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 (Lieth, 1974).

The significance of phenological studies have been recoginized for a long time (Lieth, 1970, 1971; Lieth & 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 _et_ _al_., 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 fall 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 <u>et al</u>. (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 & McClendon, 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 et al., 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 et al. (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 et al. (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.

SECTION A

SEASONAL ADAPTATION

CHAPTER I

Phenology of trees in a sub-tropical evergreen montane forest in north-east India

PHENOLOGY OF TREES IN A SUB-TROPICAL EVERGREEN MONTANE FOREST IN NORTH-EAST INDIA

INTRODUCTION

The concepts and significance of phenological studies in the understanding of ecosystem function have been discussed by Leith (1970) and Leith & Radford (1971). Studies on the phenological patterns of trees are important not only from an applied point of view for conserving gene resources and for a rational forestry management programme (Stern & Roche, 1974), but are also significant for a better understanding of the ecological adaptations of individual species as well as community level interactions. Thus, for e.g. the effects of herbivory will vary significantly between plants with short-lived leaves and those which retain them for many years. For a better understanding of productivity, individual leaf phenology is important (Bentley, 1979). Further, any understanding of the organization of tropical communities based on plant-animal species interactions must be based on a knowledge of the seasonality of production of plant parts (Mooney _et_ _al_. 1980).

Much of the studies on the phenology of trees done in tropics, present only a partial analysis of leafing, flowering and fruiting data (McClure, 1960; Rees, 1964; Nevling, 1971) and only recently has there been a systematic attempt to make comparative and quantitative studies on this problem (Frankie _et_ _al_., 1974; Putz, 1979; Opler _et_ _al_., 1980; Primack, 1980).

PLATE 1

A view of the sub-tropical evergreen montane forest at Upper Shillong.

PLATE 2

A close view of the sacred forest grove at Upper Shillong.

PLATE 1

PLATE 2

This study deals with the seasonality patterns in a subtropical, humid, evergreen montane forest community near Shillong ($25^{\circ}34'$N and $91^{\circ}56'$E) at an altitude of 1900 m. This forest community is a relict sacred forest grove which is maintained in a comparatively undisturbed state because of the faith and tradition of the local Khasi tribe who believe that sylvan deities would be offended, if trees are cut or flowers and fruits are plucked. Therefore, this is representative of the climax forest type of this area, which otherwise is highly disturbed due to slash and burn agriculture (Ramakrishnan & Toky, 1978).

CLIMATE AND VEGETATION

The climate is seasonal with monsoonic pattern of rainfall with over 80% of it occurring during May to September. The year may be divided into four more or less well marked seasons; (i) a period of heavy rain during May-September; (ii) a period which marks the retreat of monsoon charactrized by low rainfall and equable temperature in October-November; (iii) a winter period during December-February, marked by low temperature and scanty rainfall and (iv) a warm windy summer during March-April. The summer temperature does not exceed more than an average maximum of 25°C and in winter it goes down to an average minimum of 3°C (Fig 1.1).

The vegetation is a mixed evergreen broad-leaved forest consisting of Oaks and laurels as dominants. At lower levels on the hill, the tall evergreen association has <u>Quercus</u>

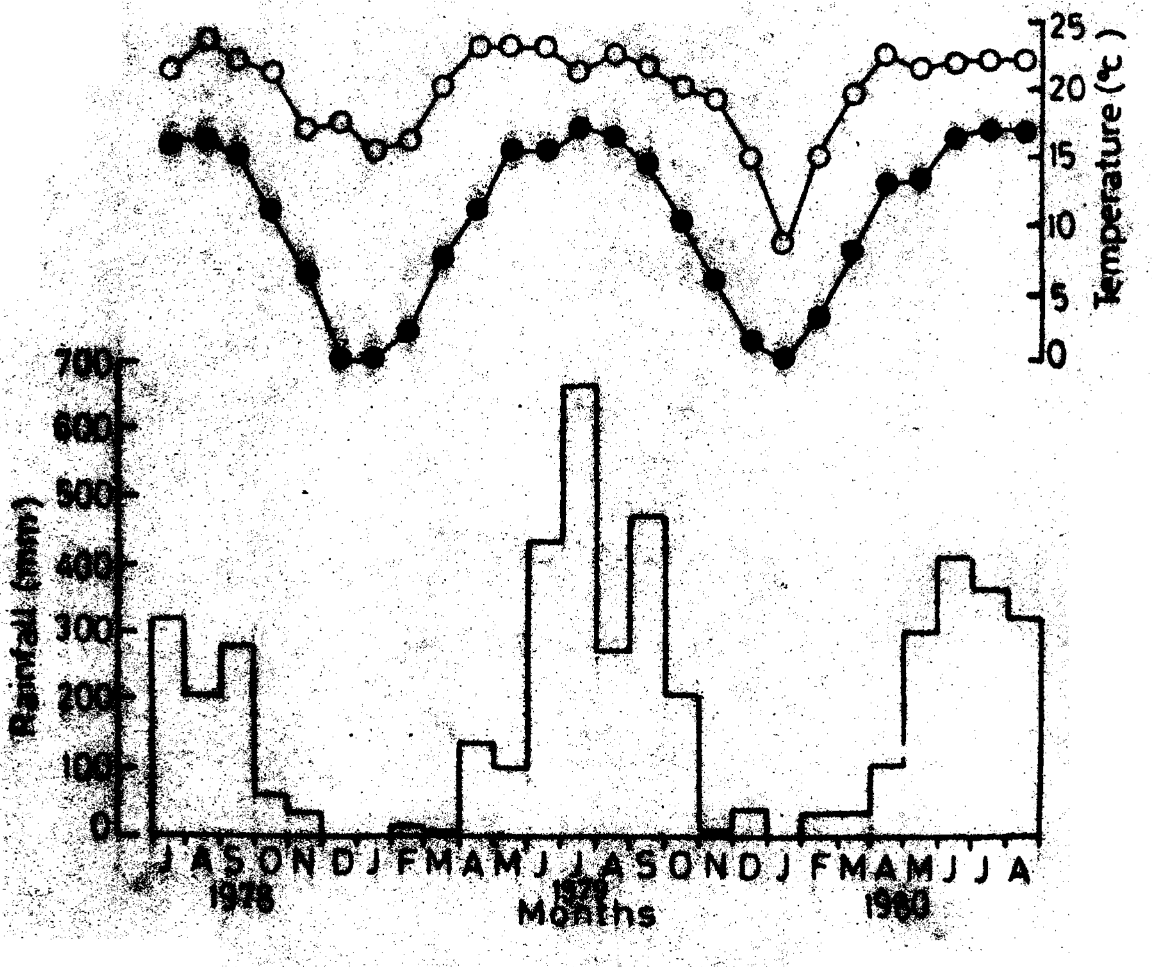
Fig. 1.1 : Ombrothermic diagram of the study area.

Mean maximum temperature (○)

Mean minimum temperature (●)

Rainfall (bars)

Fig. 1.1.



25
20
15
10
5
0
Temperature (°C)
700
600
500
400
300
200
100
0
Rainfall (mm)
J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
Months

dealbata, *Q. griffithii*, *Pasania spicata*, *Manglitia insignis*, *Schima khasiana*, *Machilus kingii* and *Cinnamomum impressinervum* with an understorey of *Eurya Japonica*, *Myrsine semiserrata*, *Lindera pulcherima*, *Symplocos* and *Litsea* species. At the summit (c.2100m) the dwarf ericaceous association consists chiefly of *Rhododendron* species alongwith other dwarf trees like *Symplocos spicata*, *Elaegnus pyriformis* and *Quercus dealbata*. The shrub stratum here consists of *Daphne shillong*, *Osbeckia Crenata* and *Coffea khasiana* as the main elements.

METHODS OF STUDY

Phenological records were noted for tagged individuals of the species along five permanent transects 200m in length. The transect records were supplemented by general phenological observations on trees at random. All the data presented here are based on 10 replicate individuals or more of each species over a period of two years (January 1978 to January 1980), at monthly intervals. For each tagged tree records were made of leaf development, leaf fall, flowering and fruiting. The categories 'none', 'few' and 'many' were employed and assigned values of 0, 1 and 2 respectively, following Opler *et al.* (1980). The monthly values for each characteritics for all individuals of each species, were summed separately and divided by the number of individuals. Thereby a mean value was obtained for each phenological characteristic of each species. Using this technique, the maximum possible value for any characteristic for any month is 2.0.

DEFINITIONS

1. Tree:

Any woody plant of perennial duration which rises from the ground with a trunk and with a minimum height of about 3m (Frankie *et al.*, 1974). Overstorey consisted of canopy and sub-canopy trees of more than 10 m. height and the understorey had trees less than this height.

2. Duration of Activity:

Brief activity (flowering or fruiting) extends for 2 weeks or less while prolonged refers to periods more than 2 weeks per episode. Flowering and fruiting activity by the members of a species population more or less continuous throughout the year is referred to as continuous activity and those having engaged in flowering/fruiting only once during the year are discontinuous.

3. Pattern of Activity:

Seasonal and extended activity refers to flowering/fruiting occurring during a given season or extending into more than one season respectively. Marginal activity refers to species that have their activity occurring during transition period of seasonal changes.

When all the members of a species population engage in flowering/fruiting simultaneously the activity is referred to as synchronous and if only some members of a species population fruit/flower during a given season, it is called as asynchronous.

4. Fruit maturation:

Fruit maturation periods of 4 months or less following fertilization are considered rapid and those greater than 4 months are termed lengthy.

RESULTS

Leafing activity

The forest community maintained its evergreen appearance throughout the year with a majority of both the overstorey and the understorey species showing continuous or periodic evergreen leafing behaviour but with only a small proportion of deciduous elements (Table 1.1). However, in the drier months of December to March evergreen aspect of the forest was less conspicuous due to marked leaf drop.

Leaf flushing periodicity

Leaf flushing in both overstorey and understorey species showed strong seasonal periodicity. The first peak of flushing was observed in April-May followed by another in July-August. The latter was less pronounced in the understorey species. There was a brief period of lesser activity in May-June. During winter months most of the species were dormant (Fig 1.2a).

Species were divided into 4 distinct categories according to their flushing behaviour (Table 1.2). In the overstorey most of the species were with double determinate flushes, followed by the species with multiple flushes of the indeterminate type but with only one species having continuous flushing activity. Species with single determinate flush were

Table 1.1 : Types of leafing activity of tree species

GROUP	ACTIVITY	OVERSTOREY Number of species	%	UNDERSTOREY Number of species	%
I	Continuous evergreen	1	4	3	7
II	Periodic evergreen	18	69	26	65
III	Periodic deciduous	7	27	11	28

Table 1.2 : Flushing behaviour of overstorey and understorey tree species

ACTIVITY	OVERSTOREY SPECIES		UNDERSTOREY SPECIES	
	Number	%	Number	%
Species with single determinate flush	0	0	12	30
Species with double determinate flushes	18	69	11	28
Species with multiple indeterminate flushes	7	27	14	35
Continuous flushing type	1	4	3	7

Fig. 1.2 : Phenological periodicity (%) of overstorey (continuous lines) and understorey (broken lines) trees. Crossed lines represent the activity level (see text for explanation).

(a) flushing
(b) leaf fall
(c) flowering
(d) fruiting.

Fig.1[illegible]a.

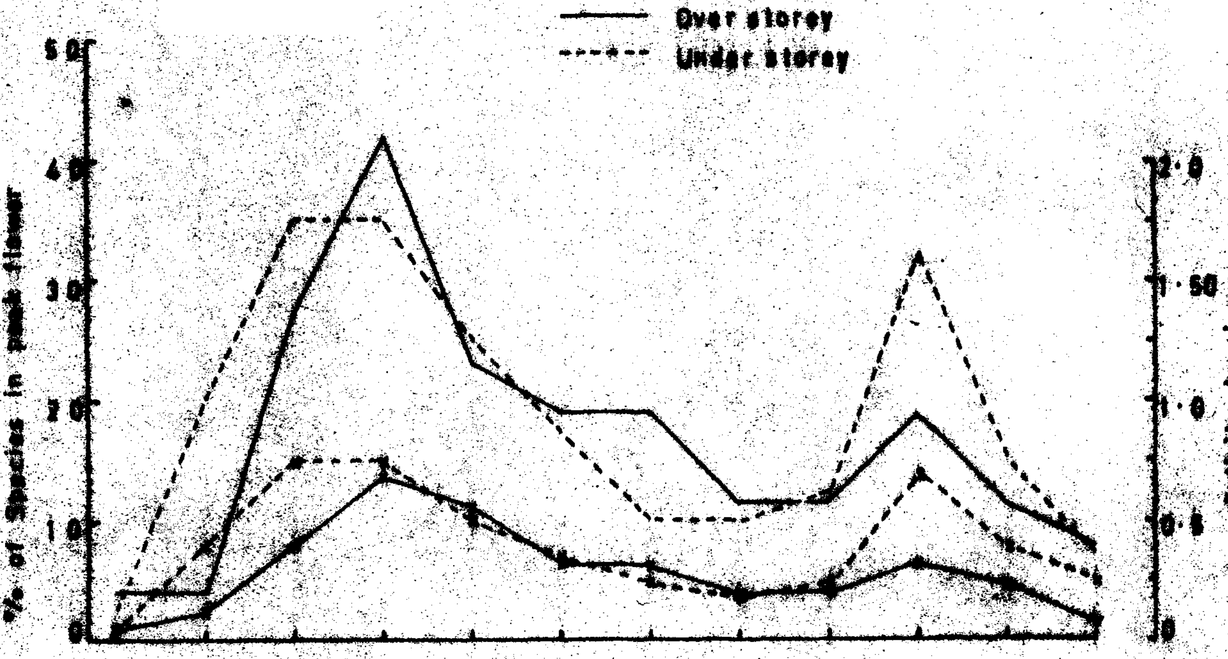
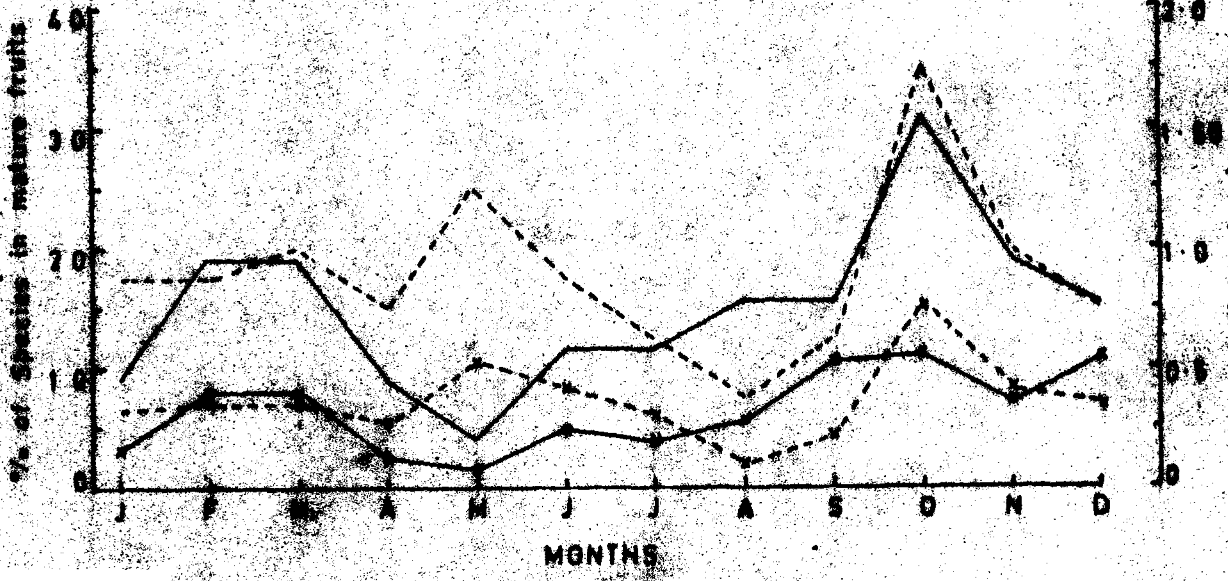

Over storey
Under storey
% of Species in peak flower
Activity level
50
40
30
20
10
0
2.0
1.50
1.0
0.5
0

Fig.1[illegible]b.


% of Species in mature fruits
Activity level
40
30
20
10
0
2.0
1.50
1.0
0.5
0
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

absent in this category. On the contrary, understorey trees had many species with single determinate flush. About an equal number of species also showed double determinate and multiple indeterminate flushes. A few species also showed continuous flushing activity.

Leaf fall periodicity

Leaf fall in the overstorey species was maximum during January to March followed by a steep fall in subsequent months. Another small peak was observed during July-August with leaf fall showed by the species like *Betula*, *Englehardtia* and *Prunus*. The leaf fall in *Quercus griffithii* started in October, becoming completely naked by December and remained so upto the end of March. The understorey trees had only a single peak of leaf fall in the month of February to March. During the rest of the year the fall was at a slow rate (Fig 1.2b).

Flowering activity

The flowering pattern of the overstorey and understorey trees (Fig 1.2c) showed that two peaks occur during the year, one major peak in April and a smaller one in October. An equal number of species belonging to both over and understoreys flowered either during dry or wet months. A few species flowered during the marginal season extending to both wet and dry periods. Two of the understorey species, namely, *Pieris ovalifolia* and *Eurya japonica* showed extended flowering over a long period (Table 1.3).

Fig.1.2.c

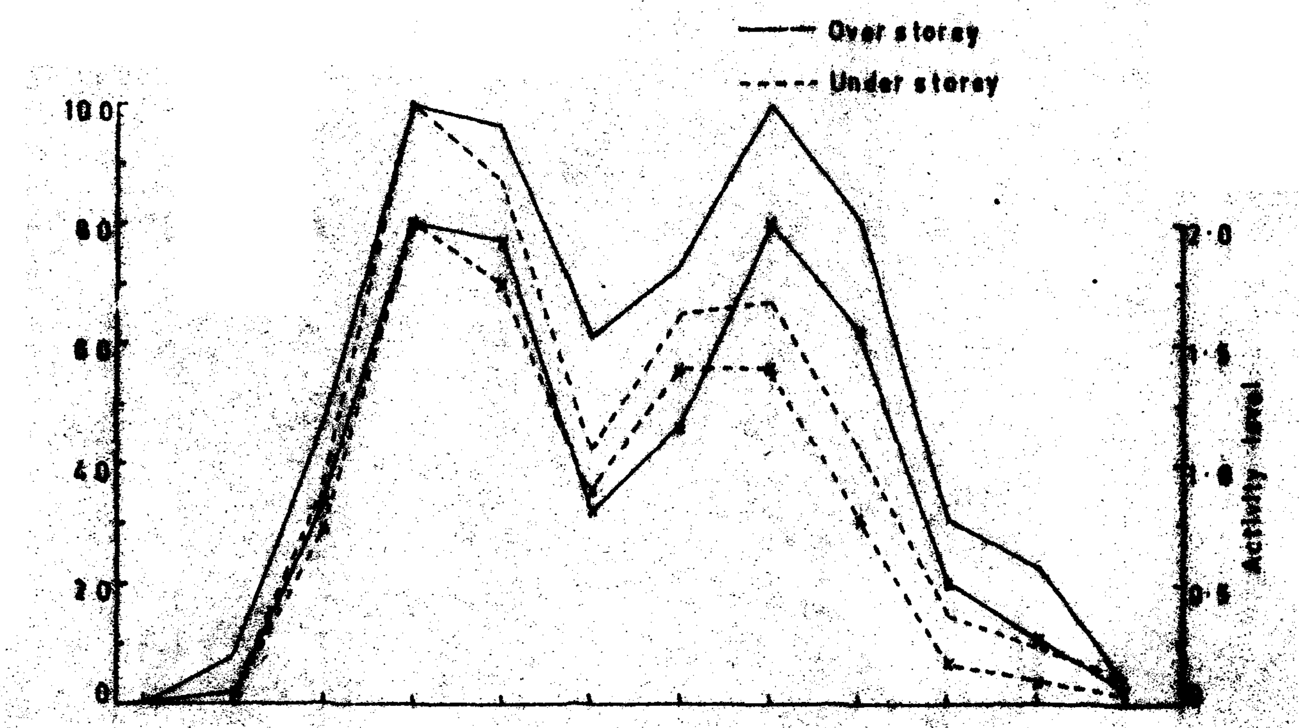


Fig.1.2.d.

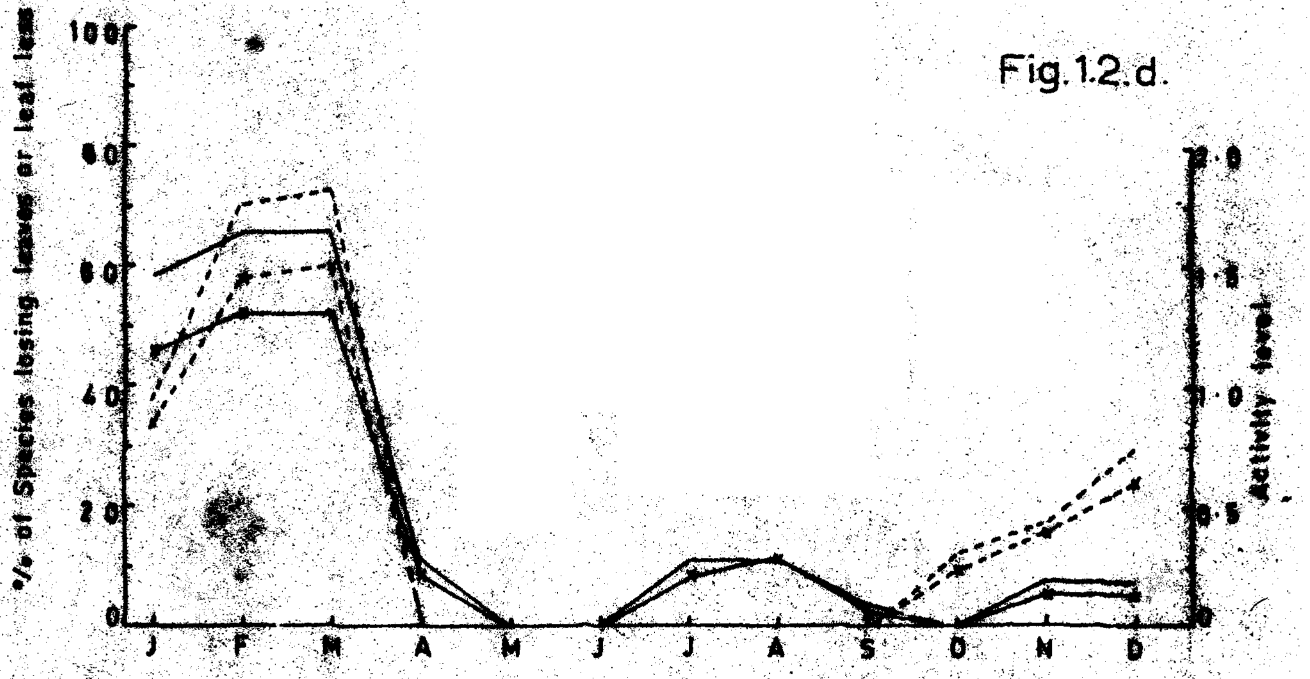


Table 1.3 : Overstorey and understorey tree species flowering in wet and dry seasons. (percentage values in parentheses).

SPECIES	SEASON DRY	WET	MARGINAL	EXTENDED	UNKNOWN
OVERSTOREY	10 (38.5)	10 (38.5)	5 (19)	- -	1 (4)
UNDERSTOREY	13 (32.5)	13 (32.5)	10 (25)	2 (5)	2 (5)

Most of the trees both of over and understoreys showed discontinuous flowering behaviour. It was only a few understorey species (Pieris ovalifolia and Eurya Japonica) which showed more or less continuous activity. Majority of the discontinuous flowering individuals had prolonged flowering activity. Asynchrony in flowering was quite pronounced for both the category of species (Table 1.4).

A large number of species of both over-and understoreys flowered at intervals more than one year. Majority of individuals of a population of 6 out of 17 overstorey and 3 out of 16 understorey species were observed to flower regularly on an annual basis (Table 1.5).

Fruiting activity

The community showed some rhythmicity in its fruiting pattern for both over-and understorey species. The overstorey species showed a major peak in October and a smaller one in February-March. The understorey species showed a major peak in October and a minor one in May (Fig 1.2d). A majority of species showed discontinuous and prolonged fruiting activity. Further a larger proportion of the species showed lengthy fruit development behaviour. Continuous fruiting activity was shown by two understorey species, Pieris ovalifolia and Eurya Japonica (Table 1.6).

Most of the species of the overstorey and understorey either fruit during the dry season or the wet season, more or

Table 1.4 : Duration of flowering activity of overstorey and understorey tree species (percentage values in parentheses)

SPECIES	ACTIVITY					
	CONTINUOUS	DISCONTINUOUS				UNKNOWN
		Prolonged synchronous	Asynchronous	Brief synchronous	Asynchronous	
OVERSTOREY	0	1 (4)	20 (77)	0	5 (19)	0
UNDERSTOREY	2 (5)	4 (10)	21 (52.5)	1 (2.5)	10 (25)	2 (5)
TOTAL	2 (3)	5 (8)	41 (62)	1 (1.5)	15 (23)	2 (3)

Table 1.5 : Overstorey and understorey tree species which flowered at intervals more than one year; I = only some individuals in population; II = all or more individuals but asynchronously; III = all individuals synchronously.

OVERSTOREY	TYPE	UNDERSTOREY	TYPE
Acer laevigatum	II	Cinnamomum tamala	II
Betula alnoides	I	Heptapleurum khasianum	III
Exbucklandia populea	III	Ilex khasiana	I
Castanopsis hystrix	II	I. theafolia	I
Cinnamomum impressinervum	II	Lindera pulcherima	II
C. obtusifolium	II	L. latifolia	II
Daphnephyllum himalayense	I	L. thomsonii	II
Englehardtia spicata	I	Litsea elongata	II
Eugenia terragona	I	Mallotus nepalensis	I
Litsea meissneri	I	Myrica esculenta	II
L. sebifera	I	M. rubra	II
Machilus kingii	II	Photinia notoniana	II
M. odoratissima	II	Symplocos Crataegoides	II
Quercus dealbata	II	S. pyrifolia	II
Q. griffithii	II	S. spicata	II
Q. paniculata	II	S. theafolia	II
Schima khasiana	II		

Table 1.6 : Duration of fruiting activity of over- and understorey tree species (percentage values in parentheses)

SPECIES	ACTIVITY						
	CONTINUOUS		DISCONTINUOUS				UNKNOWN
	Rapid	Lengthy	Prolonged Rapid	Lengthy	Brief Rapid	Lengthy	
OVERSTOREY	0 (0)	0 (0)	4 (15)	14 (54)	3 (12)	4 (15)	1 (4)
UNDERSTOREY	0 (0)	2 (5)	1 (2.5)	24 (60)	0 (0)	9 (22.5)	4 (10)
TOTAL	0 (0)	2 (3)	5 (8)	38 (59)	3 (5)	13 (20)	5 (8)

less in equal proportions. While a few understorey species showed fruiting for an extended period of time, none of the overstorey species belonged to this category (Table 1.7).

A large majority of the species had fleshy fruits, with less than 25% species having wind adapted fruits. The number of species producing fleshy fruits did not differ much between wet and dry seasons, both for over and understorey species. Only in the case of understorey species a large number of wind adapted fruits were found during the dry season compared to the wet season. Miscellaneous fruit type consisted of hard fruits such as acorns produced by Castanopsis and Quercus species (Table 1.8).

DISCUSSION

Biotic activity in a community follows the annual cycles of environmental parameters which regulate the phenological characteristics of individual species. In a forest community, the tree periodicity patterns give an idea of seasonal organization of floral and fruit resources (Frankie et al., 1974) 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 (Connell & Orias, 1964). The correlation of phenological activity in the present study with seasonally occurring events is best exemplified by the patterns of leaf fall and leaf flushing. Maximum leaf fall occurred during December to March at a time of water or cold

Table 1.7 : Seasonal fruiting pattern of tree species (Percentage values are in parentheses)

	SEASON			
SPECIES	DRY	WET	EXTENDED	BEHAVIOUR UNKNOWN
OVERSTOREY	13 (50)	12 (46)	0 (0)	1 (4)
UNDERSTOREY	19 (48)	13 (32)	4 (10)	4 (10)
TOTAL	32 (48)	25 (38)	4 (6)	5 (8)

Table 1.8 : Season of fruit maturity related to fruit type for different tree species (percentage values in parentheses)

		FRUIT TYPE		
SPECIES	SEASON	FLESHY	WIND ADAPTED	MISCELLANEOUS
OVERSTOREY	DRY	6 (43)	4 (50)	2 (50)
	WET	7 (50)	4 (50)	2 (50)
	EXTENDED	0 (0)	0 (0)	0 (0)
	UNKNOWN	1 (7)	0 (0)	0 (0)
	TOTAL	14 (100)	8 (100)	4 (100)
UNDERSTOREY	DRY	12 (42)	6 (75)	1 (33)
	WET	11 (38)	1 (12.5)	1 (33)
	EXTENDED	3 (10)	1 (12.5)	0
	UNKNOWN	3 (10)	0 (0)	1 (34)
	TOTAL	29 (100)	8 (100)	3 (100)
TOTAL		43	16	7

stress while flushing occurred mostly in the warmer months of March-April just before the rains. Thus, the leaf replacement strategy appears to be to minimize stress by leaf fall at such periods and maximize phtosynthetic activity during wet warm season of the year through flushing.

The pattern of community seasonality are the averages of the seasonal patterns of many species and though the community pattern may be generally most adaptive, certain species have evolved completely different approaches to leaf flushing and leaf fall which may be due to intrinsic factors. While the overstorey trees are mostly with double determinate flushes, understorey has quite a good number of species with a single determinate flush. The second flush in the overstorey species is in response to favourable environmental conditions during July-August. Leaves in the understorey species are retained for longer periods and this may be attributed to more homogenous environmental conditions like light and moisture which allow them to retain leaves for long periods without the risk of environmental stresses. Bentley (1979) has also reported a similar pattern of longevity of individual leaves of 27 understorey species in a Costa Rican tropical rainforest.

Though the relative number of flowerers are more or less equal in both dry (November-April) and wet (May-October) periods, the seasonal pattern of flowering for the forest has two peaks, a major and a minor one which correlates well with the relatively major (April) and minor (October) Xeric periods of the warm season. Thus this synchronization of flowering seems to be related to climatic conditions as also reported by others (Ducke & Black, 1953; Njoku, 1963; Frankie et al., 1974).

The peak production of mature fruits in the forest also corresponds with the onset of dry season after October; therefore most of the species have seeds with winter dormancy which is broken only after the warm season rains. The escape of flowering and fruiting by certain species on an annual basis as seen from the present study has also been reported by others (Ashton, 1969; Medway, 1972 and Janzen, 1978). Janzen (1978) has discussed the possible significance of this irregular behaviour as an escape from seed predation on a time basis. Departure from intraspecific synchrony in flowering and fruiting observed in a few species in the community may be the result of micro-environmental heterogeniety.

In the tropical trees dissemination of the propagule is usually considered to be by wind occurring at the end of the season of lowest vegetative activity, whereas in temperate trees, it is typically by animals and at the end of the vegetative growth season (Daubenmire, 1972). The forest community in the present case consisting of a majority of temperate elements follow the latter pattern.

SUMMARY

Phenology of a sub-tropical montane evergreen forest represented by a sacred grove at an elevation of 1900 m, near

Shillong in north-east India was done. 26 important overstorey and 40 understorey tree species were considered for this study. Leaf flushing in the majority of tree species coincided with the onset of warm period just prior to the rains to optimize production during the warm wet 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 in the month of October-November. The majority of the species were with fleshy fruits suggesting an adaptation for animal dissemination.

APPENDIX

List of species recorded and their phenological behaviour are given below. Abbreviations used in the lists are as follows:

1-12, January through to December;

P, periodic;

C, continuous;

b, brief periods - $\leq$ 2 weeks per episode;

p, extended periods - $>$ 2 weeks per episode;

M, multiple events per year;

S, synchronous;

A, Asynchronous;

D, deciduous;

F, rapid fruit maturation - $\leq$ 4 months;

L, lengthy fruit maturation - $>$ 4 months.

List 1. Phenological records for overstorey tree species

	Flowering		Fruiting		Leaf flushing		Leaf fall	
	Months	Behaviour	Months	Behaviour	Months	Behaviour	Months	Behaviour
ACERACEAE								
Acer laevigatum Wall.	3-6	PpA	8-10	PpF	4-5 & 7-8	PpM	2-3	PD
BETULACEAE								
Alnus nepalensis Don.	10-12	PpS	2-3	PpF	2-12	CS	1-3	CE
Betula alnoides Ham.	4-5	PpA	7-8	PbF	2-4 & 8-9	PpM	7-8	PD
ELAEOCARPACEAE								
Elaeocarpus braceanus Watt.	3-4	PpA	9-10	PpL	3-5 & 7-8	PpM	1-3	PE
ERICACEAE								
Rhododendron arboreum Sm.	2-3	PpS	9	PpL	4-5 & 7-9	PpM	1-3	PE
EUPHORBIACEAE								
Daphniphyllum himalayense Muell.	3-4	PpA	2-3	PpL	4-6 & 7-9	PpM	1-3	PE
FAGACEAE								
Castanopsis hystrix A.DC	10	PpA	3	PpL	3-5 & 7-9	PpM	1-3	PE
Pasania spicata Smith	4-5	PpA	8-10	PpL	3-5 & 7-9	PpM	1-3	PE
Quercus dealbata Hook F. & Thoms.	7-8	PpA	10-12	PpL	4-5 & 7-8	PpM	1-3	PE
Q. griffithii Hook F. Thoms.	8-9	PpA	10-12	PpL	4-5 & 7-8	PpM	11-12	PD
Q. paniculata	6-7	PpA	9-10	PpL	4-5 & 7-8	PpM	1-3	PE

List 1. contd.

	Flowering		Fruiting		Leaf flushing		Leaf fall	
	Months	Behaviour	Months	Behaviour	Months	Behaviour	Months	Behaviour
HAMAMELIDACEAE								
Exbucklandia populea Br.	11	PpA	12	PpL	3-11	PpM	11-12	PE
JUGLANDACEAE								
Englehardtia spicata Blume	7-8	PpA	12-3	PpL	3-5 & 7-9	PpM	8-9	PD
LAURACEAE								
Cinnamomum impressinervum Meissn.	3-4	PpA	-	-	4-5 & 8-9	PpM	1-3	PE
C. obtusifolim Nees.	3-4	PpA	7-8	PpL	4-5 & 8-9	PpM	1-3	PE
Litsea meissneri HK.F.	9-10	PpA	4	PpL	4-5 & 8-9	PpM	1-3	PE
L. sebifera Pers. Wall.	4-7	PpA	9-10	PpL	4-6 & 8-9	PpM	1-3	PE
Machil~~l~~us kingii HK. F.	1-4	PpA	6-7	PpF	4-6 & 8-9	PpM	1-3	PE
M. odoratissima Nees	3-4	PpA	5-6	PpF	4-6 & 8-9	PpM	1-3	PE
MAGNOLIACEAE								
Manglietia insignis (Wall.) Bl.	5	PbA	11-12	PbL	4-6 & 8-9	PpM	1-3	PE
MORACEAE								
Ficus nemoralis Wall.	-	-	11-12	PpL	3-11	PpM	4	PE

List 1 contd.

	Flowering		Fruiting		Leaf flushing		Leaf fall	
	Months	Behaviour	Months	Behaviour	Months	Behaviour	Months	Behaviour
MYRTACEAE								
Eugenia tetragona Wight	4-5	PbA	7-8	PbF	3-11	PpM	4	PE
OLEACEAE								
Ligustrum confusum Dcne	5-7	PbA	12-4	PbL	3-10	PpM	4	PE
ROSACEAE								
Prunus cerasoides Don.	10-12	PbA	6	PbL	3-11	PpM	7-8	PD
P. puddum Roxb.	9-10	PbA	10-11	PbF	3-11	PpM	7-8	PD
TERNSTROEMIACEAE								
Schima khasiana Dyer	4-6	PpA	2	PbL	4-10	PpM	2-3	PD

List 2 : Phenological records for understorey trees

	Flowering		Fruiting		Leaf flushing		Leaf fall	
	Months	Behaviour	Months	Behaviour	Months	Behaviour	Months	Behaviour
ANACARDIACEAE								
Rhus semialata Murray	3-5	PpA	9-10	PpL	3-4 & 7-8	PpM	1-3	PD
R. succedanea Linn.	3-5	PpA	1-5	PpL	3-5	PpM	1-3	PD
AQUIFOLIACEAE								
Ilex khasiana Purkayastha	3-4	PpA	10	PpL	4-5 & 7-8	PpM	12-3	PE
I. theafolia Wall.	4-6	PpA	7	PpL	4-5 & 7-8	PpM	12-3	PE
ARALIACEAE								
Heptapleurum khasianum Clarke	12	PpA	-	-	4-5	PpM	11-12	PE
ELAEGNACEAE								
Elaegnus pyriformis Hook F.	10-11	PpA	12-1	PpL	4-5	PpM	11-12	PE
EUPHORBIACEAE								
Mallotus nepalensis Muell	6	PbA	9-10	PpL	4-10	PpM	12-3	PE
Phyllanthus glaucus Wall.	4-5	PpS	-	-	4-10	PpM	2-3	PE
ERICACEAE								
Pieris ovalifolia Don.	6-12	CS	1-12	CL	3-12	C	12-2	CE
Rhododendron formosum Wall.	3-4	PbA	10-12	PbL	4-6	PpM	12-2	PE
FAGACEAE								
Quercus sp.	-	-	-	-	3-4	PpM	2-3	PD
HAMAMELIDACEAE								
Corylopsis himalayana Griff.	2-3	PbA	4-5	PbL	4-5 & 7-8	PpM	2-3	PD

List 2. contd.

	Flowering Months	Flowering Behaviour	Fruiting Months	Fruiting Behaviour	Leaf flushing Months	Leaf flushing Behaviour	Leaf fall Months	Leaf fall Behaviour
LABIATEAE								
Leucospectrum canum Smith	2-3	PbS	4-5	PbL	4-8	PpM	2-3	PD
LAURACEAE								
Cinnamomum tamala Fr. Nees.	2-5	PbA	6-10	PpL	4-5	PpM	2-3	PE
Lindera pulcherima Benth	3	PbA	4-5	PbL	4-5	PpM	2-3	PE
L. latifolia Hook F.	10	PbA	2	PbL	4-5	PpM	2-3	PE
L. thomsonii Allen.	10	PbA	2	PbL	4-5	PpM	2-3	PE
Litsaea elongata Wall.	10	PbA	4-5	PbL	4-5	PpM	2-3	PE
LEGUMINOSAE								
Acacia dealbata Link.	2-4	PpS	10	PpL	3-11	PpM	2-3	PD
Erythrina arborescens Roxb.	8-9	PpS	10-11	PpL	3-11	PpM	2-3	PE
MYRICACEAE								
Myrica esculenta Buch. - Ham.	10	PpA	5	PpL	3-4	PpM	2-3	PE
Erythrina arborescens Roxb.	10-11	PpA	5	PpL	3-4	PpM	2-3	PE
MYRSINACEAE								
Myrsine semiserrata Wall.	9-12	PpS	1-6	PpL	3-12	C	12-3	CE
OLEACEAE								
Ligustrum lucidum Aiton	6-8	PpA	11	PpL	3-9	PpM	3	PE
L. nepalense Wall.	6-7	PpA	10-11	PpL	3-9	PpM	3	PE
L. robustum Bl.	5-7	PpA	12-4	PpL	3-9	PpM	3	PE

List 2 contd.

