OBSERVATIONS ON ECOLOGICAL ADAPTATION OF A FOREST ECOSYSTEM WITH EMPHASIS ON SOME TREE SPECIES

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I certify that the thesis entitled "OBSERVATIONS ON ECOLOGICAL ADAPTATION OF A FOREST ECOSYSTEM WITH EMPHASIS ON SOME TREE SPECIES" submitted by Shri Ram Boojh, M.Sc. for the degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong, embodies the record of original investigation carried out by him under my supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of the Ph.D. degree. This work has not been submitted for any Degree of any other university.

Supervisor

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PREFACE

The present study was undertaken to elucidate the general adaptive phenological characteristics of a sub-tropical evergreen montane forest ecosystem represented by a sacred grove about 10 Km from Shillong in the Khasi Hills of Meghalaya at an elevation of 1900 m. Three early successional species represented by *Alnus nepalensis*, *Schima khasiana* and *S. wallichii* and three late successional species represented by *Machilus kingii*, *Quercus dealbata*, and *Q. griffithii* were considered for detailed studies on growth and architectural adaptations of the forest ecosystem. Of these, all the species except *S. wallichii* are the members of this sub-tropical montane forest. *S. wallichii*, an important tree of lower elevations was considered for a comparative study with *S. khasiana*, which is an important component of the montane forest. The comparative adaptational studies on *S. wallichii* were done taking into consideration two populations of this species, one from an elevation of 1600 m and the other from an elevation of 100 m. Such detailed studies on selected species, it is hoped, would help in a better understanding of ecosystem adaptation and apart from providing useful information on the growth strategy of sub-tropical montane forest trees, this may also be helpful for evolving better forest management and tree improvement practices.

The thesis has seven chapters arranged in 3 sections: (i) seasonal adaptation, (ii) architecture and growth pattern and (iii) seed germination and seedling establishment. Since each of these chapters are written in the form of research papers, some overlapping in writing could not be avoided.

In the first chapter important phenological characteristics of trees of the forest community are dealt with special emphasis on the seasonlity of flowering, fruiting, flushing and leaf fall. The second chapter contains information on litterfall in the forest community with special reference to its seasonality. Chapter 3, 4 and 5 deal with the architectural analysis and growth pattern of a few selected tree species. Chapter 3 is a detailed account of architecture and growth pattern of two species of Schima, namely, S. khasiana and S. wallichii along an altitudinal gradient. Growth strategy of tree species related to successional status has been dealt in two parts: Part I (Chapter 4) deals with the architecture and extension growth of two early and three late successional tree species while Part II (Chapter 5) is on leaf dynamics of these two groups of species in relation to their adaptive strategy for niche occupancy. The third section has two chapters, one dealing with germination, seedling establishment and early growth characteristics of two closely related species of Schima (S. khasiana and S. wallichii) along an altitudinal gradient and the other chapter is an account of the germination ecology of Alnus nepalensis.

The thesis starts with a general introduction, which is an extensive review of literature giving a broad perspective of the topics dealt in subsequent chapters. Literature cited, is given at the end.

GENERAL INTRODUCTION

There have been significant advances in our understanding of the integrated functioning of plants in diverse environments, during the recent past. At the same time we have expanded our knowledge of the adaptive significance of various plant structures. Now plant form is no longer considered separately from plant function and it is convenient to make predictions about the success of specific structural functional plant types in different environments. For example, it is now easy to predict about plant morphofunctional types which could be the most effective competitor under specific light, nutrient and water regimes. This marked increase in our understanding of the functional significance of various plant forms and structures has extended our knowledge of the adaptive significance of various plant structures like, leaf shapes and sizes (Parkhurst & Loucks, 1972; Taylor, 1975; Givnish & Vermeij, 1976), branching patterns (Honda & Fisher, 1978; Pickett & Kempf, 1980; Kempf & Pickett, 1981; Nelson et al., 1981) and whole tree crown characteristics (Hallé & Oldeman, 1970; Brunig, 1976; Hallé et al., 1978). Much of this work has been initiated in the tropics, no doubt, inspired by the impressive diversity of forms there. However, there is still a great paucity of information especially on the temporal and spatial adaptation of trees in tropical and sub-tropical zones, and on the specific mechanisms by which the native species (Climax and pioneer) of these areas exploit the resources in their environment. Such informations are vital for evolving rational forest management schemes.

PHENOLOGY

Phenology is the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and interpretation among phases of the same or different species. The unit of study may vary from a single species (even variety or clone) to a complete ecosystem. The area involved may be small (for intensive studies on all phenophases of entire ecosystems) or very large (for inter-regional comparison of significant pheno-phases). The unit of timing is usually the solar year with which the events to be studied are in phase. The events themselves may cover variable time spans often much shorter than the solar year (Leith, 1974).

The significance of phenological studies have been recoginized for a long time (Leith, 1970, 1971; Leith & Radford, 1974). From a practical standpoint, phenological records could be applied in wildlife, forestry and agriculture as suggested by Leopold & Jones (1947) and used with success for predicting flowering, leaf flushing and fruit ripening for some important horticultural species in Norway (Wielgolaski, 1974). Likewise *Syring vulgaris* is used as the indicator plant of local climate in Wisconsin, U.S.A. (Dana *et al.*, 1963).

