# GROWTH STRATEGIES OF TREES AND THEIR APPLICATION TO FOREST MANAGEMENT

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## ABSTRACT

Phenological characteristics as related to ecosystem function of two forest types at lower and higher elevations of Meghalaya have been considered. Germination and establishment pattern of selected early and late successional species have been related to their light requirements. Tree architecture, extension growth, radial growth and leaf dynamics of early and late successional species, both from low and high elevations have been studied. These studies suggest that the early successionals have an exploitive growth strategy while the late successionals are conservative in their approach. The growth pattern has been related to biomass production and allocation pattern of early and late successional species. Early successionals have surface feeding root system with lesser allocation to root compartment, whereas the late successionals have deep root system with more allocation to it. The allocation strategy of early successional species are geared to attain more growth in height and greater allocation to the bole. On the whole, the early successional species are more productive than late successional ones. The significance of the results for forest management is discussed.

## INTRODUCTION

With the depleting fossil fuel resources, the identification and exploitation of indigenous tree species for fuel and other energy requirements are urgently needed. With increasing population pressure, other requirements like timber are also increasing at a rapid rate. In the developing countries of the tropics and subtropics where this problem is more acute, the forests are being continuously exploited and destroyed causing serious environmental problems. According to official records the extent of forest cover in India is 75 million hectares, i.e., about 23% of the total geographical area. If one realizes that much of it is degraded vegetational types, then more than half of this forest area is not capable of ensuring ecological functions and economic usefulness.

Studies on the ecological adaptation and growth characteristics of trees are, therefore, important for the conservation and management of these forest ecosystems. Of several important aspects dealing with adaptive features of trees, the architectural pattern and growth co-ordination of trees form a basis for the differences in photosynthetic or production efficiency of these giant terrestrial producers. Though there has been a marked increase in our knowledge of the adaptive significance of various structures in trees, like branching patern[1,2], leaf shapes[3,4] and sizes[5] and whole tree architecture[6,7], there is still a strong need to find out the information regarding the reactions and adaptations of trees to varied environmental conditions and occupancy of successional niche.

Besides, an understanding of the establishment pattern of the seedlings under natural forests and the phenological adaptation of the forest community as a whole is also important from the point of view of understanding of the ecosystem function.

This account emphasizes the above aspects of the problem on the basis of extensive studies done by us in two forest types, a sub-tropical montane forest at higher elevation (alt. 1900 m) and a sub-tropical humid low elevation forest (290 m) in Meghalaya. This study tries to make a comparative analysis of a few early and late successional tree species on the basis of their growth and adaptational characteristics related to 'sun' and 'shade' tolerance, besides community adaptation as a whole. Such a study, it was felt, would be useful from the point of view of planning strategies for mixed/social forestry in the region using indigenous species and exploiting their ecological equipment for obtaining optimum production. It would also, hopefully, help in better management of existing forest resources.

## PHENOLOGY

Twenty six overstorey and forty understorey species of trees were considered for the study of high elevation forest. Leaf flushing in the majority of the tree species coincided with the warm period just prior to rains to maximize production during the more favourable period of the year. Maximum leaf fall occurred during the dry winter months and this strategy is considered to be an escape from stress conditions. Two flowering peaks observed corresponded to the relatively drier months of March–April or October of the warm season. The fruiting periodicity, though not much pronounced, had a peak during October–November. A majority of the species were with fleshy fruits suggesting an adaptation for animal dissemination. Total above-ground litter fall averaged 8.95 t/ha/yr, leaves, twigs, flowers and fruits contributing 63%, 16%, 3% and 6% respectively. The rate of litter fall in the drier part of the year (November to April) was approximately thrice the rate during the wetter season. Mean leaf-life was estimated to be an average of 20 months for the forest.