	Flowering Months	Flowering Behaviour	Fruiting Months	Fruiting Behaviour	Leaf flushing Months	Leaf flushing Behaviour	Leaf fall Months	Leaf fall Behaviour
ROSACEAE								
Photinia notoniana Wight & Arn.	2-3	PpA	6-7	PpE	3-4 & 7-8	PpM	12-1	PE
Prunus nepalensis Koch.	3-5	PpA	10	PpL	4-9	PpM	10-11	PD
Pyrus baccata L.	2-4	PpA	10	PpL	4-9	PpM	10-11	PD
P. pashia Don.	2-4	PpA	7	PpL	4-9	PpM	10-11	PD
P. polycarpa Hook. F.	2-4	PpA	10	PpL	4-9	PpM	10-11	PD
RUBIACEAE								
Wendlandia paniculata DC.	3-5	PbA	10-12	PbL	4-5 & 7-8	PpM	10-12	PE
RUTACEAE								
Skimmia laureola Sieb & Zucc.	-	-	-	-	3-4 & 7-8	PpM	2-3	PE
SYMPLOCACEAE								
Symplocos crataegoides Ham.	5	PpA	12-1	PpL	4-5 & 7-8	PpM	1-3	PD
S. pyrifolia Wall.	10	PpA	3	PpL	4-5 & 7-8	PpM	1-3	PE
S. spicata Roxb	10	PpA	3	PpL	4-5 & 7-8	PpM	1-3	PE
S. theafolia Don.	10	PpA	3	PpL	4-5 & 7-8	PpM	1-3	PE
TERNSTREOMIACEAE								
Eurya acuminate DC	9-11	PpA	1-6	PpL	4-9	PpM	1-3	PE
E. Japonica Thunb.	6-1	CS	5-11	CL	3-9	C	12-3	CE

CHAPTER II

Litterfall pattern in a sub-tropical evergreen montane forest in north-east India

LITTERFALL PATTERN IN A SUB-TROPICAL EVERGREEN MONTANE FOREST IN NORTH-EAST INDIA

INTRODUCTION

The importance of litter production in the forest ecosystem has long been recognized; therefore this is one of the aspects that has received much attention (Bray & Gorham, 1964; Jensen, 1974; Jordan & Murphy, 1978). While most of the studies on litter production have been done on temperate forests, tropical and sub-tropical forest ecosystems have also received some attention (Jenny *et al.*, 1949; Laudelot & Meyer, 1954; Nye, 1961; Cornforth, 1971; Hains & Foster, 1977; Klinge & Rodrigues, 1968; Singh, 1980). However, the data available on tropical and sub-tropical montane forests are few and scattered. A few important studies on the montane forests of the tropical and sub-tropical belt are those of Jenny *et al.*, (1949) in Colombia (1630m), Edwards (1977) at New Guinea (2400 - 2500 m), Saxena *et al.* (1978) at Nainital, India (1950 - 2200m) and Tanner (1980) at Jamaica (1500m).

The present study on litter production pattern of a sub-tropical montane forest at an elevation of 1900 m near Shillong concerns that of a mixed evergreen sacred forest grove. This sacred grove has been maintained by the local Khasi tribe with least disturbance as they believe that their sylvan deities live here and therefore this represents a relict climax community of this area which otherwise is highly disturbed due to slash and burn agriculture (Ramakrishnan & Toky, 1978) which is a prevalent form of agricultural practice of the region. Majority of the trees of this forest, although evergreen are strongly seasonal in their phenology. This study on the seasonal pattern of litterfall is, therefore, of considerable interest from phenological and production ecological points of view.

METHODS OF STUDY

The study area, climate and vegetation have been described in Chapter 1.

Litter was collected from 12 randomly placed $1m^2$ permanent quadrats, demarcated by wooden frames with a permanently fixed nylon mesh at a height of about 15 cm from the ground which permitted drainage of water without any litter loss. Litter sampling was done at monthly intervals during drier months and at fornightly intervals during the rainy season. The collection material was classified according to the tree species and the individual fractions of litter and was oven dried at 85^oC to a constant weight. Leaf litter was separated into 12 major tree species and all other species were considered under the mixed leaf category. Flowers, fruits and twigs were considered jointly for all the species. Unidentifiable plant litter other than those considered above were grouped into miscellaneous category.

The average leaf-life of the forest as a whole was based on 12 important tree species in the forest, on the basis of periodic observations of identified leaves on a number of individuals.

RESULTS AND DISCUSSION

Leaf-life

The mean leaf-life value of about 20 months for the important trees in the forest suggests the generally evergreen physiognomy of the forest. The leaves of *Cinnamomum impressinervum*, *Machilus kingii*, *Quercus dealbata* and *Q. paniculata* which are dominant species in the forest were retained for periods greater than two years. The deciduous species like *Litsea sebifera* and *Schima khasiana* showed an average leaf-life of one year only. *Acer laevigatum*, *Lindera pulcherima* and *Manglitia insignis* fall in between these two extremes (Table 2.1).

Litterfall

The total annual litterfall in the forest worked out to 8.96 t ha^{-1} yr^{-1}. A major fraction of this was represented by leaf, followed by twigs, miscellaneous litter, fruits and flowers (Table 2.2). The specieswise contribution of leaf litter was highest for *Quercus dealbata* an important overstorey species followed by *Symplocos crataegoides* a dominant of the understorey (Appendix).

Comparisons with other Montane tropical/sub-tropical forests

In any comparison of litter production it is important to consider the highly variable nature of litterfall in space and time. The results presented here showed that the standard error of the mean was usually less than 10% of the mean for the major litter fractions as well as total litter (Table 2.3). Since a

Table 2.1 : Mean leaf-life of some important tree species

Species	Average leaf-life (months)
Acer laevigatum	14
Cinnamomum impressinervum	26
Elaeocarpus pyriformis	18
Lindera pulcherima	15
Litsea sebifera	12
Machilus kingii	28
Manglitia insignis	16
Quercus dealbata	30
Q. paniculata	30
Rhododendron arboreum	20
Schima khasiana	12
Symplocos crataegoides	18
TOTAL	20

Table 2.2 : Annual contribution by different litter fractions

Litter fractions	Amount (t/ha/yr) ± S.E.	% of the total litter
Leaves	5.68 ± 0.56	63.4
Twigs	1.45 ± 0.18	16.2
Fruits	0.50 ± 0.08	5.6
Flowers	0.27 ± 0.06	3.1
Miscellaneous	1.05 ± 0.11	11.7
Total	8.96 ± 0.72	100

Table 2.3 : Accuracy of measurements for litter and litter fractions

Litter	Amount t/ha/yr	Range	S.D.	S.E.(%)
Leaves	5.68	2.94 - 8.70	1.95	9.94
Twigs	1.45	0.60 - 2.44	0.63	12.48
Fruits	0.50	0.16 - 1.07	0.27	15.35
Flowers	0.27	0.02 - 0.74	0.20	21.08
Miscellaneous	1.05	0.60 - 1.69	0.37	10.06
Total	8.96	2.66 -13.32	2.50	8.08

similar degree of variability was also found by many other workers (Klinge & Rodrigues, 1968; Brassel et al., 1980; Tanner, 1980), these values can be considered as reliably representative and it may be relevant to the comparisons of the estimates of litterfall from studies of other tropical and sub-tropical montane forests shown in table 2.4. The annual litterfall recorded in the present study is comparable to the data of others. A comparison with lowland tropical forests, however, indicates that these have generally higher litter production than those obtained in montane forests of higher elevations.

The value of leaf litter is similarly within the range of reported value (6 to 10.4 + ha^{-1} yr^{-1}, Table 2.4). The higher proportion of leaf fraction in the litter, reported in the present study is also in conformity with the results of others (Bray & Gorham, 1964; Rodin & Brazilevich, 1967).

Seasonality of litterfall

Litter fell throughout the year with a marked seasonal distribution. It was less during May to December and was maximum during January to April, with a distinct seasonal peak in the month of March. Another minor peak was seen in the month of October. These periods of maximum leaf shedding corresponded well with the dry periods of the warm season (Fig 2.1). Litter production during the dry months was 3 times more than that during the wet period and the rate of fall was also equally high (Table 2.5). The seasonal pattern of fall of litter fractions

Table 2.4 : The annual litter production in some tropical and sub-tropical forests of the world (values in t ha^{-1})

FOREST TYPE	ALTITUDE (m)	LITTER FRACTION Leaves	Bark & Twigs	fruits & flowers	Total	AUTHOR
LOWLAND FORESTS						
Semi-evergreen young secondary forest, Zaire	300	-	-	-	12.3	Laudelot & Meyer (1954)
Semi-evergreen secondary forest, Ghana	150	7.0	3.5	-	10.5	Nye (1961)
Mature secondary forest, Panama	137	5.83	2.30	1.23	11.10	Hains & Foster (1977)
MONTANE FORESTS						
Colombia	1630	-	-	-	10.1	Jenny et al. (1949)
Central site of radiation Study, Puerto Rico	460	4.8	-	-	-	Wiegert (1970)
New Guineae	2400-2500	6.35*	1.20**	-	7.55	Edwards (1977)
Nainital, India	1950-2200	-	-	-	5.5	Saxena et al. (1978)
Tropical Australia	680-820	-	-	-	9.25	Brassel et al. (1980)
Jamaica						
Gap forest	1550	5.5	0.9	-	6.4	Tanner (1980)
Mor ridge forest		4.9	1.7	-	6.6	
Mull ridge forest		5.6	0.2	-	5.8	
Wet selope forest		4.4	1.2	-	5.6	
Shillong, India.	1900	5.67	2.50	0.78	8.96	Present Study

*Leaves and other material ** Woody material

Fig. 2.1 : Temporal distribution of litterfall, temperature and rainfall in Upper Shillong montane forest. Vertical lines are Standard Errors of the mean.

Fig. 2.1.

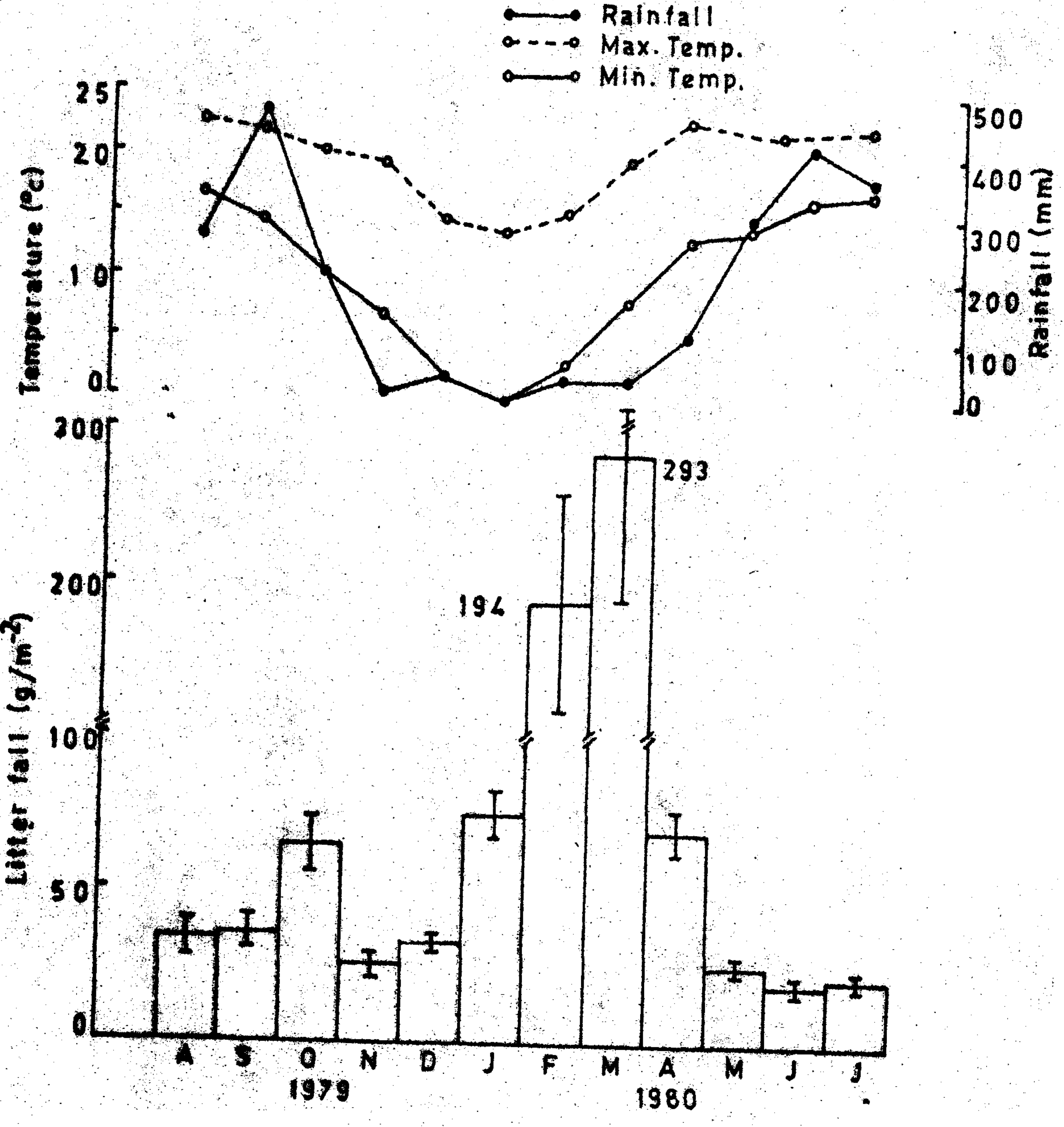

Rainfall
Max. Temp.
Min. Temp.
Temperature (°c)
25
20
10
0
Rainfall (mm)
500
400
300
200
100
0
Litter fall (g/m-2)
300
200
100
50
0
194
293
A
S
O
N
D
J
F
M
A
M
J
J
1979
1980

Table 2.5 : The seasonality of litterfall in Upper Shillong Forest during 1979-80; values in parentheses are % of the total in each column.

Period	Amount of litter-fall t/ha/yr	Rate of litterfall g/day
Dry (181 days)	6.92 (77)	3.82
Wet (184 days)	2.04 (23)	1.11
Total	8.96 (100)	2.45

is shown in Fig 2.2. This was similar to the pattern observed for total litterfall. However, maximum flower and fruit litter was found to be in the month of April. The seasonal pattern of leaf litterfall for individual species also followed a more or less similar general trend (Appendix).

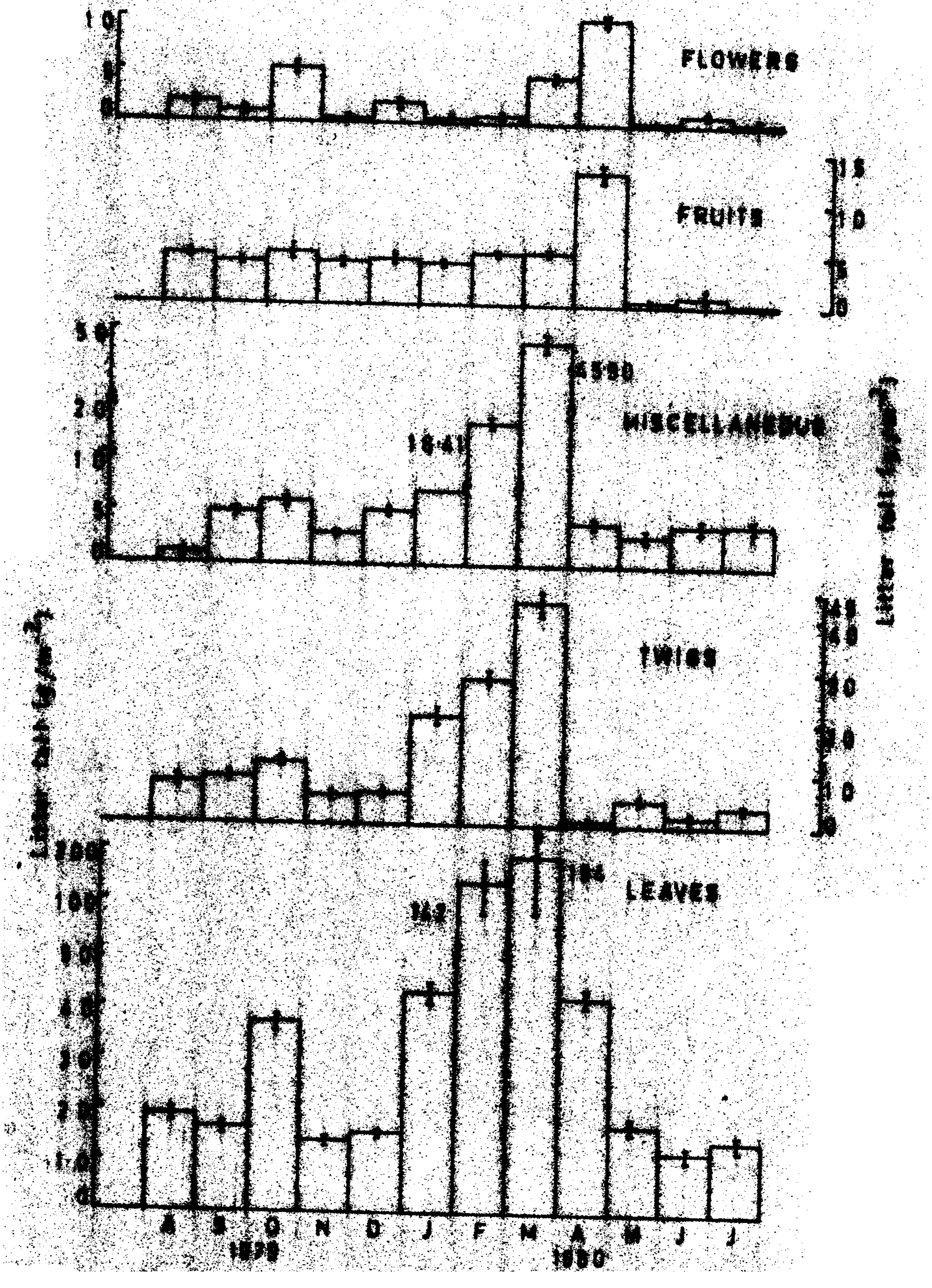
Jorgensen (1975) maintained that three main factors limit litter production - temperature, water and nutrient availability. At the present study site the temperature and rainfall variables are quite seasonal which cause large seasonal fluctuations in the fall pattern. The rate of litterfall was also almost 3 times higher during dry season compared to that during wet period. Such a pattern of coincidence of litterfall with the dry season was also reported by others (Nye, 1961; Klinge & Rodrigues, 1968; Singh, 1980; Tanner, 1980) which is related to water stress (Whitmore, 1975). While the litterfall pattern generally coincided with phenological events in the forest, fruit fall was maximum during April though majority of the species produced mature fruits in the preceding October. This is due to heavy fall of fruits of Litsea and Lindera during the month of April which contributed to the fruit litter.

SUMMARY

Total above-ground litterfall in a sub-tropical evergreen montane forest at Shillong (1900m) averaged 8.95 t $ha^{-1}yr^{-1}$; leaves, twigs, flowers and fruits contributed 63%, 16%, 3% and 6% respectively. Other miscellaneous litter fraction consisting

Fig. 2.2 : Seasonal pattern of fall of litter fractions in the Upper Shillong montane forest.

Fig. 2.2.


FLOWERS
FRUITS
MISCELLANEOUS
16·41
TWIGS
LEAVES
142
A
S
O
N
D
J
F
M
A
M
J
J
1979
1980
Litter fall (g/m²)

of fragments of leaf tissue, bark etc. accounted for 12% of the total annual litterfall. Litterfall occurred throughout the year, but with a distinct peak in the months of March. The rate of litterfall in the drier part of the year (November to April) was approximately thrice the rate during the wetter part of the year. Mean leaf-life was estimated to be an average of 20 months for the forest.

Appendix: Monthly variation of leaf litter ($gm^{-2}yr^{-1}$) in different tree species
(± S.E. of the mean and values in parentheses are % of the total)

	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Total
Acer laevigatum	-	-	-	0.2 ±0.2	0.6 ±0.5	5.2 ±1.6	8.9 ±3.9	1.9 ±0.6	0.5 ±0.4	0.1 ±0.05	0.1 ±0.1	0.05 ±0.03	17.5 (3.1)
Cinnamomum impressinervum	0.3 ±0.1	0.1 ±0.1	0.4 ±0.2	0.1 ±0.1	0.4 ±0.2	0.6 ±0.4	4.0 ±1.9	14.8 ±2.4	0.5 ±0.2	1.3 ±0.1	0.4 ±0.2	0.4 ±0.2	23.3 (4.1)
Elacocarpus lancifolius	-	1.4 ±0.8	0.5 ±0.3	0.9 ±0.4	0.3 ±0.2	0.5 ±0.3	13.6 ±5.3	16.2 ±4.6	4.2 ±2.5	1.5 ±0.9	0.3 ±0.2	0.9 ±0.5	40.2 (7.1)
Lindera pulcherima	0.4 ±0.3	0.4 ±0.2	0.5 ±0.3	0.4 ±0.2	0.4 ±0.2	3.2 ±1.3	7.8 ±3.3	7.7 ±4.3	0.7 ±0.3	0.6 ±0.3	0.8 ±0.3	0.9 ±0.3	23.9 (4.2)
Litsea sebifera	-	-	0.4 ±0.2	0.4 ±0.3	0.3 ±0.2	0.7 ±0.4	3.5 ±2.5	1.0 ±0.8	1.4 ±0.9	1.2 ±1.0	0.1 ±0.1	1.1 ±0.9	10.0 (1.8)
Machilus kingii	1.0 ±0.8	0.3 ±0.1	2.5 ±0.9	0.2 ±0.1	0.3 ±0.1	0.6 ±0.2	2.3 ±1.6	4.6 ±1.8	1.5 ±0.7	0.7 ±0.3	0.1 ±0.1	0.5 ±0.2	15.0 (2.6)
Manglitia insignis	0.7 ±0.4	0.8 ±0.7	3.2 +1.4	1.3 ±0.5	0.6 ±0.3	1.4 ±0.6	5.7 ±2.3	14.2 ±7.9	1.7 ±0.9	0.4 ±0.3	0.6 ±0.4	0.2 ±0.2	30.9 (5.4)
Quercus dealbata	4.4 ±1.4	2.5 ±1.0	2.0 ±0.9	1.1 ±0.5	1.4 ±0.7	2.5 ±1.2	18.9 ±9.8	45.5 ±17.9	10.7 ±6.0	2.6 ±0.8	2.3 ±0.6	3.0 ±1.7	96.9 (17.1)
Q. paniculata	-	0.2 ±0.2	4.1 ±4.1	1.0 ±0.4	0.8 ±0.4	3.9 ±1.4	14.2 ±5.6	19.2 ±7.4	4.6 ±2.7	3.1 ±1.8	0.6 ±0.4	0.8 ±0.5	52.4 (9.2)
Rhododendron arboreum	0.9 ±0.8	1.7 ±1.7	0.8 ±0.4	1.7 ±1.3	0.4 ±0.1	1.0 ±1.0	2.5 ±2.5	5.7 ±5.7	0.4 ±0.3	0.3 ±0.3	0.2 ±0.2	0.9 ±0.9	16.5 (2.9)
Schima khasiana	0.4 ±0.3	0.7 ±0.4	6.3 ±4.0	0.6 ±0.4	2.4 ±0.9	7.8 ±4.0	6.7 ±3.4	1.3 ±0.7	0.3 ±0.2	0.3 ±0.2	0.5 ±0.4	0.4 ±0.2	27.7 (4.9)
Symplocos crataegoides	3.4 ±1.1	2.5 ±0.7	1.5 ±1.1	2.3 ±1.3	1.5 ±0.6	5.1 ±1.9	18.9 ±5.5	21.6 ±7.1	6.4 ±2.2	1.9 ±0.7	1.0 ±0.2	1.1 ±0.5	67.2 (11.8)
Others	7.8 ±0.9	5.7 ±0.8	15.1 ±7.2	3.9 ±0.5	6.2 ±1.1	10.0 ±1.2	34.5 ±9.3	50.7 ±20.6	9.4 ±0.9	4.6 ±0.8	5.2 ±0.8	4.3 ±0.7	141.1 (25.4)
TOTAL	19.3 ± 2.7	16.5 ±2.7	37.2 ±7.7	14.1 ±2.1	15.5 ±1.8	42.6 ±4.1	141.9 ±26.6	194.3 ±42.6	42.2 ±5.0	17.4 ±1.9	12.3 ±1.8	14.4 ±2.4	567.58 (100)

SECTION B

ARCHITECTURE AND GROWTH PATTERN

CHAPTER III

An analysis of architecture and growth pattern of *Schima* species

AN ANALYSIS OF ARCHITECTURE AND GROWTH PATTERN OF SCHIMA SPECIES

INTRODUCTION

Early studies on tropical tree growth were of a phenological nature (Büsgen & Münch, 1929; Holttum, 1940; Koriba, 1958), though a few detailed investigations are also available on tea (Bond, 1942); rubber (Hallé & Martin, 1968) and *Rhizophora mangle* (Gill & Tomlinson, 1971). One of the first comprehensive studies on the vegetative architecture of tropical plants is that of Hallé *et al*. (1978) which has opened up new avenues for studies on individual tree species as well as the forest community as a whole.

While canopy structure and its relationship to light interception and yield has received some attention from forest ecologists and silviculturists (Farmer, 1976), little attention has been paid to tree architecture of closely related species or populations of the same species from different environments. Trees have evolved various strategies for niche occupancy and survival in different environments through appropriate crown development, leaf and branch orientation, and overall architecture (Horn, 1971). The understanding of these processes is a prerequisite for better forest management and tree improvement programmes. From the production point of view, the answer to the higher productivity of the tropical forests may have to be found in the growth pattern and canopy structure of tropical trees (Ramakrishnan, 1978).

The present paper reports a comparative study of the growth pattern and architecture of two closely related species of Schima Reinw. ex. Blume (Ternstroemiaceae), namely S. wallichii (DC) Korth, and S. khasiana Dyer, growing at different altitudes. These two species are economically important timber trees of the north-east India. In the north-eastern hills region of India, S. wallichii has an altitudinal range of 100 to 1600 m and S. khasiana is restricted to higher elevations (1600 to 1900m) only. These are early successional trees that come up in the secondary fallows left after slash and burn agriculture (locally known as '**Jhum**'). The species are light demanding and regenerate abundantly in the open through light, wind-dispersed seeds. The trees coppice well. In secondary forests they form canopy trees reaching an average height of 25-30m at lower altitude, 15-20m at higher altitude for S. wallichii and 12-15m for S. khasiana. S. wallichii is distributed throughout the Indo-Malayan region. In Java it is not a real pioneer tree, rather it specializes in poor ruined soils, far away from the rain-forest (Hallé, Personal Communication). Whitmore (1975) considers it to be a light demander, locally colonizing man-made clearings in lowland and lower montane forests of Malaya. According to his observations the species has some pioneer characters but lacks the aggression of true pioneers.

STUDY AREA AND CLIMATE

Three sites at different altitudes, at Upper Shillong (1900m), Shillong (1600m) and Burnihat (100m), in the Khasi

PLATE 3

A pure stand of early successional *Schima wallichii* near Umsaw (1000m).

PLATE 4

A close view of the pure stand of early successional *Schima wallichii* near Umsaw (1000 m).

PLATE 3

PLATE 4

hills of Meghalaya State in the north-eastern hill region of India (sub-tropical), were selected for the present study. The lower elevation site at Burnihat (26^{o} 02'N and $91^{o}52'$ E) is located about 90 km north of Shillong (25^{o} 34'N and 91^{o} 56'E). Studies on S. khasiana were done at one of the sites only at Upper Shillong where this species is restricted, whereas studies on S. wallichii which has a wider distributional range were done both at Shillong and Burnihat.

The climate is monsoonic with the rainfall mostly confined to a few months . The year may be divided into four more or less well marked seasons; (i) the monsoon season of heavy rain during May-September, due to the Southwest monsoon; (ii) a transitional period of low rainfall due to retreating monsoons during October-November; (iii) a winter season during December to February with scattered low rainfall; and (iv) a summer dry period during March-April. The average annual rainfall during the study period was 2350 mm at Upper Shillong, 1800mm at Shillong and 1550mm at Burnihat. The average maximum temperature during the monsoon period was 24.00°C and the average minimum was 16.13°C at Shillong whereas the average maximum at Burnihat was 32.07°C and the average minimum was 24.13°C. Shillong had an average maximum of 16.01°C and average minimum of 6.23°C during the winter whereas at Burnihat this was 24.87°C (average maximum) and 12.37°C (average minimum). The temperature conditions at Upper Shillong were generally lower than

Fig. 3.1 : Ombrothermic diagram for the study sites, mean maximum temperature (O), mean minimum temperature (●) & rainfall (△) during the study period.

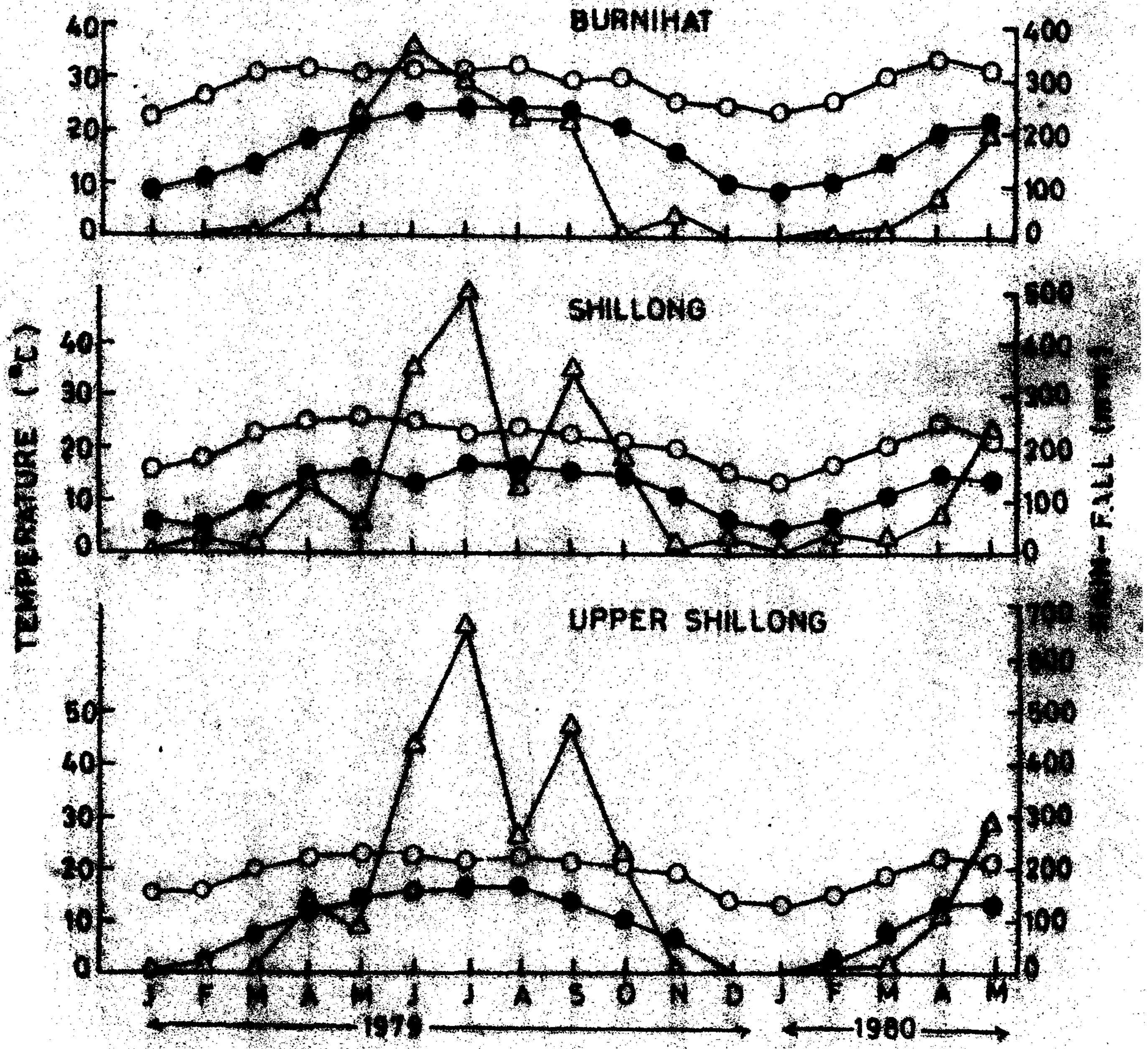

BURNIHAT
SHILLONG
UPPER SHILLONG
TEMPERATURE (°C)
FALL (mm)
0
10
20
30
40
50
0
100
200
300
400
500
600
700
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1979
1980

Fig.3·1

that of Shillong with an average maximum of 22.24°C and a minimum of 15.84°C during the monsoon and average maximum of 15.47°C and minimum of 1.18°C during the winter. (Fig. 3.1)

METHODS OF STUDY

For shoot extension measurements five replicates of 5 year old open grown trees were randomly chosen at different sites in the forest openings. The average height of S. wallichii at the lower altitude was 293 cm (dbh 1.80cm), at the higher altitude it was 219 cm (dbh 1.94 cm) and of S. khasiana at Upper Shillong was 203 cm (dbh 1.28 cm). Detailed architectural analysis of the trees was based on one typical tree at each site. A stage erected around one selected tree was used for making detailed measurements. At each site the tree was divided into the different whorls of branches, each whorl representing one year's growth. The nomenclature used to describe orders of branches was that of Hallé et al. (1978). Ordinal numbers were used, considering the trunk of the tree as the starting point order zero (0) and the branches as the first, second, and third order respectively in chronological sequence. The pattern of branch development was studied by following the fate of buds on current increments of main axis and one year old First order branches.

For the estimation of leaf production and fall each leaf was tagged using small light aluminium tags. For leaf blade area calculations a correction factor was applied by dividing the actual leaf area measured using a planimeter, by the

PLATE 5

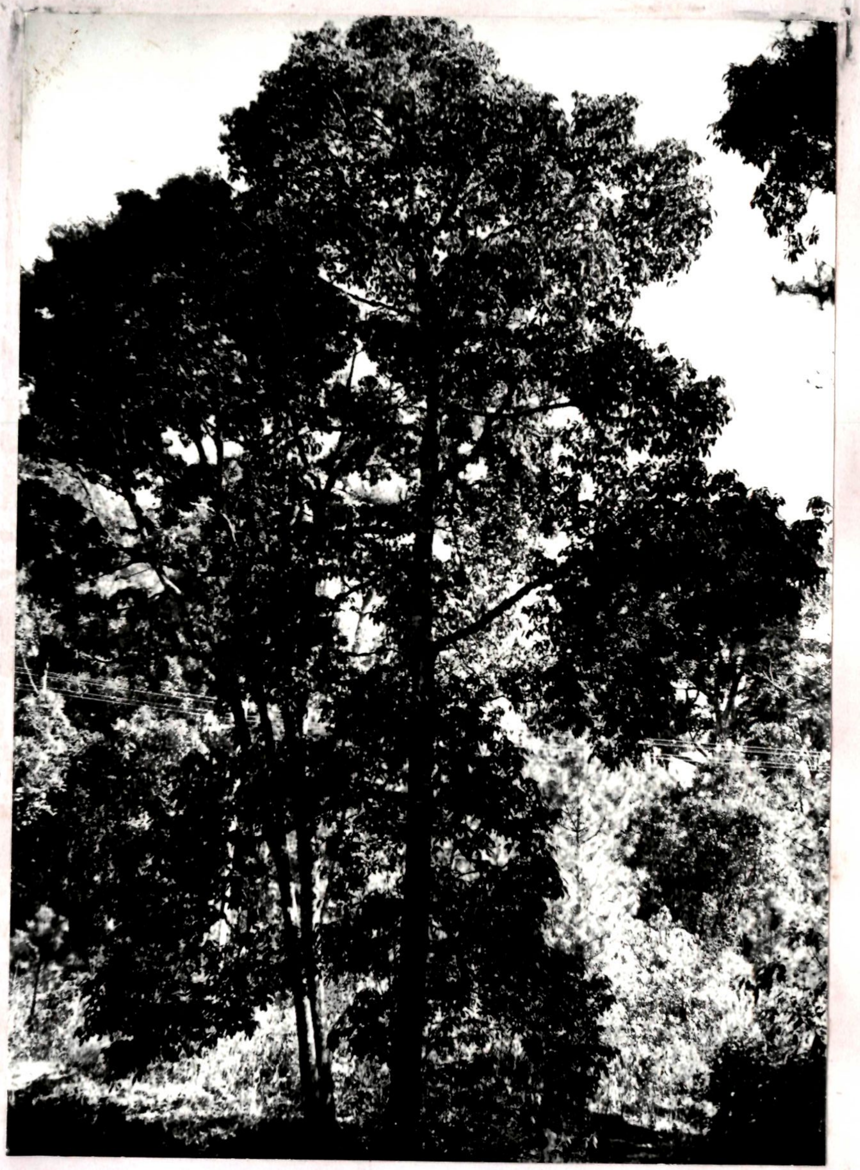
A stage erected around a tree of *Schima khasiana* to study architecture and growth pattern. The similar method has been followed for all other species.

PLATE 6

A tree of *Schima khasiana* showing a clear bole and crown geometry.

←PLATE 5

PLATE 6→



calculated leaf area (length x width). The leaf area was then calculated using the formula, $A = c \times l \times w$ (Dolph, 1977), where c is the correction factor appropriate for the species as well as the different populations.

Leaf and branch angles were measured by means of a protractor. The leaf blades deviate from the horizontal in several ways such as tilting of the apex downward or upward, folding of margins upward and twisting of the petioles. The most vertical aspect of each individual leaf was measured as degree inclination from the horizontal. Branch angles were measured as the orientations from the main trunk.

For estimating the effect of the position of leaves on the tree canopy and the consequent shading, the crown of another five year old tree was identified. At three levels of the canopy (upper, middle and lower), 25 leaves each from the periphery and centre of the crown were harvested. These leaves were referred as 'sun' and 'shade' leaves respectively. The mean leaf length and width, petiole length as well as the correction factor for calculating leaf area were estimated separately for each category. Leaf area, however, was calculated individually by using planimeter. Dry weights were estimated after over drying for 24 hours at $85^{\circ}C$ to a constant weight.

For calculation of bifurcation ratios, branches were ordered according to Horton's rule, modified by Strahler (1957). In this method segments of branch systems are ordered and a branching ratio was calculated which subsequently serves as an index of 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. 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. The bifurcation ratio is calculated by Motomura's formula (1947), $Rb = N-Nmax/N-N_1$ (Steingraeber et al., 1979) where N is the total number of branches of all orders, Nmax is the number of the branches of the highest order and N_1 is the number of branches of the first order. At each site 10 open-grown and 10 trees grown in a closed stand but not strictly under shade were ordered according to Strahler's method and the bifurcation ratio was calculated.

Phenological observations like flowering, fruiting, seed dispersal, flushing and growth cessation were made on marked trees at all the three sites.

RESULTS

Pattern of architectural development

The two species of Schima have a similar architecture development pattern, though there are quantitative and seasonal variations in growth behaviour. The architecture (Hallé et al., 1978), is determined by a monopodial trunk which grows rhythmically and so develops tiers of branches.

After winter dormancy the growth starts with flushing of new leaves when rapid unfolding and expansion of leaves as well as internodal elongation occurs. The leader axis, a monopodial trunk, is orthotropic in having radial symmetry and spiral phyllotaxy. The lateral branches are also orthotropic with radial symmetry and spiral phyllotaxy. Branch production is sylleptic, as axillary buds grow into branches without any rest period. These branches are characterized by the lack of basal bud scales or scale scars and have an extended basal internode (hypopodium). Further, there is no transition in leaf morphology along the axes of sylleptic branches, the development of sylleptic branches is closely correlated with the activity of terminal meristem i.e. the rhythm of the main leader (rhythmic branching type of Hallé *et al.*, 1978). This also confers a more or less whorled arrangement of laterals. The pattern of branch development on the main leader is repeated on lateral branches also. Branching on laterals is mainly restricts to the abaxial side, which broadens the crown structure. The lower branches in the canopy tend to become horizontal. The nodes devoid of branches bear resting buds in the axil of leaves, these may develop into inflorescences on older shoots or grow out as proleptic shoots if the axis above is damaged (reiteration - Oldeman, 1974). Both the reiterated and sequential (of unmodified architecture) axes conform to the original architecture. As the lower branches of the crown compete for space and light, they are shed gradually after the death of terminal bud and through a series

PLATE 7

Growth habit of an open grown *Schima wallichii* (Rauh's model).

PLATE 8

A closer view of *Schima wallichii* showing upper whorl of branches with finer patterns (Rauh's model).

PLATE 7

PLATE 8

PLATE 9

Sylleptic branching in <u>Schima</u> <u>wallichii</u>. Note the development of branches without a rest period of axillary buds.

PLATE 10

Development of a proleptic branch in <u>Schima</u> <u>wallichii</u> after the damage to the main leader. Note the proliferation of a latent axillary meristem.

PLATE 9

PLATE 10

of reiteration and death of the subsequent terminal bud, the branch is discarded. This gradually shifts the crown vertically. The lowest major branch in most of the cases, is a reiterated trunk representing inversion of morphological units. This level of reiterated trunk has been termed as the morphological inversion point (Oldeman, 1974). This helps in achieving a branchless bole, as well as the characteristic shape of the tree crown. The initial architecture complex of the tree undergoes several changes during its life cycle. Since the sapling is likely to be damaged through disturbances like fire, insect attack and other injuries, it then is regenerated by reiteration (Fig. 3.2 a-e). These reiterated complexes also conform to the initial complex of the model, constituting part of a supplementary process only.

In young trees, growth is synchronous in all active meristems but this is lost with age and flushings eventually become not only asynchronous but also less frequent than on saplings, yet without affecting the basic architecture. This lack of synchronism is due to reiteration, where various reiterated complexes of the same tree crown behave differently regarding phenological events like leaf flush, senescence or fall, flowering and fruiting.

From the above description, it is clear that the tree follows the architecture model of Rauh (Hallé _et_ _al_., 1978). The characteristics of this model is a monopodial trunk with rhythmic growth and a whorled arrangement of branches which

Fig. 3.2 : Observed methods of reiteration in *Schima* spp.