Phenological adaptations of Trees in the forest allow the utilization of specific resources which exhibit temporal periodicity and may lead to temporal separation of species. This has been viewed as a mechanism of niche separation, whereby competition between the species is reduced (McDougall, 1922). Also, temporal separation increases diversity of the community which may influence production and stability (Connell & Orias, 1964). However, phenological divergence exposes a species to different environmental characteristics which may lead to the evolution of new adaptations. Tree periodicity patterns provide insight into seasonal organization of floral and fruit resources. Frankie et al. (1974) mention several ways of breaking down these patterns for analyses at finer levels of organization within the respective communities of each ecosystem. They also suggest how these patterns may provide clues as to which animals interact with them for the food resources they provide (Plant-animal interaction).

The phenological studies in the tropics were of inverstigative type lacking comparative and quantitative informations. only recently systematic attempts in this direction have been made by ecologists (Frankie et al., 1974; Putz, 1979; Borchert, 1980; Opler et al.,1980; Primack, 1980).

Seasonality of phenological events:

In areas with distinctive seasons, organisms respond to climatic rhythms and their environmental cues. This is particularly evident in areas such as the temperate deciduous forests, where the community dominants have similar patterns of bud burst, foliage development, senescence and leaf fall (Anderson, 1974; Schemske, 1977). Synchronized growth cycles are also apparent in tropical climates with distinctive wet and dry seasons (Janzen, 1967; Daubenmire, 1972). Many of the investigations of phenology of tropical forests have been carried out in markedly seasonal climates (Njoku, 1963, 1964; Fournier & Salar, 1966; Boaler, 1966; Jeffers & Boaler, 1966; Janzen, 1967; Croat, 1969, 1975; Hopkins, 1970; Smythe, 1970; Nevling, 1971; Daubenmire, 1971; Foster, 1973; Burger, 1974; Frankie et al., 1974; Malaisse, 1974; Opler et al., 1967). Strong annual phenological cycles are evident in these areas.

In tropical areas with relatively constant temperature and rainfall, phenological activities are not constrained by climate as they are in the sub-tropics and the temperate zone. When reproductive and vegetative growth can proceed virtually unimpeded throughout the year, it is not expected for the communities of trees to follow the annual patterns observed under more limiting conditions. Such studies in more or less seasonal climates are limited to those of Holttum (1930, 1940), Corner (1952), Koriba (1958), McClure (1966), Medway (1972), Ng (1977) and Putz (1979) in Malaysia and Singapore; Baker & Baker (1936) in the New Hebrides; Brookfield (1969) in the Solomon islands, Koelmayer (1959) in Srilanka and Frankie et al., (1974) in Costa Rica. In these studies, by and large, strong seasonality in flower, fruit and leaf production was not apparent in tree species and there was apparent lack of seasonality at the community level.

Flowering and fruiting periodicity:

The synchronization of flowering with particular seasons and periodicity in flowering have been commonly observed in rainforest trees (Richards, 1952; Holttum, 1953; Rees, 1964; Ashton, 1969; Croat, 1969; Medway, 1972; Frankie et al., 1974). Of interest is the general observation made by several investigators that most wet forest flowering occurs chiefly during periods of dry weather as shown by Holttum (1953) in Singapore, Ducke & Black (1953) in Brazil and Njoku (1963) in Nigeria. This pattern has been attributed to a triggering mechanism for flowering in response to the sequences of dryness and wetness (Opler et al., 1976). Although moisture related factors may play an important role in flowering periodicity of tropical trees, a change in photoperiod has also been suggested to stimulate flowering (Njoku, 1958, 1963).

Stiles (1977) suggested that tropical trees have a regular spacing of flowering times, but Poole & Rathcke (1979) re-analysed his data and concluded that the flowering pattern was aggregated, because no species bloomed during a transition period between a wet and dry season. Tree species have various levels of overlap in blooming time and vary in their pattern of flower initiation. Three hypothetical phenological tactics have been proposed for flowering (Stearns, 1976; Anderson & Schelfhout, 1980). In the first tactic the sum of the blooming times for all species does not exceed the time available for flowering i.e., there is no overlap in flowering time among the species and thus minimal competition for pollinators. The second tactics is followed by species which have a maximum amount of overlap in flowering time, in potential competition for pollinators and in the length of blooming time. An equal number of species is in flower during each interval but there is a significant departure from the expected equal number of species in flower (i.e. number of species/number of intervals). In the third tactic, the number of species in flower approximates normal distribution and there is a significant departure from an expected equal number of species in flower at each interval. This pattern has potentially reduced competition for pollinators more than the second one because of the staggered pattern of flower initiation and blooming among the species (Mosquin, 1971; Heinrich & Raven, 1972; Frankie <u>et al</u>., 1974; Stiles, 1975, 1977; Feinsinger, 1978).

The pattern of fruit maturation and seeding have been discussed in detail by Janzen (1978) from the angle of animal-plant interactions. He has related the timing of seed production to be of adaptive significance for dispersal agent activity, seed predator behaviour, resource allocation options within the plant and germination demands by the seedlings.