The lower elevation forest had a greater proportion of evergreen compared to deciduous species. These observations are based on 76 overstorey and 46 understorey species. Here too leaf fall coincided with the dry season. Flushing in the majority of the species started towards the end of the dry period after different degrees and periods of leaflessness. Leaf production in the overstorey species extended over a longer period of time compared to the understorey species. For most of the species, flowering coincided with leaflessness. Proportionately higher number of overstorey species flowered during the dry season but wet season flowering was more for understorey species relating probably to the micro-environmental differences at these two levels. A majority of the species produced fruits during wet season and the fruits were mostly fleshy. Fruits produced during the dry season were mostly of dry type and could be related to the seasonal differences in moisture availability.

Thus the biotic activity in the community follows the annual cycle of environmental parameters which regulate the phenological characteristics of individual species. In the forest community, the tree periodicity patterns give an idea of seasonal organization of floral and fruit resources[8] which have been viewed as a mechanism of niche separation whereby competition between species is reduced and temporal separation increases diversity of the community which may influence production and stability[9].

## SEED GERMINATION AND SEEDLING ESTABLISHMENT

Germination and establishment are two critical phases in the life-history of a species[10]. After its escape from predation and pathogens, the chance that a non-dormant surface-lying seed will develop into an established seedling, is dependent on its fixation in a safe site which provides the specific condition for its germination and establishment. Observations on seed germination of 12 important low elevation tree species of different successional status suggest that the germination percentage of early successional species was higher in the open at shallower depths in the soil. Mid- and late successional species responded little to the differences in these conditions. This was related to the light demanding nature of early successionals[11]. The survivorship of seedlings of early successionals at the end of rainy season was more adversely affected than that of mid- and late successional species. This was related to the generally lighter seeds of early