(a) Bayonet joint (b) Forked trunk (c) Coppice

(d) Proleptic branch replacing a damaged bud

(e) An old tree showing reiteration complexes

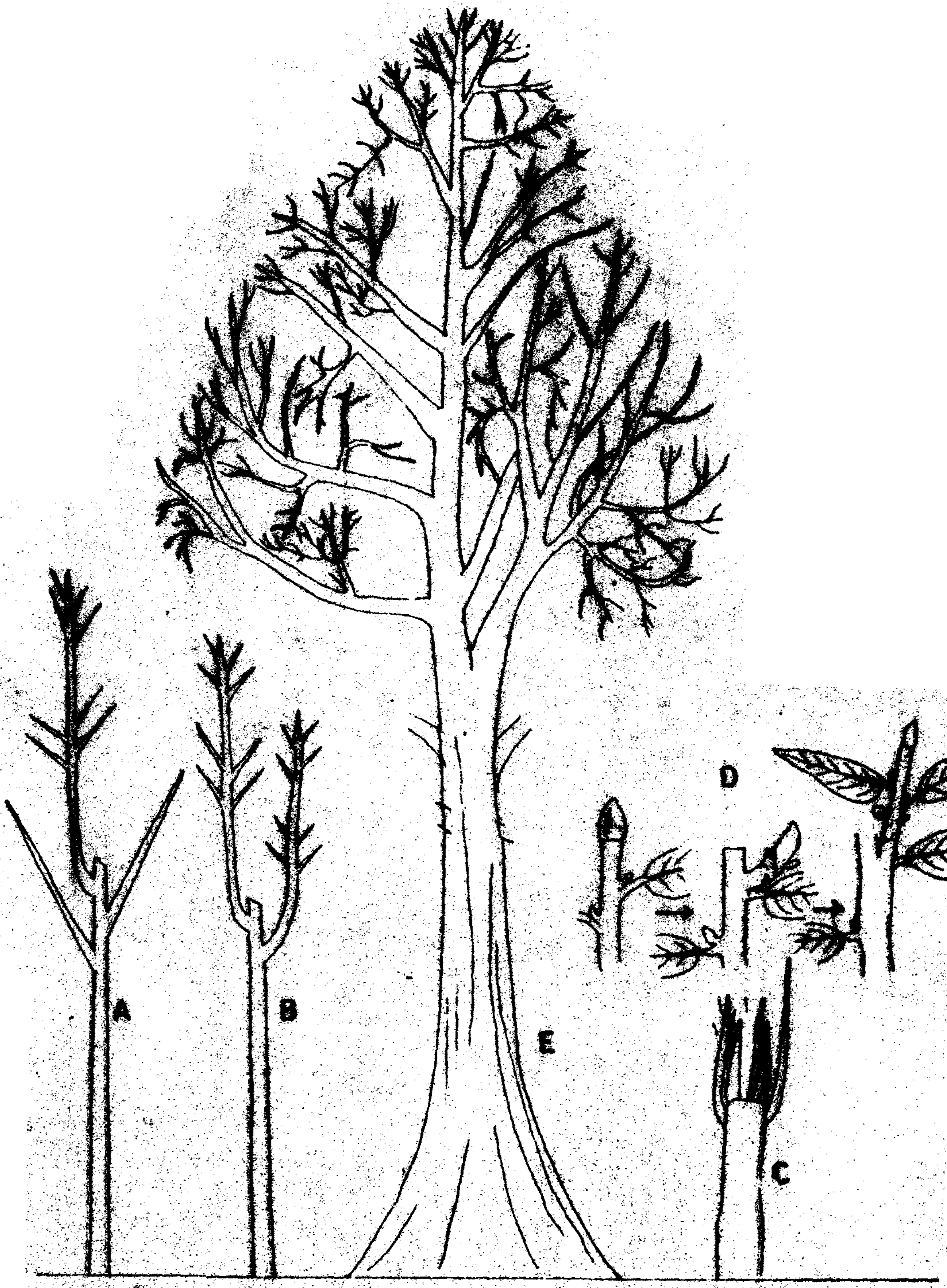


Fig. 3·2

are morphogenetically identical to the trunk. Flowers are borne laterally on the branches and, therefore, have no direct impact on the geometry of aerial vegetative axes (Fig. 3.3). The conspicuous feature of the rhythmic growth in the tree is the presence of shorter internodes with leaves of somewhat reduced sizes along the axis alternating with longer internodes (Fig. 3.4). This morphological indication of rhythmic growth results in the more or less pronounced segmentation of the axis. At the end of the growing season a series of short internodes delimits articulation (Tomlinson & Gill, 1971), and is helpful in determining the age of the tree. The presence of internodes shorter than the average inbetween two articulations (i.e. one growth year) shows the tendency to have more than one flush of growth during the growing season.

Bud dynamics

Fig 3.5 (a), shows the dynamics of bud populations on the main axis and on one year old First order branches. The axillary buds on the main axis produced branches as soon as they were formed (syllepsis) in the same growth year, but a large number of them subsequently remained dormant. *S. wallichii* at lower altitude produced two whorls of branches; one in April and nother again in July (7-8 branches in each whorl). At higher elevations, however, both in *S. wallichii* and *S. khasiana* only a single whorl of 4-6 branches was produced in the month of May. The pattern of branch development on the main axis is repeated on lateral branches also.

Fig. 3.3 : Rauh's model as exemplified by *Schima* spp. Dotted lines represent limits of one season's growth.

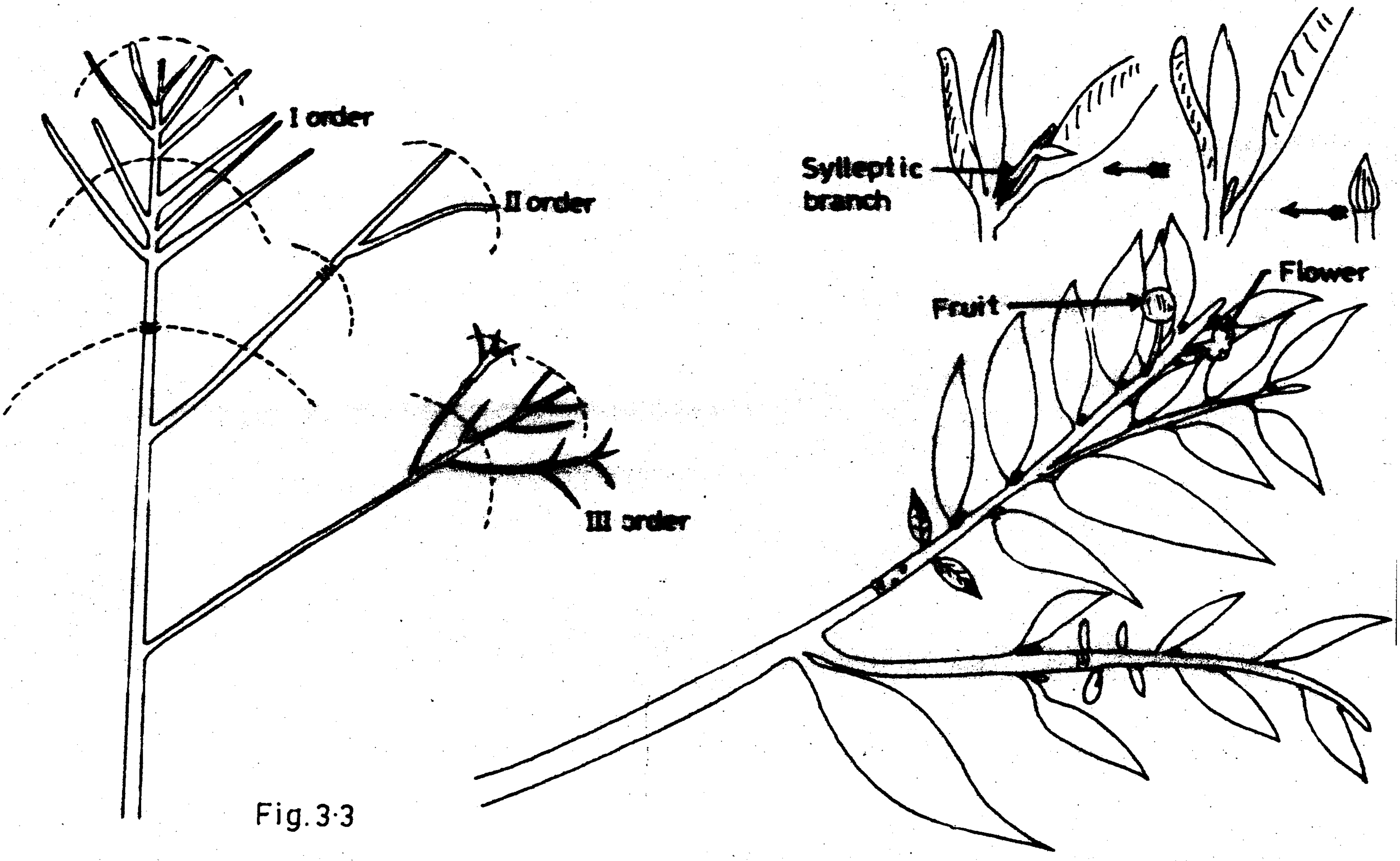


Fig. 3·3

Fig. 3.4 : Growth rhythms in Schima spp. represented by internodal elongation (bars) and leaf area changes (Undulating line, above the bars) on leader axis. (Time period one year)

Fig. 3·4

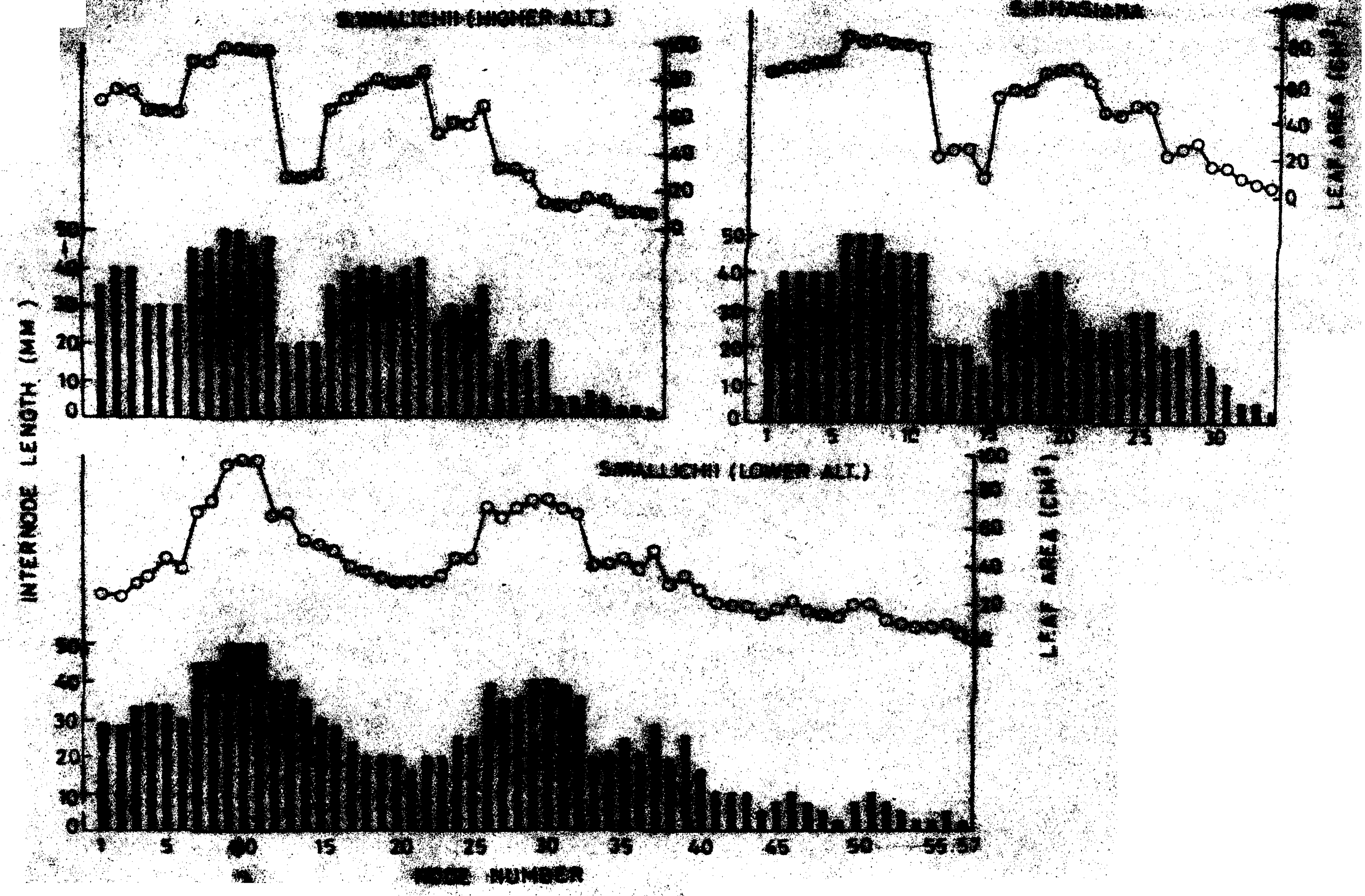

S. WALLICHII (HIGHER ALT.)
S. KHASIANA
S. WALLICHII (LOWER ALT.)
INTERNODE LENGTH (MM)
LEAF AREA (CM²)
NODE NUMBER
0
10
20
30
40
50
0
20
40
60
80
100
1
5
10
15
20
25
30
35
40
45
50
55
57

Fig. 3.5 : Bud dynamics (a) Dynamics of axillary bud populations (b) The percentage component composition of the axillary bud bank. ░ dormant buds ▨ branches formed □ buds died.

SWH = *Schima wallichii* (higher altitude)

SWL = *Schima wallichii* (lower altitude)

SK = *S. khasiana*

I = First growing season; II = Second growing season.

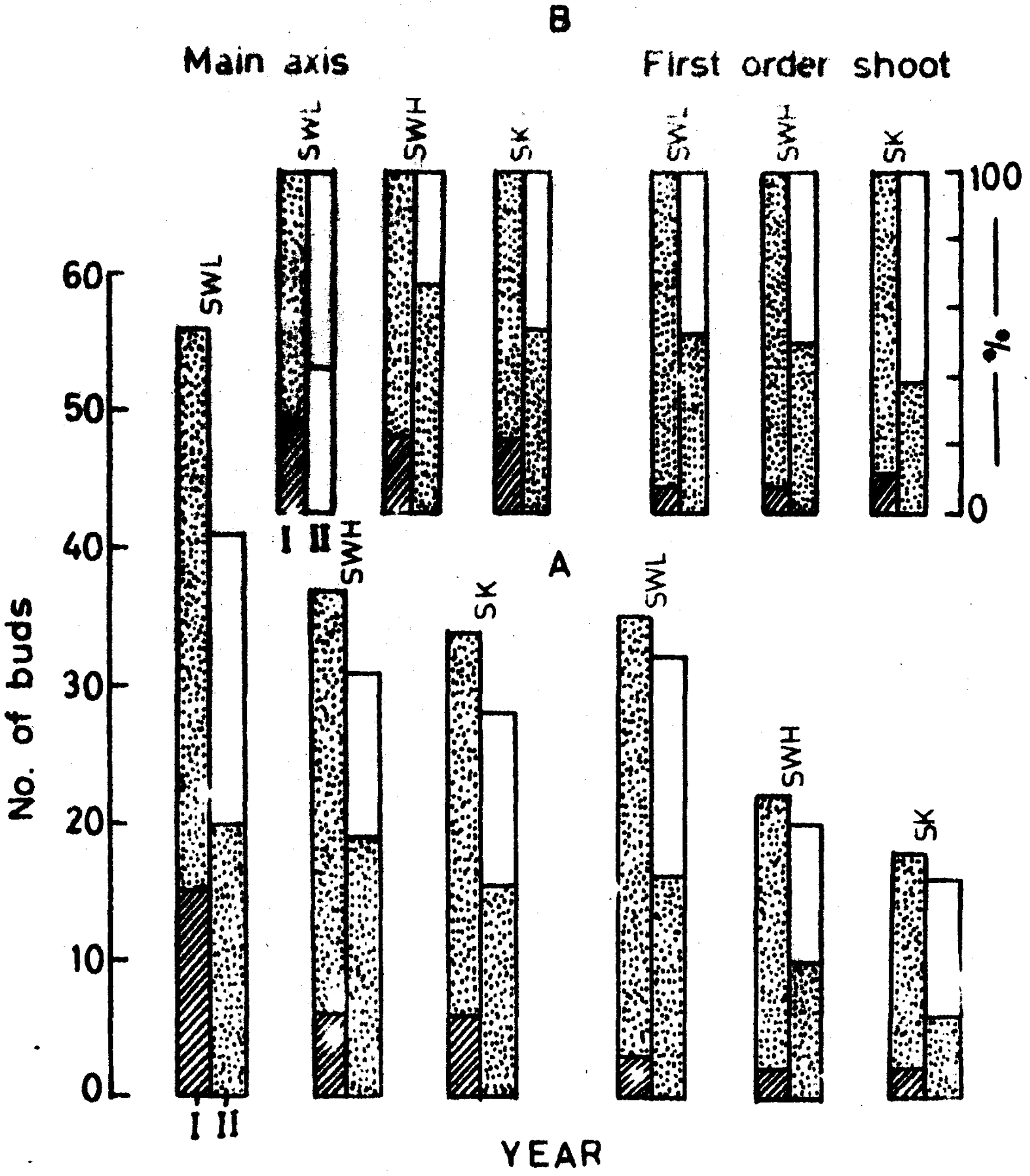

B
Main axis
First order shoot
SWL
SWH
SK
SWL
SWH
SK
100
%
0
I II
A
60
50
40
30
20
10
0
No. of buds
SWL
SWH
SK
SWL
SWH
SK
I II
YEAR

Fig. 3·5

The first order branches of the current year did not produce second order branches within the same growing season in S. khasiana, but it did so in S. wallichii with greater numbers at lower than at higher altitude.

An examination of the relative percentage composition of various bud bank components revealed quite distinct trends (Fig 3.5 b). Of the total bud sites potentially present on the main axis shoot **less than** 30% could produce branches and about 15% did so on the first order shoot and the rest remained dormant. In the next growth year about 35% of the total dormant buds on main leader and more than 50% on first order branches died and the rest remained as dormant reserve buds.

Extension and Radial growth

Extension growth in S. wallichii at lower altitude starts earlier and ends later than at higher altitude, with the result the growing period at lower elevation is longer. S. khasiana on the other hand has the shortest growing period due to the onset of dormancy much earlier than that for S. wallichii at the same altitude. Flowering and fruiting is earlier in S. wallichii at lower altitude compared to that at higher altitude. It is delayed even more in the case of S. khasiana at higher altitude (Table 3.1).

During the growth period, the internodal elongation showed a distinct rhythmic pattern with two major peaks in April-May and in July, in both the species. However, at

This is 3.1

Table 3.2 : Phenology of growth and reproduction in Schima spp.

	Flushing date	Beginning of dormancy	Growing period (days)	Dormant period (days)	Flowering date	Fruiting date	Seed dispersal
S. wallichii (Lower altitude)	Mar 1	Dec 25	300	65	Apr 1 - May 15	May 25	Feb 20 - Mar 15
(Higher altitude)	Mar 20	Nov 25	250	115	Apr 25 - May 30	Jun 1	Mar 1 - Apr 15
S. khasiana	Apr 5	Oct 1	180	185	May 15 - July 31	Jul 25	Jan 20 - Feb 15

lower altitude in *S. wallichii* another less pronounced peak was observed in the month of September. This rhythmicity is also related to the changes in leaf area pattern at the nodes (Fig 3.4).

The growth in height has two peaks one in April-May and another in July, the latter being lesser than the former (Fig 3.6 b). In all the cases more than 50% of extension growth was completed in the early growing season by May (Fig 3.6 c). Radial growth in all the cases was maximum on a date subsequent to the maximum for extension growth (Fig 3.6a).

ok

Table 3.2 shows the shoot elongation pattern on different locations of the tree. Both the species of *Schima* showed strong correlative growth inhibition. The extension growth in the main axis was more than in the branches which showed a sequence of first order > second order > third order and so on. Also the elongation of the current year (terminal whorls) shoot was maximum and decreased progressively down the tree in the second, third and fourth year whorls. Generally speaking branches of different orders of *S. wallichii* at low elevation showed greater elongation compared to those at high elevation (Fig 3.7)

Branch orientation and bifurcation ratio

The branch angle of open grown and forest grown (not strictly under shade) trees are compared in Table 3.3, which showed that the branch angle is more acute in all the forest grown situations at all canopy positions. Generally, branch

Fig. 3.6 : Radial (a) extension growth (b) cumulative % of season's total growth (c) in *Schima* spp. *S. wallichii* (lower altitude) (o), *S. wallichii* higher altitude (●) and *S. khasiana* (Δ).

Fig.3·6

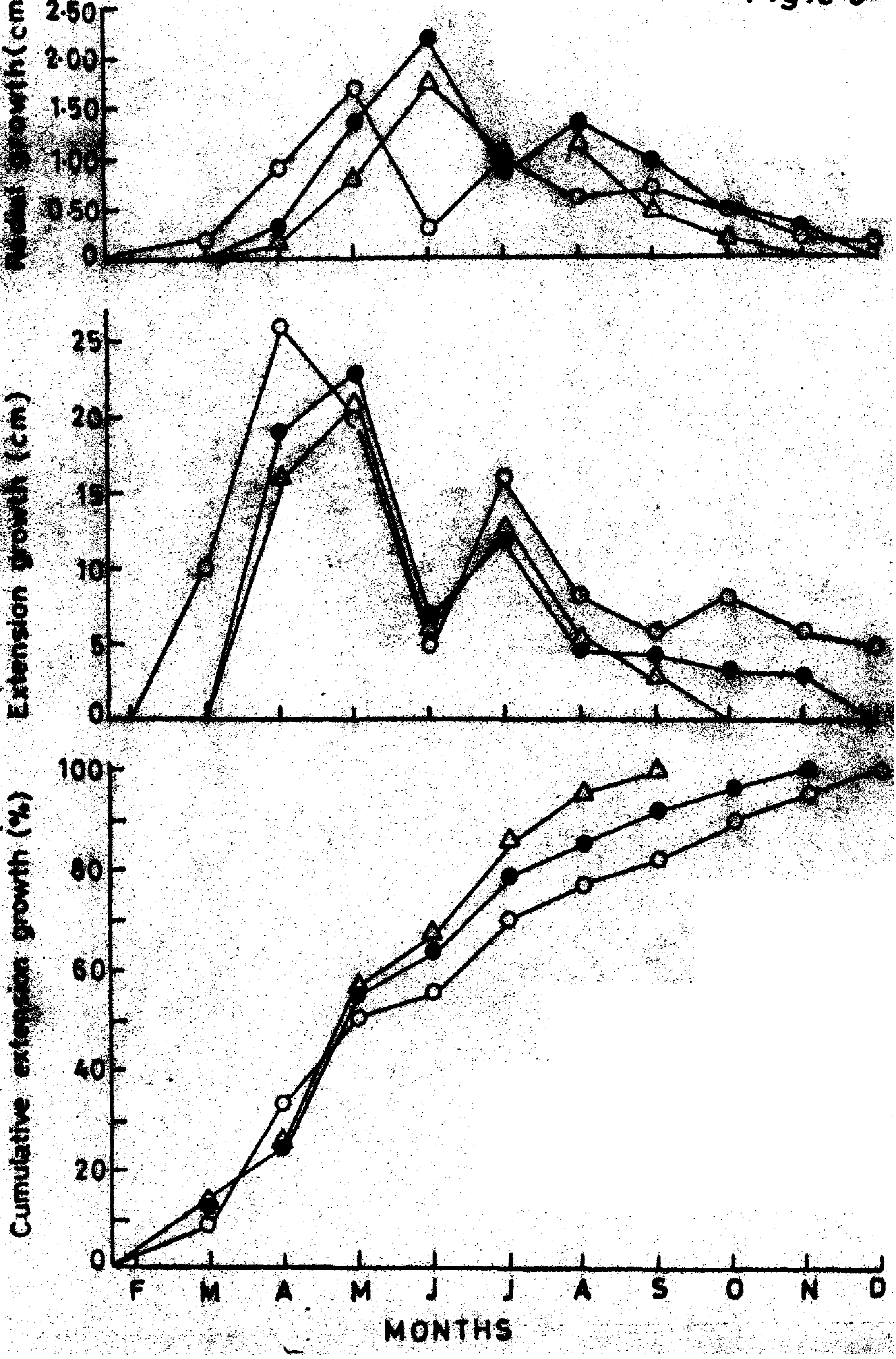

Radial growth (cm)
2·50
2·00
1·50
1·00
0·50
0
Extension growth (cm)
25
20
15
10
5
0
Cumulative extension growth (%)
100
80
60
40
20
0
F
M
A
M
J
J
A
S
O
N
D
MONTHS

Fig. 3. 7 : Branching pattern in Schima spp.

Fig. 3·7

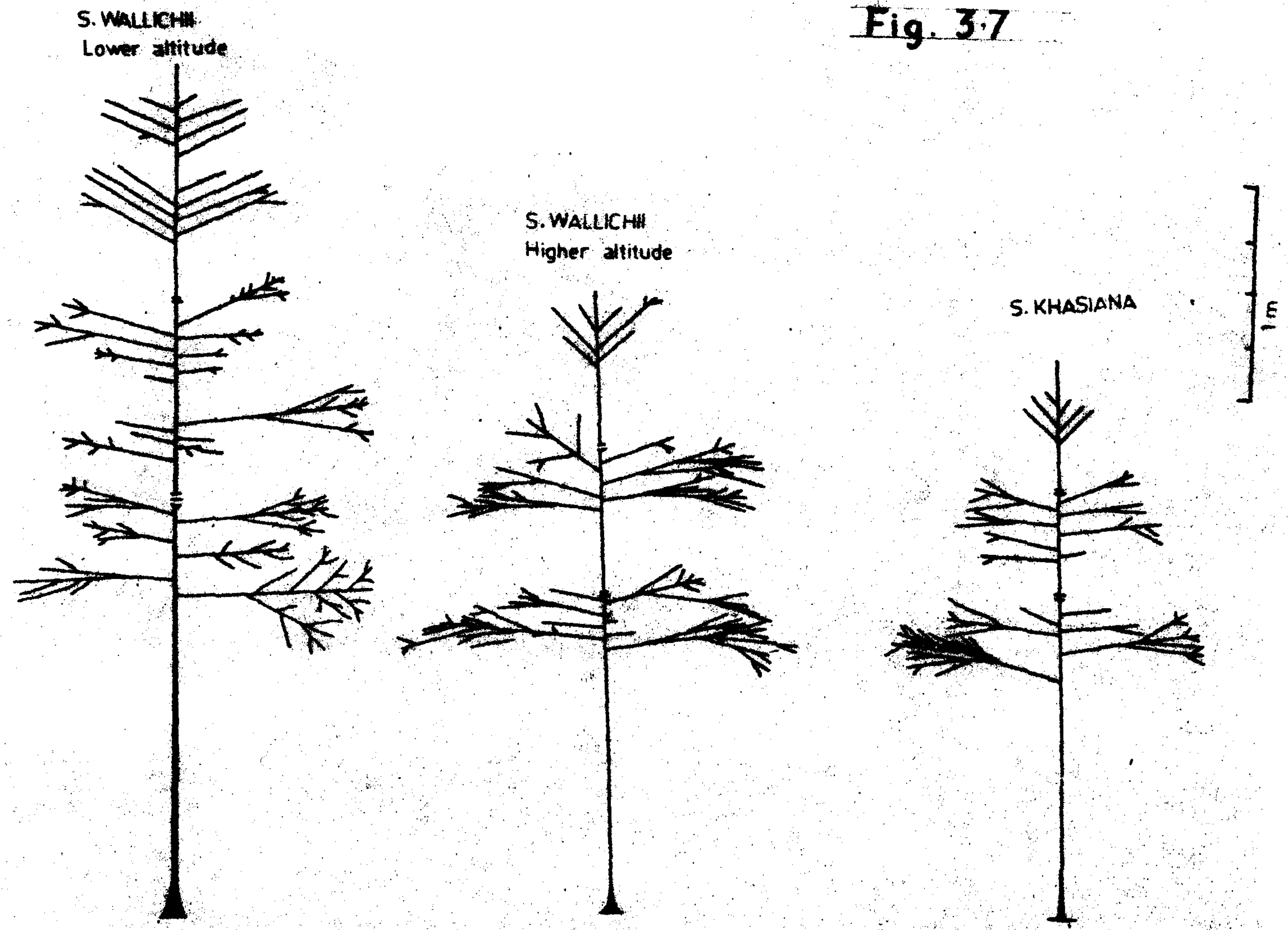

S. WALLICHII
Lower altitude
S. WALLICHII
Higher altitude
S. KHASIANA
1m

Table 3.2: Variations in shoot elongation (cm. ± Standard error of the mean) on different locations of young *Schima wallichii* and *S. khasiana* trees during one growing season.

	ORDER OF BRANCHES												
	0	First Order				2nd Order				3rd Order			4th Order
	MAIN AXIS	Year whorl numbers 1	2	3	4	1	2	3	4	2	3	4	4
S. wallichii (Lower alt)	110.00	32.00	15.94	10.44	1.50	15.30	12.32	9.97	1.38	10.62	10.17	5.00	---
	± 3.67	±3.86	±4.34	±4.02	±1.49	±3.62	±1.38	±0.78	±0.56	±2.30	±1.08	±2.04	
S. wallichii (Higher alt)	77.00	24.40	17.00	11.00	6.00	10.00	14.23	10.68	6.73	13.50	10.25	5.97	4.50
	±5.24	±3.51	±2.69	±5.27	±0.78	±0	±1.94	±1.48	±1.58	±0.95	±1.30	±1.09	±1.14
S. khasiana	64.00	23.50	16.20	13.67	12.75	-	15.38	7.94	4.87	-	15.27	5.03	9.50
	±3.09	±1.63	±2.63	±3.86	±4.33		±1.75	±1.09	±0.70		±1.79	±1.22	±3.51

Table 3.3 : Branch-angles (orientation from the main trunk) for *Schima* spp. (± S.E.)

	OPEN GROWN TREES			FOREST GROWN TREES		
	Upper Canopy	Middle canopy	Lower canopy	Upper canopy	Middle canopy	Lower canopy
S. wallichii (Lower alt)	56.33 ±2.17	77.64 ±1.79	80.30 ±2.11	42.50 ±3.18	60.50 ±2.52	77.00 ±3.18
S. wallichii (Higher alt)	55.00 ±2.44	70.00 ±3.42	79.87 ±2.50	45.00 ±2.67	66.00 ±3.06	72.50 ±3.41
S. khasiana	46.43 ±1.43	58.57 ±2.06	87.14 ±1.49	34.29 ±2.02	56.43 ±3.25	59.38 ±2.75

angle increased from the top to the base of the canopy. S. khasiana, in general showed more acute branches compared to S. wallichii at two altitudes.

A linear relationship was obtained between the branches of a given order (Strahler's ordering) and their frequency for all the three populations (Fig 3.8). The bifurcation ratio values were not significantly different (at 5% level) between the open and forest grown trees of S. wallichii though in the latter case the values are somewhat lower. In case of S. khasiana differences are significant (at 1% level) between forest and open grown situations (Table 3.4).

Leaf Dynamics

Morphologically leaves of S. wallichii and S. khasiana differed with the former having an entire leaf margin while the latter strongly serrate margin. Sun and shade leaves of all the populations showed significant (5% level) differences with sun leaves showing greater petiole length, blade length, blade width, blade area as well as blade and petiole dry weights, than those of shade leaves. The differences in leaf characteristics between S. wallichii from lower and higher altitude and S. khasiana were also significant (5% level) (Table 3.5). Both sun and shade leaves of lower altitude S. wallichii had greater blade length, blade width, petiole length and leaf blade area than at higher altitude; however, the latter showed greater petiole and blade dry weight than the former. The correction factor computed for leaf area calculation was constant for all the populations and also for sun and shade leaves.

Fig. 3.8 : Branch order/Frequency relationship in *Schima* spp.

Fig. 3·8

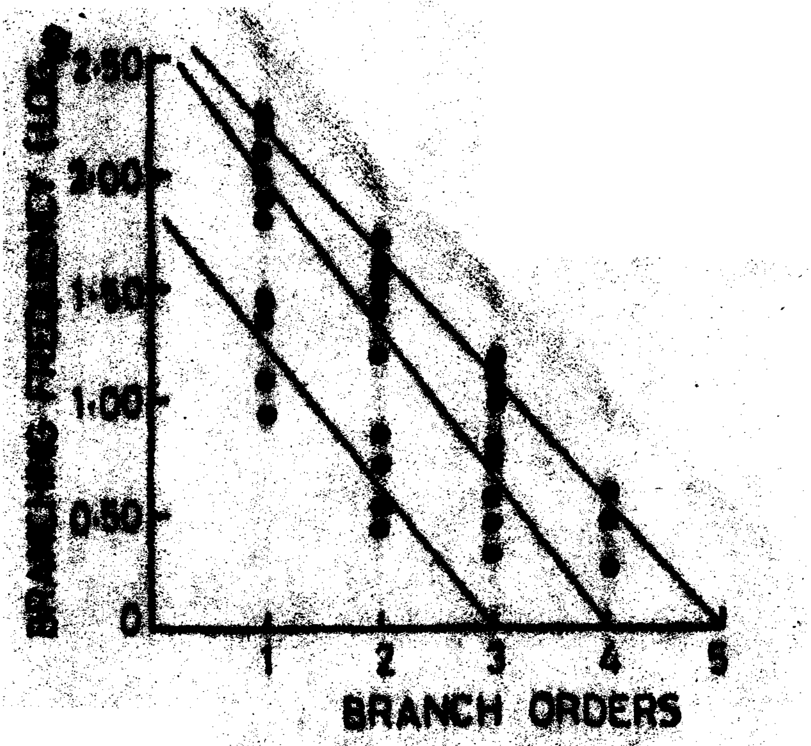

BRANCHING FREQUENCY (LOG)
2·50
2·00
1·50
1·00
0·50
0
1
2
3
4
5
BRANCH ORDERS

Table 3.4: Bifurcation ratio (Rb) values (± S.E.) for *Schima* spp.

	OPEN GROWN			FOREST GROWN	
	Mean ± S.E.	Range	t	Mean ± S.E.	Range
S. wallichii (Lower alt)	3.99 ± 0.49	3.31 — 4.76	0.76 N.S.	3.44 ± 0.19	3.00 — 4.14
S. wallichii (Higher alt)	3.85 ± 0.20	3.00 — 4.20	1.81 N.S.	3.40 ± 0.14	3.00 — 3.95
S. khasiana	3.91 ± 0.14	3.38 — 4.75	4.06*	3.24 ± 0.09	3.00 — 3.59

*Significant at 1% level, N.S., not significant.

Table 3.5 : Variations in leaf characteristics (± S.E.) of *S. wallichii* and *S. khasiana*

Leaf characteristics	*S. wallichii*				*S. khasiana*	
	Lower altitude		Higher altitude			
	SUN	SHADE	SUN	SHADE	SUN	SHADE
Petiole length (cm)	1.11 ±0.03	1.02 ±0.03	0.93 ±0.02	0.88 ±0.02	1.09 ±0.02	1.03 ±0.03
Blade length (cm)	16.02 ±0.31	11.95 ±0.46	13.85 ±0.33	10.01 ±2.94	15.92 ±0.29	12.24 ±0.40
Blade width (cm)	6.48 ±0.12	5.02 ±0.20	5.69 ±0.15	4.22 ±0.16	4.45 ±0.09	3.27 ±0.11
Correction factor	0.67 +0.01	0.67 +0.01	0.67 +0.01	0.68 +0.01	0.65 +0.01	0.64 +0.01
Leaf area (cm^2)	71.49 ±2.46	45.17 ±2.54	54.72 ±2.54	30.91 ±2.20	46.49 ±1.64	26.74 ±1.59
Leaf biomass (mg)						
Petiole	16.50 ±0.80	12.80 ±0.80	18.50 ±0.70	15.50 ±1.00	11.00 ±0.60	7.20 ±0.70
Blade	381.80 ±16.00	248.90 ±18.00	437.70 ±22.00	251.30 ±20.00	279.10 ± 9.80	155.80 ±20.00

Flushing occurred with the production of pink coloured young leaves, during early March for S. wallichii at lower altitude and about 20 days later at higher altitude; S. khasiana, on the other hand, started flushing another 15 days later in early April. Leaf production during the growth period showed two major peaks in April and July for the two high altitude species populations. S. wallichii at lower altitude also showed a smaller peak of production in September. Leaf production declined sharply in subsequent months with complete stoppage in late December in the case of the low altitude population of S. wallichii and late November and early October for the high altitude S. wallichii and S. khasiana respectively. S. wallichii at lower altitude produced more leaves than either the same species at higher altitude or than S. khasiana. All species and populations produced more than 50% of their annual leaf production by June (Fig 3.9).

Considering the cohort of leaves produced in 1979, leaf area production reached its peak in September-October in the case of all the three populations with maximum values attained for S. wallichii at lower altitude followed by the same species at higher altitude and with least values for S. khasiana. Annual production of leaf area was, 63 x $10^3 cm^2$, for the low altitude population of S. wallichii, 48 x $10^3 cm^2$, for the high altitude population of S. wallichii and 41 x $10^3 cm^2$ for S. khasiana. In months subsequent to peak leaf production, leaf area started decreasing sharply due to leaf fall and all the leaves of that cohort were shed by February in the case

Fig. 3.9 : Pattern of leaf production in S. *wallichii* at lower altitude (○), at higher altitude (●) and S. *khasiana* (△).

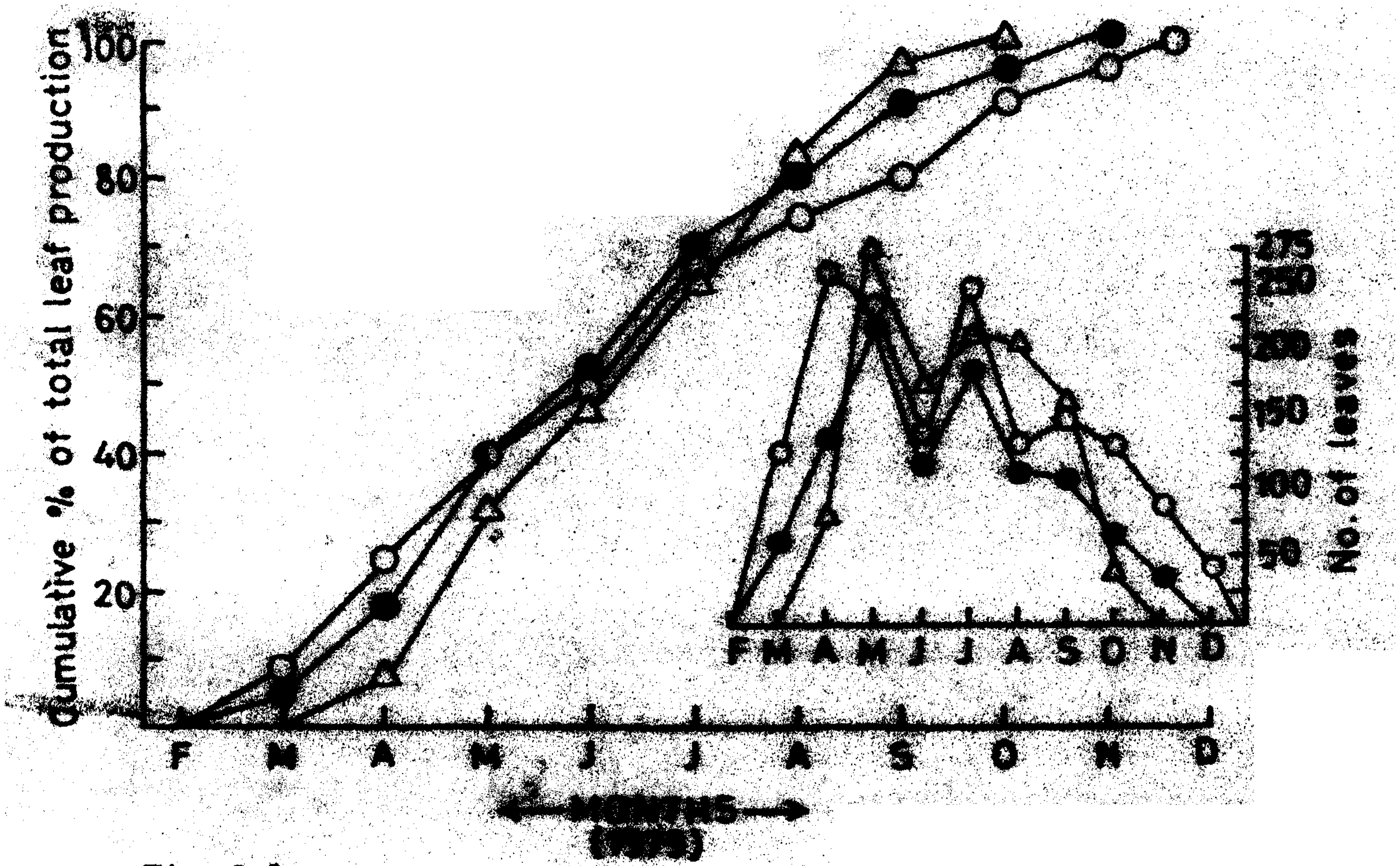

Cumulative % of total leaf production
20
40
60
80
100
F
M
A
M
J
J
A
S
O
N
D
MONTHS
No. of leaves
50
100
150
200
250
275
F M A M J J A S O N D

Fig. 3·9

of S. wallichii at low altitude and by March-April in the case of high altitude population of both the species (Fig 3.10).