Flushing and leaf fall:

The adaptive significance of different types of leaf replacement strategies have not received the kind of analysis that Janzen (1967) provided for flowering and fruiting phenology. Jackson (1978) has discussed the adaptive advantages of different kinds of leaf replacement activities in forests. He has proposed that the most advantageous strategy of leaf replacement in a perennial plant in an aseasonal environment would be retention and photosynthetic use of an old leaf until a new leaf is grown. Such a strategy would result in maximum leaf fall during the optimal growing season or to a continuous level of leaf fall if new leaf growth were to be continuous. In fact, seasonal cold or drought stress is usually present and leaves must be shed to minimize the effects of this stress. Because cold stress in cold temperate forests has a relatively sudden and predictable onset, cold temperate forests normally have a pulse of leaf fall at the end of the warm season (Bray & Gorham, 1964). In most of the lowland tropical forests, leaf fall has been found to be maximum in the dry season particularly at the end of this season (Hopkins, 1966; Fittkau & Klinge, 1973; Frankie _et_ _al_., 1974). In some tropical forests the maximal leaf fall has been reported during the wet season (Cornforth, 1970; Edwards, 1977; Jackson, 1978; Brassel _et_ _al_., 1980). The only forests found to have non-seasonal leaf fall are Malaysian dipterocarps (Mitchell, cited in Bray & Gorham, 1964), which are characterized by relatively uniform climate.

LITTER PRODUCTION

Since the classic work of Ebermayer (1876) a vast amount of literature concerning litterfall in forest stands has accumulated. The subject is discussed in detail by Lutz & Chandler (1946) and Aaltonen (1948). Bray & Gorham (1964), Jordan (1971a), Jensen (1974) and Jordan & Murphy (1978) have excellently **reviewed** the subject. Most of the early work was done on forest stands in the temperate zone of the northern hemisphere, but during recent years a number of studies have been carried out in other parts of the world too. Bray & Gorham (1964) in their review of the work on litter production have emphasized that, "the study of the quantitative aspects of litterfall remains an important part of forest ecology, dealing with a major pathway for both energy and nutrient transfer." The dynamics of litter accummulation processes are of particular interest in the humid tropical forests where rates of litter production and decomposition are very high.

Seasonality of litter production:

The pattern of litterfall varies greatly throughout the different climatic zones. In deciduous forests of the northern hemisphere, leaf fall is normally concentrated in a rather short autumnal period, often with a pronounced peak in October and November (Viro, 1955; Witkemf & Van der drift, 1961; Carlisle _et_ _al_., 1966; Duvigneaud _et_. _al_, 1969; Anderson, 1973). In a mixed Oak forest (_Quercus_ _ellipsoides_ & _Q_. _alba_) in Minnesota, U.S.A., Reiners & Reiners (1970) found that 20% of the litter fell in September, 50% in October, 9% in the 5 winter months and 21% (probably flowers, bud scales etc.) in April to August. In the evergreen Quercus ilex woodlands in southern France, the leaves have a life span of about 2 years and they are shed mainly in the period from April to June with a peak in May (Rapp, 1969).

In humid equatorial forests litter fall is more or less continuous throughout the year although with a tendency for extensive falls during or shortly after relatively dry periods. Thus, Laudelot & Meyer (1954) found that litter fall at Yangambi (Congo) was low during the rainy season and reached a peak at the end of the dry season. Nye (1961) found in the moist tropical forests of Ghana a relatively high litterfall during February and March due to a short dry season in January and February. Madge (1965) and Hopkins (1966) both working in Nigeria, found that maximum leaf fall occurred during the dry season months of November to March. The former stated that leaf fall fluctuated little during the wet season, at the start of dry season it progressively increased, culminating during the driest months and then falling off again. A similar pattern was found in South-east China in forests dominated by Gironniera subaequalis (Rodin & Brazilevich, 1967). Here the leaves fell all the year round, but with a peak period from March-May, where March-April is the dry season followed by the wet season starting in May.

Jorgensen et al. (1975) maintained that three main factors limit litter production: temperature, water and nutrient availability. The seasonal pattern of litterfall largely depends upon the factors responsible for leaf senescence and abcission in the component species and have been discussed in detail by Whitmore (1975), Addicott (1978) and Jackson (1978). Jackson (1978) suggested that the timing in litterfall is a response to the degree of seasonality in both temperature and moisture. Rain has also been considered to be a factor for increase in litterfall, as the increased weight of wet senesced material in the canopy causes them to fall (Brassel et al. 1980). John (1973), Hopkins (1966) and Brassel et al. (1980) associated litterfall rates with wind velocity. Tanner (1980) has observed that litterfall per day during the dry season was about twice and during the hurricane period was about 4 times to that during the wet period.