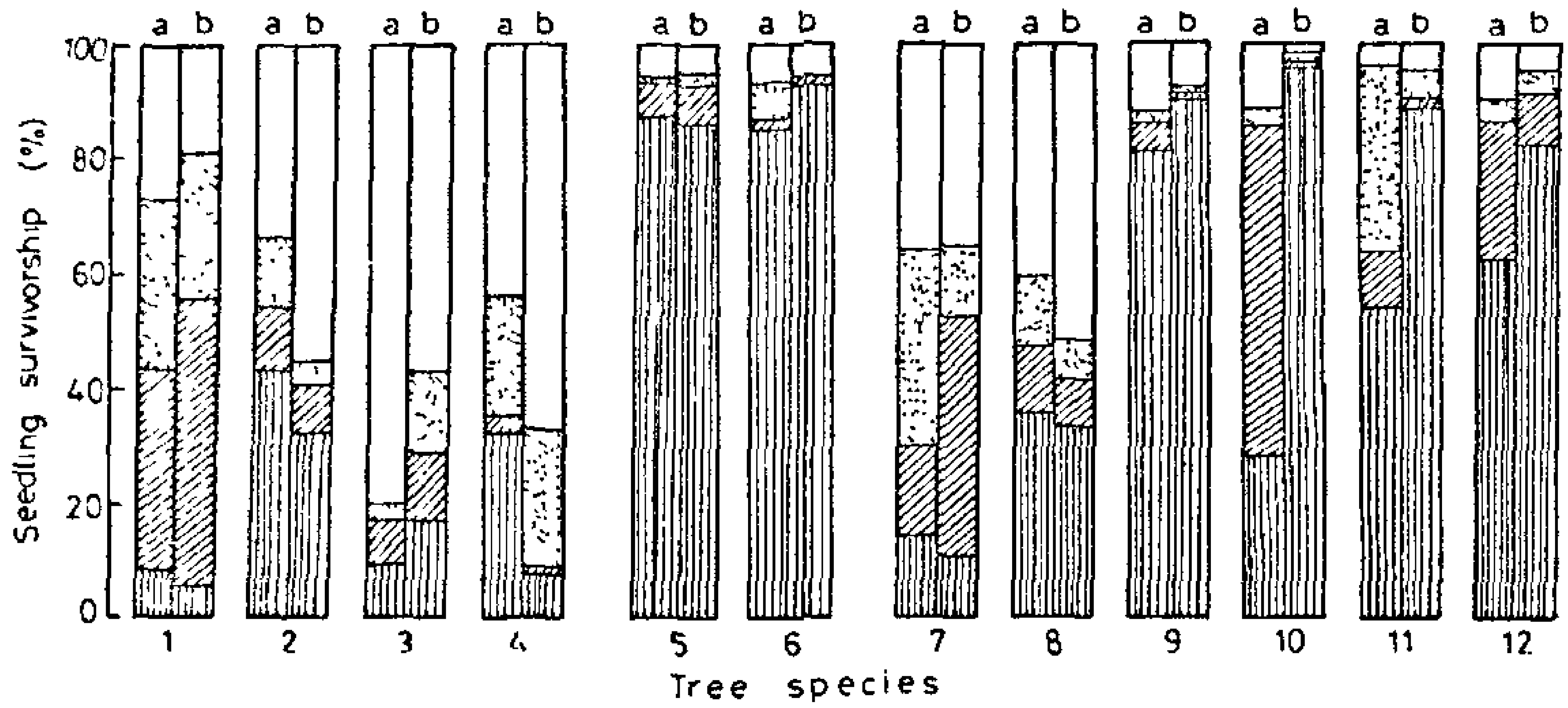


**Figure 1.** Mortality % of seedlings growing in the open (a) and under forest canopy (b) during rainy season (open column) winter season (stippled column) and drought (hatched column) with final establishment % (column with vertical lines) after one year in early successional (1–4), mid-successional (5–6) and late successional (7–12) species. 1, *Sterculia villosa*; 2, *Erythrina stricta*; 3, *Premna miliflora*; 4, *Lagerstroemia parviflora*; 5, *Bauhinia purpurea*; 6, *Amoora wallichii*; 7, *Dillenia pentagyna*; 8, *Artocarpus chaplasha*; 9, *Sterculia coccinea*; 10, *Pithecolobium longan*; 11, *Mesua ferrea*; 12, *Garcinia cowa*. (After Shukla and Ramakrishnan[25])

successionals. The higher seedling survival of late successional species in shade as compared with the open and the reverse behaviour of early successional species are related to their adaptation to different light regimes in the forest community (figure 1).

## GROWTH PATTERN CHARACTERISTICS OF TREES

Three early successional species namely *Alnus nepalensis*, *Schima khasiana* and *S. wallichii* and three late successional species namely *Machilus Kingii*, *Quercus dealbata* and *Q. griffithii* form the basis of this study at higher elevation forests. The growth characteristics of these species are contrasting (table 1). Thus, for the same age, the early successionals are taller than the late successionals. Further, the former have indeterminate growth strategy with sylleptic branching whereas the latter are all determinate in growth pattern with proleptic branching. It may be noted that the broad architectural model[7] does not appear to be related to the ecological niche characteristics of these tree species.

Early successional species generally showed a prolonged period of indeterminate growth, having shorter dormancy period, more extension and radial growth and leaf production than the late successional species. Early successionals do not restrict their growth to the contents of overwintering buds, rather they continue growing either rhythmically (*Schima* species) with periods of slower activity, or continuously (*Alnus nepalensis*) with more or less uniform growth throughout the growing season. Late successional species on the other hand, have determinate growth scheme where the growth is usually limited to winter bud contents. There is a rapid flush of shoot extension and leaf production for only a brief period of growing season, followed by a long dormant period. Though this is the basic determinate scheme, these species respond to light and other favourable environmental conditions by producing another flush of shoot growth in the month of July–August similar to the lamma's shoot of the temperate region[12]. The different stem-crown ratios tend to emphasize vertical growth in early successional species and lateral spread in late successional ones.

The study of growth pattern of two early successional (*Duabanga sonneratioides* and *Anthocephalus cadamba*) and two late successional (*Dillenia pentagyna* and *Artocarpus chaplasha*) species at lower elevation forests also showed marked differences. The extension and

