interaction between the endogenous shoot growth periodicity and

the variations in the water status of the environment and observed that along an altitudinal gradient with increasing water stress *Erythrina poeppigiana* ranged from evergreen to deciduous habit. The shorter life span and the consequent faster turnover rate of leaves of the lower altitude population compared to the higher altitude one may be an adaptation of the former to capitalize upon the more favourable environmental conditions available for an extended time period at lower altitude. It may also be attributed partly to site dependent higher moisture stress at lower elevation where rainfall is lesser and evapotranspiration is higher.

The rate and duration of growth, period of active extension and leaf production as well as cessation of growth are of much importance to a tree's ability to survive competition in the forest (Longman & Jenik 1974) and also for the productivity of the

forest (Ramakrishnan 1978). The results presented here where an early successional tree with the capacity for rapid and prolonged growth, and ability to grow more at the lower altitude have practical implications in forestry programmes particularly forest management and agroforestry.

Acknowledgements

We are grateful to Professor Francis Hallé of the Institut Botanique, Montpellier, France; Professor Rolf Borchert of the University of Kansas, USA; and Dr Jack B Fisher of Fairchild Tropical Garden, Miami, USA, for their interest and appreciation of this work and for suggestions. This research was supported by a research grant of the Department of Science and Technology, Government of India, under its SERC programme. The assistance to one of us (RB) from CSIR, New Delhi during the preparation of this paper is also acknowledged.

References

- Boojh R and Ramakrishnan P S 1982a Growth strategy of trees related to successional status: I. Architecture and extension growth; *Forest Ecol. Manage.* (in Press)
- _____ and _____ 1982b Growth strategy of trees related to successional status: II. Leaf dynamics; *Forest Ecol. Manage.* (in Press)
- _____ and _____ 1982c On bifurcation ratio in *Schima* species; *Curr. Sci.* 51 436-437
- Borchert R 1980 Phenology and ecophysiology of tropical trees: *Erythrina poeppigiana* O. F. Cook; *Ecology* 61 1065-1074
- _____ and Slade NA 1981 Bifurcation ratios and the adaptive geometry of trees; *Bot. Gaz.* 142 394-401
- Bruning E F 1976 Tree forms in relation to environmental conditions: An ecological viewpoint; in *Tree Physiology and Yield Improvement* 139-156 eds M G R Canell and F T Last (New York: Academic Press)
- Champagnat P 1965 Physiologie de la croissance et de l'inhibition des bourgeons: dominance apicale et phenomenes analogues. Rameux courts et rameaux longs. Problems physiologiques; in *Encyclopedia of Plant Physiology* Vol. 15 pt 1 pp 1106-1177 (Berlin: Springer Verlag)
- Coombe D E 1960 An analysis of the growth of *Trema guineensis*; *J. Ecol.* 48 219-231
- _____ and Hadfield W 1962 An analysis of the growth of *Musanga cecropioides*; *J. Ecol.* 50 221-234
- Dolph G E 1977 The effect of different calculational techniques on the estimation of leaf area and the construction of leaf size distributions; *Bull. Torrey Bot. Club* 104 264-269
- Fisher J B 1978 A quantitative study of Terminalis branching; in *Tropical Trees as Living Systems* 285-320 eds P B Tomlinson and M H Zimmermann (Cambridge University Press)
- Gill A M and Tomlinson P B 1971 Studies on the growth of red mangrove (*Rhizophora mangle* L.) 3-Phenology of the shoot; *Biotropica* 3 109-124
- Hallé F and Martin R 1968 Studies on the growth rhythm in *Havea brasiliensis* (Euphorbiaceae-crotonoideae); *Adansonia* 8 407-503

- _____ and Oldeman R A A 1970 In, *An Essay on the Architecture and Dynamics of Growth of Tropical Trees* (English Translation by Stone B C in 1975 Penerbit University Malaya)
- _____, _____ and Tomlinson P B 1978 *Tropical Trees and Forests: An Architectural Analysis* (Berlin: Springer Verlag)
- Holttum R E 1940 Periodic leaf change, and flowering and fruiting of trees in Singapore; *Gdn. Bull. (Singapore)* 11 119-175
- Honda H and Fisher J B 1978 Tree branch angle-maximizing effective leaf area; *Science* 199 888-890
- Horn H S 1971 In *The Adaptive Geometry of Trees* (New Jersey : Princeton University Press)
- Horton R E 1945 Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology; *Bull. Geol. Soc. Am.* 56 275-370
- Koriba K 1958 On the periodicity of tree growth in the tropics with reference to the modes of branching, the leaf fall and the formation of the resting bud; *Gdn. Bull. Singapore* 17 11-81
- Kozlowski T T 1971 In *Growth and Development of Trees Vol. I Seed germination, Ontogeny and Shoot growth* (New York : Academic Press)
- Kramer P J and Kozlowski T T 1979 In *Physiology of Woody Plants* (New York : Academic Press)
- Longman K A and Jenik J 1974 In *Tropical Forests and its Environment* (London : Longman Group Ltd.)
- McMillan G G and McClendon J H 1979 Leaf angle: an adaptive feature of sun and shade leaves; *Bot. Gaz.* 140 437-442
- Milthorpe F L 1976 Quantitative aspects of leaf growth; in *Perspectives of Experimental Biology 1*, *Botany* 33-40 ed N Sunderland (Oxford: Pergamon Press)
- Motomura I 1947 Further notes on the law of geometrical progression of the population density in animal association; *Physiol. Ecol.* 1 55-60
- Oldeman R A A 1974 In *L' Architecture de la Forêt Guyanaise* (Paris: Mem. Orstom 73)
- Oohata S and Shidei T 1971 Studies on the branching structure of trees. 1. Bifurcation ratio of trees in Horton's law; *Jap. J. Ecol.* 21 7-14
- 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 the biological productivity of forest ecosystems; in *Glimpses of Ecology: Prof. R. Misra Comm. Vol.* 193-199 eds. J S Singh and B Gopal (Jaipur: Internat. Sci. Publ.)
- _____, Toky O P, Misra B K and Saxena K G 1981 Slash and burn agriculture in north eastern India; in *Fire Regimes and Ecosystem Properties* eds H A Mooney, T M Bonnicksen, N L Christensen, J E Lotan and W A Reiners (Washington DC: USDA Forest Service) General Technical Report; WO-26 570-586
- Steingraeber D A, Kascht L J and Franek D H 1979 Variation of shoot morphology and bifurcation ratio in sugar maple (*Acer sacharrum*) Saplings; *Am. J. Bot.* 66 441-445
- Strahler A M 1957 Quantitative analysis of watershed geomorphology; *Trans. Am. Geophys. Un* 38 913-920
- Tomlinson P B and Gill A M 1973 Growth habits of tropical trees; some guiding principles; in *Tropical Forest Ecosystems in Africa and South America: A Comparative Review* 129-143 eds B J Meggers, E S Ayensu and W D Duckworth (Washington D C : Smithsonian Institution Press)
- Wheat D 1980 Sylleptic branching in *Myrsine floridana* (Myrsinaceae); *Am. J. Bot.* 67 490-499
- Whitmore T C 1975 In *Tropical Rain forests of the Far East* (London : Oxford University Press)
- Whitney G G 1976 The bifurcation ratio as an indicator of adaptive strategy in woody plant species; *Bull. Torrey Bot. Club* 103 67-72