Litter production pattern:

Litter production pattern is greatly influenced by the prevailing climatic conditions at different climatic zones. Bray & Gorham (1964) have shown the predominant influence of climate upon litter production. The mean litter production averages 1t/ha, for Artic-Alpine zone, 11 t/ha for equatorial forests and 3.5 and 5.5 t/ha for cool and warm temperate forests respectively. Recent estimates of litterfall from tropical forests range from 5.5 to 15.3 t/ha per year

(Madge, 1965; Muller & Neilson, 1965; Hopkins, 1966; Kira & Iwata, 1967; Wiegert, 1970; Hains & Foster, 1977; Jackson, 1978; Brassel _et al._, 1980; Tanner, 1980). Rate of litter production is thus highest in the tropics and decreases with increase in latitude. Also, it has been shown that the rate of litterfall decreases with decrease in light available during the growing season along a world-wide gradient of decreasing light availability (Jordan, 1971 a).

The major role of temperature in controlling litterfall is revealed when total annual litterfall is plotted against latitude, the relationship is inverse and linear, with a maximum level of over 11 t/ha at the equator, declining steadily to a little less than 1 t/ha at latitude 65°N in Europe, where forest grades into Tundra (Bray & Gorham, 1964). Litterfall pattern may vary even at the same latitude, if coastal and montane forests are compared. Both sites may receive equal amounts of solar radiation but the mountain top site may have a shorter growing season and consequently the total amount of light available for growth there is less (Jordan & Murphy, 1978).

Also, litter production pattern may vary according to topography, vegetation type, species composition and many other biotic and abiotic factors which have been dealt at length by Bray & Gorham (1964).

Litter fractions:

Leaf litter by and large constitute the major portion of the total litter all over the world, its contribution being 60 - 76% to the total litter (Bray & Gorham, 1964). In tropical forests leaf litter contribution vary from 4.4 to 6.9 t/ha (Klinge & Rodrigues, 1968, Cornforth, 1970; Wiegert, 1970; Edwards, 1977, Tanner, 1980). Litter fractions other than leaf have been less investigated except the wood litter which have been brilliantly reviewed by Jordan & Murphy (1978). Jordan (1971 a,b) has found that there is no difference in annual rate of wood production between mesic forests of tropical and temperate zones, but the ratio of wood production to litter production increases with increasing latitude and suggested that a high ratio confers a greater competitive advantage in areas with a short growing season than in areas with a long growing season.

ARCHITECTURE AND GROWTH PATTERN

Early works on growth characteristics of trees are largely confined to their north temperate representatives (Büsgen & Münch, 1929; Kozlowski, 1964). The generalizations made from such studies can not be representative for all tree species (Tomlinson & Gill, 1973) comparatively fewer investigations have been carried out on trees of tropical zones. Studies specific to tropical tree growth in older literature largely refer to comprehensive investigations of phenology (Büsgen &

Münch, 1929). In addition, there are several detailed reports on trees of specific areas (Coster, 1923 in the monsoon region of Java; Holttum, 1953 in Singapore; Medway, 1972 in Malaya). The studies of Koriba (1958) in Singapore are generalized and essentially comparative in approach. This work refers to periods during which species are visibly flushing i.e. exhibiting a crop of new leaves usually associated with shoot extension and it has been concluded that trees exhibit endogenous rhythms in their growth.

Some specific studies which have investigated the dynamics of shoot initiation and expansion in tropical trees include those by Bond (1942 , 1945) on tea; Hallé & Martin (1968) on rubber; Purohit & Nanda (1968) on *callistemon*; Greathouse & Laetsch (1969, 1973) and Greathouse *et al*. (1971) on cocoa; Borchert (1969) on *oreopanax*; Holdsworth (1963), Taylor (1970, 1975), Scarrone (1965) on Mango and Gill & Tomlinson (1971) on *Rhizophora*.

The monumental works of Hallé & Oldeman (1970, 1975) and Hallé *et al*. (1978) on the growth and dynamics of tropical trees have opened up new avenues of systematic researches on the forests and trees of these areas.

Extension growth:

Extension growth or the elongation of the branch axes of a shoot system, varies widely among tree species in its rate, phenology and underlying morphogenetic basis. A wide range of extension growth patterns have been recognized in tree species. On the one hand there are species with a single flush of shoot growth wholly preformed in the previous year's overwintering bud (determinate growth) as exemplified by many north temperate species. Typically shoot elongation in such species is completed rapidly (less than eight weeks), during favourable growing conditions which include the longest photoperiod of the year. On the other hand, there are species where more leaves are produced along the leader in a growing season than there are embryonic leaves and primordia in the winter bud. This has been referred to as indeterminate growth.

These two patterns of growth have been widely recognized in temperate trees. The growth in tropical trees is more diverse than that in the temperate regions and the periodicity of shoot growth in tropical trees has been a centre of controversy. If recurrent flushes occur at regular intervals the growth has been termed as rhythmic or periodic, the same at irregular intervals has been called as episodic, intermittent or recurrent (Romberger, 1963; Zimmermann & Brown, 1971). Hallé et al. (1978) have collectively placed all these under one broad category of rhythmic growth mainly in the context of tropical trees where time-lag between different growth flushes are very small. Thus, they have distinguished two main patterns of growth:-

(i) Rhythmic growth - as defined by Hallé & Martin (1968) in which shoots have a marked enodgenous periodicity of extension. This term may be regarded as synonymous with episodic (Romberger, 1963) or with intermittent growth (Koriba, 1958). The term 'rhythmic' may imply a regular cycle, though this is not intended in the definition by Hallé *et al.* (1978).