TABLE 1

*Growth Characteristics of Early and Late Successional Tree Species (After Boojh and Ramakrishnan[23])*

| | Early Successional | | | Late Successional | | |
|---|---|---|---|---|---|---|
| | S. wallichii | S. khasiana | A. nepalensis | Q. dealbata | Q. griffithii | M. kingii |
| Growth period (Days) | 250 | 180 | 334 | 73 | 63 | 72 |
| Dormancy period (Days) | 115 | 185 | 31 | 292 | 302 | 293 |
| Extension growth/ Yr. (cm) | 77 | 64 | 104 | 49 | 46 | 44 |
| Diameter (Dbh)growth/ Yr. (cm) | 0.79 | 0.57 | 0.95 | 0.55 | 0.42 | 0.49 |
| Leaf production/ Yr. | 1029 | 1167 | 647 | 225 | 169 | 206 |
| Leaf area production/ Yr. ($cm^2$ $10^3$) | 48.00 | 41.00 | 43.17 | 8.81 | 10.51 | 6.18 |
| Total ht./crown width ratio | 2.51 | 2.75 | 3.12 | 1.71 | 1.98 | 1.78 |
| Total ht.: ht. to lowest branch | 2.16 | 2.63 | 2.56 | 4.32 | 3.61 | 3.02 |

radial growth of axes of early successional species were very rapid and more in comparison to those of the late successional ones. The sparse branch arrangement, facilitating leaf exposure to a greater degree and longer growth period of early successional species accounted for the faster growth. On the other hand, the late successional species showed shorter growth period and densely packed canopies with mutual shading of leaves which accounts for their slower growth rate. In the early successional species, the production and the contribution of I order branches to the total framework of branch complex was much higher than that in late successional species. Plasticity in orientation and overall display of branches in relation to light intensity was noted in these species.

It may be pointed out that the early successional species show exploitive strategy where the aim is to maximize vertical growth over a short period of time when light is not a limiting factor whereas late successional species have a conservative strategy where the aim is to make growth, though slowly, even under shaded situations and survive till such a time they are capable to make more rapid growth either through gap formation or after gradual emergence over the general canopy of the forest. Different workers have attributed different ecological characteristics of the early and the late successional species to varied physiological attributes. Thus, Coombe and Hadfield[13] have suggested that the fast growth rate of early successional tropical tree species is not due to higher photosynthetic rate but to unrestricted capacity of leaf production, and others[14,15] have shown differential LAI, leaf display angle and allocation patterns for early versus late successional temperate species, as also observed in the present study.

## TREE ARCHITECTURE

The architectural models of trees[7] are mainly based on morphological expression of growth though there are numerous ways in which growth may be expressed in tropical trees[16]. Thus, though both early and late successional species at higher elevation follow Rauh's model (monopodial trunk, rhythmic growth, arrangement of branches in tiers which are morphogenetically identical to trunk), the finer architectural development patterns suggest that in early successional species growth rhythms are much more in number than in the late successional species. Also, while the late successional species produce branches proleptically (after a rest period for lateral buds), early successional species produce them sylleptically (without a rest period for lateral bud, *i.e.*, *simultaneous with the* main axis). Branch production through syllepsis is exclusively a tropical phenomenon and is a mechanism to deploy an extensive branching system. The Attim's architecture model with continouous growth in *A. nepalensis* is understandable for an early successional species.

At lower elevations, however, the early successional species showed heterogeneous axes (trunk orthotropic and branches plagiotropic) and conform to Massart's model (*D. sonneratiodes*) or Roux's model (*A. cadamba*), the late successional species showed heterogeneous axes (all axes orthotropic) and conform to Scarrone's model (*D. pentagyna*) or Rauh's model (*A. chaplasha*) of tree architecture. The early successional species with their synchronous sylleptic I order branch production, seems to achieve quick growth and rapid extension of plagiotropic branches ensuring least overlapping of the leaves so that they are able to capitalize upon the resources before light becomes a limiting factor. Further the hypopodium of sylleptic branches helps extending the branch to avoid the shade offered by the leaves of parent shoot[17]. This growth pattern with heavy shoot tip abortion in the II order branches and in the I order ones of the lower canopy positions, helps in the development of an excurrent crown form. On the other hand, the production of proleptic I and II order branches in the late successional species, over a brief period of time with greater emphasis being placed on production and extension of II order branches, helps in developing broader tree crown, where the leaves are placed more peripherally, so that they are able to maximize photosynthesis under the shade of forest canopy.