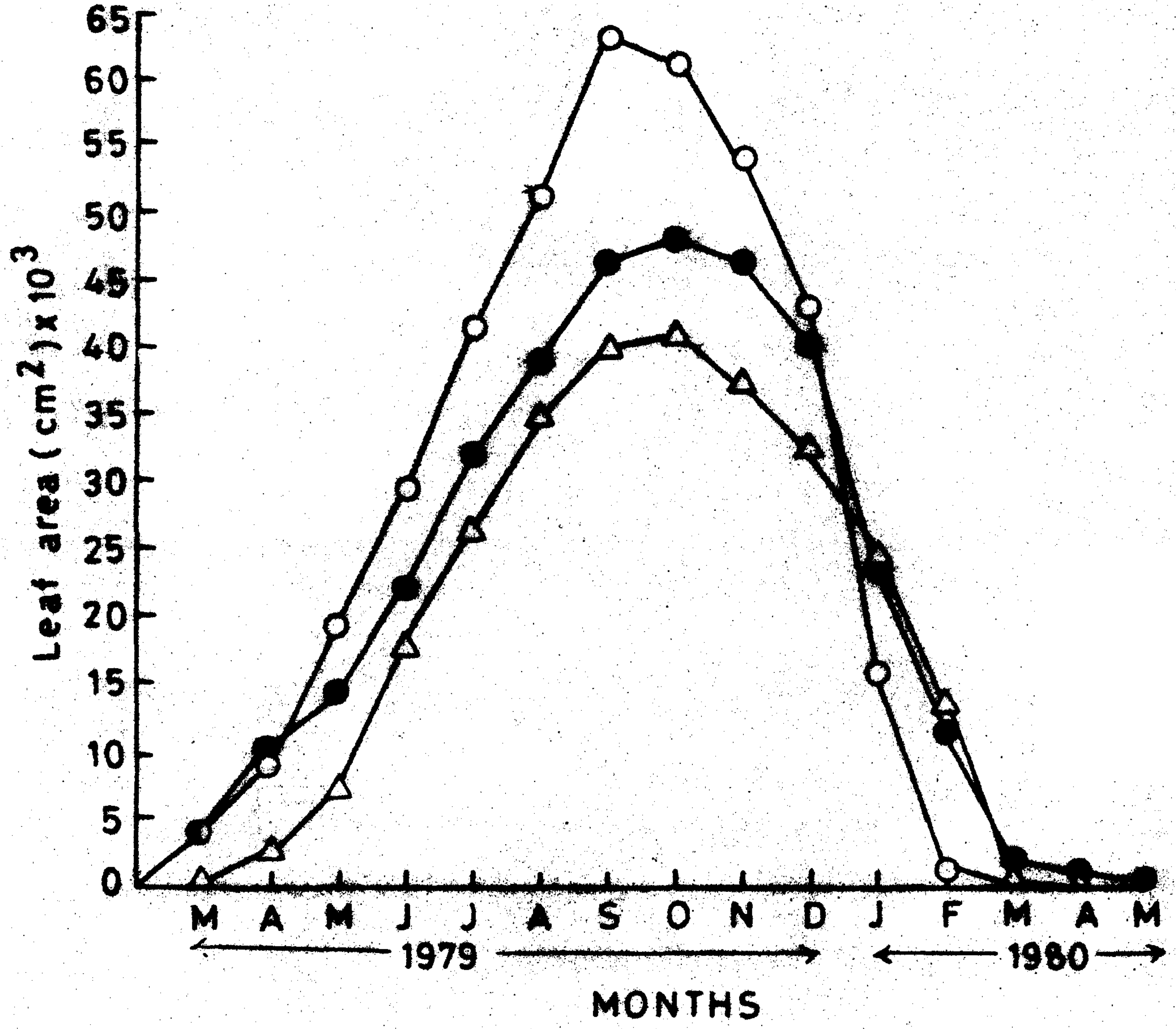
Considering the cohort of leaves produced in 1979, leaf fall began as early as August with a peak in the month of January for S. wallichii at both the altitudes and in the month of March for S. khasiana. Both the species thus follow the 'periodic growth, deciduous pattern of leafiness' (Longman and Jenik 1974). In this pattern of leafiness the branch or whole tree is leafless or nearly so far a period varying from a few weeks to several months. The degree of deciduousness differs for both the species (Fig 3.11). At lower altitude S. wallichii had a complete deciduous period of one month but at higher altitude it retained nearly 15% of its leaves at the time of new flush. S. khasiana had complete deciduousness for about 20 days before the new flush occurs.

Life span of leaves produced early in the season in general was longer compared to those produced late in the season. Leaves of the high altitude species populations in general had longer life span compared to the low altitude population of S. wallichii (Fig 3.12).

Leaf angles taken an inclinations from the horizontal (Table 3.6) showed that leaves in all the species populations are placed more acutely in full sun and are less so in the shade. This is more markedly seen in the low altitude population of S. wallichii than those at high altitude and those of S. khasiana.

Fig. 3.10 : Leaf area dynamics for one cohort of leaves *S. wallichii* lower altitude (○), higher altitude (●) and S. khasiana (△).

Fig. 3·10



Leaf area (cm^2) x 10^3
0
5
10
15
20
25
30
35
40
45
50
55
60
65
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1979
1980
MONTHS

Fig. 3.11 : Pattern of leaf fall in _S. wallichii_ at lower altitude (o), higher altitude (●) and _S. khasiana_ (△) % leaf fall for a particular month (solid lines), cumulative % of leaf-fall (broken lines) and standing leaves (dotted lines).

Fig. 3·11

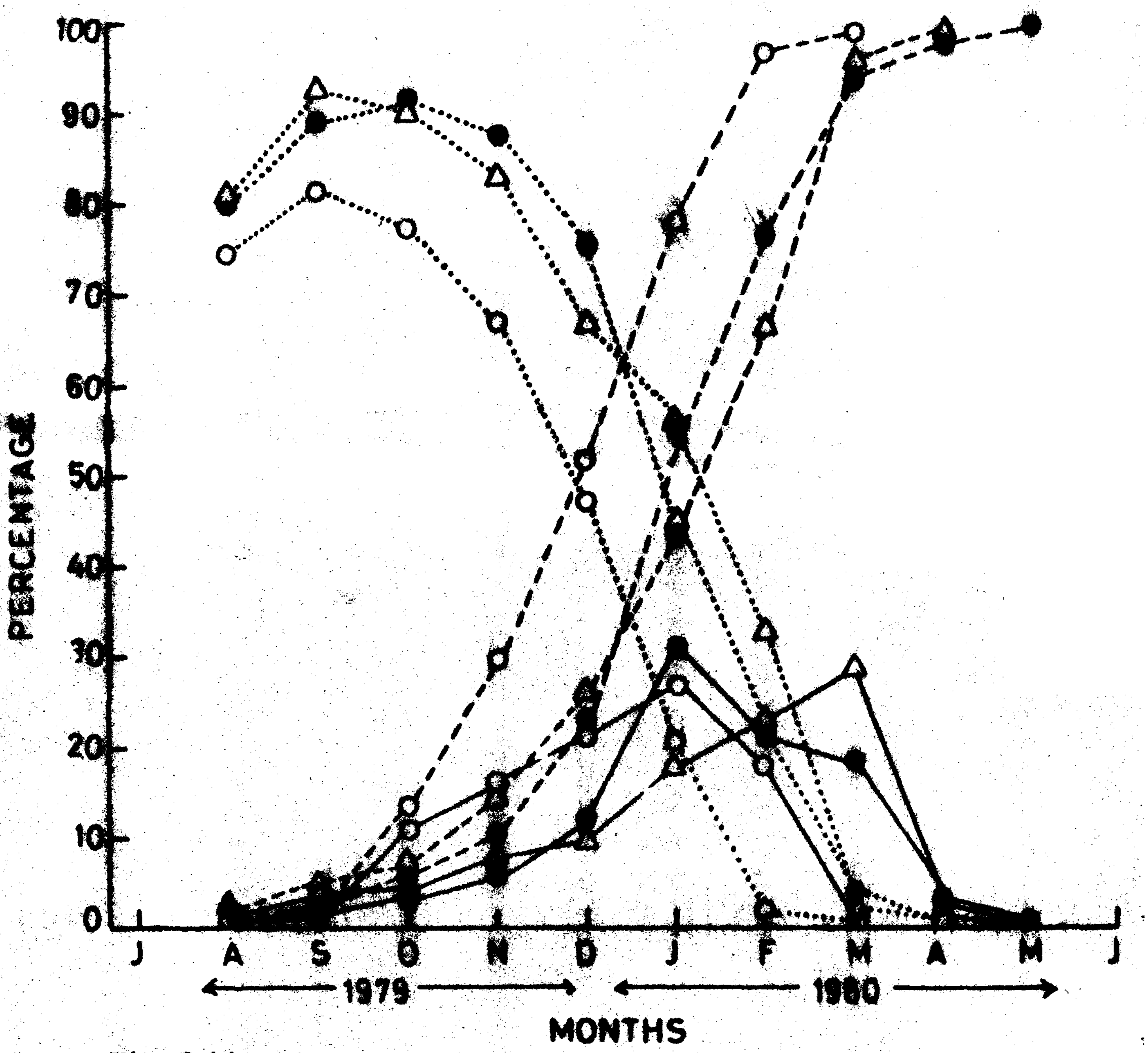


Fig. 3·11

Fig. 3.12 : Life span of leaves of *S. wallichii* at lower altitude (open bars), at higher altitude (hatched bars) and *S. khasiana* (filled bars).

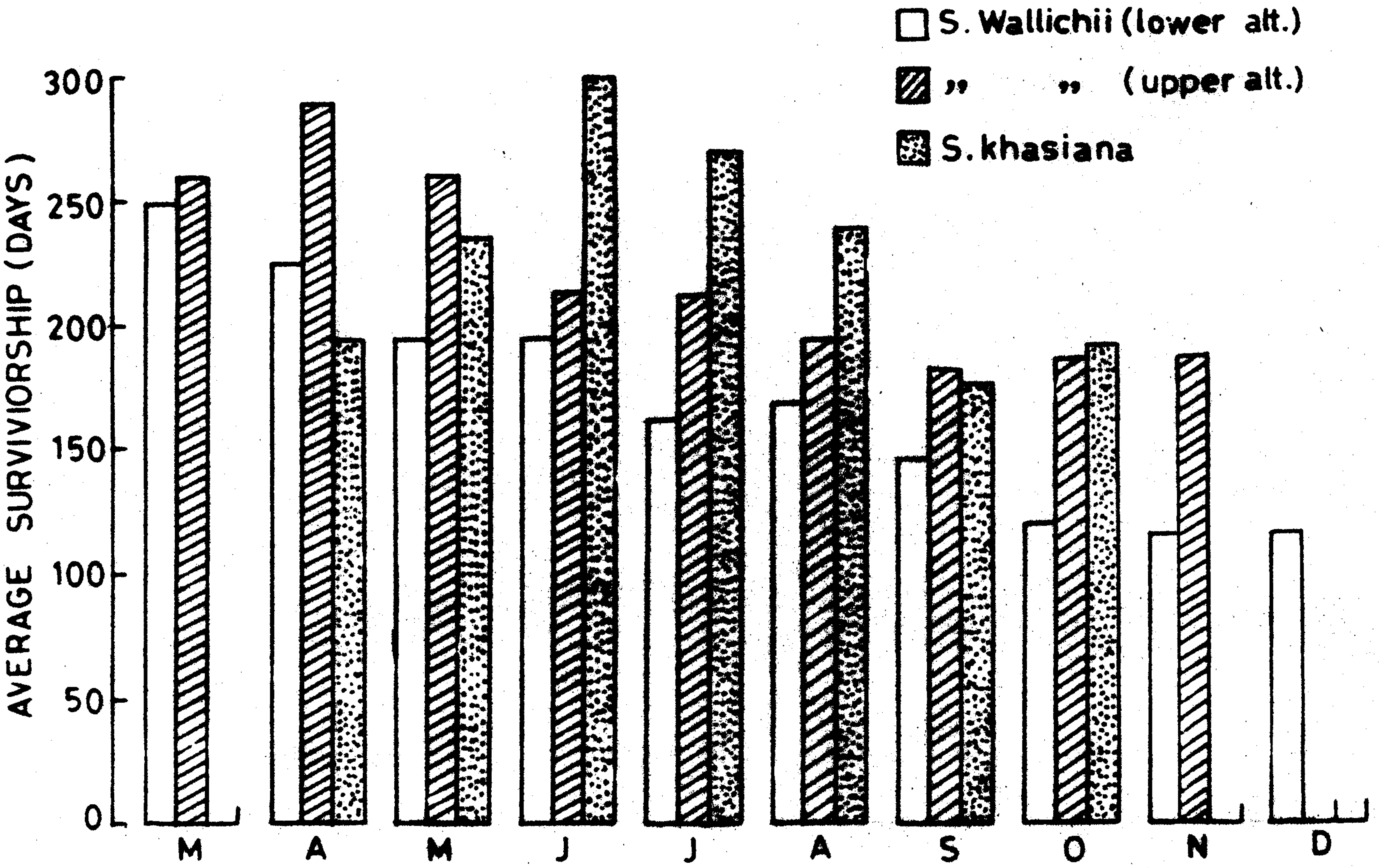

□ S. Wallichii (lower alt.)
▨ ,, ,, (upper alt.)
▩ S. khasiana
AVERAGE SURVIVIORSHIP (DAYS)
300
250
200
150
100
50
0
M
A
M
J
J
A
S
O
N
D
MONTHS OF PRODUCTION

Fig. 3·12

Table 3.6: Leaf angles (inclinations from horizontal) (± S.E.) in *Schima wallichii* (Lower and Upper altitude) and *S. khasiana*

	SUN LEAVES			SHADE LEAVES		
	Upper Canopy	Mid. Canopy	Lower Canopy	Upper Canopy	Mid. Canopy	Lower Canopy
Schima wallichii	85.00	72.50	71.50	60.50	55.10	50.50
(Lower alt)	±1.30	±3.22	±2.79	±2.88	±3.43	±2.84
Schima wallichii	69.50	62.92	58.00	49.50	44.83	40.77
(Higher alt)	±1.53	±3.23	±2.81	±3.42	±3.19	±2.24
S. khasiana	75.00	61.50	50.00	31.80	27.00	17.50
	±1.30	±2.53	±1.97	±1.49	±4.34	±3.21

DISCUSSION

S. khasiana and S. wallichii from low and high altitudes, basically follow the same architectural pattern, the variations being related to periodicity and the amount of growth, probably related to temperature differences. The pattern of shoot growth and architecture build up by this species are well suited to its role as an early successional tree species. The apical as well as lateral meristems being morphogenetically equivalent and rhythmic are very adaptable. The entire pattern of growth is regulated by the apical meristem of the trunk, which may grow repeating the same pattern throughout its life cycle. However, if the trunk meristem is destroyed, it is readily replaced by the uppermost lateral meristem or if the damage is more extreme, by the uppermost branch which rapidly substitutes as a leader. This is possibly due to the equivalence of all the axes and the regeneration involves minimum distrubance in growth pattern. Thus in this species reiteration is essentially a repetition of the original architecture, the difference being the mode of delopment of the reiterated complexes. All sequential branching in Schima is by syllepsis and reiterated branches can be produced proleptically. This can easily be recognized by the morphology of the proleptic shoot. However, both sequential and reiterated branches are produced only through prolepsis in S. wallichii in Indonesia (Hallé, personal communication) even this difference becomes unrecognizable in the Indonesian population of this species. As each wave of reiteration activates meristems, the chances of survival of the tree is increased. Thus, an old tree could be said to be made of several reiterated complexes.

The dynamic concept of architecture (Hallé et al; 1978) interprets the growth in terms of organized flux of specific constructional units (buds), their subsequent proliferation and survival. The branch production through syllepsis in the two species is during periods of rapid shoot growth, as was also seen in Alnus (Champagnat, 1954); Avicennia (Gill, 1971b) and Rhizophora (Gill & Tomlinson, 1971). Tomlinson & Gill (1973) hypothesized that the switch from a 'lower' state which determined prolepsis of a lateral meristem to another 'higher' state which determines syllepsis is conditioned by a 'threshold' which in turn is determined by the growth vigour of the parent shoot. Thus, in the low altitude population of S. wallichii which has faster shoot extension growth, more branches are produced sylleptically, than at higher altitude species populations. The branches in Indonesian population of S. wallichii (Hallé, Personal Communication) are produced proleptically, suggesting an intraspecific diversity, which could be attributed to its specialization to poor ruined soils under sub-optimal growth conditions. The production of first and second order branches during the same growth season which is more marked in the low altitude population, makes quick growth under fast diminishing light resources in a developing community. The growth of a hypopodium in sylleptic branches might be a mechanism by which the leaves are put outside the shade created by the leaves of the parent shoot (Wheat, 1980).

The Schima spp. are adapted to survive and make efficient growth after damage through fire, insects or other reasons.

The lateral buds that failed to produce sylleptic branches may produce proleptic branches if damaged. Thus, the species produce a basic type of meristem which can adapt itself to any of the functions either become dormant as a resting bud or grow out as a sylleptic branch, or assume the function of the main axis through reiteration.

The periodicity of shoot growth in tropical trees has been a centre of controversy. If recurrent growth flushes occur at regular intervals, the growth has been termed as rhythmic or periodic, if flushes occur at irregular intervals it has been called as episodic, intermittent or recurrent (Romberger, 1963). Hallé et al., (1978) have collectively placed all these under one broad category of 'rhythmic growth' mainly in the context of tropical trees species where the time-lag between different flushes are very small. In Schima spp. the growth rhythms are endogenous as they are not related to noticeable climatic fluctuations during the growing season. Even under the most favourable environmental conditions during May-June there are periods of slower growth for all the species populations. Further, it was noted that different individuals under the same environment may also not show synchrony in their rhythm. Duration of growth seems to determine the number of rhythms being more frequent at lower altitude. While many workers have attributed various environmental parameters like wet and dry season to rhythmicity (Alvium, 1964; Gaertner, 1964), absence of correlations with the environment has prompted others (Koriba, 1958; Borchert, 1969; Greathouse et al., 1971) to consider this phenomenon as endogenous as in the present case.

Differential elongation of different axes usually determines the form of the woody plants. In Schima spp. growth of the main axis far exceeds that of I order branches, which grow faster than II order branches and so on. Also the branches of current year's whorl grew more than others from previous years. Thus there is strong correlative growth inhibition, with apical control over the growth of the branches beneath (Brown et al., 1971) resulting in an excurrent crown form.

The growth period for the low altitude population of S. wallichii was longer than that for the high altitude population. S. khasiana has the shortest period. The number of cycles of shoot extension were more for low elevation population compared to that of the two species at higher altitude. This obviously is related to the duration of the favourable climate at different altitudes though intrinsic factors of the species are often implicated (Kozlowski, 1971; Kramer & Kozlowski, 1979). Radial growth started earlier and terminated later than the extension growth for all the species populations. Similar results are reported for many temperate trees (Kozlowski, 1971) and also for some of tropical trees (Choudhury, 1958).

The orientation of branches in space and time shape the geometry of the tree crown, and this has been related to its adaptive strategy for light interception (Horn, 1971; Brunig, 1976; Honda & Fisher, 1978). In *Schima* spp. lateral branches were vertical at first, and became progressively more horizontal with increasing distance from the leader apex. This reorientation may be due to increased branch weight related to branch growth and the active bending caused by reaction (tension) wood or a combination of these two factors.

Oohata & Shidei (1971) and Whitney (1976) analysed bifurcation ratio which is a measure of morphological adaptation of the crown structure to a particular niche and showed that it reaches to a species specific constant, suggesting that species have limited ability to modify the crown structure under different environments. This has been contradicted by the studies of Steingraeber *et al.*, (1979), who indicated that bifurcation ratio could vary with changes in light environments. Our studies on *Anthocephalus cadamba* (Shukla & Ramakrishnan unpublished) and *S. khasiana* in the present case support the latter viewpoint. The bifurcation ratio which is more or less constant in the case of *S. wallichii* under forest and open grown situations may be due to less marked differences in light environment of the open grown and forest grown trees. In fact, the forest grown trees were growing under sufficient light except for some restriction in the space available for growth. Also, being an early successional and light demanding species it cannot establish naturally under forest shade. The branching pattern in the species is such that the order/frequency relation is fairly linear and is maintained by the restriction of new twig growth to the top of the crown and by the death of the older twigs near the base.

The variation in leaves exposed to sun and those of inner crown (shade leaves) of the same tree is due to mutual shading of leaves and their variable exposure to light. The variation of leaves between different populations are due to inherent genetic differences as well as environmental factors (altitude). The greater size and leaf area at the lower altitude in comparison to that at the higher altitude may be due to the differences in temperature conditions existing at a particular habitat which may affect leaf expansion (Longman & Jenik, 1974; Milthrope, 1976). The general decrease in size of leaves at the higher altitude and interior of the crown of individual trees may be attributed to the light availability and temperature conditions as they affect photosynthesis. Jackson (1967) showed that the leaf structure of shade intolerant species are altered more by shading than that of shade tolerant species. In a light demanding species like <u>Schima</u> the marked differences in leaf characteristics in sun and shade is therefore understandable. The differences in the orientation of sun and shade leaves on the branch where the former is held more vertically than the latter is also achieved through the twisting of the petiole where necessary. Such differences in leaf orientation have also been recorded by others (McMillan & McClendon, 1979). Such a light interception strategy presumably enhances phtosynthesis of shade leaves under limited light conditions and promotes leaf cooling during high solar radiation in sun leaves (McMillan & McClendon, 1979).

A variety of patterns of leafiness (renewal and fall) have been described for tropical trees (Holttum 1940; Koriba 1958; Longman & Jenik, 1974), mostly with the cases of prerain or equinoctial flushing (Alvim, 1964; Frankie et al., 1974) which may perhaps be related to the display of the newly expanded leaves at the time of maximum solar irradiation and other favourable growth conditions (Longman & Jenik, 1974). In Schima spp. too leaf flushing is triggered just before the rains and leaf fall is mostly during the xeric periods of the year. The periodic growth-deciduous type of pattern of leafiness of Schima spp. is adaptive since losing photosynthetic area during dry periods of the year may help in avoiding water stress. It is an evergreen tree in Indonesia, where there is no such stress (Hallé, Personal Cummunication). The differences in degree of deciduousness between the lower and higher altitude populations, where the latter has a longer life span may be partly intrinsic and partly environmental.

The rate and duration of shoot 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 and also for the productivity of the forest (Longman & Jenik, 1974; Ramakrishnan, 1978). Bormann & Likens (1979) have described two types of growth strategies for niche occupancy in tree species. An exploitive strategy characteristics of early successional species with rapid and prolonged growth and a conservative strategy adapted for late successional environments. Marks (1975) and Ramakrishnan, Bormann & Siccama (Unpublished) have shown that early successional tree species with an indeterminate growth pattern are exploitive strategists; late successional tree species have mostly determinate growth and are conservative ones. These studies for temperate trees and those of others for tropical trees (Coombe, 1960; Coombe & Hadfield, 1960) alongwith the results presented here; where continuous leaf production is maintained for a major part of the year in an early successional light demanding species like Schima; tend to substantiate the view point that more prolonged production of photosynthetic leaf surface compared to that of late successional species is primarily responsible for their faster growth rate and productivity.

SUMMARY

Architecture and growth pattern of two closely related deciduous tree species of Schima, namely S. wallichii from lower (100m) and higher (1600m) altitudes and S. khasiana (restricted to higher altitude 1900m only) were analysed comparatively. Both the species conform to Rauh's model of architecture in having a monopodial trunk with rhythmic growth and morphogenetically equivalent branches. Branch production through syllepsis suggests a high growth vigour of the tree and a mechanism to achieve fast growth. Extension

and radial growth of the stem as well as leaf production continues throughout the growing season. The favourable growth conditions at the lower altitude favours fast extension growth with greater rhythmicity in S. wallichii in comparison to the higher altitude population of the species. The architectural and growth pattern characteristics of the two species are related to their ecological niche as early successional exploitive species.

CHAPTER IV

Growth strategy of trees related to successional status: I. Architecture and extension growth

GROWTH STRATEGY OF TREES RELATED TO SUCCESSIONAL STATUS

I. ARCHITECTURE AND EXTENSION GROWTH

INTRODUCTION

Much of our knowledge of the growth characteristics of tree species is based on their north temperate representatives (Kozlowski, 1964). Only recently has there been an attempt to understand the architecture and growth pattern of tropical and sub-tropical trees (Hallé et al., 1978). The ecological approach to the studies on canopy structure and its relationships to light interception strategy (Horn, 1971) and extension growth characteristics related to successional status of north temperate dediduous trees (Marks, 1974; Ramakrishnan, Bormann & Siccama, Unpublished) has reaulted in a better understanding of growth strategies of developing temperate forest communities. The architectural characteristics of the successional communities in French Guiana, have been analysed by Lescure (1978), which is a significant contribution on some aspects of revegetation occurring in different plots previously used for shifting agriculture. The present study attempts to look at growth strategy of trees from these viewpoints. Such an approach is not only important for a better understanding of the production strategies of the individual species and community as a whole (Ramakrishnan, 1978) but would also contribute towards more rational forestry management (Stern & Roche, 1974).

The forest where the present study has been done is a sub-tropical montane, humid, evergreen forest (Raju, 1964) and is located at Upper Shillong ($25^\circ 34'$N and $91^\circ 56'$E) near Shillong peak (1900m) in the Khasi Hills of Meghalaya State of north-eastern India. The forest is characterised both by sub-tropical elements like *Schima khasiana*, *Machilus kingii*, *Manglitia insignis*, *Eugenia terragona* and *Ficus nemoralis*; alongwith a number of temperate species like *Quercus dealbata*, *Q. griffithii*, *Alnus nepalensis*, *Rhododendron arboretum* and *Betula alnoides*. For the present study two early (*A. nepalensis* and *S. khasiana*) and three late (*Machilus kingii*, *Quercus dealbata* and *Q. griffithii*) successional tree species have been considered. The architecture and growth patterns of these two categories of trees are compared and related to their niche occupancy in the forest.

CLIMATE

The climate is monsoonic with most of the rainfall confined to a few months. The year may be divided into four more or less well marked seasons: (1) the monsoon season of heavy rains during May-September with over 80% of the total average annual rainfall (2350mm) occurring at this time; (ii) a transitional period of low rainfall due to the retreating monsoons during October-November; (iii) a winter season during December to February with scattered showers, and (iv) a short summer dry period during March-April. The average maximum and minimum temperatures were 22.24°C and 15.84°C during the monsoon and 15.47° and 1.18°C during the winter (Fig 1.1)

METHODS

Both the early and late successional trees of 5 years' age were identified at the study site. While the early successional species were studied only under open grown situations as they were not to be found to grow in shade, late successional species were studied both from open and forest grown situations. The detailed architectural analysis of trees was made by tagging buds and shoots and observing them at monthly intervals using a wooden platform erected around the tree to reach upto the top of the canopy. During active growth period the observations were made daily/weekly depending on the situation, to understand the changes in finer architectural pattern. The branches were ordered according to Hallé et al. 1978) using ordinal numbers, considering the trunk of the tree as the starting point order zero and branches as First, Second and Third orders respectively in chronological sequence. The pattern of branch development was studied by following the fate of buds on current increment of main leader and one year old First order branches. Branch angle was measured using a protractor and plumb bob and was expressed as degree orientation from the main trunk. Leaf display angle i.e. deviation from horizontal was also measured using a protractor equipped with a plumb bob, the protractor was aligned with the midrib of the leaf and the angle read. All observations are based on 5 replicates of trees.

For calculation of the bifurcation ratio alone the branches were classified according to their position in crown using Horton's (1945) method as modified by Strahler (1957). The terminal branches are designated as first order. The juncture of two first order branches defines a segment of a second order; the juncture of two second order branches makes a third order branch and so on down the system. The meeting point of branches of two unequal orders does not affect the classification of either. The bifurcation ratio (Rb) is calculated by Motomura's (1947) formula: $Rb = N-Nmax/N-N_1$, where N is the total number of the branches of all orders, Nmax is the number of branches of the highest order and N_1 is the number of branches of the first order (Steingraeber et al., 1979). The results are based on 10 replicates. For branch angle and bifurcation ratio studies a few forest grown trees of S. khasiana which were mostly stump sprouts were also considered.

GENERAL GROWTH CHARACTERISTICS AND ARCHITECTURE

General Growth pattern

For a precise description of growth pattern of the early and late successional tree species under consideration, the determinate/indeterminate terminology used for temperate trees, is adopted here, along with the broad categorization under rhythmic/continuous growth by Hallé et al. (1978) used with special reference to the tropical tree species. Early successional species can be grouped under indeterminate type. In S. khasiana after a period of dormancy (from October to March) the 'flush' of new pink coloured leaves is preformed in winter bud but growth is continued through neoformation during the growing season. The tree has characteristics of rhythmic growth expressed in rhythmic branches (whorls) and periodicity of internode elongation and leaf area production. A. nepalensis, has continuous growth, through neoformation involving the continued extension of primordia immediately after they are initiated without a rest period. In this species the terminal meristem consistently consists of single leaf associated with stipule and branch primordia enclosed by the mature stipule of youngest leaf to form a distinct terminal bud. In unfavourable winter period though the activity is stopped but when resumed it again produces the same number of leaf primordia.

The late successional species follow determinate pattern of shoot growth where the leaf and internode primordia are wholly preformed i.e. initiated entirely in the previous growth year in the overwintering bud. Late season activity of the terminal meristem continues after shoot extension has ceased and involves the formation of the following years' leaves. Though this is the basic pattern of determinate scheme, plants growing under more favourable conditions in the open, produce another flush of determinate shoots (lama growth) from pre-formed leaves of the dormant bud laid out before the second flush. This pattern of growth can obviously be grouped under rhythmic growth type of Hallé *et al.* (1978).

Architecture development

The architecture development pattern of A. nepalensis follows Attim's model (Fig 4.2a) (Hallé *et al.*, 1978). In

Fig. 4.1 : Growth rhythms represented by internodal elongation (bars) and leaf area changes (undulating lines above the bars) on leader axis.

a. *A. nepalensis*;

b. *S. khasiana*;

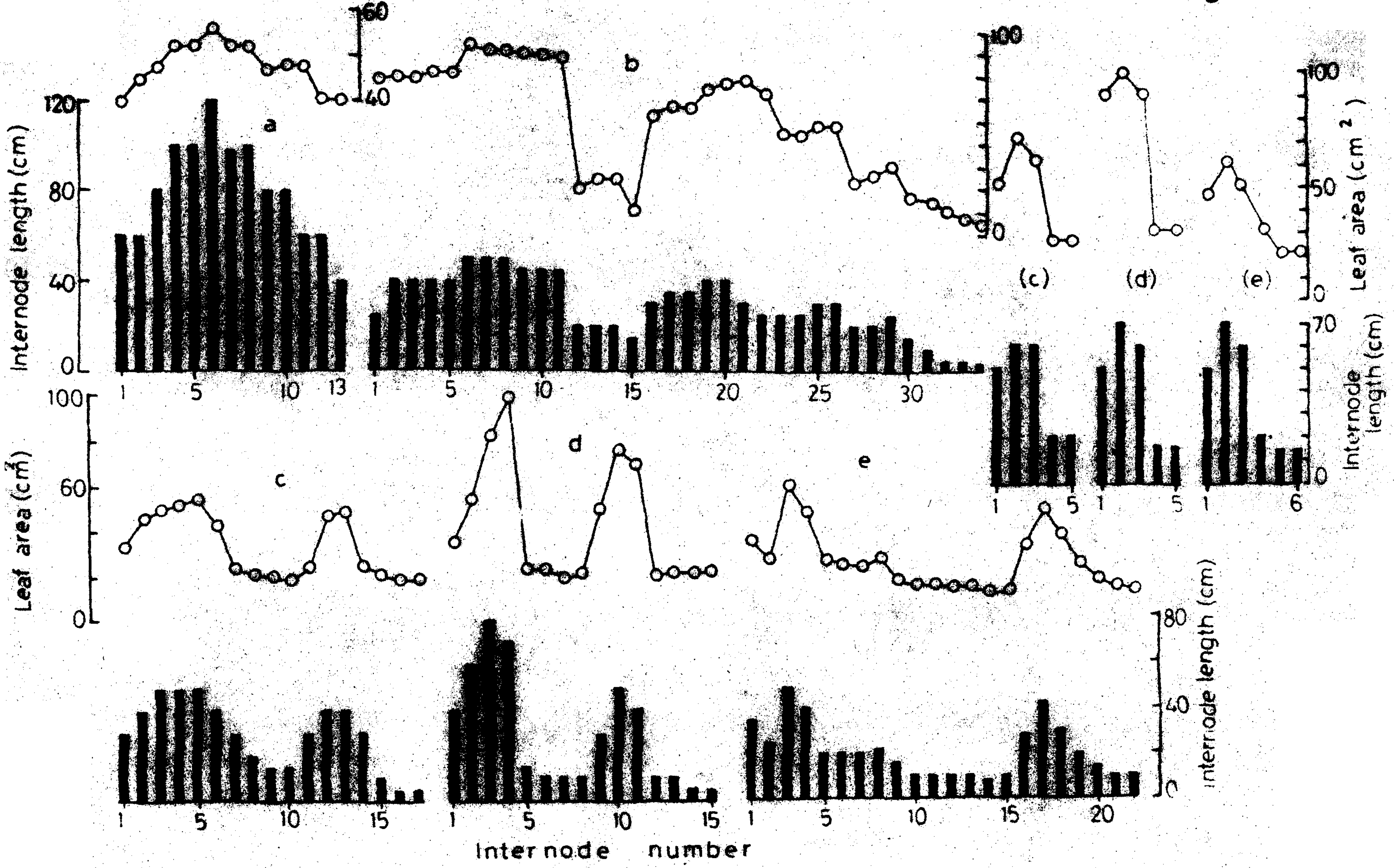
c. *Q. dealbata*;

d. *Q. griffithii*;

e. *M. kingii*

Inset figure for forest grown individuals.

Fig. 4.1.


a
b
c
d
e
(c)
(d)
(e)
Internode length (cm)
0
40
80
120
40
160
1
5
10
13
1
5
10
15
20
25
30
0
100
Leaf area (cm²)
0
50
100
Internode length (cm)
0
70
1
5
1
5
1
6
Leaf area (cm²)
0
60
100
internode length (cm)
0
40
80
1
5
10
15
1
5
10
15
1
5
10
15
20
Internode number

this species the formative meristem has continuous growth, differentiated into monopodial trunk and morphogenetically equivalent branches. Branching is continuous during the growing season but becomes intermittent during the winter due to the failure of branch formation. This helps in determining age of the tree. The continuous activity of the meristem is expressed in the more or less constant bud composition and little variation in leaf shapes and sizes along the axis. But growth rate is not uniform as is clear from the rhythmicity of internode length and leaf area pattern on the main axis (Fig 4.1a) as well as temporary suspension of growth during the winter. Branches are produced through syllepsis without a rest period of axillary meristems. These branches are characterized by the lack of basal bud scales or scale scars and have an extended basal internode (hypopodium). Further, there is no transition in leaf morphology along the axes of the sylleptic branches. Branches are inherently orthotropic, as they have spiral phyllotaxy and radial symmetry, but due to apical control they tend to become horizontal, arranging leaves in one plane through twisting of petioles (secondary orientation). The inherent orthotropy of such branch is revealed in damaged trees, where leader is readily replaced by an adjacent lateral which conforms to the original architecture.

All other species follow Rauh's model (Fig 4.2b, c, d, and e) which is characterised by a monopodial trunk with rhythmic growth and a whorled arrangement of laterals which

Fig. 4.1 : Attim's model as exemplified by

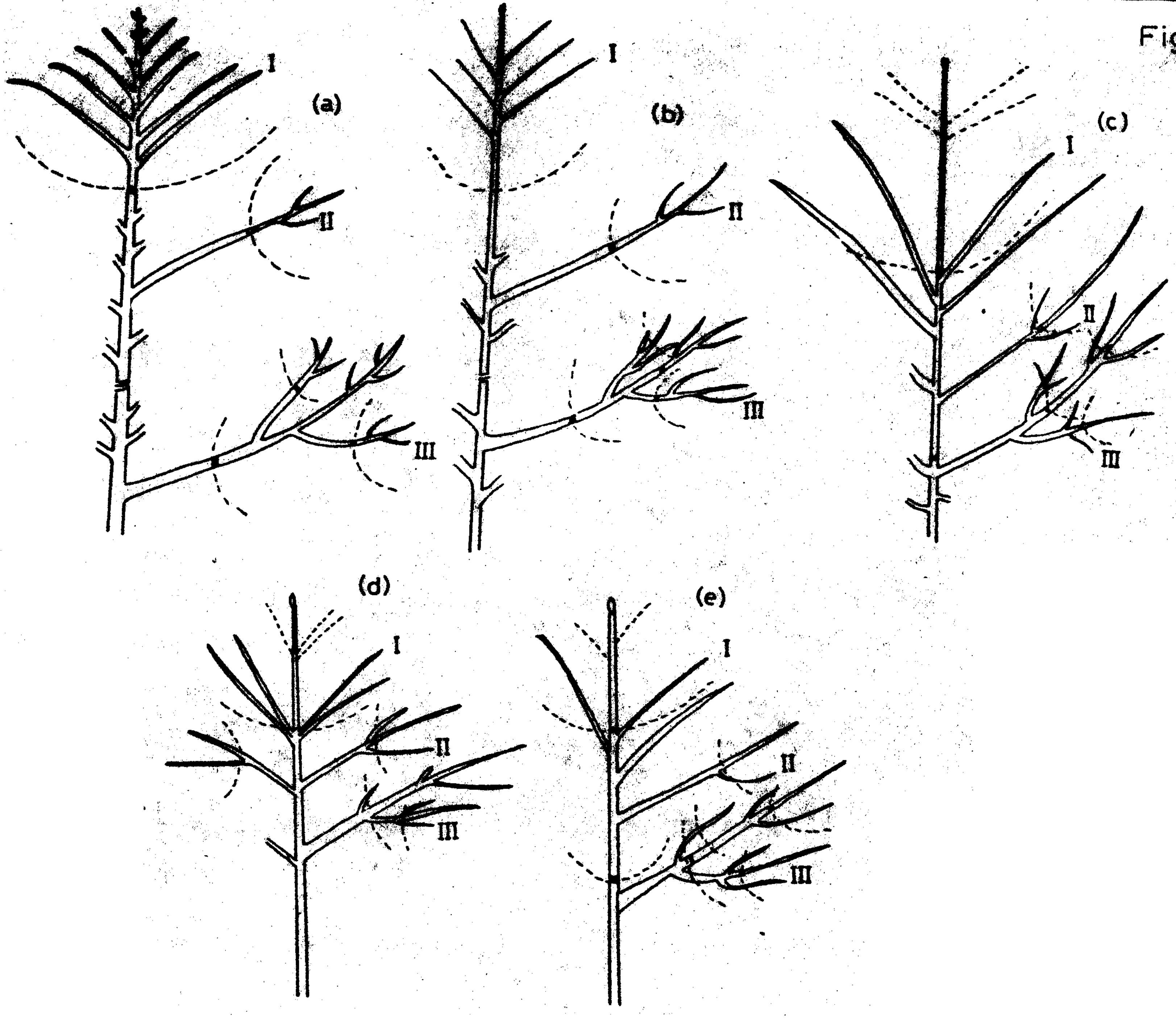
A. nepalensis, a; and

Rauh's model as exemplified by

b. *S. khasiana*; c. *Q. dealbata*; d. *Q. griffithii*;

e. *M. kingii*

Fig. 4.2



are morphogenetically equivalent to the trunk. This rhythmicity helps in aging the tree. The leader axis as well as the laterals are orthotropic with radial symmetry and spiral phyllotaxy. The early successional *S. khasiana* which follows this model showed more rhythms of internodal elongation and leaf area production than the late successional species (Fig 4.1). *S. khasiana* produces branches through syllepsis whereas all late successional species produce branches through prolepsis - through the proliferation of latent or resting buds, thus they have basal bud scales and usually a transition in leaf shape and size on their axes.