After a period of dormancy flushing in tropical trees or bud burst in temperate trees, most strikingly demonstrates rhythmic growth. Flushing largely indicates rapid expansion of preformed leaves. In many trees with essentially rhythmic growth expansion is less rapid and less obvious, so that the term may have limited application.

The morphological indication of rhythmic growth in the mature shoot is a more or less pronounced segmentation of the axes (referred to by Tomlinson & Gill (1973) as 'articulate growth). In trees which develop bud scales, there may be a series of short internodes or small leaves. For many trees with rhythmic growth the most conspicuous feature is the development of groups or tier of branches and the periodic production of branches in relation to rhythmic growth has been referred to as 'rhythmic branching.'

(ii) Continuous growth - in which shoots have no marked endogenous periodicity of extension. It implies that the apical meristem undergoes no 'rest' or in the more precise usage of

Romberger (1963) 'quiescence'. The trees in the tropics which have been described as evergrowing by Koriba (1958), come in this category. As little is known about the physiology of dormancy, the continuous growth is distinguished by the absence of pronounced morphological segmentation. A more or less continuous process of leaf production is involved in continuous growth. This is implicit in Koriba's (1958) description and in the type of shoot referred to as 'non-articulate' by Tomlinson & Gill (1973).

Tree architecture:

Organization in trees reflects the precisely controlled genetic programme which determines their development. This has been comprehensively described by the pioneer works of Hallé & Oldeman (1970, 1975) by means of their concept of architecture, which has permitted a typological categorization of growth models. The visible morphological expression of the genetic blueprint of a tree at any one time is referred to as its architecture. For a tree the growth programme which determines the successive architectural phases is called as its architectural model or shorter, its model (Hallé et al. 1978). Thus the architectural model of a tree, refers to its plan of growth.

Architecture is a dynamic **concept distinct** from shape or physiognomy which is static. Similarly, it is not synonymous to growth habit, which refers essentially to the ultimately expressed form of the organism (herb, shrub or tree) and implicates size. Architecture does not involve size and diminutive herbs and giant forest trees may exhibit precisely the same architecture. Hallé & Oldeman (1970) have described 21 architectural models. Each model is named after a botanist who has contributed to a knowledge of the model or has done morphological research exhibiting the model. Architectural models have been recognized mainly by criteria which relate to primary extension growth.

Branching and axis differentiation:

Unbranched trees are those like single stemmed palm of which the coconut is a familiar example, remain vegetatively unbranched because they lack lateral meristems completely. A number of dicotyledons, of which carica papaya is a familiar example are architecturally unbranched and belong to the same model (Corner's).

Branched trees have two modes of branching. The simplest mechanism for proliferation of a meristem is by its equal division into two daughter meristems of initially equal growth potential. This is called as dichotomy or terminal branching. Only one architectural model (Schout's) has been accounted for such trees. The axillary or lateral branching involves the development at each node of one or more lateral meristems from the terminal meristem, which may or may not continue its activity. Axillary branches are formed by two methods: Syllepsis or prolepsis. The definition of Späth (1912) as restated by Hallé *et al.* (1978) for syllepsis is 'the continuous development of a lateral meristem to establish a branch, without an evident intervening period of rest of the lateral meristem.' Hallé *et al.* (1978) define prolepsis as 'the discontinuous development of a lateral bud from a terminal meristem to establish a branch, with some intervening period of rest of the lateral meristem.'

Morphology of branch expression:

In monopodial branching, lateral branch meristems are produced (continuous or rhythmic) by a permanent terminal meristem. In sympodial branching, lateral branch meristems successively function for a limited period as a terminal shoot and are successively evicted, there is no permanent meristem. Sympodial growth by substitution occurs when the terminal meristem either aborts or becomes reproductive and makes no further contribution to the vegetative architecture of the tree. Sympodial growth by apposition occurs when both terminal and lateral meristems of each unit are evicted into a sub-ordindate position and extension growth of the axis is continued by a vigorous lateral which in its turn eventually becomes abruptly erected (Koriba, 1958; Tomlinson, 1978).

An orthotropic shoot has an erect orientation (negatively geotropic), radial symmetry and phyllotaxis most commonly decussate or spiral. A plagiotropic shoot has a horizontal or oblique orientation (more or less diageotropic) and dorsiventral symmetry either by virtue of a distichous phyllotaxis or if spiral or decussate, by secondary orientation (petiolar or pulvini or twisting of internodes). The degree of differentiation of a meristem may be changed either by external influences or by modifications of internal correlations. Of special interest are those woody plants in which there is no inherent change of expression within a single meristem producing axes of architectural significance. Such axes are described by Hallé & Oldeman (1970) as mixed axes. Among the several possibilities of the most distinctive type are those axes in which an initial orthotropic phase shows a pronounced distal curvature, the site of a future branch complex.

Reiteration

The concept of reiteration of the tree model exists as an ecological extension of the architectural concept (Oldeman,1974). At the beginning of tree's life after germination, it produces the initial model, which is one of those described by Hallé & Oldeman (1970). Later and under propitious ecological conditions, meristems which do not initiate any growth during the model's development, may copy all or part of the model. This copy should not be confused with a ramification and is called a 'reiteration'. Thus, the process of reiteration is a mechanism of architectural adjustment by which the damaged tree accommodates itself to its environment.