*Branch and Leaf Display Characteristics*

The orientation of branches and leaves in space and time usually shape the geometry of the tree crown[1] and this has been related to its adaptation for light interception[18]. Branch angles generally increase from top to bottom of the canopy along a vertical gradient of tree crown for both early and late successional species. While the early succesionals show more acute placement of the branches under forest grown conditions in order to put their canopy as high as possible which is in keeping with their light demanding nature, the late successional species under similar situations show more horizontally oriented branches in order to maximize photosynthesis under low light regimes. The leaf display angles of early successional species, in general, are more acute than the same in the late successional ones where the orientation is closer to horizontal. This becomes more obvious when the shade leaves from the inner crown are considered.

*Bifurcation ratio (Rb)*

Bifurcation ratio has often been used as an index of branch organization and pattern of branching. According to Whitney[19] the early successional species should have a higher Rb value in view of the fact that the first order branches (Strahler's ordering) are vertically placed with less forking. This conclusion is not generally true for the high elevation species but is in agreement for the low elevation species. However, the lower bifurcation ratio of forest-grown individuals in comparison to that of open grown ones, is consistent with the contention of Steingraeber *et al*[20], that trees may show plastic response in forking of branches under different light conditions to arrange their leaves for maximum light interception.

*Leaf dynamics*

The demography of the leaf populations revealed fluxes that determine the net population size. For early successional species, the net population size was greater during the favourable growing season. Also, these show greater fluxes of births and deaths of leaf population than late successional species. Thus, these species have developed a competitive attribute in the form of large size of leaf populations. This in turn is dependent upon an extended period of photosynthtic activity under conditions conducive to high productivity. In late successional species the lower flux of leaf modules especially in forest-grown situations can be attributed to their rapid adjustment in growth in response to local depletion in resources arising during competition.