Reiteration

The initial architecture of the tree is likely to get modified due to damages like insect attack, fire and breakages due to natural calamities, or environmental modifications like canopy openings, light availability and also canopy closure. The tree then reiterates its initial architecture to adjust itself to such changes (Fig 4.3). This has been termed as reiteration (Oldeman, 1974). Reiterated complexes of early successional species generally show more vigorous growth with prolonged growth period. Late successional species reiterated complexes, instead of making determinate growth exhibit indeterminate growth pattern.

In *A. nepalensis*, if the apex is damaged, an adjacent lateral starts growing upwards, subsequently substituting the role of the damaged part. In certain cases instead of a single,

Fig. 4.3 : Reiteration processes in early and late successional tree species.

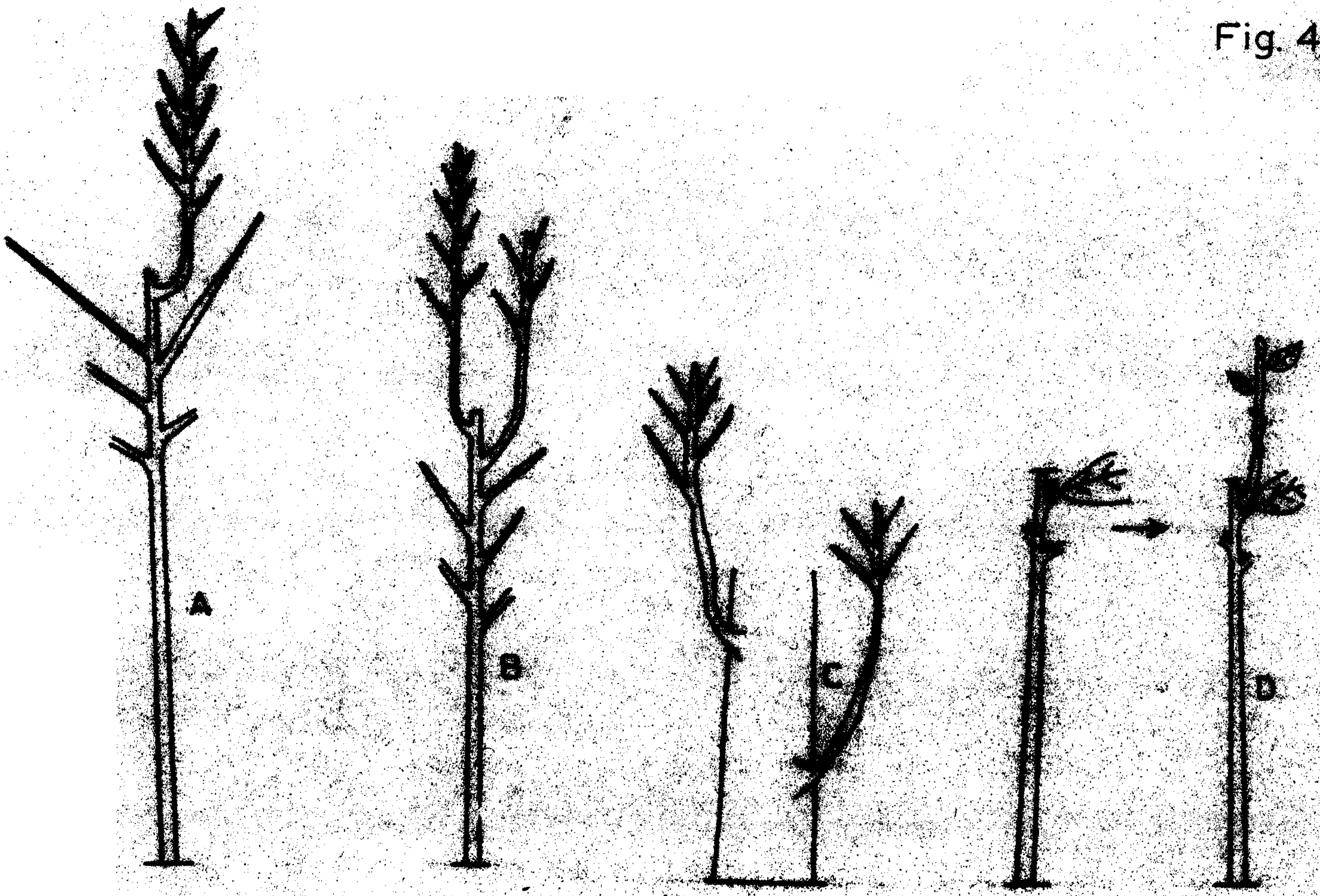
a. Substitution trunk;

b. Same but producing a forked trunk;

c. Stem suckers from an old tree, and

d. Regeneration by activating a dormant axillary bud upon the loss of terminal bud.

Fig. 42.



two laterals are made functional to substitute the damaged leader axis, their reiteration is only through substitution process due to the short life span of the axillary meristems hindering the reiteration through activating dormant buds. In S. khasiana and all other late successional species, on the other hand, reiteration may be achieved either through the activation of lateral meristem, substitution process or even through coppicing of stumps. In S. khasiana branching in initial architecture is through syllepsis only but if reiteration is by the activation of a dormant meristem it is through prolepsis.

RESULTS

Bud dynamics

Fig 4.4 shows the dynamics of bud populations on the main axis and one-year old First order branches. Early successional species though produced branches through syllepsis had some dormant buds. The proportion of dormant to non-dormant buds was very high in S. khasiana compared to A. nepalensis. In the next growth year some of these dormant buds died and the rest remained dormant again forming reserve bud banks; in A. nepalensis their number was very few. In the late successional species where branches are formed through prolepsis, buds underwent a rest period and produced branches in the next growth season only. But in open grown situations however some of these buds proliferated into branches in the second flush of the same growth year producing lamma shoots.

Fig. 4.4 : Dynamics of bud populations in

a. *A. nepalensis*;

b. *S. khasiana*;

c. *Q. dealbata*;

d. *Q. griffithii*, and

e. *M. kingii*

on A main leader axis and B.

First order shoot of previous year. Inset figure for forest grown individuals.

▨ branches produced;

░ dormant buds and

□ dead buds.

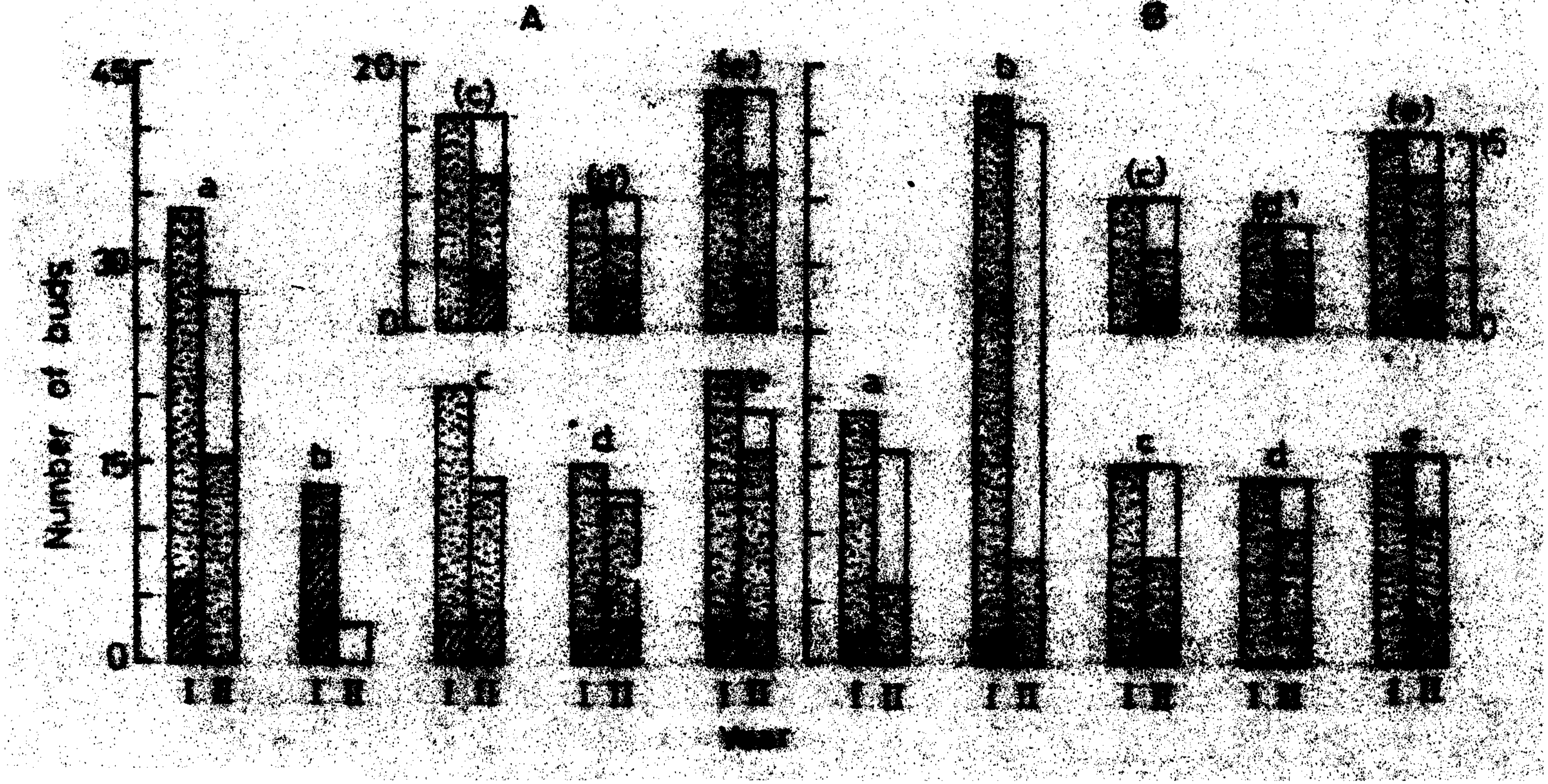


Fig. 4.4.

The pattern of branch production on the main axis was repeated on the first order branches also. But the chief difference between early and late successional lies in the fact that while the first order branches produce second order ones sylleptically in the former; these are produced proleptically in the latter with the result branch position for the second order branches on these two categories are different as shown in Fig 4.2.

An examination of the relative percentage composition of various bud bank components revealed quite distinct trends (Fig 4.5) for both groups of species. Of the total bud sites potentially present on the main axis shoot of _A. nepalensis_ about 80% produced branches and the rest remained dormant of which none could survive in the next growth year. But on the first order shoot only a small proportion of the buds produced branches making 90% buds dormant. Of these dormant buds 20% formed reserve bud bank in the next growth season and the rest died. In _S. khasiana_ only 22% buds proliferated into branches, of the remaining ones about 50% formed reserve buds and the rest died on the main axis shoot. On the first order branches of this species, only 10% buds were active, 40% formed reserve buds and the rest died. In open grown late successional trees less than 20% of the dormant buds on the main axis proliferated in the first growth year as lamma shoots. In the next growth year some of these dormant buds (10% to 20%) produced branches. On the main axis of forest grown late successional trees and

Fig. 4.5: The percentage component composition of the axillary bud bank on A main axis and B. Previous year's First order shoot of open grown trees of,

a. *A. nepalensis*;

b. *S. khasiana*;

c. *Q. dealbata*;

d. *Q. griffithii*, and

e. *Q. dealbata*,

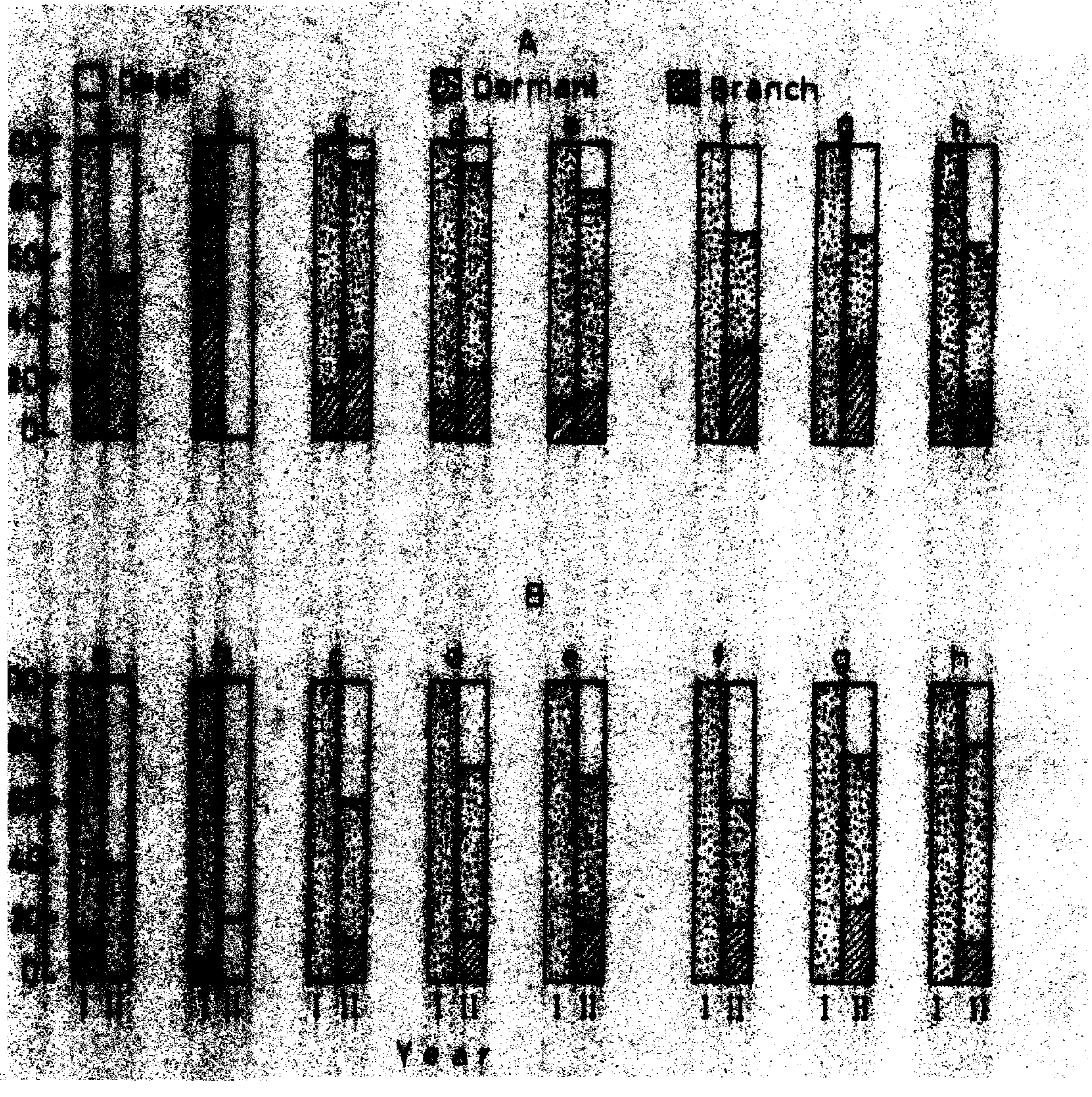
and forest grown trees of the last three (f, g, h)

▨ branches proliferated,

⊡ dormant buds,

☐ dead buds.

Fig. 4·5



on first order branches of both open and forest grown trees of this category, the buds in the first year remained dormant while in the second growth year 20-30% of them proliferated into branches, 40-50% remained dormant (reserve buds) and the rest died.

Extension and Radial growth

Table 4.1, summarises the important growth characteristics of both early and late successional tree species. Early successional species had prolonged growth period, shorter dormancy period, more extension and radial growth than the late successional species. The early successional species were either with larger number of internodes or greater internodal length than the late successional ones. The tree height/crown width value was higher in early successional species, while the ratio of the total height to the height upto the lowest branch was higher for the late successional species.

Early successional trees exhibited either more frequent rhythms of internode elongation and leaf area production on the leader axis as in the case of S. khasiana or it had more or less continuous growth but with a distinct peak as in A. nepalensis, whereas, the late successional tree species showed invariably two distinct peaks in open grown situations. Further the shade grown late successionals showed only a single peak with a fairly short growth duration. (Fig 4.1)

Table 4.1 : Growth characteristics of early and late successional tree species. All measurements are based on 5 replicate individuals.

	EARLY SUCCESSIONAL		LATE SUCCESSIONAL					
	A. nepalensis	S.khasiana	Q. dealbata		Q. griffithii		M. kingii	
	OPEN	OPEN	OPEN	FOREST	OPEN	FOREST	OPEN	FOREST
1. Dimension of the experimental trees								
a. height (m)	5.05 ±0.68	2.03 ±0.39	1.96 ±0.75	1.54 ±0.90	1.74 ±0.35	1.25 ±0.60	1.85 ±0.25	1.37 ±0.26
b. dbh* (cm)	3.55 ±0.35	1.28 ±0.34	1.14 ±0.29	0.73 ±0.29	1.05 ±0.29	0.68 ±0.30	1.14 ±0.30	0.74 ±0.30
2. Growth period (days)	334 ±10.50	190 ±9.18	73 ±1.88	35 ±0.69	63 ±2.00	30 ±1.35	72 ±4.63	33 ±1.00
3. Dormancy period (days)	31 ±10.50	175 ±9.18	292 ±1.88	330 ±0.69	302 ±1.99	335 ±1.35	293 ±4.63	332 ±1.00
4. Extension growth/ Yr (cm)	104 ±6.50	64 ±3.09	49 ±2.50	21 ±1.90	46 ±1.60	21 ±2.60	44 ±2.30	23 ±2.35
5. Radial (dbh) growth/Yr (cm)	0.95 ±0.09	0.57 ±0.15	0.55 ±0.06	0.27 ±0.03	0.42 ±0.05	0.25 ±0.05	0.49 ±1.12	0.20 ±0.02
6. Internode No. on main leader/Yr	13 ±4.40	34 ±9.50	17 ±6.60	5 ±3.33	15 ±3.30	5 ±3.00	22 ±3.00	6 ±4.60
7. Mean internode length (cm) on main leader/yr	8.00 ±4.80	1.88 ±3.90	2.88 ±2.20	4.20 ±2.90	3.07 ±1.50	4.32 ±1.33	2.00 ±1.60	3.93 ±1.30
8. Ratio of total height to crown width	3.12 ±0.22	2.75 ±0.12	1.71 ±0.04	1.56 ±0.06	1.98 ±0.20	1.62 ±0.02	1.78 ±0.09	1.62 ±0.02
9. Ratio of total height to height at lowest branch	2.56 ±0.16	2.63 ±0.24	4.32 ±0.74	5.66 ±0.22	3.61 ±0.28	5.25 ±0.23	3.02 ±0.30	4.86 ±0.36
10. Tolerance to shade	Intolerant	Intolerant	Tolerant	Tolerant	Tolerant	Tolerant	Tolerant	Tolerant

* diameter at breast height (1.20m) in the present case

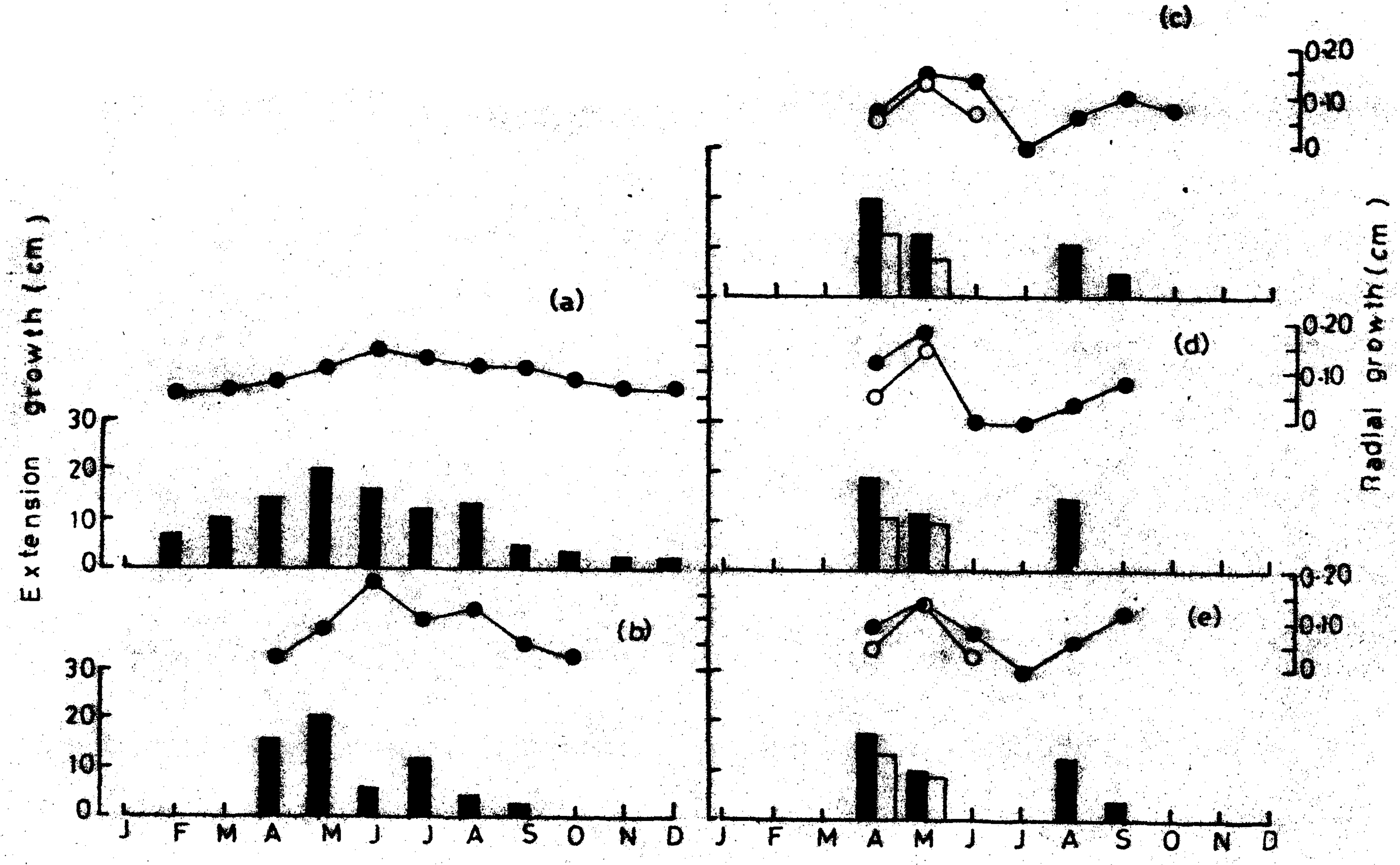
Extension growth in A. nepalensis started in February and continued upto December with one month dormancy in January whereas that of S. khasiana started in April and continued upto September with a dormancy for the rest of the period. Both species showed maximum extension growth in the month of May. On the other hand the open grown late successional species all had a similar pattern of extension growth whereby two peaks of extension growth were noted with a gap of two months' dormancy in June and July. Thus the growth was confined for a very brief period during April-May (First flush) and August (Second flush) with peaks in the beginning of the both flushes itself. Shade grown late successionals, however had only one flush of extension growth with a rapid peaking in April (Fig 4.6). Monthly radial growth also showed a similar pattern as extension growth except that the growth as well as peaking was postponed by a month (Fig 4.6).

Early successional species completed more than 50% of their total extension growth early in the growing season by May-June but had continued activity throughout the favourable growing season. Late successional species growing in the open achieved more than 50% of the total growth in the first determinate flush and the rest in the second flush while forest grown individuals completed 100% growth in one determinate flush only (Fig 4.7).

Table 4.2, shows the shoot elongation pattern at different locations on the tree of both early and late successional

Fig. 4.6: Extension (vertical bar diagram) and radial (linear diagram) growth in a. A. nepalensis, b. S. khasiana, c. Q. dealbata, d. Q. griffithii and e. M. kingii. Open bars and open circles are for forest grown individuals.

Fig. 4.6.



Extension growth (cm)
Radial growth (cm)
(a)
(b)
(c)
(d)
(e)
0
10
20
30
0
0·10
0·20
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 4.7: Cumulative percentage of extension growth completed during the growing season at various dates.

a. Early successional species.

A. nepalensis (●),

S. khasiana (○) and

b. Late successional species

Q. dealbata (●),

Q. griffithii (○),

M. kingii (▲) Dotted lines for forest grown individuals.

Fig. 4.7

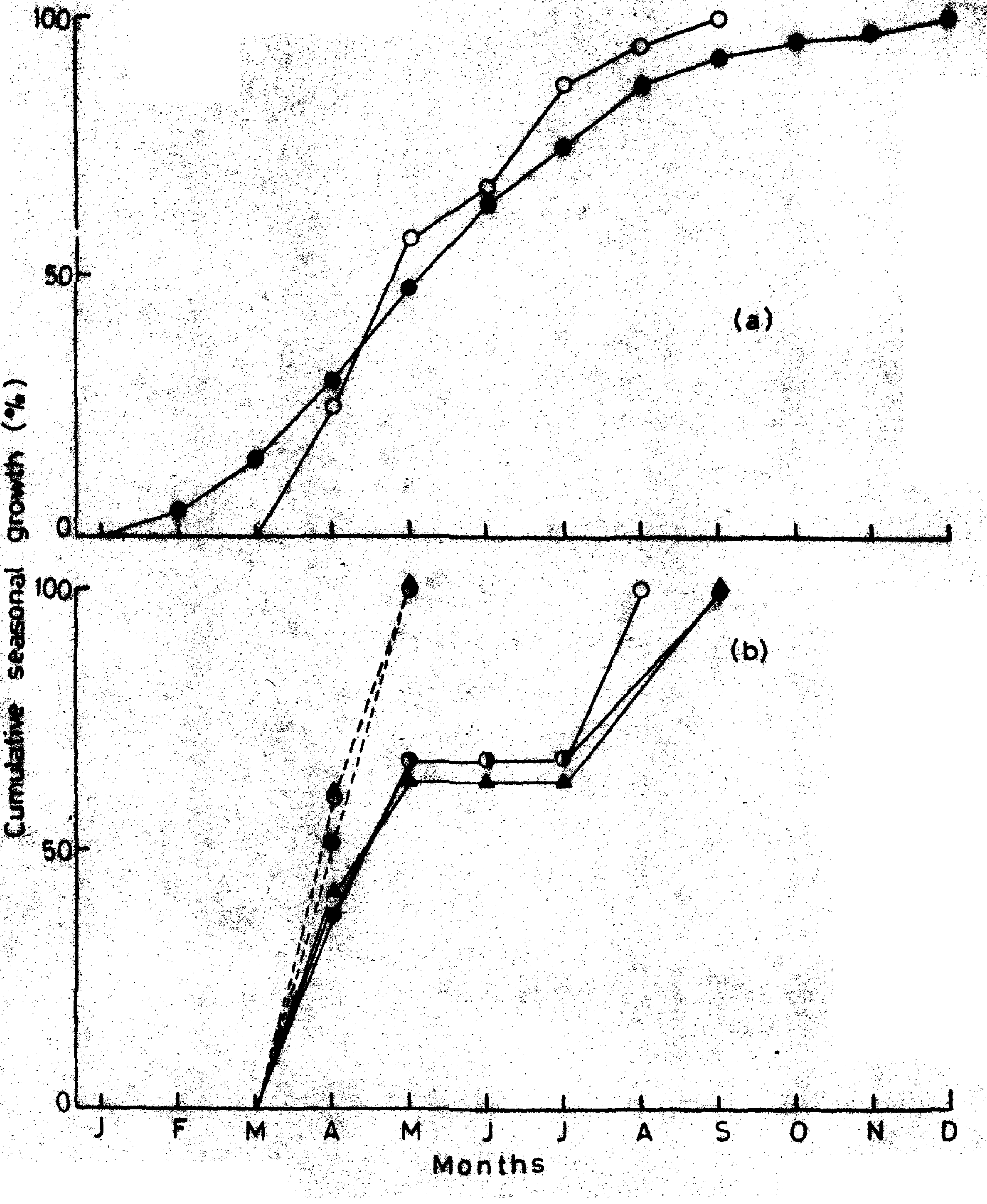

100
50
0
(a)
100
50
0
(b)
Cumulative seasonal growth (%)
J
F
M
A
M
J
J
A
S
O
N
D
Months

Table 4.2 : Variation in shoot extension (cm/year) on different locations of early and late successional tree species

		ORDER OF BRANCHES									
		I				II			III		IV
		WHORL NUMBER/YR									
	MAIN LEADER	I	II	III	IV	II	III	IV	III	IV	IV
A. nepalensis	104.00 ±10.60	49.96 ±5.68	33.58 ±2.87	15.29 ±2.44	- -	30.00 ±3.79	13.88 ±3.11	- -	12.50 ±1.89	- -	- -
S. khasiana	64.00 ±3.09	23.50 ±1.63	16.20 ±2.63	13.67 ±3.86	12.75 ±4.33	15.38 ±1.75	7.94 ±1.09	4.87 ±0.70	15.27 ±1.79	5.03 ±1.22	9.50 ±3.50
Q. dealbata	49.00 ±3.50	16.18 ±3.12	9.96 ±3.55	7.33 ±2.67	-	9.17 ±1.66	4.17 ±1.02	-	4.00 ±1.00	-	-
Q. griffithii	46.00 ±3.60	13.25 ±2.40	10.00 ±0.98	9.25 ±2.69	-	8.25 ±4.26	7.25 ±1.42	-	7.12 ±1.50	-	-
M. kingii	44.00 ±3.30	18.53 ±0.60	11.32 ±1.98	10.42 ±1.46	-	6.44 ±1.25	5.09 ±0.59	-	4.65 ±2.16	-	-

species. Both the groups showed strong correlative growth inhibition. Thus the extension growth of the main leader was more than the branches which showed the sequence of first order > second order > third order and so on. Also, the elongation of the current year (terminal whorls) shoot was maximum and decreased progressively down the tree in the second, third and fourth year whorls prior to it (Fig 4.8). Generally, branches of different orders in early successional species showed greater elongation compared to those in late successional species.

Branch and leaf orientation

Branch angles generally increased from top to the base of the canopy for both early and late successional species. Early successional species had more acute branch angles than the late successional ones at all canopy positions. The forest grown trees of S. khasiana showed even more acute branch angles compared to late successional species. The latter category under forest grown situations had more horizontal branches. (Table 4.3)

Leaf display angles showed that the leaves in all the species are placed more acutely in the periphery and less so in the inner crown at all the canopy positions. Generally, early successional species had more acutely placed leaves than the open grown late successional ones under all canopy positions. A. nepalensis is an exception to this where its large megaphylls were placed near to horizontal and in one

Fig. 4.8 : Crown form and branching pattern in a. *A. nepalensis*, b. *S. khasiana*, c. *Q. dealbata*, d. *Q. griffithii*, and e. *M. kingii*.

Fig. 4.8.

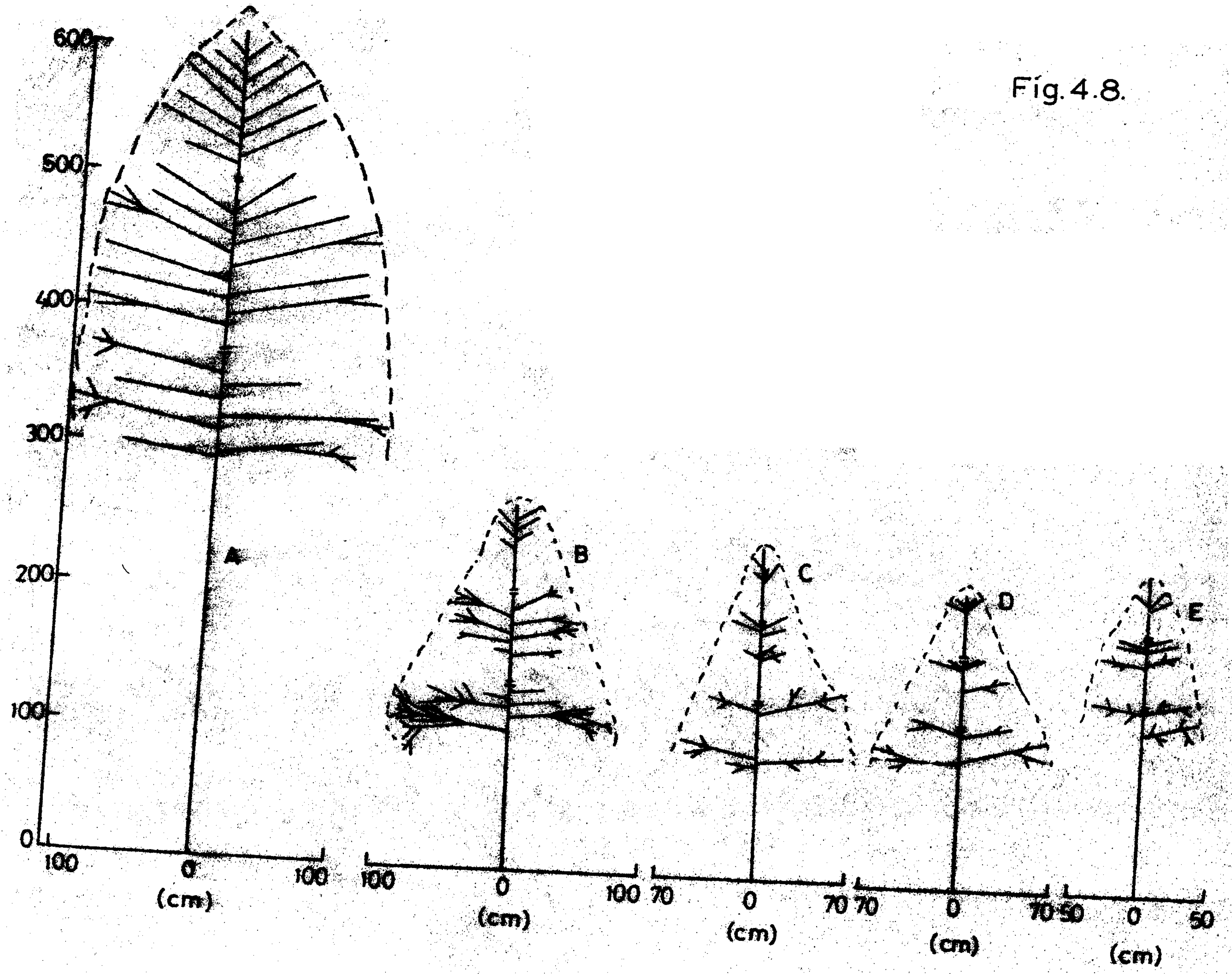

600
500
400
300
200
100
0
A
B
C
D
E
100
0
100
(cm)
100
0
100
(cm)
70
0
70
(cm)
70
0
70
(cm)
50
0
50
(cm)

Table 4.3 : Orientation of branches (degrees) with respect to main axis (trunk) for early and late successional tree species (± S.E.)

	OPEN GROWN			FOREST GROWN		
	Upper Canopy	Middle Canopy	Lower Canopy	Upper Canopy	Middle Canopy	Lower Canopy
EARLY SUCCESSIONAL						
A. nepalensis	52.20 ± 3.74	64.70 ± 2.36	79.10 ± 2.11	-	-	-
S. khasiana	46.43 ± 1.43	58.57 ± 2.06	87.14 ± 1.49	34.29 ± 2.02	56.43 ± 3.25	59.38 ± 2.75
LATE SUCCESSIONAL						
Q. dealbata	60.00 ± 3.16	77.00 ± 2.33	84.00 ± 2.66	78.00 ± 2.20	87.50 ± 0.89	89.33 ± 2.36
Q. griffithii	58.40 ± 2.97	73.83 ± 1.38	81.67 ± 3.34	62.17 ± 2.98	78.86 ± 4.42	92.67 ± 3.02
M. kingii	57.75 ± 3.17	72.20 ± 2.08	84.00 ± 1.87	67.57 ± 1.70	79.17 ± 2.09	88.83 ± 1.01

plane due to secondary orientation in the middle and lower canopy positions only in the peripheral leaves and all canopy positions in the inner crown leaves. Generally, the leaves of forest grown individuals were placed more horizontally than open grown ones (Table 4.4).

Bifurcation ratio

The bifurcation ratio (Rb) values for open grown trees of all the species indicated that A. nepalensis had much higher ratio compared to S. khasiana and all other late successional species. Open grown trees of S. khasiana and all the late successional species had significantly higher bifurcation ratio compared to forest grown trees. If the open grown early successionals are compared with forest grown late successionals the former had higher ratio compared to the latter (Table 4.5).

DISCUSSION

The pattern of growth and architecture build-up of early and late successional species are well suited to their strategy of niche occupancy in the forest ecosystem. The early successional species, chiefly through indeterminate pattern of prolonged growth and leaf production achieve much more extension growth than the late successional ones, which are determinate, confining the growth for a brief period of the growing season. Thus the growth design of early successional species which are shade intolerant favours increase in height to put up their crown under a high light regime in the forest. On the other hand, the presence of two determinate flushes in the open

Table 4.4 : Leaf display angles (+ S.E.) with respect to horizontal for early and late successional tree species (values in parentheses are for Forest Grown situations)

	PERIPHERAL (SUN) LEAVES			INNER CROWN (SHADE) LEAVES		
	Upper canopy	Middle canopy	Lower canopy	Upper canopy	Middle canopy	Lower Canopy
A. nepalensis	62.20 ±1.97	27.27 ± 2.00	10.73 ±1.46	7.20 ±1.56	4.60 ± 0.78	3.47 ± 0.65
S. khasiana	75.00 ±1.30	61.50 ± 2.53	50.00 ±1.97	31.80 ±1.49	27.00 ± 4.34	17.50 ± 3.21
Q. dealbata	52.27 ±2.39	47.33 ± 1.29	43.53 ±1.86	37.13 ±2.19	30.87 ± 1.38	28.60 ± 1.62
	(40.80 ±2.18)	(39.47 ± 1.57)	(35.13 ±1.91)	(35.00 ±1.21)	(27.33 ± 1.07)	(16.80 ± 1.12)
Q. griffithii	50.87 ±2.94	43.67 ± 3.53	47.73 ±1.98	30.60 ±1.32	24.13 ± 0.85	14.60 ± 0.90
	(44.13 ±1.14)	(39.00 ± 1.04)	(30.27 ±0.89)	(26.07 ±2.79)	(22.20 ± 1.53)	(12.53 ± 0.88)
M. kingii	49.67 ±3.47	43.33 ± 1.51	31.27 ±1.68	44.13 ±1.19	24.40 ± 1.03	19.07 ± 1.19
	(39.47 ±1.37)	(33.60 ± 0.94)	(29.20 ±1.15)	(29.67 ±1.06)	(23.13 ± 0.70)	(14.47 ± 1.01)

Table 4.5 : Bifurcation ratio values for early and late succesional trees

	OPEN GROWN			FOREST GROWN	
	Mean ± S.E.	Range	t	Mean ± S.E.	Range
EARLY SUCCESSIONAL					
A. nepalensis	6.18 ± 0.20	5.50 - 7.41	-	-	-
S. khasiana	3.91 ± 0.14	3.38 - 4.75	4.06**	3.24 ± 0.09	3.00 - 3.59
LATE SUCCESSIONAL					
Q. dealbata	4.72 ± 0.22	3.75 - 5.45	7.27**	2.91 ± 0.12	2.35 - 3.64
Q. griffithii	4.62 ± 0.49	3.64 - 7.00	2.77*	3.62 ± 0.14	3.20 - 4.67
M. kingii	4.02 ± 0.34	3.50 - 4.40	5.84**	3.23 ± 0.08	2.93 - 3.71

** Significant at 1% and * significant at 5% level of significance grown late successional trees and only one in the case of forest grown ones is indicative of the ability of these species to adapt their growth strategy, at least to some degree, depending upon the light availability. It is possible that the late successional species have evolved with a strategy to grow under low light regimes where resources are often limiting, but also have the ability to adjust its growth pattern favourably in open situations which chiefly arise due to canopy openings.

The Attim's architecture model of A. nepalensis is particularly geared to make fast and efficient growth through continued actitivity of its apical meristems. Ideally, the continued meristematic activity should be the case all the year round but in the present case there is a very brief dormancy for about a month during winter which often is not obvious. All the late successional species and the early successional S. khasiana though have the same architecture model (Rauh's), the differences between them are quantitative, with less rhythmicity and lesser extension growth and leaf production in the latter category of species. Early successional species produce branches sylleptically and the late successionals branch through prolepsis. The switch from a 'lower state' which determined prolepsis of a lateral meristem, to another state which determines syllepsis, is conditioned by a 'threshold' which in turn is determined by the growth vigour of the parent shoot (Tomlinson & Gill, 1973).

Such a sylleptic branch production in early successional species, it seems, is intended to make quick growth under fast diminishing light resources in a developing community as also reported in <u>Schima wallichii</u> (Boojh & Ramakrishnan, unpublished). The growth of a hypopodium in sylleptic branches is presumably a mechanism by which the leaves are put outside the shade created by the leaves of the parent shoot (Wheat, 1980).