Trees in the forest which conform to the initial model or those having fewer reiterations constitute the set of future, those which have developed a lot of reiterations constitute the set of the present. A tree of the 'future' is not always younger than one of the 'present', but it still keeps its growing potential. Last, the set of the past is constituted by the trees of which the old age or poor ecologic conditions lead to the architecture's degradation.

In each structural ensemble in the forest, the different points where bigger reiterations occur, constitute an irregular space which is called the inversion surface. The levels of those surfaces correlate with different storeys where the tendency to produce always bigger organs such as stems, reverses and becomes a tendency to produce smaller organs such as little branches around the crown. This architectural inversion involves the regulation of vertical gradients of light and humidity which change to a lower or higher degree than in the average gradient.

Branch and leaf orientation

Branching pattern is one of the most conspicuous features of woody plants. Efficacious leaf-display, minimization of non-photosynthetic tissue (Horn, 1971; Whitney, 1976; Honda & Fisher, 1978), structural strength (McMahon & Kronhaur, 1976) and optimization of translocation (Leopold, 1971; Leigh, 1975) are the potential adaptive functions of branching design of trees. Thus, it provides the structural support and leaf exposure of woody plants. Species growing in different environments have adopted differing branching pattern and leaf display characteristics, Whitney (1976) proposed that the species of closed forests growing under canopy shade are selected to favour minimization of shading within the crown. Horn (1971) categorized this type of leaf display as a non-random, highly structured monolayer. In contrast to this, trees adapted to open situations would be expected to approach a multilayer state, having a number of small overlapping leaves randomly distributed through the crown (Horn, 1971).

The geometry of phtosynthetic apparatus is an important feature in the adaptive mechanism of trees and has been related to their strategy for light interception (Horn, 1971; Douglas & Ramsaden, 1973; Lang, 1973; Monsi *et al.* 1975). Generally, the orientation of leaves in sun positions of the crown or the leaves of the upper canopy is such as to enhance photosynthesis and promote leaf cooling during high solar radiation. In shade positions, leaves orient to maximize the individual leaf photosynthesis by displaying themselves in horizontal monolayers (Horn, 1971; Baker *et al.*, 1973; Honda & Fisher, 1978; McMillan & MoClendon, 1979; Pickett & Kempf, 1980).

Bifurcation ratio:

Differences in branching in trees are demonstrated by the bifurcation or branching ratio, which is the ratio of numbers of distal to proximal branches. This type of ratio was first used to quantify the drainage patterns of stream basins (Horton, 1945). More recently it has been used to characterize the branch networks of biological systems, such as trees (Holland, 1969; Leopold, 1971; Oohata & Shidei, 1971; Baker et al., 1973; McMahon & Kronauer, 1976; Whitney, 1976; Thornley, 1977; Niklas, 1978; Steingraeber et al., 1979; Pickett & Kempf, 1980; Kempf & Pickett, 1981).

Oohata & Shidei (1971) subjected seedlings of Quercus phillyraeoides to different planting densities and levels of light intensity and found that bifurcation ratio was insensitive to changes in light environment. Whitney (1976) compared bifurcation ratios of open and shade grown Fraxinus americana and similarly concluded that bifurcation ratio values approach a species specific constant. Whitney (1976), further suggested that bifurcation ratio is a measure of morphological adaptation to a particular successional status. Thus, the lower bifurcation ratios are associated with the monolayer late successionals, while higher ratios are associated with multilayer display of leaves, characteristics of early successional species (Whitney, 1976). Recently, Steingraeber et al. (1979) and Pickett & Kempf (1980) have shown that bifurcation ratio varies within a single species growing under different environments. Thus, they found that individuals from exposed habitats had higher branching ratios and in addition also possessed longer terminal branches than those beneath the canopy.

However, bifurcation ratio, is considered to be a relatively crude index of tree architecture, while branch angle and branch length have been found in both real and model trees to have a major effect on the acrhitecture (Honda & Fisher, 1978; Steingraeber et al., 1979; Pickett & Kempf (1980; Kempf & Pickett, 1981; Nelson et al., 1981).

LEAF DYNAMICS

Higher plants are all organised as iterations of a basic construction module and leaf with its axillary bud is the construction unit in the shoot (Harper & White, 1970; Harper & Bell, 1979; White, 1979). As a plant grows new modules are added to the structure and old ones die. The parts of a modular organism have their own birth and death rates; a genet has its own internal population dynamics and the relative placement of the modular units determines the forms of the organism. Form is a consequence of dynamics (Harper & Bell, 1979), and the dynamic concept of architecture (Hallé et al. 1978) also interprets the plant growth in terms of the organized accumulation and flux of specific constructional units (buds, leaves etc.) at the blueprint.

Leaf and its axillary bud are the smallest module of the organized structure in higher plants and leaves may have many properties associated with members of populations, e.g. they may increase in number exponentially in a rapidly growing plant, they have juvenile, mature and senescent phases; death-rates and survivorship curves. Bazzaz & Harper (1977) have shown that it is relatively easy and rewarding to describe the growth and reaction of plants to different environments by applying demographic procedures for the analysis of populations of leaves.