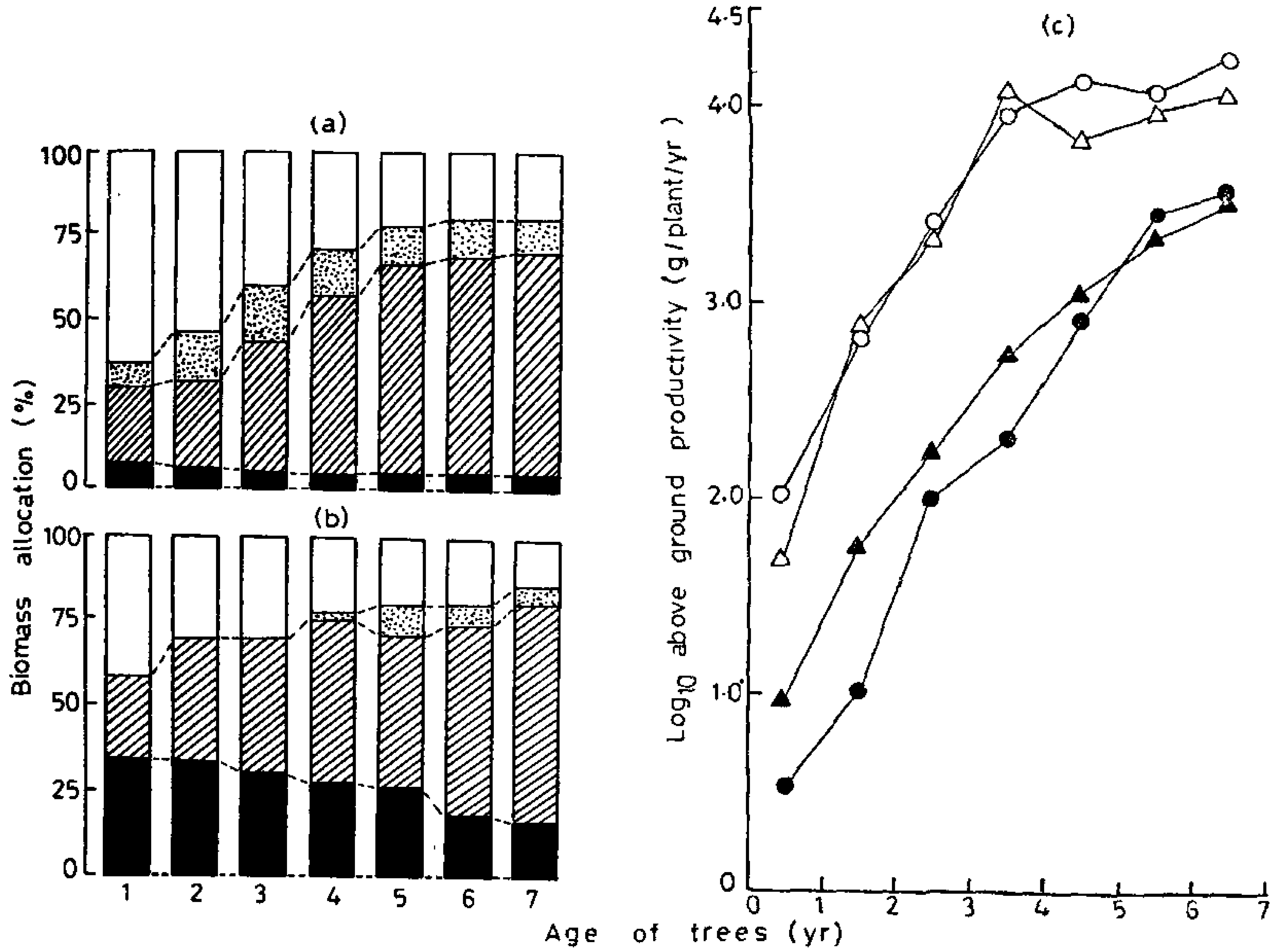


**Figure 2.** Allocation pattern of total biomass in four different compartments *viz.*, root (solid column), bole (hatched column), branch (stippled column) and leaf (open column) of an early successional, *D. sonneratioides* (a) and a late successional, *A. chaplasha* (b). (c), Pattern of change in above ground productivity of early successional (open symbols) and late successional (closed symbols) species with increase in tree age. *A. chaplasha* open triangle, *D. sonneratioides*, open circle, *A. cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*. (After Shukla[24])

## BIOMASS PRODUCTION AND ALLOCATION PATTERN

The different low elevation tree species from a successional gradient which could broadly be categorized into early-, mid- and late successional species, showed a number of differences in their production and allocation pattern of biomass. The early successional species of the community, in general, were found to allocate less to the root system (figure 2a) compared to the late successional ones (figure 2b). These observations suggest firstly, that the early successionals tend to maximize allocation to their shoot system with higher productivity[21] in order to put up their canopy as high as possible for exploiting the high light environment. The greater allocation to bole compartment supports this strategy. Secondly, the spreading root systems mostly in the upper soil profile (20 cm) provide enough absorptive system though poor physical support. This type of root system may exploit the short term increase in nutrient and water available in disturbed sites[22]. On the other extreme, the late successionals have higher allocation to their roots in order to draw upon the nutrient pool from deeper soil layers and exhibit deeper roots with little lateral spread. Between these two extremes are the mid-successional species which are intermediate, having a tap root system with considerable lateral spread to exploit disturbed sites as well as to occur in more developed communities.

The productivity pattern could be related to the successional status which in turn is related to the growth characteristics of the trees. Root productivity of the early successional species was only slightly higher than that for the late successional ones. On the other hand, the shoot productivity was much higher for early successional species (figure 2c).

## CONCLUSIONS

The forestry practices in India, unfortunately, have often not been based on sound scientific principles, much less so on the basis of sound ecology. In this country, as elsewhere, forestry plantations are monocultures of tree species identified as economically important. Very often, in our enthusiasm to obtain fast returns from man-made forests, we tend to go in for exotic species without knowing our own resources in this regard. This often results in many environmental problems which are often realized after many years after the damage has been done. Eucalypt plantations, sometimes introduced into geographical areas which are basically not suited to them and without sufficient baseline information on their impact is a case in point. Identification and utilization of fast growing indigenous tree species which may have all the desired attributes of an exotic, has the advantage of its being more in harmony with the local environment. Understanding the growth characteristics of indigenous trees, as shown in the present study, is, therefore,important.