The reiteration process through which the tree adjusts its architecture to environmental modifications and disturbances may be helpful to early successional species, for adjustment to changing light environments. These species being shade intolerant try to put their crown always in high light environments and each wave of reiteration offers the tree to activate dormant meristems to grow more vigorously for achieving such a strategy. Likewise, for late successional species, this process may often be triggered after canopy openings. Thus, reiteration allows the tree to exploit the changes in the environmental energy level. The larger quantities of incoming energy due to environmental changes or disturbances is utilized by the trees by increasing the numbers or sizes of the producing organs. Branching and reiteration in tree crown are examples of this process. Thus, the branching within the model is a standard solution to bio-energetic relationship, whereas reiteration allows for ecological opportunism (Hallé <u>et al</u>., 1978).

Bud dynamics, which takes into account the number and longevity of meristems, their positions, time and potential of development leads directly to the dynamic concept of architecture (Hallé et al., 1978) and allows plant growth to be interpreted in terms of organized flux of constructional units. While the early successional species proliferate their axillary buds synchronously with that of the terminal bud growth, late successional species proliferate their buds after a dormant period and the activity is dependent upon the resources of the environment. Thus the branches proliferate continuously in A. nepalensis as the meristem activity is continuous; while in S. khasiana the branching is rhythmic due to rhythmic activity of the terminal leader. This allows the two early successionals to achieve faster growth by utilizing the current years energy. The lesser number of reserve buds and their high mortality or inability to proliferate in the following year also tends to suggest that all resources are directed exclusively for the current year's growth and branch production. The late successional species in open grown situations are able to make some bud proliferation during the current year through lamma's shoot formation in the second flush; shade grown trees, however, produce branches in the next year only. This may be due to the limiting light conditions that exist in late successional environments. The early successional species though they make about 50% of their annual extension growth in the beginning of the growing season by April-May, continue their growth almost all through the favourable growth season. This pattern allows them to use, more effectively temporary conditions of increased resource availability and reduced competition of the early successional environments. The modest extension growth that the late successional species make which is confined only to a brief period in the early part of the growing season may be an adaptation to the relatively predictable and highly competitive environments of closed forests. Radial growth started and terminated later than the extension for all the species and similar results are reported for many temperate trees (Kozlowksi, 1971) and also for some tropical trees (Choudhury, 1958).

Differential elongation of different axes usually determines the form of woody plants. The excurrent crown form which was more pronounced in early successional species is achieved through stronger correlative growth inhibition with apical control over the growth of the branches beneath (Brown <u>et al</u>., 1967) compared to late successional species.

The aspect of stem architecture documented through various ratios between stem and crown shows that early successional species tend to maintain a higher, narrower crown than the late successional species which have lower, wider and deeper crowns. Early successional species tend to emphasize height growth in order to attain a superior competitive position, while late successional species have more lateral crown growth. This would help early successional species to exploit high light regime while late successional species would be able to put out a larger leaf surface area to exploit low light intensity.

The orientation of branches and leaves in space and time usually shape the geometry of tree crown and this has been related to its adaptive strategy for light interception (Horn, 1971; Brunig, 1976; Honda & Fisher, 1978). The increase in branch angles down the tree along the vertical gradient of sunlight results in greater increase in gap between the two first order branch complexes. The highly acute branch angles of early successional _S._ _khasiana_ under forested situations show its inability to tolerate shade, while the reverse situation for late successional species under forest grown situations increase the spread of the crown to provide maximum effective leaf surface area possible. The leaf display angles in the late successional species are more near to horizontal and arranged in one plane for both sun and shade leaves than the early successional species which have its leaves disperesed into several layers (multilayer - Horn, 1971) with sun leaves placed vertically and shade leaves to near horizontal. Such a light interception strategy as also reported by Pickett & Kempf (1980), is meant to enhance photosynthesis of leaves of late successional species and shade leaves of early successional species under limited light conditions and to promote leaf cooling during high solar radiation in sun leaves of early successional species (McMillan & McClendon, 1979).

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

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

SUMMARY

The architecture and growth pattern of early (*Alnus nepalensis* Don. and *Schima khasiana* Dyer) and late (*Machilus kingii* H.K.F., *Quercus dealbata* Hook. F. & Thoms. and *Q. griffithii* Hook F. & Thoms.) successional tree species in a

sub-tropical montane humid evergreen forest at Upper Shillong (1900 m) in north-east India were analysed and related to their ecological strategy for niche occupancy in the forest ecosystem. The early successional species have geared their architectural development pattern and growth design to maximize production under high light environments. These have indeterminate pattern of shoot growth, prolonged growth period with greater extension growth and leaf production, greater rhythmicity (except for A. nepalensis which showed almost a continuous growth) and branch mainly through syllepsis. Various stem crown ratios suggest for these species, to emphasize vertical growth at the expense of lateral spread.

In contrast, the late successional species make modest growth under a determinate scheme, the growth being confined to preformed bud primordia for a brief period of the growing season. Growth has lesser rhythmicity and branch production is through prolepsis. The stem crown ratios show a tendency of late successional species to emphasize lateral spread, as an adaptation to the highly competitive environments. Under forest grown situations these species tended to have only one determinate flush of shoot growth, however, under open grown situations there were two such flushes. Bifurcation ratio values are found to vary in forest and open grown situations, suggesting the capacity of the species to adjust their architecture to changed light conditions.

PLATE 11

Branching pattern in *Alnus nepalensis* showing Attim's model.

PLATE 12

A tree of *Quercus griffithii* showing Rauh's model.

PLATE 11

PLATE 12

PLATE 13

Quercus dealbata showing rhythmic branching and Rauh's model of architecture.

PLATE 14

Quercus dealbata showing a new flush of branch and leaves from overwintering buds.

PLATE 14

PLATE 13

PLATE 15

A tree of Machilus kingii showing branching pattern as exemplified by Rauh's model.

PLATE 16

Machillus kingii showing new flush of leaves and branches from overwintering buds.

PLATE 15

CHAPTER V

Growth strategy of trees related to successional status: II. Leaf dynamics

GROWTH STRATEGY OF TREES RELATED TO SUCCESSIONAL STATUS

II LEAF DYNAMICS

INTRODUCTION

Higher plants are built of repeating modules of structures or iterations of a basic constructional module in which the construction unit in the shoot is the leaf and its axillary bud (Harper & White, 1970; Harper & Bell, 1979; White, 1979). As a plant grows new modules are added to the structure and old ones die. The growth pattern of trees as a population of parts, therefore, needs to quantify the births anddeaths of these parts.

The leaf, with its axillary bud, is the smallest module of organized structure in higher plants and leaves may have many of the properties associated with members of a population, e.g. they may increase in number exponentially in a rapidly growing plant, they have juvenile, mature and senescent phases, death rates, birth rates and survivorship curves. Bazzaz & Harper (1977) in the case of Linum usitatissimum, have shown that the use of demographic techniques to study the populations of leaves on a plant is feasible. It may, in some cases, allow more comprehensive understanding of plant growth and primary production processes in the canopy.

Though individual trees have been considered as aggregates of repeating and somewhat independent units in the pipe model theory of Shinozaki et al, (1964), and others have considered branches as individuals (Oldeman, 1971; Gill & Tomlinson, 1971) or dealt with leaf characteristics such as census (Busgen & Munch, 1929), longevity (Gill & Tomlinson, 1971,) age-structure

(Kinerson *et al*, 1971) or abcission rates (Kozlowski 1973; Addicott 1978), comprehensive demographic studies on leaves in a canopy have received little attention.

This chapter attempts to analyse the growth pattern of early (*Alnus nepalensis Don* & *Schima khasiana Dyer*) and late (*Machilus kingii* H K F., *Quercus dealbata* Hook F. & Thomas & *Q. griffithii* Hook F. & Thomas) successional tree species of a sub-tropical montane, moist evergreen forest at Upper Shillong (1900m) by considering the structural demography of key constructional units namely the leaves. Such a comparative study of trees of diverse ecological equipment and niche occupancy in the forest is expected to contribute towards a better understanding of their adaptation to the environment in which they grow.

METHODS

The study area and climate have been described in Part I of this series. For both group of the species one 5-year old normal growing tree of seed origin was selected taking care to ensure that they were not damaged. Early successional species were from open grown situations only as they were not found to grow in forest shade but the late successional species were considered both from open and forest grown situations. The census of leaf numbers, was made for each individual tree at the beginning of the study. Leaves were classed into different age groups by using their position on the branch. Some broader categorization into age classes could also be made on the basis of leaf texture and colour in the case of *Q. dealbata* and *M. kingii*. The fate of individual leave of each age group (cohort) was followed to estimate the distribution of ages of dead leaf populations at the end of the study. Monthly estimates of leaf production/birth and fall/death were made by tagging all previous leaves and constantly giving fresh tags to newly recruited ones using light, small, colour-coded aluminium tags.

RESULTS

Leafing characteristics

Table 5.1 gives a summary of the important leafing characteristics of early and late successional tree species. The leaf production period was more for early successional species and consequently they had lesser number of dormant days than the late successional species. The latter in open grown situations had more production period and lesser dormancy period than in the forest grown situations. Early successional species produced greater number of leaves and a larger leaf area than the late successional ones which in open grown situations had more number of leaves and a larger leaf area than in the forest grown situations.

Leaf production and population flux

Early successional A. nepalensis had prolonged leaf production with a peak in the month of May while S. khasiana showed two seasonal peaks of leaf production, one in May and the other in July. Open grown late successional tree species showed two major peaks of leaf production corresponding to their two determinate flushes (see Part I) one in April and the other in August. In forest grown trees of this category there was only one seasonal rhythm of leaf production in the month of April. (Fig. 5.1 a)

Fig 5.1 : (a) Pattern of leaf production in early and late successional tree species

(b) Cumulative % of total annual leaf production completed at various dates.

Alnus _nepalensis_ (●), _Schima_ _khasiana_ (○), _Quercus_ _dealbata_ (▲), _Q._ _griffithii_ (△), _Machillus_ _kingii_ (□).

Fig. 5.1.

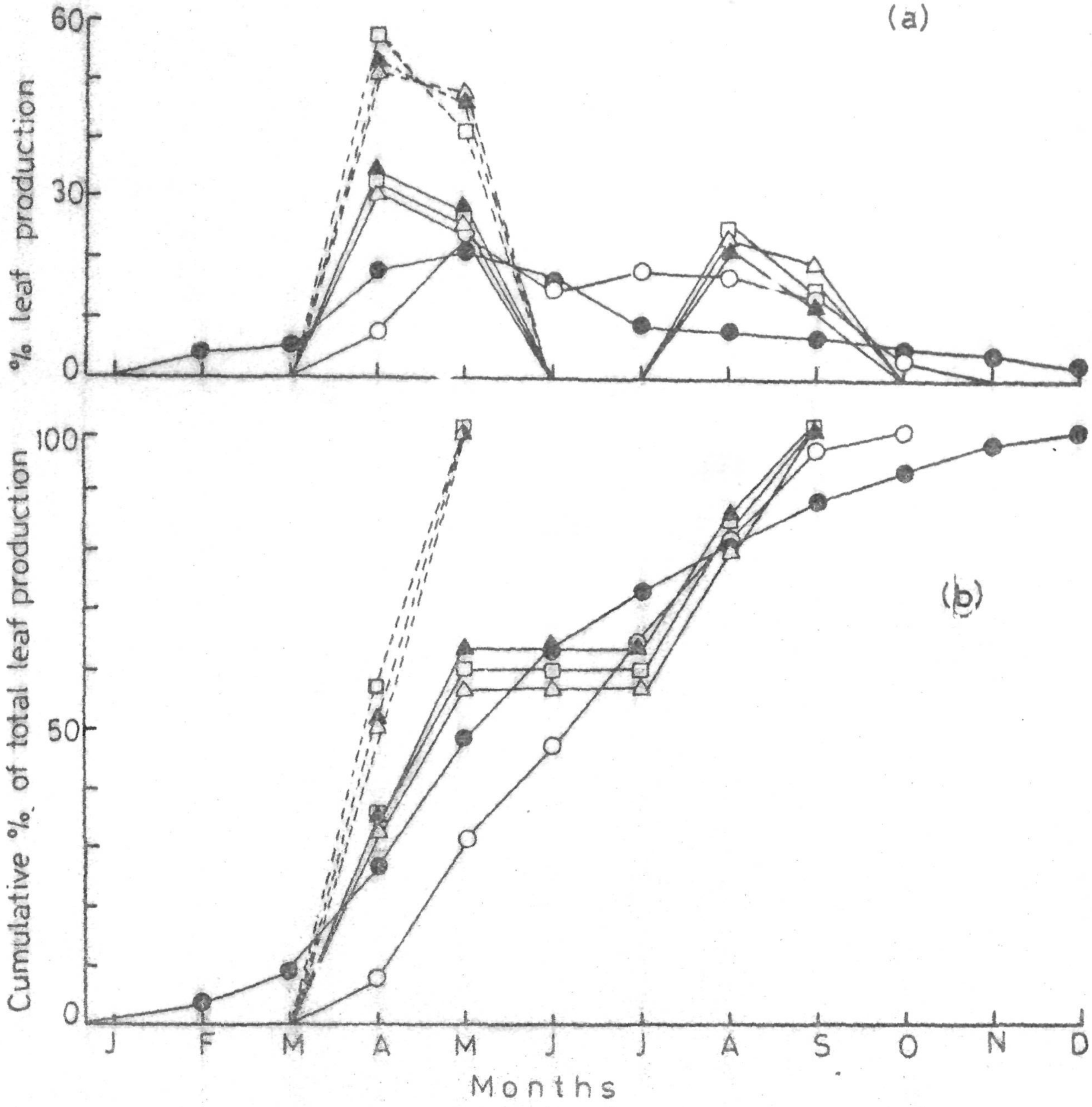

(a)
% leaf production
0
30
60
(b)
Cumulative % of total leaf production
0
50
100
J
F
M
A
M
J
J
A
S
O
N
D
Months

Table 5.1 : Leafing characteristics of early and late successional tree species

	EARLY SUCCESSIONAL		LATE SUCCESSIONAL					
	A. nepalensis	S.khasiana	Q. dealbata		Q. griffithii		M. kingii	
	OPEN	OPEN	OPEN	SHADE	OPEN	SHADE	OPEN	SHADE
Flushing date	Feb 1	Mar 25	Apr 1 & Aug 5	Apr 20	Apr 5 & Aug 5	Apr 20	Apr 10 & Aug 5	May 1
Date of onset of dormancy	Dec 31	Oct 1	May 15 & Aug 30	May 25	May 20 & Aug 23	May 20	May 25 & Sep 1	May 3
Leaf production period (days)	334	190	73	35	63	30	72	33
Dormant period (days)	31	175	292	330	302	335	293	332
Total leaf production/year	647	1167	225	114	169	78	206	92
Total leaf area production/year ($cm^2 \times 10^3$)	43.17	41.00	8.81	4.46	10.51	4.85	6.18	2.76
Leafing behaviour*	E	D	E	E	D	E	E	E

*E = evergreen; D = deciduous

Early successional species completed more than 50% of their total annual leaf production early in the growing season by June-July but continued the production till the end of the favourable period. Late successional species under open situtations completed more than 55-65% of the total annual leaf production in the first flush only. In forest grown trees, however, all leaves were produced within a very brief period of about a month (April - May) in a single flush. (Fig. 5.1, b)

Table 5.2 gives a summary of the population flux of leaves for early and late successional species. The total number of leaves produced by early successional species was far more than the late successional ones. Further the total number of leaves recorded on the tree during the study period was also greater for early successional species. Percentage annual mortality of all leaves was in general much higher for early successional species compared to late successional ones, the only exception being open grown *Q. griffithii*. But the dynamics of the leaf populations i.e. loss and gain (the flux) depended on the pattern of leafiness, whether a tree was deciduous or evergreen. Thus, in the case of two deciduous species the expected time for complete turnover was one year in open grown trees whereas it was more for the rest. Further the percentage mortality of all leaves in open grown *S. khasiana* and *Q. griffithii* was more compared to others. However a comparison of open grown trees of *Q. griffithii* with forest grown ones of the same species suggests that the expected time for complete turnover was more than one year with lower annual mortality in the latter. This was true also for evergreen *Q. dealbata* and *M. kingii*.

Table 5.2 : Population flux of leaves of early and late successional tree species

	EARLY SUCCESSIONAL		LATE SUCCESSIONAL					
	A. nepalensis	S. khasiana	Q. dealbata		Q. griffithi		M. kingii	
	OPEN	OPEN	OPEN	SHADE	OPEN	SHADE	OPEN	SHADE
a) No. of leaves/tree, April 1979	320	97	354	198	55	96	226	181
b) No. of leaves/tree, April 1980	331	129	356	228	70	108	286	201
c) Net change (b-a)	+11	+32	+ 2	+30	+15	+12	+60	+20
d) Rate of increase (b/a)	1.03	1.33	1.01	1.15	1.27	1.12	1.26	1.11
e) No. of leaves produced between April 1979 and April 1980	647	1167	225	114	169	78	206	92
f) Total No. of leaves lost between April 1979 and April 1980	626	1160	229	93	169	75	155	79
g) Leaves present April 1979 alive by April 1980	9	0	204	166	0	21	71	102
h) Percentage survival of leaves in (a), (g/a x 100)	2.81	0	57.63	83.84	0	21.87	31.42	56.35
i) Expected time for complete turnover (Yrs) $(\frac{1}{100-h} \times 100)$	1.03	1.00	2.36	6.19	1.00	1.28	1.46	2.29
j) Total leaves recorded during study	842	1192	500	251	169	133	361	220
k) Percentage annual mortality of all leaves $(\frac{f}{j} \times 100)$	74.35	97.31	45.80	37.05	100	56.39	42.94	35.91

Fig. 5.2 shows the changes in the net population size with time and the cumulative gains and losses that determine them. It shows the seasonal patterns of population flux. The early successional species showed pronounced flux in leaf populations compared to the late successional species. The gain in the population was very sharp extending upto October-November in the case of S. khasiana and almost for the entire period in A. nepalensis. The losses became pronounced after October-November in both the species, more so in the case of S. khasiana. The late successional species on the other hand had less pronounced population flux with leaf gains being confined to a shorter period with two short flushes in the case of open grown trees. The forest grown trees however showed only one flush of leaf gain. The loss pattern in the case of two evergreen trees Q. dealbata and M. kingii was more or less steady throughout with a sharper decline after January. The deciduous Q. griffithii showed leaf fall confined to October-December after which the tree became naked. The losses in forest grown late successional species occurred at a slower rate and even the deciduous Q. griffithii did not become totally naked.

Age Structure of living leaf populations

Fig. 5.3 shows the age structure of the living leaf populations categorized according to their year of birth. There is a normal age distribution with greater representation of younger age classes in the case of Q. dealbata and M. kingii. The shade grown trees of both these species had more wider age classes present with a good proportion originating prior to

Fig 5.2: The flux of leaf modules in early and late successional species.

a. Early successional species

A. nepalensis

(●) Cumulative gains.

(○) Cumulative losses.

(▲) Net population size

S. khasiana

(△) Cumulative gains,

(■) Cumulative losses,

(□) Net population size

b. Late successional species

(●) Cumulative gains,

(○) Cumulative losses,

(▲) Net population size.

Solid lines for open grown and broken lines for forest grown trees.

Fig. 5.2.

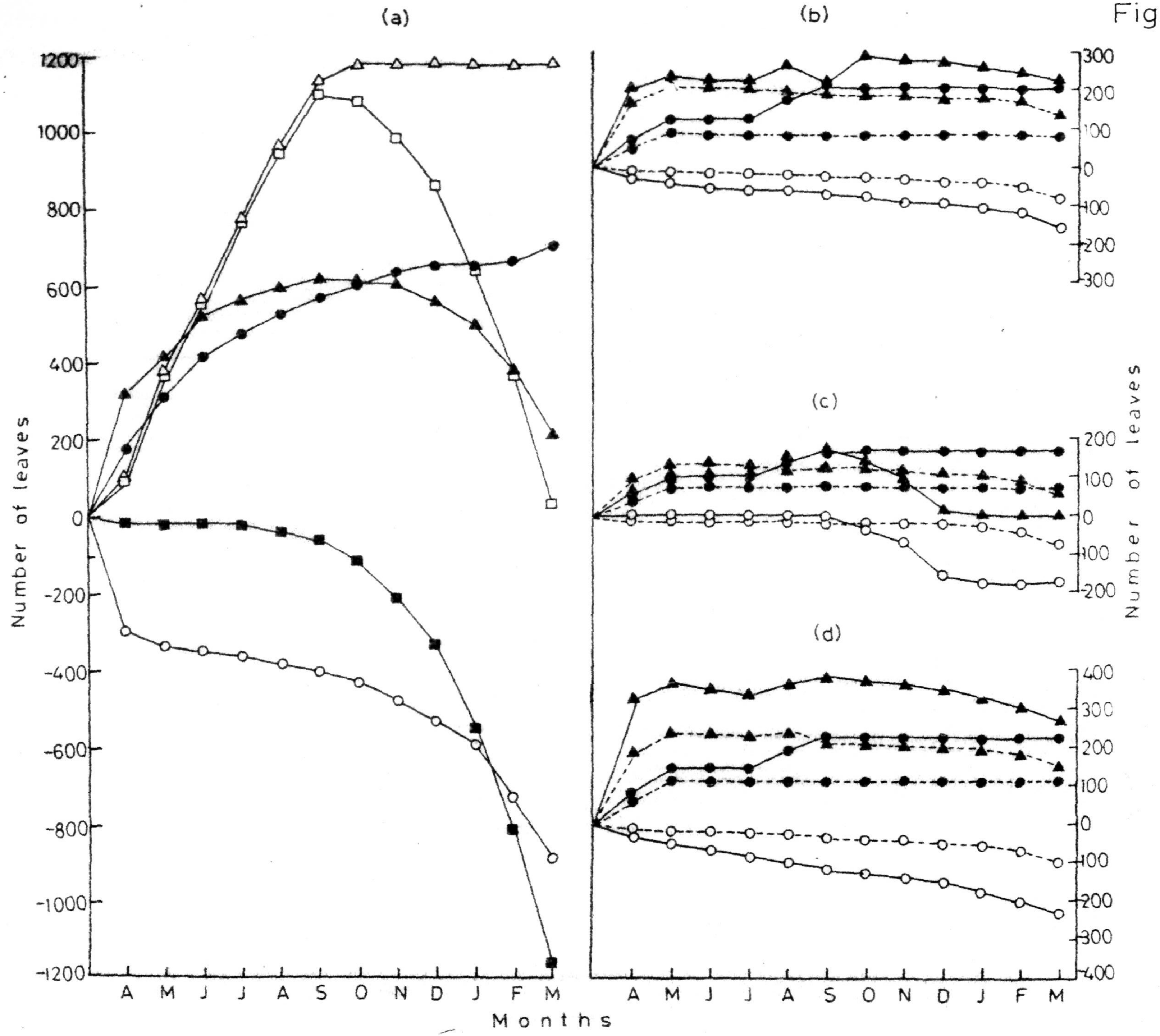

(a)
(b)
(c)
(d)
Number of leaves
1200
1000
800
600
400
200
0
-200
-400
-600
-800
-1000
-1200
300
200
100
0
100
200
300
400
A M J J A S O N D J F M
Months

Fig. 5.3: Age structure of living leaf populations for late successional

a. *Q. dealbata* (open grown), (a) forest grown

b. *Q. griffithii* (open grown), (b) forest grown

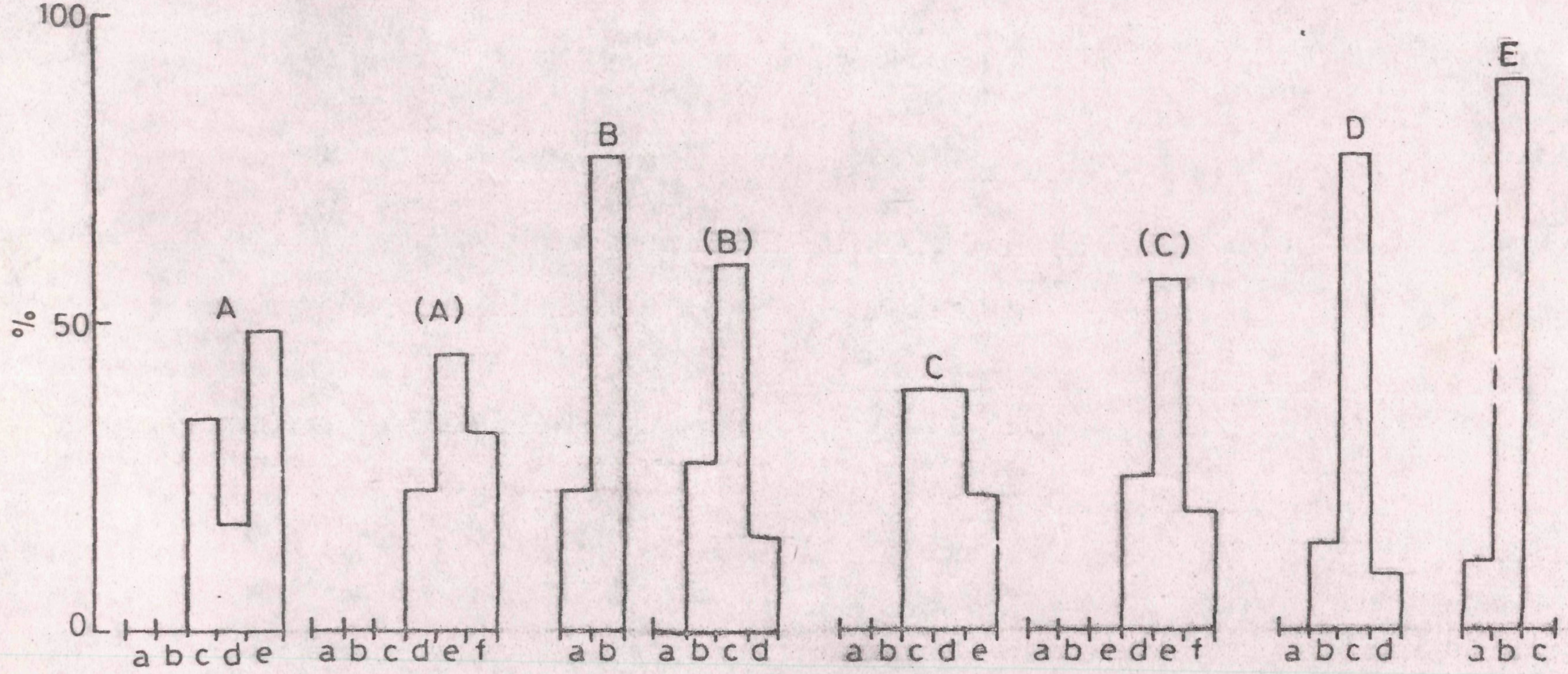
Machillus kingii c, open grown, (c), forest grown.

Early successional tree species.

d. *A. nepalensis*

e. *S. khasiana*

Fig.5.3.



the study period. In the case of deciduous Q. griffithii particularly in open grown trees only the current year's leaves were present whereas in the forest grown trees of this species two years leaves were present with a greater representation for the current year ones. The early successional S. khasiana had only current year's leaves present on the tree whereas A. nepalensis had a greater proportion of leaves from the previous year.

Age distribution of dead leaves

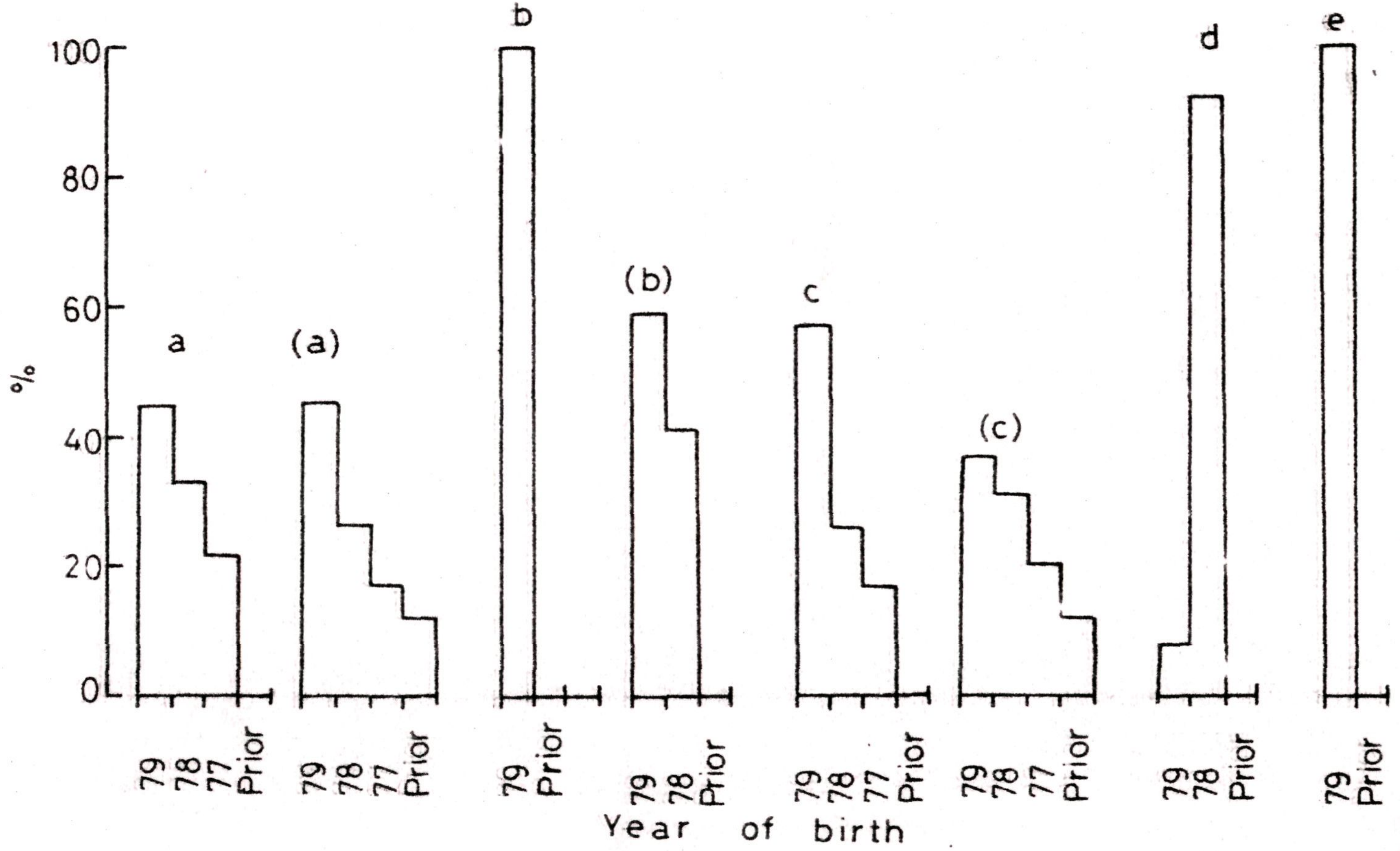
The fate of leaf populations from individual cohorts is shown in Fig. 5.4. In early successional A. nepalensis, cohort of leaves produced in 1978 showed high mortality and by April all the leaves of this cohort were shed. In 1979 cohort there was a steady decline of leaf populations after October with more mortality rate after January. In S. khasiana there was a rapid mortality in the 1978 cohort resulting the death of all leaves by June. But the leaf populations of 1979 started declining in the month of August and the rate increased sharply after November.

Late successional Q. griffithii under open grown situations had only the current year's cohort of leaves, which showed a rapid decline in October followed by complete mortality by February. In the forest grown trees of this species mortality occurred at a slower rate and 1978 cohort of leaves could survive till March 1979 while 1979 cohort started declining after December with 75% of leaves still present in March. In

Fig. 5.4: The age distribution of leaf populations at the time of death for late successional
Q. dealbata A, open grown; (A) forest grown.
Q. griffithii B, open grown; (B) forest grown.
M. kingii C, open grown; (C) forest grown.
and early successional
A. nepalensis, D; *S. khasiana*, E. tree species.

Age groups: a = 0 - 0.5 years;
b = 0.6 - 1.0 years;
c = 1.1 - 1.5 years;
d = 1.6 - 2.0 years;
e = 2.1 - 2.5 years;
f =>2.6 years.

Fig. 5.4.



Q. dealbata and M. kingii (both open and forest grown), current year's (1979) cohort of leaves showed no mortality whereas the rate and final mortality increased with the age of the cohort. In general the individual cohorts under forest grown situations showed greater survivorship than those of the open grown situations. (Fig. 5.5)

DISCUSSION

The ecological strategy of trees has been linked to shoot morphogenesis (Marks, 1975; Bormann & Likens, 1979). Conservative species which make relatively modest amounts of height growth during the earliest part of their life-span and complete annual height growth early in the growing season are adapted to the relatively predictable and highly competitive environments of closed forests. Growth of the exploitive species, on the other hand, is geared to temporary conditions of increased resource availability and reduced competion associated with recently disturbed sites such as those resulting from fire, clear cutting, wind throw or abandonment of agricultural land. Thus the species that are exploitive ecologically are exploitive phenologically and developmentally and vice versa (Marks, 1975). These expectations are related to the slower growth (Marks, 1975) of late as compared to the early successional species and ultimately to the generally lower resource demand of the former (Grime, 1979; Bazzaz, 1979).

The dynamics of leaf populations of early and late successional species indicates some of the potentitals that enables

Fig. 5.5: Survivorship curves for leaf populations of A. early successional : *A. nepalensis*, a; *S. khasiana*, b, and B. late successional: *Q. dealbata*, C, *Q. griffithii*, d; *M. kingii*, e tree species,

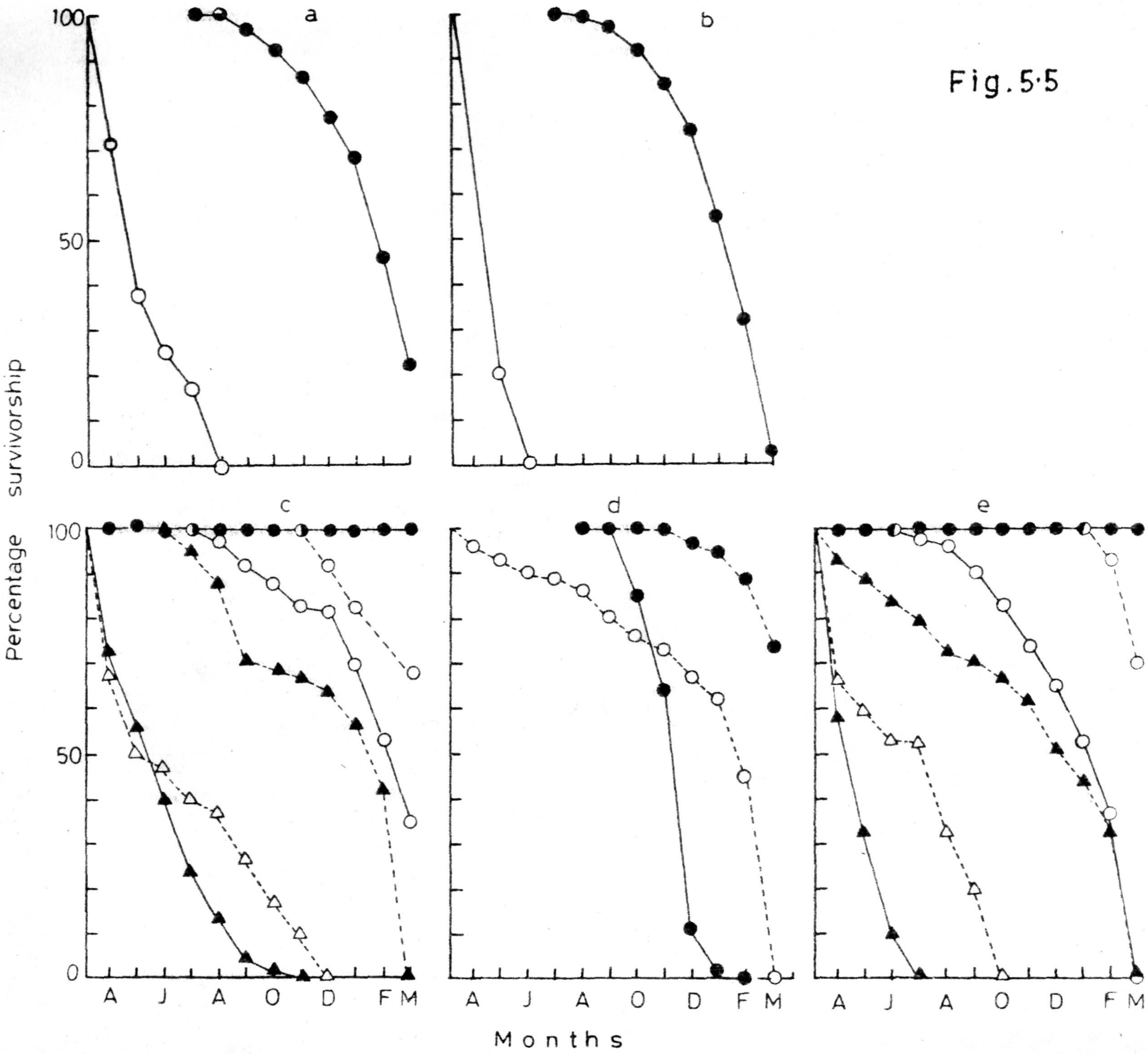
1979 cohort of leaves (●)

1978 cohort of leaves (○)

1977 cohort of leaves (▲)

1976 cohort of leaves (△)

Fig.5·5



them to perform their role in the ecological niche they occupy in the forest. Early successional species through their extended period of leaf production are able to produce a large photosynthetic area to exploit effectively temporary conditions of resource availability which follow disturbance. The high turnover rates of leaves may be associated with the tendency of these species to achieve fast growth through putting their leaves always in a favourable light environment. Further, growth of these species are dependent mainly on the current photosynthates. The growth analysis of some tropical trees (Coombe, 1960; Coombe & Hadfield, 1962) has revealed that the rapid growth of early successional species does not lie in particularly efficient energy converstion but rather in their capacities for unrestricted leaf production. Late successional species, which have a brief leaf production period and produce only a determinate number of leaves, have evolved this strategy to suit the competitive late successional environments.

Leaves change their activity with age; in particular, their photosynthetic activity rises to a plateau and then declines. Hence the population of leaves that constitute a canopy should have an activity determined by the age structure and age specific phtosynthetic activity of the leaves. Thus, apart from having more leaves of younger age groups, early successional species have lesser number of age groups as mutual shading of a large number of age groups would reduce their performance. The late successional species, being shade adapted and having a monolayer arrangement of their leaves (Horn, 1971), pack leaves of various age groups in their crown and this is more pronounced in the forest grown trees of this category.

The study of births and deaths 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 populations than late successional species. Thus, these species have developed a competitive attribute in the form of large size of leaf populations. This in term is dependent upon an extended period of phtosynthetic 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. Short-term experiments involving artificial shading have also shown such adjustments (Grime & Jefferey, 1965; Loach, 1970).

Leaf populations undergo mortality over a time period. The leaf populations in the present study follow a Deevey Type I (Deevey, 1947) survivorship curve, having very slight mortality during early life, but increasing with age. In several other studies also similar survivorship curves have been observed for leaf populations (Kimura et al, 1968; Williamson, 1976; Bazzaz & Harper, 1977; Yuwaka et al, 1977: Reader, 1978; Solbrig, Newell & Kincaid, 1980).

A variety of patterns of leafiness (renewal and fall) have been reported for tropical trees (Holttum, 1940; Koriba, 1958; Longman & Jenik, 1974), mostly with a pattern of prerain or equinoctial flushing (Alvim, 1964; Frankie et al, 1974) which may perhaps be related to the display of the newly expanded leaves at the time of maximum solar irradiation and other favourable growth conditions. This is also true in the present case. The foliage deciduousness patterns that appear to be beneficial adaptations have evolved in response to seasonal climatic changes. A large number of factors have been implicated to trigger the leaf sheeding in tropical trees like water or cold stress, photoperiod and intrinsic factors (Addicott, 1978). Maximum leaf sheeding occurring during the winter season as seen from the present study seems to be an adaptation to avoid cold stress.

SUMMARY

The leaf dynamics of two early (Alnus nepalensis and Schima khasiana) and three late (Machillus kingii, Quercus dealbata and Q. griffithii) successional tree species of a subtropical, humid, evergreen, montane (1900m) forest at Upper Shillong in north-east India, have been analysed by applying demographic techniques to study the leaf populations. The early successional species show greater leaf production, higher leaf turnover rate and a greater flux of births and deaths of leaf populations than the late successional ones. The latter, under forest grown situations, though having a lesser flux of leaf populations consisted of leaves of several

age-groups. The dynamics of leaf populations indicates exploitive potentials of the early successional species suitable for such environments of temporary resource availability. The late successional species on the other hand have conservative strategy adapted to the relatively predictable and highly competitive environments of closed forests. The leafing characteristics of both the groups of species are discussed with respect to their ecological strategy for niche occupancy.