Though some aspects of leaf demography of tree species have been worked out like census (Büsgen & Münch, 1929), longevity (Gill & Tomlinson, 1971a), age-structure (Kinerson et al., 1971) or abcission strategies (Kozlowski, 1973; Addicott, 1978), no detailed demographic studies are available on the leaves in the canopy of trees.

Leaf production:

Leaf production estimates have been of interest to foresters and horticulturists (usually as a part of wider studies on productivity). The early studies on leaf production estimates have been reviewed by Büsgen & Münch (1929). With the increased emphasis on the role of leaf biomass in ecosystem studies and primary productivity (Baskerville, 1965; Satoo, 1970), later investigations were carried out on changes in leaf production over time in mono-specific stands (Rennie, 1955; Ovington & Heitkamp, 1960; Switzer et al., 1967; Wiegert & Monk, 1972; Marks, 1974) and mixed-species forests (Covington & Aber, 1980). But the studies from demographic point of view considering the dynamics of leaf populations (flux), are lacking for tree species.

Leaf longevity:

Most leaves are determinate in growth (though a few are not and retain a functioning apical meristem, Hallé et al., 1978) and have a determinate life span. Within a species this life span may be environmentally determined. Leaf populations undergo mortality over a time period. Survivorship curves best represent this pattern and have been constructed for various species: *Abies veitchii* (Kinerson et al., 1974); *Actinodaphne longifolia* (Yuwaka et al., 1977); *Ledum groenlandicum*, *Kalmia polifolia*, *Chamaedaphne calyculata* (Reader, 1978); *Linum usitatissimum* (Bazzaz & Harper, 1977); and *viola sororia* (Solbrig et al., 1980). Without exception they all show Deevey Type I survivorship curve (Deevey, 1947), where there is an initial period of constant low probability of death followed by a rapidly increasing risk.

In plants that carry cohort of leaves for more than one year an age structure may develop if successive annual cohorts overlap. Studies on leaf age-structure exist for certain species since the physiological significance of leaves of different age classes affect tree productivity (Linzon, 1958; Woodman, 1971; Kinerson et al., 1974).

SEED GERMINATION, SEEDLING ESTABLISHMENT AND INITIAL GROWTH CHARACTERISTICS

Germination and establishment are two critical phases in the life cycle of a plant. While much is known about the physiological processes which occur at the time of germination, its adaptive aspects have received little attention (Kozlowski, 1972; Hydecker, 1973). It has been argued by Harper et al. (1961, 1965) and Silverton (1980) that the number of plants established from seed may be regulated by the availability of 'safe germination' sites. 'Gap detection' is the term coined by Thompson et al. (1977) which enables a seed to avoid germination until conditions are favourable. The most direct means of gap detection for a seed would probably involve a mechanism of germinability to the degree of shading which the seedling would encounter if the seeds were to germinate. Thus, the pioneer species have evolved a mechanism of dormancy till the availability of gap (dormant/Buried seed strategy - Marks,1974) or for the transportation of seeds from outside sources (fugitive strategy - Hutchinson, 1951).

Germination requirements of different species or the populations of the same species represent the normal conditions for their germination under natural conditions and these have been related to the distribution and adaptation pattern of species/populations (Koller et al., 1962; Harper, 1965; Cohen, 1967; Ramakrishnan, 1972; Ross & Harper, 1972; Kapoor & Ramakrishnan, 1973; Thompson, 1973). Widely distributed tree species encounter different environmental conditions over their distribution range. This brings into a consideration of role of ecotypic differences in seed germination, seedling establishment and initial growth of tree species. Adaptive differentiation of this kind for germination requirements have been observed by Ramakrishnan (1961, 1965, 1968) and Ramakrishnan & Kapoor (1974) in the case of herbaceous species and by **Winstead** (1971), Williams & Winstead, (1972), Wearstler & Barnes (1977) for tree species. Whilst the ecotypic studies have received considerable attention in this country with respect to herbaceous species (Ramakrishnan & Khosla, 1971; Kapoor & Ramakrishnan, 1973; Ramakrishnan & Kapoor, 1974), the forest trees have received no attention.

Differences in early growth characteristics of ecotypic populations of trees are exemplified by many temperate tree species, the work on which has been reviewed by Wareing (1956) and Vaartaja (1959), and there is considerable evidence that indicates the role of day length and temperature in breaking winter dormancy. In a study of *Picea* ecotypes, Roche (1969) has also related photothermal regime to cessation of growth and initiation of dormancy, the differential behaviour of populations being related to local habitat conditions. The differences in cone scale morphology in *Picea* populations along an altitudinal belt observed by this worker was related to dormancy patterns and ultimately to the overwhelming influence of environment.