With our emphasis on optimization in output under a mixed forestry system, identification of mutually compatible species is important. Thus, fast growing but light demanding species has to be grown along with one or more moderately growing or even may be somewhat slow growing but shade tolerant species in order to make a mixed forestry system compatible. This would also ensure optimum output from a given area. An understanding of the architectural design, growth strategies and production pattern of trees under different light conditions in the forest and the way in which their growth strategy has evolved to occupy different ecological niches, as brought in this study, would be useful for the development of forestry programme in the country as a whole and the north-eastern region in particular.

## ACKNOWLEDGEMENT

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# ANNOUNCEMENTS

## ASSOCIATION OF GERONTOLOGY (INDIA)

The first Conference of the Association of Gerontology (India) shall be held from October 2 to 4, 1982, in the Department of Zoology, Banaras Hindu University. It will cover Biological, Clinical and Socio-psychological aspects of aging. Each of the three areas shall have a Symposium of 30 min. duration and several free papers of 15 mins. All correspondence regarding participation should be addressed to Prof. M.S. Kanungo, Department of Zoology, Banaras Hindu University, Varanasi 221 005. May 31, 1982 is the last date for acceptance of papers.

## INTERNATIONAL CONFERENCE ON LEAF PROTEIN RESEARCH

An International Conference of Leaf Protein Research will be held on 5–8 October 1982 at Aurangabad in India, under the host-auspices of the Botany Department of Marathwada University. This Conference is being orgnaised by the Society for Green Vegetation Research and co-sponsored by the Indian Universities and institutes involved in leaf protein research. Conference programme includes five scientific sessions covering of vegetation for choice of raw materials, cultivation and agronomic studies for asessment of yields of leaf protein, technical and technological aspects of processing and production, nutritional and biochemical investigations for quality assessment and improvement, and the results of bulk production and utilisation studies. Last day has been kept aside for equipment demonstration and farm visits. Intending participants are requested to write as soon as possible and send the paper abstract before July end 1982.

The orgnisers, with no funds for travel and other grants, will support requests, being made to the funding agencies. British Commonwealth Foundation will sympathetically consider application for travel grant from the citizens within the Commonwealth; F.A.O. suggests for the people from developing countries to make request directly through their national authorities for use of UNDP funds.

Details can be had from the following Conference Secretariat: Organising Secretary: Dr. Narendra Singh, Central Food Technological Research Institute, Mysore 570 013; Local Secretary: Dr. R. N. Joshi, Department of Botany, Marathwada University, Aurangabad 431 004; International Adviser: Prof. N. W. Pirie, F.R.S., Rothamsted Experimental Station, Harpenden AL5 2JQ, UK.

## IX INTERNATIONAL LIQUID CRYSTAL CONFERENCE

Following the conferences at Kent, Ohio (1965, 1968, 1972 and 1976). West Berlin (1970), Stockholm (1974), Bordeaux (1978) and Kyoto (1980), the Ninth International Liquid Crystal Conference will be held in Bangalore, India, from December 6-10, 1982 under the chairmanship of Professor S. Chandrasekhar, Raman Research Institute. The conference will cover all aspects of the subject: (A) Synthesis and Characterization of Liquid Crystals, (B) Structure and Dynamics, (C) Thermodynamics and Phase Transitions, (D) Mechanical Properties and Defects, (E) Magnetic, Electric and Optical Properties, (F) Interfacial Effects and Anchoring, (G) Liquid Crystals of Disc-like Molecules, (H) Polymer Liquid Crystals, (I) Amphiphilic and Biological Systems, (J) Display Devices and other Applications.

Those interested in participating should write immediately to

Professor S. Chandrasekhar
IX International Liquid Crystal Conference,
Raman Research Institute, Bangalore 560 080.

The Proceedings of the conference will be published in **Molecular Crystals and Liquid Crystals** (Gordon & Breach Science Publishers). The next conference, the tenth in the series, will be held in 1984 in York, England under the chairmanship of Professor G. W. Gray.