SECTION C

SEED GERMINATION AND SEEDLING ESTABLISHMENT

CHAPTER VI

Seed germination and seedling establishment of two closely related *Schima* species

CHAPTER VII

Germination ecology of *Alnus nepalensis* Don

SEED GERMINATION AND SEEDLING ESTABLISHMENT OF TWO CLOSELY RELATED *SCHIMA* SPECIES

INTRODUCTION

Germination and establishment represent two critical phases in the life-cycle of a plant species and these two aspects have been related to adaptation and distribution pattern of species in space (Koller *et al*., 1962; Harper, 1965; Cohen, 1967; Ramakrishnan, 1972; Ross & Harper 1972; Thompson, 1973; Boojh & Ramakrishnan, 1981_a) and in time (Kapoor & Ramakrishnan, 1973). However, this aspect of the problem in relation to adaptive strategy of tree species has received little attention (Kozlowski, 1971; 1979). Although the size of a single species population is to some extent related to seed supply, it is ultimately determined by favourable conditions available for germination and establishment (Harper *et al*., 1961). Further, a large gap often exists between the seeding potential of a species and the actual number of seedlings established in that area, depending on environmental conditions.

S. khasiana Dyer and *S. wallichii* D.C. (Korth) are two closely related and economically important timber tree species of north-eastern hills of India. These species show a distribution pattern on an altitudinal basis where *S. khasiana* is restricted to higher elevations (1800 - 1900m), while *S. wallichii* shows a wide distribution ranging from 100 to 1600m. These two species are early successional and come up in the secondary fallows after slash and burn agriculture (Jhum). It is light demanding and regenerate profusely in the open, through light wind dispersed seeds. The present study is a comparative investigation of seed germination and seedling establishment of these two species along an altitudinal gradient in the Khasi Hills of Meghalaya.

CLIMATE

All the three sites are characterised by marked seasonal changes in climate. The year could be divided into 3 distinct seasons: (i) Monsoon season of high temperature and humidity extending from May to October when over 80% of the rainfall occurs (ii) Winter season (November to February) of lower temperature which is comparatively dry except for a few winter showers, & (iii) A warm, dry and windy summer in March-April (Table 6.1).

METHODS OF STUDY

Mature fruits of S. khasiana were collected from Upper Shillong and that of S. wallichii from 3 sites at Shillong, Umsaw and Burnihat, in the months of February-March, 1978. Seeds were separated out by air drying. The fruit and seed weight measurements were based on 100 fruit/seed with 20 replications.

Seeds were stored at 20 ± 5^{o}C and at 0^{o}C, in tightly closed plastic bottles in the laboratory. In nature, seeds were similarly stored 5 cm. below the soil surface. Viability

Table 6.1 : Comparison of climatic data at study sites during 1978-79

	Upper Shillong	Shillong	Umsaw	Burnihat
LOCATION				
Latitude (N)	25.34	25.34	25.45	26.02
Longitude (E)	91.56	91.56	91.54	91.52
Altitude (m.)	1900	1400	800	100
TEMPERATURE (°C)				
Mean Monsoon Maximum	22	24	30	32
Mean Monsoon Minimum	15	16	22	24
Mean winter maximum	16	16	20	25
Mean winter minimum	3	6	10	12
PRECIPITATION (mm)	2400	2000	1800	1600

tests with tetrazolium trichloride solution and germination tests in petri-dishes on moist filter paper were done at intervals of 3 months.

Seeds were tested under two conditions, of continuous light under an incandescent fluorscent tube (500 - 600 lx.) or under continuous darkness by covering the petri-dishes inside thick black paper, at a constant temperature of 20°C. Seed germination in dark was counted under green light. Different constant (15, 20, 25, 30 and 35°C) and alternating (25/15 and 25/20°C) temperature regimes were tried in B.O.D. incubators maintained at these temperatures. The effect of different soil depths of 0, 2, 4, 6, 8 and 10 cm. in pots filled with soil, by placing seeds at the appropriate depth.

All germination experiments were replicated 4 times with 50 seeds in each test. The emergence of radicle was taken as an indicator of germination. Tests in all cases were done for 20 days after the seeds were placed for germination.

Ten replicates of 100 viable seeds of each species/population were sown at a depth of 5 cm at all the 4 study sites both in the open and under forested situations, in May 1978. Observations on the seedling emergence and establishment were taken at monthly intervals. Seedlings were harvested at the end of one year period and after noting plant height and leaf area using a planimeter, the root and shoot portions were separated and dried to a constant weight at 85°C.

RESULTS

Fruit and seed characters:

The capsules and seeds of *S. khasiana* were heavier than of the populations of *S. wallichii*. While the fruit weight of the populations of *S. wallichii* were not very different, significantly higher seed weight was noticed for the Burnihat population of this species compared to that of the two other populations (Table 6.2).

Germination studies

(i) Effect of storage

When seeds were stored in the soil or in the laboratory at a temperature of 25°C, both viability and germinability of the seeds of all the populations decreased markedly with passage of time so that after one year, seeds were totally non-viable or gave very poor germination. However, storage at 0°C maintained better viability and germinability after 1 year storage (Fig 6.1).

(ii) Depth of burial

As seen from Fig 6.2, the depth of burial affected both the time and the final percentage of germination. Maximum germination was found to occur at 2 cm. depth and it decreased at the depths greater than this for all the species and populations. At soil surface though faster germination occurred the total percentage was lesser than at 2 cm. depth.

Fig. 6.1 : Viability and germinability (hatched columns) of Schima seeds after different storage periods.

First column - Storage under 0°C;

Second column - Storage at 20 ± 5°C; and

Third column - Storage under soil.

Fig. 6.1.

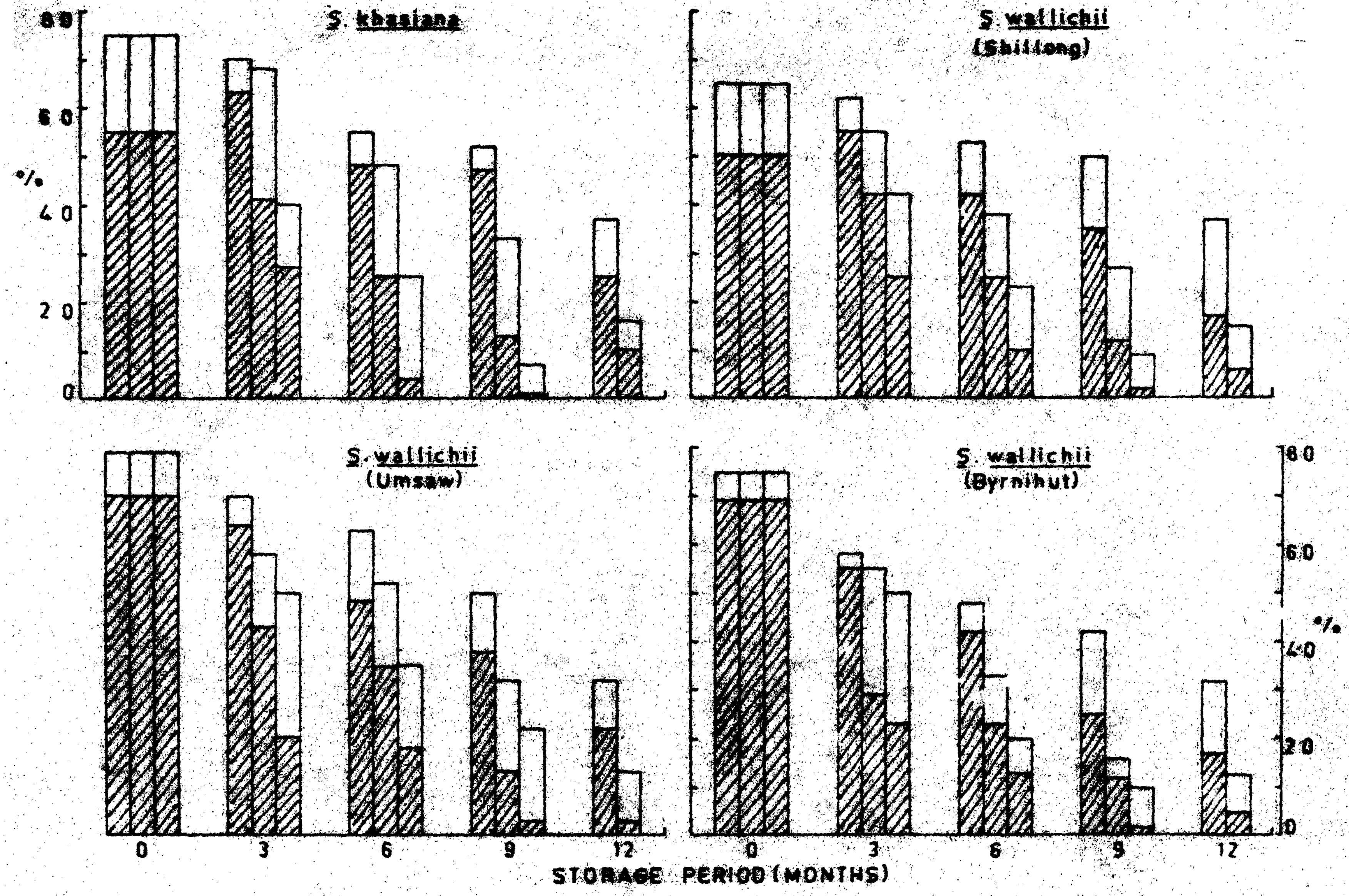

S. khasiana
S. wallichii (Shillong)
S. wallichii (Umsaw)
S. wallichii (Byrnihut)
%
0
20
40
60
80
0
3
6
9
12
STORAGE PERIOD (MONTHS)

Fig. 6.2 : The relationship between seed depth, germination and emergence period of seedlings of Schima species/populations over a period of 35 days after sowing.

Fig. 6.2.

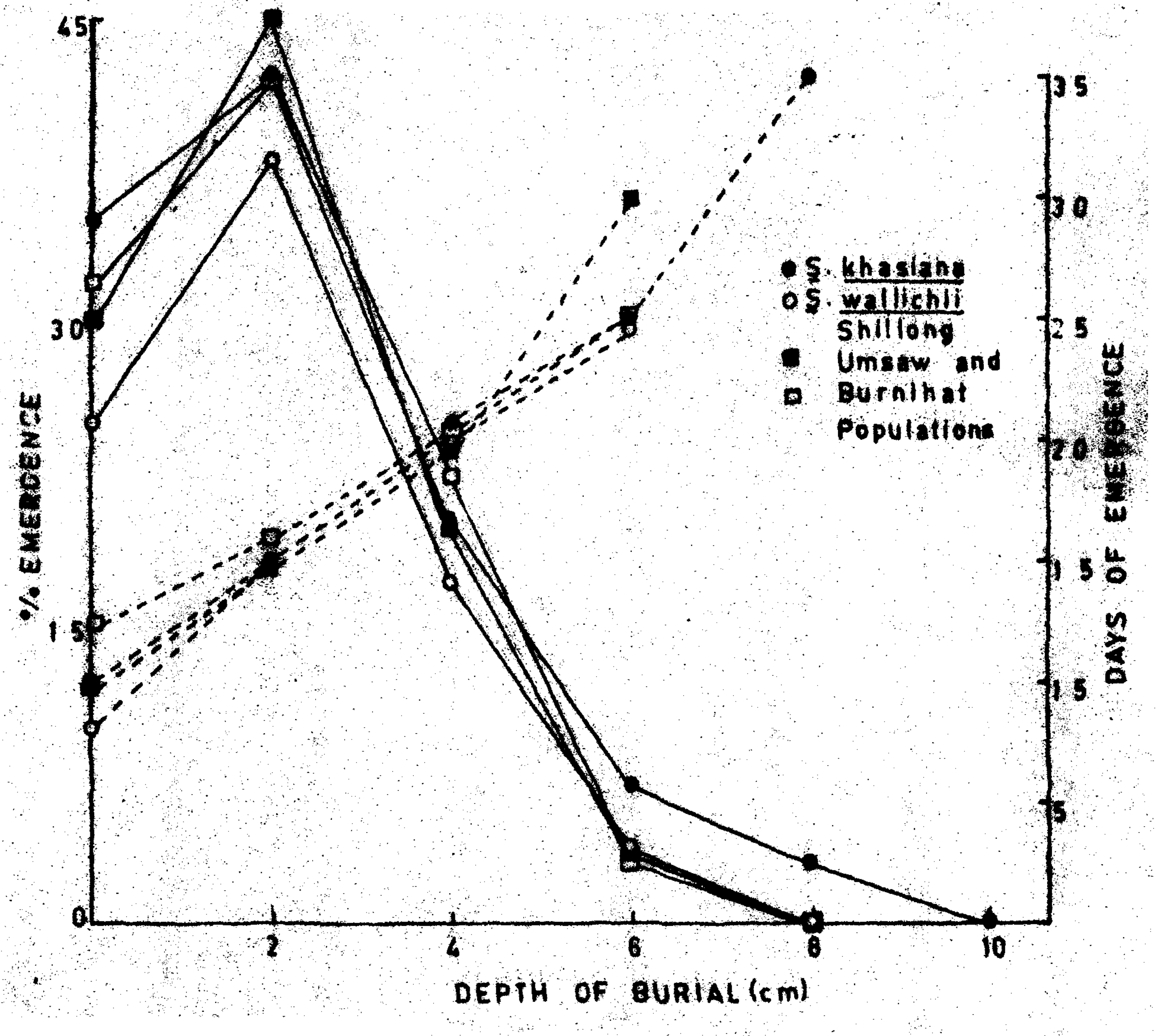

45
30
15
0
% EMERGENCE
2
4
6
8
10
DEPTH OF BURIAL (cm)
35
30
25
20
15
15
5
DAYS OF EMERGENCE
● S. khasiana
○ S. wallichii
Shillong
■ Umsaw and
□ Burnihat
Populations

Table 6.2 : Fruit and Seed weight of *Schima* species/pouplations (± S.E. of the mean)

	Fruit weight (g)	Seed weight (mg)
S. KHASIANA	1.67 ± 0.09	1.18 ± 0.03
S. WALLICHII		
SHILLONG	1.13 ± 0.07	0.46 ± 0.06
UMSAW	1.04 ± 0.03	0.44 ± 0.02
BURNIHAT	1.07 ± 0.05	0.53 ± 0.01

(iii) The effect of light and darkness

There was germination both in the dark and light and the results obtained were not significantly different under these two conditions (Table 6.3).

(iv) The effect of temperature

Table 6.4, reveals the effect of various temperature regimes on the germination of the seeds of *Schima* species and populations. *S. khasiana* showed maximum germination at constant 15°C, with a gradual decrease with increase in temperature, so that at 35°C no seeds of this species germinated. Populations of *S. wallichii* showed maximum germination at 20 and 25°C with decrease in germination on either side. Two alternating temperature regimes tried were favourable for germination for all the species/populations.

The rate of germination was faster at 15°C for *S. khasiana* and 20 and 25°C or alternating (25/20°C) for *S. wallichii* populations (Fig 6.3).

Seedling establishment

(i) Seedling emergence

Only a small proportion of seedlings could emerge under field conditions at all the study sites. Further, the differences in emergence were not significant (at 5% level) between species/populations (Table 6.5).

(ii) Survivorship

No seedlings could survive under forested situations beyond

Fig. 6.3 : Percentage germination of <u>Schima</u> species/populations on different periods, at constant and alternating temperatures of - 15°C (●); 20°C (o); 25°C (■); 30°C (□); 35°C (▲); 25/15°C (△) & 25/20°C (×).

Fig. 6.3.

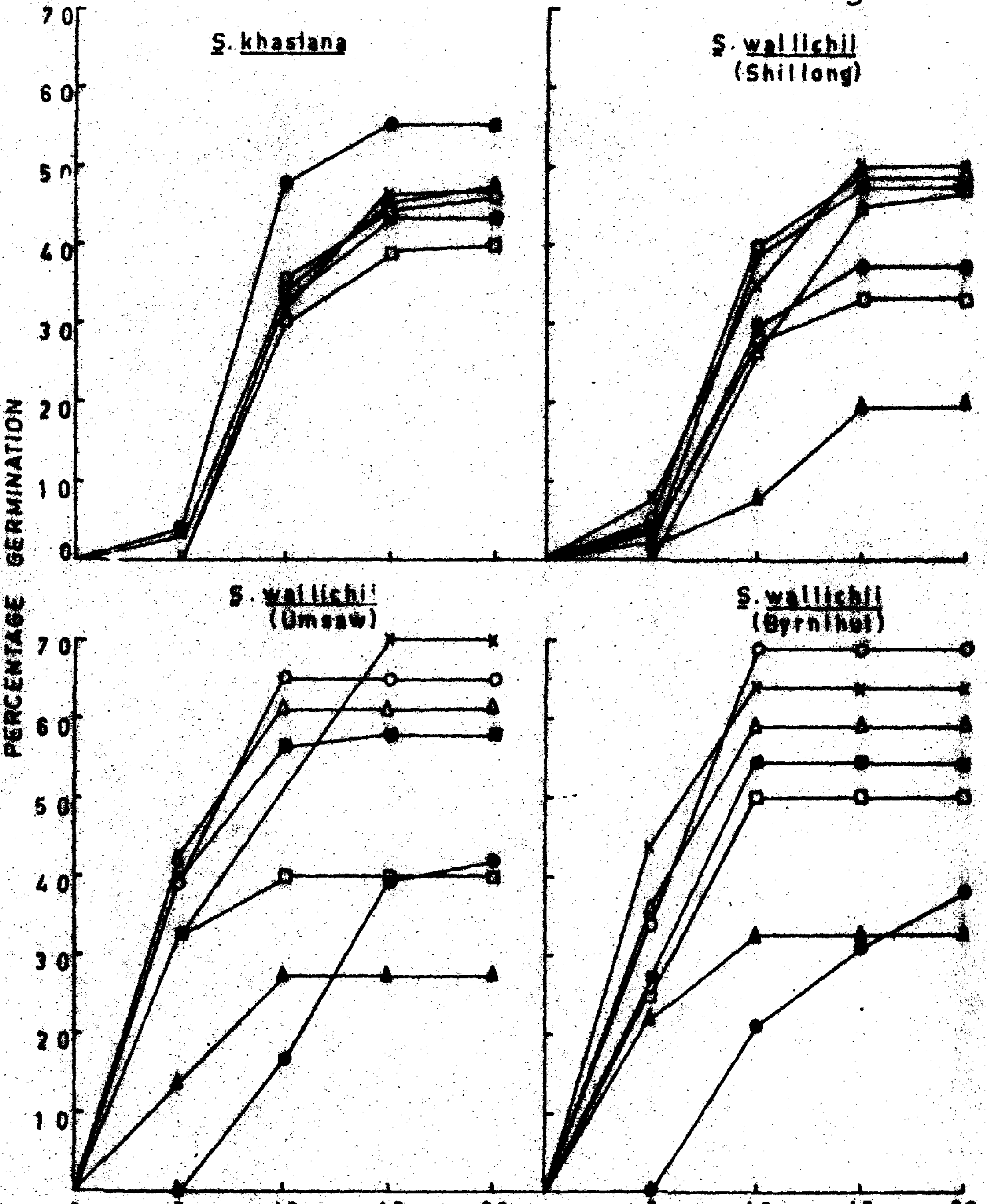

S. khasiana
S. wallichii (Shillong)
S. wallichii (Umsaw)
S. wallichii (Byrnihat)
PERCENTAGE GERMINATION
DAYS OF GERMINATION
0
10
20
30
40
50
60
70
0
5
10
15
20

Fig. 6.4 : Survivorship of *Schima* seedlings under field conditions (open). No seedlings could survive beyond 2 months under forested situations.

S. khasiana (●);
S. wallichii, Shillong (o);
S. wallichii, Umsaw (■) &
S. wallichii, Burnihat (□) populations.

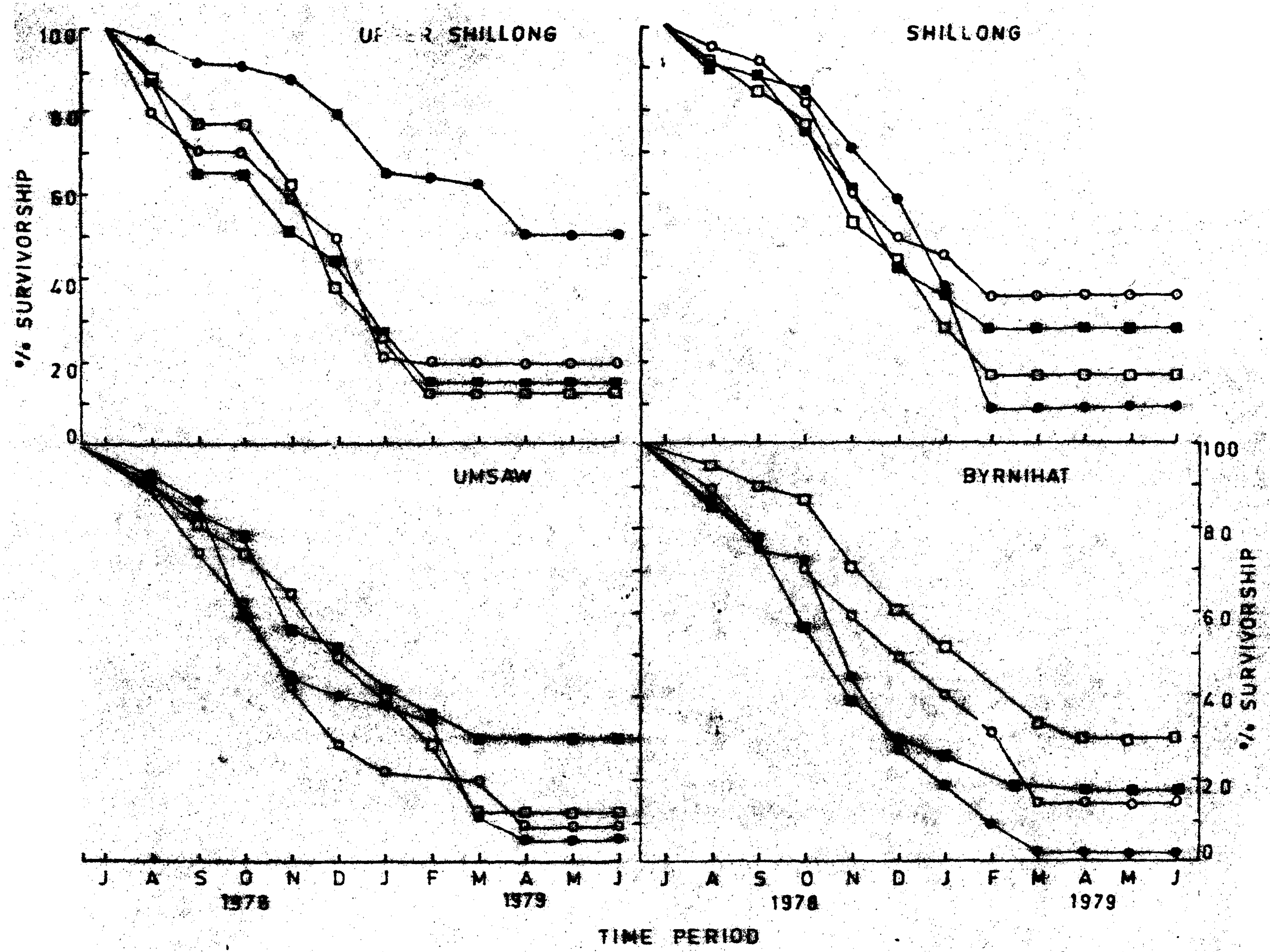

U R SHILLONG
SHILLONG
UMSAW
BYRNIHAT
% SURVIVORSHIP
100
80
60
40
20
0
% SURVIVORSHIP
100
80
60
40
20
0
J
A
S
O
N
D
J
F
M
A
M
J
1978
1979
J
A
S
O
N
D
J
F
M
A
M
J
1978
1979
TIME PERIOD

Fig. 6·4

Table 6. 3 : The effect of light and dark treatment on seed germination of *Schima* species (± S.E. of the mean)

	CONTINUOUS LIGHT 20°C	CONTINUOUS DARK 20°C
S. KHASIANA	50 ± 5.4	48 ±3.4
S. WALLICHII	62 ± 6.4	57 ± 1.3

The seeds & populations of *S. wallichii* were pooled.

Table 6.4 : Germination (%) of S. khasiana and S. wallichii seeds at various constant and alternating temperatures
(± S.E. of the mean)

	CONSTANT TEMPERATURES (°C)					ALTERNATING TEMPERATURES (°C)	
	15	20	25	30	35	25/15	25/20
S. KHASIANA	55 ± 2.7	46 ± 3.6	44 ± 2.9	42 ± 2.2	0	46 ± 2.3	45 ± 5.5
S. WALLICHII							
SHILLONG	37 ± 4.3	48 ± 6.0	48 ± 6.8	33 ± 4.1	20 ± 7.5	48 ± 4.1	50 ± 4.6
UMSAW	42 ± 5.3	65 ± 3.7	58 ± 3.7	40 ± 6.8	27 ± 2.9	61 ± 3.7	70 ± 9.9
BURNIHAT	38 ± 2.2	69 ± 3.7	56 ± 5.4	50 ± 4.8	33 ± 7.6	59 ± 3.4	64 ± 3.6

Table 6.5 : Seedling emergence (%) of *S. khasiana* and *S. wallichii* at different altitudinal sites.

FIELD STATIONS	SPECIES/POPULATIONS			
	S. KHASIANA	S. WALLICHII		
		SHILLONG	UMSAW	BURNIHAT
Upper Shillong	20 ± 4.6	10 ± 2.3	11 ± 1.8	14 ± 1.8
Shillong	19 ± 2.4	21 ± 3.9	10 ± 3.3	10 ± 2.1
Umsaw	16 ± 1.7	13 ± 2.7	13 ± 1.2	13 ± 2.5
Burnihat	16 ± 3.9	12 ± 1.7	11 ± 2.3	11 ± 0.6

a period of 2 months. Under open grown situations, mortality was generally very high resulting in a steep decline in population upto January-February, at all the sites. At Upper Shillong, however, the rate of decline in population was slower for S. khasiana with an ultimately large population size compared to the populations of S. wallichii. At the other 3 experimental sites, however, the pattern of survivorship was not very different for the populations of Schima, though the local populations showed better survivorship than the introduced ones. S. khasiana gave the lowest final survival at these three sites (Fig 6.4).

(iii) Plant performance

The growth characteristics of the different species/populations at different sites given in Fig 6.5, shows that the naturalized population for a given site was superior compared to the other introduced populations. Thus, S. khasiana gave better growth yield under Upper Shillong site, while the populations of S. wallichii from 3 different sites did better in their other natural habitats.

DISCUSSION

Schima species being an early successional colonizers depend for regeneration on the availability of open sites which favour their germination, establishment and growth. The most important factor limiting the ability of such species to colonize disturbed sites is the availability of seed, which must come either from a stand in close proximity or from storage in the soil. The

Fig. 6.5 : Growth performance of *Schima* species/populations at different field conditions. a = Upper Shillong site; b = Shillong site; c = Umsaw site and d = Burnihat site. *S. khasiana*, filled bars and *S. wallichii*, Shillong, hollow bars; Umsaw, hatched bars and Burnihat, dotted bars.

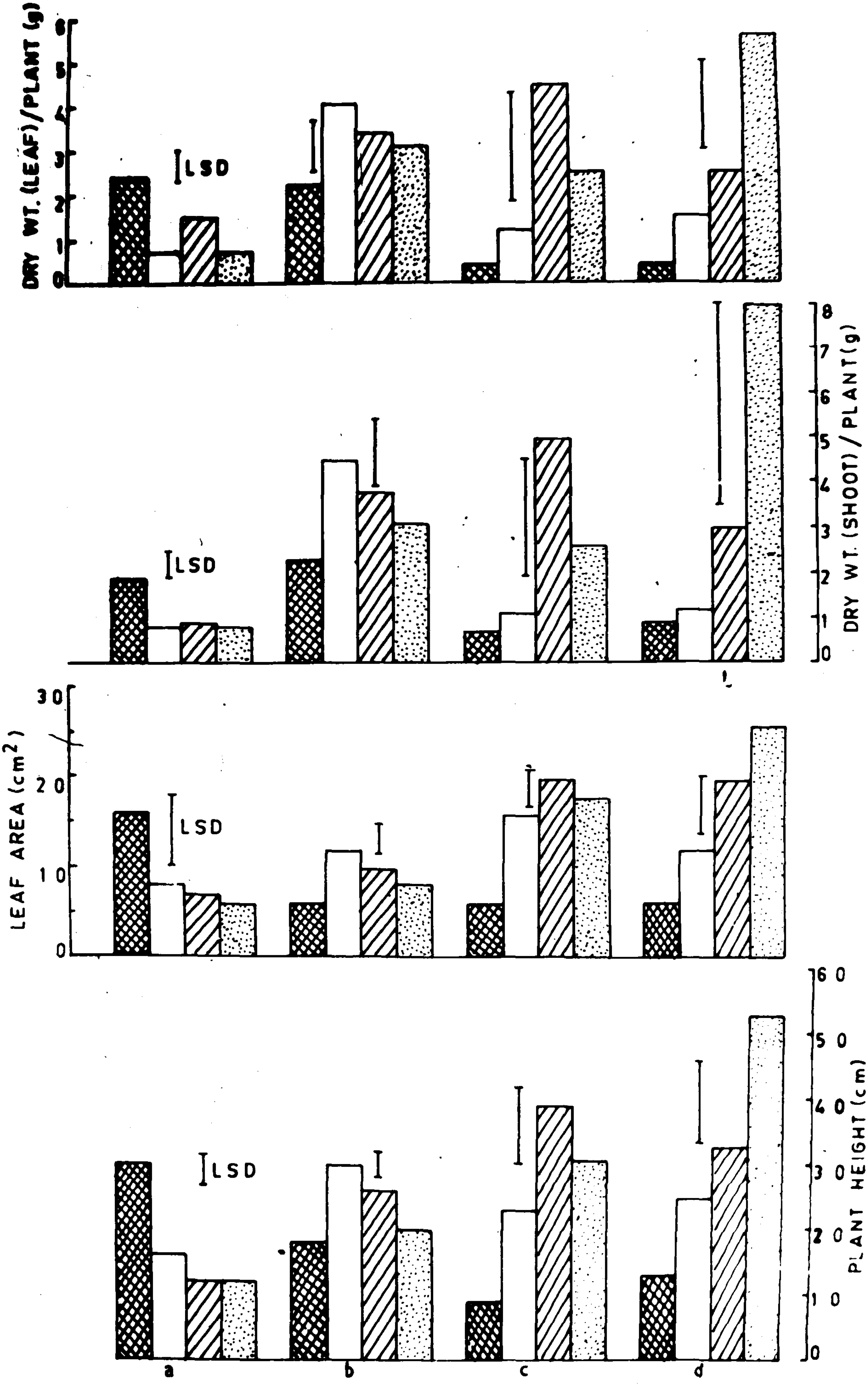

DRY WT. (LEAF)/PLANT (g)
0
1
2
3
4
5
6
LSD
DRY WT. (SHOOT)/PLANT (g)
0
1
2
3
4
5
6
7
8
LSD
LEAF AREA (cm^2)
0
10
20
30
LSD
PLANT HEIGHT (cm)
0
10
20
30
40
50
60
LSD
a
b
c
d

Fig. 6·5

latter is not possible for Schima as seeds do not remain viable in the soil for an extended period of time as seen from the present study where the viability of seeds is completely lost after storage in soil for one year. Thus, the species is fugitive in nature (Hutchinson, 1951), where good dispersal mechanism would play an important role permitting the species to colonize new habitats (Salisbury, 1942). Schima due to its light, mobile (winged) seeds often invades highly disturbed areas after slash and burn agriculture in the region. Similarly in temperate forests it has been reported that light seeded species Fraxinus and Betula play an important role in revegetation after clear cutting (Bormann & Likens, 1979). The variation in seed weight in between species/populations may partly be related to climate (Baker, 1972; Wearstler & Barnes, 1977) and partly to ecotypic differences related to altitude which is supported by growth studies of the different Schima populations done at different altitudes discussed below.

The differences in germination behaviour in response to temperature as seen in the present case where S. khasiana germinated at a comparatively lower temperature compared to S. wallichii population, have often been correlated with climatic conditions and seed source (Callaham, 1960; Thompson, 1973), whereby seeds from cold areas germinate better at lower temperature than those from warmer regions. Grose (1957) have demonstrated that montane species of Eucalyptus germinated best at a lower temperature of 16°C, in contrast to somewhat higher temperatures for species of warmer areas. Though the total number of seeds of a species which ultimately germinate at a given temperature is a good indicator of that species potential, however, the time taken to germinate is of much significance since the early germinating individuals enjoy a considerable competitive advantage (Ross & Harper, 1972). The germination rate which was higher at 15°C for S. khasiana and at 20 or 25°C for S. wallichii populations is consistent with the temperature optima for their germination. The rapidity of germination in this species without a dormancy mechanism is advantageous in colonizing new areas by producing a profusion of seedlings and this has been reported for a majority of tropical trees which has been termed as biological nomads (Ng, 1978).

Schima seeds come under microbiotic category (Crocker & Barton, 1953) as they normally lose viability and germinability within a year. Small and light seeds are reported to lose their viability faster (Quick, 1961) and this has been reported in species of Salix, Populus and Ulmus (Waering, 1963) and Alnus (Boojh & Ramakrishnan, 1981b). The better retention of viability and germinability under lower temperature storage may be attributed to slow biological and biochemical processes at such temperatures (Kamra, 1967).

There exists a large gap between seeding potential of a species and the number of seedlings emerged at a given site. The failure of survival of seedlings under a forest canopy may be attributed to the shade intolerance of the seedlings. The differences in survival pattern for different species/populations under field conditions are suggestive of the adaptation of a given population to the natural climatic conditions in which they grow. This is suggested by the relatively better survival and performance of local species/populations to that habitat compared to the introduced ones. Thus, the lower altitude population of S. wallichii which is adapted to longer growing season, higher temperature and frost free winter is adversely affected at higher altitude.

SUMMARY

Seed germination of S. khasiana from Upper Shillong and S. wallichii from Shillong, Umsaw and Burnihat and seedling establishment and growth of these species/populations in reciprocal cultivation, were studied. Seeds lost viability and germinability gradually within a year when stored in the soil or at 20°C in the laboratory but storage at 0°C permitted retention of some viability. Seeds in nature germinated better in the surface layers of the soil. S. khasiana had a low temperature optimum for germination while the lower altitude populations of S. wallichii had a higher temperature optimum. Similarly a given species/population of Schima gave better seedling establishment and growth in its own natural habitat as compared to the introduced populations from the other altitudinal sites. This is indicative of the close adaptation of the natural populations to their habit and the possible ecotypic differentiation in this species.

CHAPTER VII

Germination ecology of Alnus nepalensis Don

GERMINATION ECOLOGY OF ALNUS NEPALENSIS DON

INTRODUCTION

Alnus nepalensis, Nepalese alder is a native of India and Burma and is fairly common in Eastern Himalayas. This is an early successional tree species and among the first to become established naturally on many denuded areas particularly at higher altitudes in north-eastern hilly parts of India. It frequently represents as stand lines along streams or areas of standing water and low lying alluvial lands. The wind disseminated seeds help in its wide distribution. Cultivators in parts of Nagaland and Manipur states of North-east India, grow it for soil improvement, after slash and burn agriculture (Jhum), as it is a symbiotic nitrogen fixer and is also important for timber and watershed management.

The germination ecology of A. nepalensis is not known, though studies on its other temperate species like A. glutinosa (McVean, 1955) and A. inokumai (Asakawa & Nagao, 1963) are available.

MATERIALS AND METHODS

Mature cones of A. nepalensis collected from Upper Shillong (alt. 1800m) in March 1978 were air dried to extract the seeds. Seeds were stored at 20 ± 5°C and 0 ± 2°C in tightly closed plastic bottles. The seeds were similarly stored at 5 cm below soil surface and were tested for viability and germination. Germination tests in petri-dishes were done at constant temperatures of 15, 20, 25 and 30°C where exposure to light was only for a brief period during the day at the time of recording germination counts. Germination tests were also done under continuous light or dark at a constant temperature of 20°C. The test under an alternating temperature regime had 25/15°C. Light (550-600 lx) was provided from fluorescent tubes and this was given for the alternating temperature at higher temperature (8 hrs.) in the cycle. For dark treatment petri-dishes were placed in light proof card board boxes. The tests were carried out for a period of 20 days, as no seed germination could be recorded for the next consecutive 10 days. Germination percentages were expressed on the basis of viable seeds. Germination values were calculated using the formula (Czabator, 1962), GV = (Pv) (MDG), where PV is the maximum value of cumulative germination percentage divided by days of test and MDG is mean daily germination. Seeds were buried at different soil depths of 0 (with or without moss cover), 0.5, 1.0 and 1.5 cm. in pots maintained with sufficient moisture and tested for germination.

RESULTS AND DISCUSSION

The viability and germinability of <u>A. nepalensis</u> seeds stored at 20 ± 5°C were lost gradually and no seed could germinate after one year (Table 7.1). Seeds stored under 0 ± 2°C, however, showed better viability and germination and after one year storage gave about 22% germination. Seeds stored below the soil surface in nature, lost their viability after 6 months of storage. Even at the end of 3 months storage period, germination was very poor. Thus the seeds of <u>A. nepalensis</u> are

Table 7. 1 : Viability (%) (a) and germination (% of the total seeds) (b) after storage (± S.E. values)

		Duration of Storage (months)				
Storage conditions		0	3	6	9	12
20 ± 5°C	(a)	63.30 ± 5.55	39.80 ± 4.49	13.40 ± 1.91	6.40 ± 1.53	1.60 ± 0.40
	(b)	45.33 ± 6.70	28.67 ± 1.86	8.33 ± 2.03	4.20 ± 0.86	0 ± 0
0 ± 2°C	(a)	65.30 ± 5.55	63.67 ± 1.83	39.67 ± 2.91	34.67 ± 0.88	27.33± 1.77
	(b)	45.33 ± 6.70	49.33 ± 3.48	36.00 ± 2.08	29.00 ± 1.73	22.33± 1.46
Below soil surface	(a)	65.30 ± 5.55	13.33 ± 0.88	0	0	0
	(b)	45.33 ± 6.70	4.00 ± 1.53			

microbiotic (Crocker & Barton, 1953), as they lose their viability within a year. Small and light seeds are reported to lose their viability very fast (Quick, 1961) and is also reported (Wareing & Taylor, 1963) for species of *Salix, Populus* and *Ulmus*; and Boojh and Ramakrishnan (unpublished) for *Schima*. The seeds of *A. nepalensis* with an average number of 2769 ± 200.19 seeds/gm., also falls into this category. The better retention of viability and germinability under low temperature storage conditions may be due to slow biological and biochemical processes at such temperatures (Kamra, 1967).

The seeds of *A. nepalensis* showed maximum germination percentage and germination value at a constant temperature of 20°C under continuous light. Germination under continuous darkness was very poor (Table 7.2) Better seed germination was also obtained under alternating temperature. Thus the seeds are light sensitive as also reported for *A. inokumai* (Asakawa & Nagao, 1963). The light requirement for seed germination of early successional tree species as in the present case is consistent with their ecology and suggests a mechanism whereby the seeds of these species might be prevented from germination beneath a closed canopy (Barton, 1961; Grime & Jarvis, 1976). Generally, the temperature optima for seed germination represent the normal season for germination and emergence under field conditions, subject to availability of water (Ashby & Hellmers, 1965). In present case too, better germination at 20°C is close to the temperature conditions prevailing in

Table 7.2 : Germination total (% of viable seeds) and germination values of seeds of <u>Alnus nepalensis</u> at different temperatures and light conditions (± S.E. values)

	Constant temperatures (°C)						Alternating temperatures (°C)
	15	20	25	30	20 (continuous light)	20 (continuous dark)	25 / 15 (light) (dark)
Germination total	17.95 ± 1.36	45.13 ± 4.11	26.67 ± 1.36	14.87 ± 2.72	69.74 ±10.30	2.05 ±0.89	43.08 ± 2.35
Germination value	0.53 ± 0.08	4.56 ± 0.64	2.06 ± 0.21	0.77 ±0.21	21.73 ± 6.70	0.15 ±0.07	5.52 ± 0.59

nature at the time of seed germination. The inability of seeds to germinate at depths below 1 cm (Table 7.3) is probably related to their light requirement. Better germination of seeds placed on the surface layers of the soil with moss cover may be related to good moisture supply.

SUMMARY

The seeds of Alnus nepalensis were microbiotic in nature but low temperature storage retained viability to some extent. The seeds were found to be light sensitive for germination and germinate favourably at moist soil surface. The germination behaviour is consistent with the species' role as an early successional colonizer.