ECOLOGICAL STRATEGY OF TREES

Strategy, in an economic or military sense, is the reciprocal set of actions and reactions between two conflicting groups directed to the attainment of the ends of each group. The concept has been widely used in animal ecology and has recently penetrated the fields of plant ecology and evolution. There have been strong objections to its usage in animal and plant ecology (Grubb, 1980) and a plea has been made by Stevens (Communicated by Whitmore at Harward Symposium 'Tropical trees as living systems' at Petersham, U.S.A. 1976) to replace this word so charged with notions of planning and tactics, with a more anthropogenic word 'syndrome'. Disregarding its teleologic interpretation it has been used with an analogous meaning by ecologists to refer to the way an organism partitions or deploys its resources in the struggle for existence. Grime (1979) broadens the meaning of strategy by encompassing all ecologically significant attributes of an organism.

For trees, occupation of space is an inherent mechanism without which a population cannot survive, and it is towards the interpretation of such mechanisms that much of the concept of strategy in plant ecology is directed (Hallé <u>et al</u>., 1978). The idea of two main trends in selection of specific strategies from the work of animal biologists (McArthur & Wilson, 1967; Pianka, 1974; Blondel, 1975) i.e. 'r' and 'K' selection with relation to tree species have been discussed in detail by Hallé <u>et al</u>. (1978). It is stated that each architectural tree model represents standard solution to the utilization of energy offered by the environment. Each of the architectural models proposed by Hallé <u>et al</u>. (1978) are more or less suited to an 'r - determined or K- determined life cycle and are in accord with Pianka (1974) in thinking of an r to K selection continuum along which an organism can have a different position according to the particular environment. Most tree architectural models can be recognized as intermediates between extreme r and K plants.

For trees, there is a useful representation of the energy distribution between vegetative (K-oriented) and reproductive (r-oriented) strategies. Any defence against predators is incorporated into the complex of K-oriented factors (competitive). And because of a tree's immobility, physical flight from predators is possible only in the seed-phase and it is then linked to the reproductive (r -oriented) behaviour of trees. Reiteration which represents a shift towards more abundant flowering and fruit set, a result of the progress towards neoteny in the successive reiterated models, is a shift towards r-strategy in trees (Hallé et al., 1978).

Bormann & Likens (1979) have proposed two growth strategies of tree species to occupy the different stages of ecosystem development after disturbance. The two contrasting strategies are, exploitive strategy best adapted to conditions immediately after disturbance suited for early successional environments where there is minimum competition and abundant natural resources, and a conservative strategy better adapted to late successional environments, of high competition and lesser resource availability. Similar patterns of plant adaptation or species strategies have been implicated or proposed in a number of other studies (Grime, 1974; 1979; Harper & White, 1974). Harper & White's (1974) concept of shade-intolerant colonizing (r-type) species, for instance, is closely related to the exploitive growth strategy. By way of contrast, shade-tolerant species possessing fewer and larger seeds and a long juvenile period could be considered representative of the conservative (K) strategy.

THE PRESENT STUDY

The present study on the ecological adaptation of a forest ecosystem is aimed at the analysis of important adaptive strategies of the forest, in terms of its constituent units, the individual trees. The tree has been considered as an active, adaptable unit and the forest being made up of a vast number of such units interacting with each other.

The seasonal adaptation of the forest community has been studied by considering the phenological activities of important over-and understorey tree species in the forest. The correlations of different phenological events — flowering, fruiting, flushing and leaf fall - with the seasonal environmental triggers have been considered as the adaptation of trees and the forest community as a whole to the climate. The studies on litterfall pattern deals with the pattern of litter - production, taking into account both seasonality and rate of production. The total litter as well as the contribution of litter fractions to the total litter have been quantified. This study is compared with other relevant works in tropical and sub-tropical climates.

Studies on growth pattern and architecture have been done keeping in view the dynamic process of architectural development from bud-proliferation, branching dynamics, leaf arrangement to overall geometry of the tree. This technique separates growth into component processes and their effects on adaptive strategy of trees for niche occupancy have been analysed. The architecture build-up and growth pattern of two ecologically contrasting group of species namely early and late successional species of the forest ecosystem have been studied. Branch and leaf display characteristics and bifurcation ratios of these species have been quantified and related to their strategy of growth and dynamics in the forest community.

The demographic technique has been applied to the study of leaf populations. The study takes into account the dynamics of leaf populations (i.e. birth and death and resultant flux), their age-structure and age-distribution, mortality and survivorship. The survivorship curves have been constructed for the different cohort of leaves and compared with the patterns of survivorship in other studies. This has revealed the seasonality of birth and death of leaves as well as the overall pattern of leafiness. The dynamics of leaf populations is discussed in relation to the ecological strategy of tree species.

Schima khasiana and *S. wallichii* are two important early successional components of forest ecosystems of north-eastern India. The growth pattern and architecture of these species have been considered along their altitudinal distribution pattern. The overall architectural development pattern and growth strategy of *Schima* have been analysed in relation to its success and role in the forest ecosystem as an early successional colonizer as well as its altitudinal distribution pattern.

Studies on germination ecology of *Schima khasiana* and *S. Wallichii* populations have been done under laboratory conditions and seedling establishment and growth performance at different altitudinal field conditions. These have been discussed in relation to the species adaptation at different altitudes. Germination ecology of the early successional *Alnus nepalensis* has been studied under laboratory conditions and related to its role in the forest ecosystem.