Table 7.3 : Effect of depth of burial on seed germination of *Alnus nepalensis*. (± S.E. Values)

Depth of burial (cm)	Germination total (%)	Days of emergence
0.0 (wihtout moss cover)	43 ± 4.17	7
0.0 (with moss cover)	53 ± 2.31	7
0.5	22 ± 1.53	15
1.0	8 ± 2.08	20
1.5	0 ± 0	-

LITERATURE CITED

LITERATURE CITED

AALTONEN, V.T. (1948). Boden Und Wald. Paul Parey, Berlin & Hamburg, 457 p.

ADDICOTT, F.R. (1978). Abcission strategies in the behaviour of tropical trees. In: Tropical Trees as Living Systems (P.B. THOMLINSON & M.H. ZIMMERMANN, Eds.) Cambridge University Press, p. 381-398.

ALVIM, P. DE T. (1964). Tree growth periodicity in tropical climates. In: The Formation of Wood in Forest Trees (M.H. ZIMMERMANN, Ed.) Academic Press, New York, p. 479-495.

ALVIM, P. DE. T. (1978). Relation of climate to growth periodicity in tropical trees. In: Tropical Trees as Living Systems (P.B. TOMLINSON & M.H. ZIMMERMANN, Eds.) Cambridge University Press, p. 445-464.

ANDERSON, J.M. (1973). Stand Structure and Litterfall of a coppiced beech Fagus sylvatica and sweet chestnut Castanea sativa woodland. Oikos, 24, 128-135.

ANDERSON, R.C. (1974). Seasonality in terrestrial primary producers. In: Phenology and Seasonality modeling H. LEITH, Ed.) Springer-Verlag, New York, p. 103-111.

ANDERSON, R.C. & SCHELFHOUT, S. (1980). Phenological patterns among Tallgrass Prairie plants and their implications for pollinator competition. American Midland Naturalist, 104, 253-263.

ASAKAWA, S. & NAGAO, A. (1963). Germination behaviour of *Alnus inokumai* seeds. *Journal of Japanese Forestry Society*, 45, 331-334.

ASHBY, W.C. & HELLMERS, H. (1965). Temperature requirements for germination in relation to wild-land seeding. *Journal of Range Management*, 8, 80-83.

ASHTON, P.S. (1969). Speciation among tropical forest trees: Some deductions in the light of recent evidence. *Bilogical Journal of Linnean Society*, 1, 155-196.

BAKER, H.G. (1972). Seed weight in relation to environmental conditions in California. *Ecology*, 53, 997-1010.

BAKER, J.R. & BAKER, I. (1936). The seasons in a tropical rain-forest (New Hebrides). Part 2. Botany. *Journal of Linnean Society, Zoology*, 39, 507-519.

BARKER, S.B.; CUMMING, G. & HORSFIELD, K. (1973). Quantitative morphology of the branching structure of trees. *Journal of Theoretical Biology*, 40, 33-43.

BARTON, L.V. (1961). *Seed preservation and longevity*. Leonard Hill, London. 216p.

BASKERVILLE, G.L. (1965). Dry matter production in immature fir stands. *Forest Science Monograph 9. Society of American Foresters*, Washington, District of Columbia, U.S.A. 42p.

BAZZAZ, F.A. & Harper, J.L. (1977). Demographic analysis of the growth of *Linum usitatissimum*. *New Phytologist*, 78, 193-208.

BAZZAZ, F. A. (1979). The physiological ecology of plant succession. Annual Review of Ecology and Systematics, 10, 352-371.

BENTLEY, B.L. (1979). Longevity of individual leaves in a tropical reinforest understorey. Annals of Botany, 43, 119-121.

BLONDEL, J. (1975). La dynamique des populations d'oiseaux. In: La Demographie des populations de Vertebres. (M. LAMOTTE & F.BOURLIERE, Eds.). Mason & Co., Paris.

BOALER, S.B. (1966). Ecology of a miomba site, Lupa North Forest Reserve, Tanzania. II Plant communities and seasonal variation in the vegetation. Journal of Ecology, 54, 465-479.

BOND, T.E.T. (1942). Studies in the vegetative growth and anatomy of Tea plant (Camelia thea Link.) with special reference to the phloem I. The flush shoot. Annals of Botany, 24, 607-629.

BOND, T.E.T. (1945). Studies in the vegetative growth and anatomy of Tea plant (Camelia thea Link.) with special reference to the phloem. II. Further analysis of flushing behaviour. Annals of Botany, 9, 183-216.

BOOJH, R. & RAMAKRISHNAN, P.S. (1981 a). Temperature responses to seed germination in two closely related tree species of Schima Reinw. Current Science, 50, 416-418.

BOOJH, R. & RAMAKRISHNAN, P. S. (1981 b). Germination behaviour of seeds of Alnus nepalensis Don. National Academy Science letters, 4, (In press).

BORCHERT, R. (1969). Unusual shoot growth pattern in a tropical tree, Oreopanax (Araliaceae). American Journal of Botany, 56, 1033-1041.

BORCHERT, R. (1980). Phenology and ecophysiology of tropical trees: Erythrina poeppigiana O.F. Cook. Ecology, 61, 1065-1074.

BORMANN, F. H. & LIKENS, G.E. (1979). Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, 253 p.

BRASSELL, H.M.; UNWIN, G.L. & STOCKER, G.C. (1980). The quantity, temporal distribution and mineral element content of litterfall in two forest types at two sites in tropical Australia. Journal of Ecology, 68, 123-139.

BRAY, J. R. & GORHAM, E. (1964). Litter production in forests of the world. In: Advances in Ecological Research, Vol. 2 (J.B. CRAGG, Ed.) Academic Press, New York, p. 101-157.

BROOKFIELD, H.E. (1969). Some notes on the climate of the British Solomon Islands. Philosophical Transactions of Royal Society, B., 255, 207-210.

BROWN, C.C.; McALPINE, R.G. & KORMANICK, P.P. (1967). Apical dominance and form in woody plants: A reappraisal. American Journal of Botany, 54, 153-162.

BRUNIG, E.F. (1976). Tree form in relation to environmental conditions: an ecological viewpoint. In: Tree physiology and Yield Improvement, (M.G.R. CANNELL & F.T. LAST, Eds.) / Academic Press, New York, p. 139-156.

BURGER, W.C. (1974). Flowering periodicity at four altitudinal levels in eastern Ethiopia. Biotropica, 6, 1148-1153.

BÜSGEN, M. & MÜNCH, E. (1929). The Structure and Life of Forest Trees. Chapman and Hall, London.

CALLAHAM, R.Z. (1960). Geographic variation in forest trees. In: Genertic Resources in Plants - Their Exploration and Conservation (O.H. FRANKEL & E. BENNETT, Eds.) Blackwell Scientific Publications, Oxford, Edinburgh, 1970. p. 43-48.

CARLISLE, A.; BROWN, A.H.F. & WHITE, E.J. (1966). Litterfall, leaf production and the effects of defoliation by Tortrix Viridana in a sessile oak (Quercus petraea) woodland. Journal of Ecology, 54, 65-85.

CHOWDHURY, K.A. (1958). Extension and radial growth in tropical perennial plants. Modern Developments in Plant Physiology, Proceedings Delhi University Seminar, 1957. p. 138-139.

COHEN, D. (1967). Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. Journal of Theoretical Biology, 16, 1-14.

CONNELL, J.H. & ORIAS, E. (1964). The ecological regulation of species diversity. American Naturalist, 98, 399-414.

COOMBE, D.E. (1960). An analysis of the growth of Trema guinensis. Journal of Ecology, 48, 219-231.

COOMBE, D.E. & HADFIELD, W. (1962). An analysis of the growth of Musanga cecropioides. Journal of Ecology, 50, 221-234.

CORNER, E.J.H. (1952). Wayside Trees of Malaya. Government Printing Office, Singapore.

CORNFORTH, I.S. (1970). Leaf fall in a tropical rainforest. Journal of Applied Ecology, 7, 603-608.

COSTER, C.H. (1923). Lauberneuerung und andere periodische Lebensprozesse in dem trockenen Monsungebiet Ost-Javas. Ann. Jard. Botan. Buitenzorg, 33, 117-189.

COVINGTON, W.W. & ABER, J.D. (1980). Leaf production during secondary succession in northern hardwoods. Ecology, 61, 200-204.

CROAT, T.B. (1969). Seasonal flowering behaviour in Central Panama. Annals of Missouri Botanical Garden, 56, 295-307.

CROAT, T.B. (1975). Phenological behaviour of habit and habitat classes on Barro Colorado Island (Panama Canal Zone). Biotropica, 7, 270-277.

CROCKER, W & BARTON, L.V. (1957). Physiology of Seeds. Chronical Botanica, Waltham, Mass., 267 p.

CZABATOR, F. J. (1962). Germination value: an index combining speed and completeness of pine seed germination. Forest Science, 8, 386-396.

DANA, M.N.; ZIMMERMAN, J. & LETTAU, K. (1963). Lilac blossoming and Wisconsin weather. Wisconsin Academy Review, Wisconsin Academy of Sciences, Arts and Letters, Madison, p. 33-36.

DAUBENMIRE, R. (1972). Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. Journal of Ecology, 60, 147-170.

DEEVEY, E.S. (1947). Life-tables for natural populations of animals. Quarterly Review of Biology, 22, 283-314.

DOLPH, G.E. (1977). The effect of different calculational techniques on the estimation of leaf area and the construction of leaf size distributions. Bulletin of the Torrey Botanical Club, 104, 264-269.

DOUGLAS, G.W. & RAMSDEN, J. (1973). Representation of leaf orientation data by equal-area projection techniques. American Journal of Botany, 51, 1080-1088.

DUCKE, A. & BLACK, G.A. (1953). Phytogeographical notes on the Brazilian Amazon. Anais Acad. Bras. Cienc., 25,1-46.

DUVIGNAEAUD, P.S.; DENAEYER-DE, S & MARBAISE, J.L. (1969). Littere totale annuaue et restitution an sol des polythelements hiogenes. Bulletin Society Royale Bot. Belg., 102, 339-354.

EDWARDS, P.J. (1977). Studies of mineral cycling in a montane rain forest in New Guinea II. The production and disappearance of litter. Journal of Ecology, 65, 971-992.

FARMER, R. E. (1976). Relationships between genetic differences in yield of deciduous tree species and variation in canopy size, structure and duration. In: *Tree Physiology and Yield Improvement* (M.G.R. CANNELL & F.T. LAST Eds.) Academic Press, New York, p. 119-137.

FEINSINGER, P. (1978). Ecological interactions between plants and hummingbird in successional tropical communities. *Ecological Monographs*, 48, 269-287.

FITTKAU, E. J. & KLINGE, H. (1973). On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica*, 5, 2-14.

FOUNIER, L.A. & SALAR, S. (1966). Algunas observaciones sobre la dinamica de la floracion en el basque tropical Lumelo de Villa Colon. *Revista Biol. Trop*. 14,75-85.

FRANKIE, G.W.; BAKER, H.G. & OPLER, P.A. (1974). Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, 62, 881-919.

GAERTNER, E.E. (1964). Tree growth in relation to its environment. *Botanical Review*, 30, 393-436.

GILL, A.M. (1971 a). The formation, growth and fate of buds of *Fraxinus americana* L. in Central Massachusetts. *Harvard Forest Paper*, 20, 1-16.

GILL, A.M. (1971 b). Endogenous control of growth-ring development in *Avicennia*. *Forest Science*, 17, 462-465.

GILL, A.M. & TOMLINSON, P.B. (1971). Studies on the growth of red mangrove (Rhizophora mangle L.) 3. Phenology of the shoot. Biotropica 3, 109-124.

GIVINISH, T. & VERMEIJ, G. (1976). Sizes and shapes of liane leaves. American Naturalist, 110, 743-778.

GOSZ, J.R.; LIKENS, G.R. & BORMANN, F.H. (1972). Nutrient content of litterfall on the Hubbard Brook Experiment forest, New Hampshire. Ecology, 53, 769-784.

GREATHOUSE, D.C. & LAETSCH, W.M. (1969). Structure and development of the dimorphic branch system of Theobroma cacao. American Journal of Botany, 56, 1143-1151.

GREATHOUSE, D.C.; LAETSCH, W.M. & PHINNEY, B.O. (1971). The shoot growth of a tropical tree, Theobroma cacao. American Journal of Botany, 58, 281-286.

GRIME, J.P. (1974). Vegetation classification by reference to strategies. Nature, 250, 26-31.

GRIME, J.P. (1979). Plant strategies and Vegetation Process. Wiley & Sons, New York.

GRIME, J.P. & JARVIS, B.C. (1976). Shade avoidance and shade tolerance in flowering plants II. Effects of light on the germination of species of contrasted ecology. In: Light as an Ecological Factor (G.C. EVANS, R. BAINBRIDGE & O. RACKHAM, Eds.) Blackwell Scientific Publications, London, p. 525-532.

GRIME, J.P. & JEFFREY, D.W. (1965). Seedling establishment in vertical gradients of sunlight. Journal of Ecology, 53, 621-542.

GROSE, R.J. (1957). Notes on dormancy and effects of stratification on germination of some eucalypt ends. Bull. For. Commn. Victoria, 3, 1.

GRUBB, P.J. (1980). Review of Plant Strategies and Vegetation Processes by J.P. GRIMME. New Phytologist, 86, 123-124.

HAINS, B & FOSTER, R. B. (1977). Energy flow through litter in a Panamanian forest. Journal of Ecology, 65, 147-155.

HALLÉ, F. & MARTIN, R. (1968). Studies of the growth rhythm in Hevea brasiliensis (Euphorbiaceae - Cretonoideae). Adansonia, Paris, 8, 470-503.

HALLÉ, F. & OLDEMAN, R.A.A. (1970). Essai sur l' architecture et la dynamique de croissance des arbes tropicaux. Collection de Monographies de Botanique et de Biologie Vegetable, No. 6, Masson et Cie, Paris.

HALLÉ, F. & OLDEMAN, R.A.A. (1975). An Essay on the Architecture and Dynamics of Growth of Tropical Trees. English translation by B.C. STONE, Penerbit University Malaya, Kua Lumpur, Malaysia.

HALLÉ, F.; OLDEMAN, R.A.A. & TOMLINSON, P.B. (1978). Tropical Trees and Forests: An Architectural Analysis. Springer Verlag, Berlin. 441 p.

HARPER, J.L. (1965). Establishment, aggression and cohabitation in weedy species. In: The Genetics of colonizing species (H.G. BAKER & G.L. STEBBINS, Eds.) Academic Press, New York, p. 243-268.

HARPER, J. L. & BELL, A.D. (1979). The population dynamics of growth form in organisms with modular construction. In: *Population Dynamics* (R. M. ANDERSON, B.D. TURNER & L.R. TAYLOR, Eds.), the 20th Symposium of the British Ecological Society, London, p. 29-52.

HARPER, J. L. & WHITE, J. (1974). The demography of plants. *Annual Review of Ecology and Systematics*, 5, 419-463.

HARPER, J. L.; LOVELL, P.H. & MOORE, K.G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, 1, 327-356.

HARPER, J. L.; CLATWORTHY, J.N.; McNAUGHTON, I.H. & SAGAR, G.R. (1961). The evolution and ecology of closely related species living in the same area. *Evolution, Lancaster, Pa.*, 15, 209-227.

HEINRICH, B. & RAVEN, P.H. (1972). Energetics and pollination ecology. *Science*, 176, 597-602.

HEYDECKER, W. (1973).(Ed.) *Seed Ecology*, Penn. State University, University Park. Penn. U.S.A.

HOLDSWORTH, M. (1963). Intermittent growth of the mango tree. *Journal of West African Science Association*, 7, 163-171.

HOLLAND, P.G. (1969). The maintenance of structure and shape in three Mallee eucalypts. *New Phytologist*, 68, 411-421.

HOLTTUM, R.E. (1931). On periodic leaf change and flowering of trees in Singapore. *Gardens' Bulletin, Singapore*, 5, 173-206.

HOLTTUM, R.E. (1940). Periodic leaf-change and flowering of trees in Singapore. Gardens' Bulletin, Singapore, 11, 119-175.

HOLTTUM, R.E. (1953). Evolutionary trends in an equatorial climate. Society for Experimental Biology Symposium (Evolution), 7, 159-173.

HONDA, J.B. & FISHER, J.B. (1978). Tree branch angle: maximizing effective leaf area. Science, 199, 888-890.

HOPKINS, B. (1966). Vegetation of the Olokemeji Forest Reserve, Nigeria. IV. The litter and soil with special reference to their seasonal changes. Journal of Ecology, 54, 687-703.

HOPKINS, B. (1970). Vegetation of the Olokemeji Forest Reserve, Nigeria. IV. The plants on the forest site with special reference to their seasonal growth. Journal of Ecology, 58, 765-793.

HORN, H.S. (1971). The Adaptive Geometry of Trees. Princeton University Press, New Jersey, 144p.

HORTON, R.E. (1945). Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. Bulletin Geological Society of America, 56, 275-370.

HUTCHINSON, G.E. (1951). Copepodology for the ornithologist. Ecology, 32, 571-577.

JACKSON, J. F. (1978). Seasonality of flowering and leaf-fall in a Brazilian subtropical lower Montane moist forest. Biotropica, 10, 38-42.

JACKSON, L.W.R. (1967). Effect of shade on leaf structure of deciduous tree species. Ecology, 48, 498-499.

JANZEN, D.H. (1967). Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21, 620-637.

JANZEN, D.H. (1978). Seeding patterns in tropical trees. In: Tropical Trees as Living Systems (P.B. TOMLINSON & M.H. ZIMMERMANN, Eds.), Cambridge University Press, p. 83-128.

JEFFERS, J.N.R. & BOALER, S.B. (1966). Ecology of a Miombo site, Lupa North Forest Reserve, Tanzania. I. Weather and Plant growth, 1962-1964. Journal of Ecology, 54, 447-464.

JENNY, H.; GESSEL, S.P. & BINGHAM, F.T. (1949). Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Science, 68, 419-432.

JENSEN, B. (1974). Decomposition of angiosperm tree leaf litter. In: Biology of Plant Litter Decomposition. Vol.I. (C.H. DICKINSON & G. J. F. PUGH, Eds.) Academic Press, London, p.69-104.

JOHN, D.M. (1973). Accumulation and decay of litter and net production of forest in tropical wet Africa. Oikos, 24, 430-435.

JORDAN, C.F. (1971 a). A world pattern in plant energetics. American Scientist, 59, 426-433.

JORDAN, C.F. (1971 b). Productivity of a tropical forest and its relation to a world pattern of energy storage. Journal of Ecology, 59, 127-142.

JORDAN, C.F. & MURPHY, P.G. (1978). A latitudinal gradient of wood and litter production and its implication regarding competition and species diversity in trees. The American Midland Naturalist, 99, 415-434.

JORGENSEN, J.R.; WELLS, G.G. & METZ, L.J. (1975). The nutrient cycle: Key to continuous forest production. Journal of forestry, 73, 400-403.

KAMRA, S.K. (1967). Studies on storage of mechanically damaged seeds of Scots pine (Pinus sylvestris L.). Studia Forestalia Suecica, 42, 1-19.

KAPOOR, P. & RAMAKRISHNAN, P.S. (1973). Differential temperature optima for seed germination and seasonal distribution of two populations of Chenopodium album L. Current Science, 42, 838-839.

KEMPF, J.S. & PICKETT, S.T.A. (1981). The role of branch length and angle in branching pattern of forest shrubs along a successional gradient. New Phytologist, 88, 111-116.

KIMURA, M.; MOTOTANI, I. & HOGETSU, K. (1968). Ecological and physiological studies on the vegetation of Mt. Shimagare, VI. Growth and dry matter production of young Abies Stands. Botanical Magazine, Tokyo, 81, 287-296.

KINERSON, R.S.; HIGGINBOTHAM, K.O. & CHAPMAN, R.C. (1974). The dynamics of foliage distribution within a forest canopy. Journal of Applied Ecology, 11, 347-353.

KIRA, T & IWATA, K. (1967). Comparative ecological studies on three main types of forest vegetation in Thailand. IV. Dry matter production. Nature and Life in South East Asia, 5, 149-174.

KLINGE, H. & RODRIGUES, W.A. (1968). Litter production in an area of Amazon Terra Firme forest. I. Litterfall, Organic carbon and nitrogen contents of litter. Amazoniana 1, 287-310.

KOELMEYER, K.O. (1959). The periodicity of leaf change and flowering in the principal forest communities of Ceylone. Ceylone Forester, 4, 308-364.

KOLLER, D.; MAYER, A.M.; POLJAKOFF-MAYBER, A. & KLEIN, S. (1962). Seed Germination. Annual Review of Plant Physiology, 13, 437-464.

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. Gardens' Bulletin, Singapore, 17, 11-81.

KOZLOWSKI, T.T. (1964). Shoot growth in woody plants. Botanical Review, 30,335-392.

KOZLOWSKI, T.T. (1971). Growth and Development of Trees. Vol.I. Seed germination, Ontogeny and shoot growth. Academic Press, New York, 444p.

KOZLOWSKI, T.T. (1972)(Ed.) <u>Seed Biology, Vol. I, Importance, development and germination</u>. Academic Press, New York.

KOZLOWSKI, T.T. (1973). Extent and significance of shedding of plant parts. In : <u>Shedding of Plant Parts</u> (T.T. KOZLOWSKI, Ed.) Academic Press, New York, p. 1-44.

KOZLOWSKI, T.T. (1979). <u>Tree growth and Environmental Stresses</u>. Washington University Press, Seattle, 192 p.

KRAMER, P.J. & KOZLOWSKI, T.T. (1979). <u>Physiology of Woody Plants</u>. Academic Press, New York.

LANG, A.R.G. (1973). Leaf orientation of a cotton plant. <u>Agricultural Meteorology</u>, 11, 37-51.

LAUDELOT, H. & MEYER, J. (1954). Mineral element and organic material cycles in the equatorial forest of the Congo. <u>Oecologia Plantarum</u>, 7, 1-21.

LEIGH, E.G. (1975). Structure and climate in tropical rain-forests. <u>Annual Review of Ecology & Systematics</u>, 6, 67-86.

LEITH, H. (1970). Phenology in productivity studies. In: <u>Ecological studies Vol. I. Analysis of Temperate Forest Ecosystems</u> (D.E. REICHIE, Ed.) Springer-Verlag, Hiedelberg, p.29-56.

LEITH, H. (1971). The phenological viewpoint in productivity studies. In: <u>Productivity of.Forest Ecosystems</u> (P. DUVIGNEAUD, Ed.) Proceedings Brussels Symposium, UNESCO, Paris, p. 71-84.

LEITH, H. (1974). Purposes of a phenology book. In: <u>Phenology and Seasonality Modeling</u> (H.LEITH, Ed.) Chapman & Hall Ltd., London, p. 3-19.

LEITH, H. & RADFORD, J.S. (1971). Phenology, resource management and synagraphic computer mapping. *Bio Science*, 21, 62-70.

LEOPOLD, A. & JONES, S.E. (1947). A phenological record for Sauk and Dane Countries, Wisconsin, for 1935-1945. *Ecological Monographs*, 17, 81-122.

LEOPOLD, L.B. (1971). Trees and Streams: the efficiency of branching processes. *Journal of Theoretical Biology*, 31, 339-354.

LESCURE, J.P. (1978). An architectural study of the vegetation's regeneration in French Guiana. *Vegetatio*, 37, 53-60.

LINSON, S.N. (1958). The effect of artificial defoliation of various leaves upon white pine growth. *Forest Chronicle* 34, 50-56.

LOACH, K. (1970). Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. *New Phytologist*, 69, 273-286.

LONGMAN, K.A. & JENIK, J. (1974). *Tropical Forests and its Environment*. Longman Group Ltd., London, 196p.

LUTZ, H.J. & CHANDLER, R. F., JR. (1946). *Forest Soils*. John Wiley, New York, 514 p.

MACARTHUR, R.H. & WILSON, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, 203p.

MADGE, D.S. (1965). Litterfall and litter disappearance in a tropical forest. *Pedobiologia*, 5, 273-288.

MALAISSE, F. (1974). Phenology of the Zambezian woodland area with emphasis on the Miombo ecosystem. In: Phenology and Seasonality Modeling (H. LIETH, Ed.) Chapman & Hall Ltd., London, p. 269-286.

MARKS, P.L. (1974). The role of pin cherry (Prunus pensylvanica L.) in the maintenance of stability in northern hardwood ecosystem. Ecological Monographs,44,73-88.

MARKS, P.L. (1975). On the relation between extension growth and successional status of deciduous trees of the north-eastern United States. Bulletin of the Torrey Botanical Club, 102, 172-177.

McCLURE, H.E. (1966). Flowering, fruiting and animals in the canopy of tropical rainforest. Malasian Forester, 29, 182-203.

McDOUGALL, W.B. (1922). Symbiosis in a deciduous forest. Botanical Gazette, 73, 200-212.

McMAHON, T.A. & KRONAUER, R.E. (1976). Tree Structures: deducing the principle of mechanical design. Journal of Theoretical Biology, 59, 443-466.

McMILLAN, G.G. & McCLENDON, J.H. (1979). Leaf angle: an adaptive feature of sun and shade leaves. Botanical Gazette, 140, 437-442.

McVEAN, D.N. (1955). Ecology of Alnus glutinosa (L.) Gaertn. II. Seed distribution and germination. Journal of Ecology, 43, 61-71.

MEDWAY, L. (1972). Phenology of a tropical rainforest in Malaya. Biological Journal of Linnean Society, 4, 117-147.

MILTHROPE, F.L. (1976). Quantitative aspects of leaf growth. In: Perspectives of Experimental Biology. I. Botany (N. SUNDERLAND, Ed.), Pergamon Press, Oxford, p.33-40.

MONSI, M.; UCHIJIMA, Z. & OIKAWA, T. (1973). Structure of foliage canopies and phtosynthesis. Annual Review of Ecology & Systematics, 4, 301-327.

MOONEY, H.A.; BJORKMAN, O.; HALL, A.E.; MEDINA, E & TOMLINSON, P.B. (1980). The study of physiological ecology of tropical plants - Current status and needs. BioScience, 30, 22-26.

MOSQUIN, T. (1971). Competition for pollinators as a stimulus for the evolution of flowering time. Oikos, 22, 298-402.

MOTOMUMRA, I. (1947). Further notes on the law of geometric progression of the population density in animal association. Physiology & Ecology, 1, 55-60.

MULLER, D. & NIELSEN, J. (1965). Production brute, pertes par respiration et production nette dans la foret ombrophile tropicale. Det Forstlige Forsogsvaesen i Danmark, 29, 69-160.

NEVLING, L.T. JR. (1971). The ecology of an elfin forest in Puerto Rico, 16. The flowering cycle and an interpretation to its seasonality. Journal of Arnold Arboretum, 52, 586-613.

NELSON, N.D.; BURK, T. & ISEBRANDS, J.G. (1981). Crown architecture of short-rotation, intensively cultured Populus, I. Effects of clone and spacing on first order branch characteristics. Canadian Journal of Forest Research, 11, 73-81.

NG, F.S.P. (1977). Gregarious flowering of Dipterocarps in Kepong 1976. Malaysian Forester, 40, 126-137.

NG, F.S.P. (1978). Strategies of establishment in Malayan forest trees. In: Tropical Trees as Living Systems (P.B. TOMLINSON & M.H. ZIMMERMANN, Eds.), Cambridge University Press, p. 129-162.

NIKLAS, K. J. (1978). Branching patterns and mechanical design in palaeozoic plants: a theoretic assessment. Annals of Botany, 42, 33-39.

NJOKU, E. (1963). Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees. Journal of Ecology, 52, 617-624.

NJOKU, E. (1964). Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. Journal of Ecology, 52, 19-26.

NYE, P.H(1961). Organic matter and nutrient cycles under moist tropical forest. Plant and Soil, 13, 333-346.

OLDEMAN, R.A.A. (1974). L' Architecture de la Foret Guyannaise. Memoirs O.R.S.T.O.M. No. 73, Paris.

OOHATA, S & SHIDEI (1971). Studies on the branching structure of trees I. Bifurcation ratio of trees in Horton's Law. Japanese Journal of Ecology, 21, 7-14.

OPLER, P.A.; FRANKIE, G.W. & BAKER, H.G. (1976). Rainfall as a factor in the release, timing and synchronization of anthesis by tropical trees and shrubs. Journal of Biogeography, 3, 231-236.

OPLER, P.A.; FRANKIE, G.W. & BAKER, H.G. (1980). Comparative phenological studies of treelet and shrub species in New Zealand. Journal of Ecology, 68, 849-862.

OVINGTON, J.D. & HEITKAMP, D. (1960). The accumulation of energy in forest plantations in Britain, Journal of Ecology, 48, 639-646.

PARKHURST, D. & LOUCKS, D. (1972). Optimal leaf size in relation to environment. Journal of Ecology, 60, 505-537.

PIANKA, E.R. (1974). Evolutionary Ecology. Harper & Row, New York, 356 p.

PICKETT, S.T.A. & KEMPF, J.S. (1980). Branching pattern in forest shrubs and understorey trees in relation to habitat. New Phytologist, 86, 219-228.

POOLE, R.W. & RATHCKE, B.J. (1979). Regularity, randomness, and aggregation in flowering phenologies. Science, 203, 470-471.

PRIMACK, R.B. (1980). Variation in the phenology of natural populations of montane shrubs in New Zealand. Journal of Ecology, 68, 849-862.

PUROHIT, A.N. & NANDA, K.K. (1968). Morphophysiological studies of the shoot apex. I. Recurrent growth flushes and their relationship with structural changes in the growing apex of Callistemon viminalis. Canadian Journal of Botany, 46, 1287-1295.

PUTZ, F.E. (1979). Aseasonality in Malaysian tree phenology. Malaysian Forester, 42, 1-24.

QUICK, C.R. (1961). How long can a seed remain alive? In: Seeds, The Yearbook of Agriculture, U.S. Govt. Printing Office, Washington, D.C., p.94-99.

RAJU, D.C.S. (1964). Studies on the flora of sacred groves near Shillong. Journal of the Assam Science Society, 7, 21-30.

RAMAKRISHNAN, P.S. (1961). Calcicole and Calcifuge problem in Euphorbia thymifolia Linn. The Journal of the Indian Botanical Society, 40, 66-81.

RAMAKRISHNAN, P.S. (1965). Studies on edaphic ecotypes in Euphorbia thymifolia L. I. Seed germination. Journal of Ecology, 53, 157-162.

RAMAKRISHNAN, P.S. (1968). National requirements of the edaphic ecotypes in Melilotus alba Medic I. pH, Calcium and Phosphorus. New Phytologist, 67, 145-157.

RAMAKRISHNAN, P.S. (1972). Individual adaption and its significance in population dynamics. In: Biology of Land Plants (V. PURI, Y.S. MURTI, P.K. GUPTA & D. BANERJI, Eds.) Sarita Prakashan, Meerut, India, p. 344-355.

RAMAKRISHNAN, P.S. (1978). Observations on Biological aspects of productivity of forest ecosystems. In: Glimpses of Ecology (Professor R. Misra Commemoration Volume) (J.S. SINGH & B. GOPAL, Eds.) International Scientific Publications, Jaipur, India. p. 194-199.

RAMAKRISHNAN, P.S. & KAPOOR, P. (1974). Photoperiodic requirements of seasonal populations of Chenopodium album L. Journal of Ecology, 62, 67-73.

RAMAKRISHNAN, P.S. & KHOSLA, A.K. (1971). Seed dormancy in Digitaria adscendens (H.B.K.) Henr. and Echinochloa colona Link. with particular reference to covering structures. Tropical Ecology, 12, 112-122.

RAMAKRISHNAN, P.S. & TOKY, O.P. (1978). Preliminary observations on the impact of Jhum (Shifting agriculture) on the forested ecosystem. In: Resources, Development and Environment in the Himalayan Region. Department of Science & Technology, Government of India, New Delhi, p. 343-354.

RAPP, M. (1969). Production de litiere et apport en sol d' elements mineraux dans deux ecosystemes mediterances: la forest de Quercus ilex L. et la gariggue de Quercus cocifera L. Ecologia Plantarum, Gauthier Villars, IV, 377-410.

READER, R.J. (1975). Competitive relationships of some bog ericads for major insect pollinators. Canadian Journal of Botany, 53, 1300-1305.

READER, R. J. (1978). Contribution of overwintering leaves to the growth of three broad-leaved evergreen shrubs belonging to the Ericaceae family. Canadian Journal of Botany, 56, 1248-1261.

REES, A.R. (1964). Some observations on the flowering behaviour of Coffea rupestris in southern Nigeria. Journal of Ecology, 52, 1-7.

REINERS, W.A. & REINERS, N.M. (1970). Energy and nutrient dynamics of forest floors in three minnesota forests. Journal of Ecology, 58, 497-519.

RENNIE, P.J. (1955). The uptake of nutrients by mature forest frowth. Plant and Soil, 7, 49-95.

RICHARDS, P.W. (1952). The Tropical Rain Forest: An Ecological Study. Cambridge University Press, London.

ROCHE, L. (1969). A genecological study of the genus Picea in British Columbia. New Phytologist, 68, 505-554.

RODIN, L.E. & BRAZILEVICH, N.I. (1967). Production and Mineral Cycling in Terrestrial Vegetation. (English translation), Oliver and Boyd, Edinburgh and London.

ROMBERGER, J.A. (1964). Meristems, growth and development in woody plants. U.S.D.A. Forest Service Technical Bulletin, 1293.

ROSS, M.A. & HARPER, J.L. (1972). Occupation of biological space during seedling establishment. Journal of Ecology, 60, 77-88.

SATOO, T. (1970). A synthesis of studies by the harvest method: primary production relations in the temperate deciduous forest of Japan. In: Analysis of Temperate Forest Ecosystems. (D.E. REICHLE, ed.), Springer-Verlag, New York, p. 55-72.

SAXENA, A.K.; PANDEY, U. & SINGH, J.S. (1978). On the ecology of oak forests in Naini Tal hills, Kumaun Himalaya. In: Glimpses of Ecology (J.S. Singh & B. Gopal, Eds.) International Scientific Publications, Jaipur, India, p. 167-180.

SCARRONE, F. (1965). Role respectif des rythmes endogenes et des facteurs climatiques dans la croissance du Manguier (Mangifera indica L.). C.R. Acad. Sci (Paris), 260, 3469-3472.

SCHEMSKE, D. W. (1977). Flowering phenology and seed set in Claytonia virginica (Portulacaceae). Bulletin of Torrey Botanical Club, 104, 254-263.

SHINOZAKI, K. ; YODA, K.; HOZUMI, K. & KIRA, T. (1964). A quantitative analysis of plant form - the pipe model theory. I. Basic analysis. Japanese Journal of Ecology, 14, 97-105.

SILVERTON, J. (1980). Leaf canopy induced seed dormancy in a grassland flora. New Phytologist, 85, 109-118.

SINGH, JASBIR (1980). Studies on Structural and Functional Aspects of two sub-tropical Humid Forest types of Meghalaya. Ph.D. Thesis, North-Eastern Hill University, Shillong. 278 p.

SMYTHE, N. (1970). Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. American Naturalist, 104, 25-35.

SOLBRIG, O.T.; NEWELL, S.J. & KINCAID, D.T. (1980). The population biology of the genus Viola. I. The demography of Viola sororia. Journal of Ecology, 68, 521-546.

STEARNS, S.C. (1976). Life-history tactics: a review of the ideas. Quarterly Review Biology, 51, 3-47.

STEINGRAEBER, D.A.; KASCHT, L.J. & FRANCK, D.H. (1979). Variation of shoot morphology and bifurcation ratio in sugar maple (Acer saccharum) saplings. American Journal of Botany, 66, 441-445.

STERN, K. & ROCHE, L. (1974). Genetics of Forest Ecosystems. Chapman & Hall Ltd., London, 330 p.

STILES, F.G. (1975). Ecology, flowering phenology and pollination of some Cost Rican Heliconia species. Ecology, 56, 285-301.

STILES, F.G. (1977). Co-adapted competitors: The flowering seasons of humming bird - pollinated plants in a tropical forest. Science, 198, 1177-1178.

STILES, F.G. (1979). Comments on Poole and Rathcke (1979). Science, 203, 302-471.

STRAHLER, A.M. (1957). Quantitative analysis of watershed geomorphology. Transaction American Geophysics Union, 38, 913-920.

SWITZER, G.L.; NELSON, L.E. & SMITH, W.H. (1967). The mineral cycle in forest stands. In: Forest Fertilization theory and Practice, National Fertilizer Development Center, Tennessee Valley Authority, Muscle Sholas, Albama, U.S.A. p. 1-9.

TANNER, E.V.J. (1980). Litterfall in montane rainforests of Jamaica and its relation to climate. Journal of Ecology. 68, 833-848.

TAYLOR, F.J. (1970). Some aspects of the development of Mango (Mangifera indica L.) Leaves. 1. Leaf area, dry weight and water content. New Phytologist, 69, 377-394.

TAYLOR, S.E. (1975). Optimal leaf form. Ecol. Stud. 12, 73-86.

THOMPSON, K.; GRIME, J.P. & MASON, G. (1977). Seed germination in response to diurnal fluctuations of temperature. Nature, 267, 147-149.

THOMPSON, P.A. (1970). Characterization of the germination response to temperature of species and ecotypes. Nature, 225, 827-831.

THOMPSON, P.A. (1973). Geographical adaptation of seeds. In: Seed Ecology (W. HEYDECKER, Ed.), Pennsylvania State University Press, University Park, p. 31-58.

THORNLEY, J.H.M. (1977). A model of apical bifurcation applicable to trees and other organisms. Journal of Theoretical Biology, 64, 165-176.

TOMLINSON, P.B. (1978). Branching and axis differentiation in tropical trees. In: Tropical Trees as Living Systems (P.B. TOMLINSON & M.H. ZIMMERMANN, Eds.) Cambridge University Press, p. 187-207.

TOMLINSON, P.B. & GILL, A.M. (1973). Growth habits of tropical trees: Some guiding principles. In: Tropical Forest Ecosystems in Africa and South America: A Comparative Review (B.J. MEGGERS; E.S. AYENSW & W.D.DUCKWORTH, Eds.) Smithsonian Institution Press, Washington, D.C. p.129-143.

VAARTAJA, O. (1959). Evidence of photoperiodic ecotypes in trees. Ecological Monographs, 29, 91-111.

VIRO, P.J. (1955). Investigations on forest litter. Commun. Inst. For. Fenn., 45, 65.

WAREING, P.F. (1956). Photoperiodism in woody plants. Annual Review of Plant Physiology, 7, 91-111.

WAREING, P.F. (1963). The germination of seeds. In: Vistas in Botany Vol. II (R.C. ROLLINS & C. TAYLOR Eds.) The MacMillan Co, New York, p. 195-227.

WEARSTLER, K.A. & BARNES, B.V. (1977). Genetic diversity of yellow birch seedlings. Canadian Journal of Botany, 55, 2778-2788.

*WEIGERT, R.G. & MONK, C.D. (1972). Litter production and energy accumulation in three plantations of longleaf pine (Pinus palustris Mill.) Ecology, 53, 949-953.

WHEAT, D. (1980). Sylleptic branching in Myrsine floridana (Myrsinaceae). American Journal of Botany, 67, 490-499.

WHITE, J. (1979). The plant as a meta-population. Annual Review of Ecology and Systematics, 10, 109-145.

WHITMORE, T.C. (1975). Tropical Rainforests of the Far East. Oxford University Press, London, 282p.

WHITNEY, G.G. (1976). The bifurcation ratio as an indicator of adaptive strategy in woody plant species. Bulletin of the Torrey Botanical Club, 103, 67-72.

WIEGERT, R.G. (1970). Effects of ionizing radiation on leaf fall, decomposition and litter microarthropods of a montane rainforest. In: A Tropical Rainforest (H.T. ODUM & R.F. PIGEON, Eds.) Atomic Energy Commission, Oak Ridge, Tennessee, p. H- 89-100.

WIELGOLASKI, F.E. (1974). Phenology in Agriculture. In: Phenology and Seasonality Modeling (H. LIETH, Ed.), Chapman & Hall Ltd., London, p. 369-381.

WILLIAMS, R.D. & WINSTEAD, J.E. (1972). Population variation in seed germination and stratification of Acer negundo. Transactions of Kentucky Academy of Sciences, 33, 43-48.

WILLIAMSON, P. (1976). Aboveground primary production of chalk grassland allowing for leaf death. Journal of Ecology, 64, 1059-1075.

WINSTEAD, J.E. (1971). Population differences in seed germination and stratification requirements of sweetgum. Forest Science, 17, 34-36.

WITKAMP, M. & Van der DRIFT, J. (1961). Breakdown of forest litter in relation to environmental factors. Plant & Soil, 15, 295-311.

WOODMAN, J.N. (1971). Variation of net photosynthesis within the crown of a large forest grown conifer. Photosynthetica, 5, 50-54.

YUWAKA, J.; YAMAUCHI, S.; NAGAI, S. & TOKUHISA, E. (1977). Leaf longevity and the defoliating process in saplings of Actinodaphne longifolia. Japanese Journal of Ecology, 27, 171-175.

ZIMMERMANN, M.H. & BROWN, C.L. (1971). Trees - Structure and Function. Springer-Verlag, New York.

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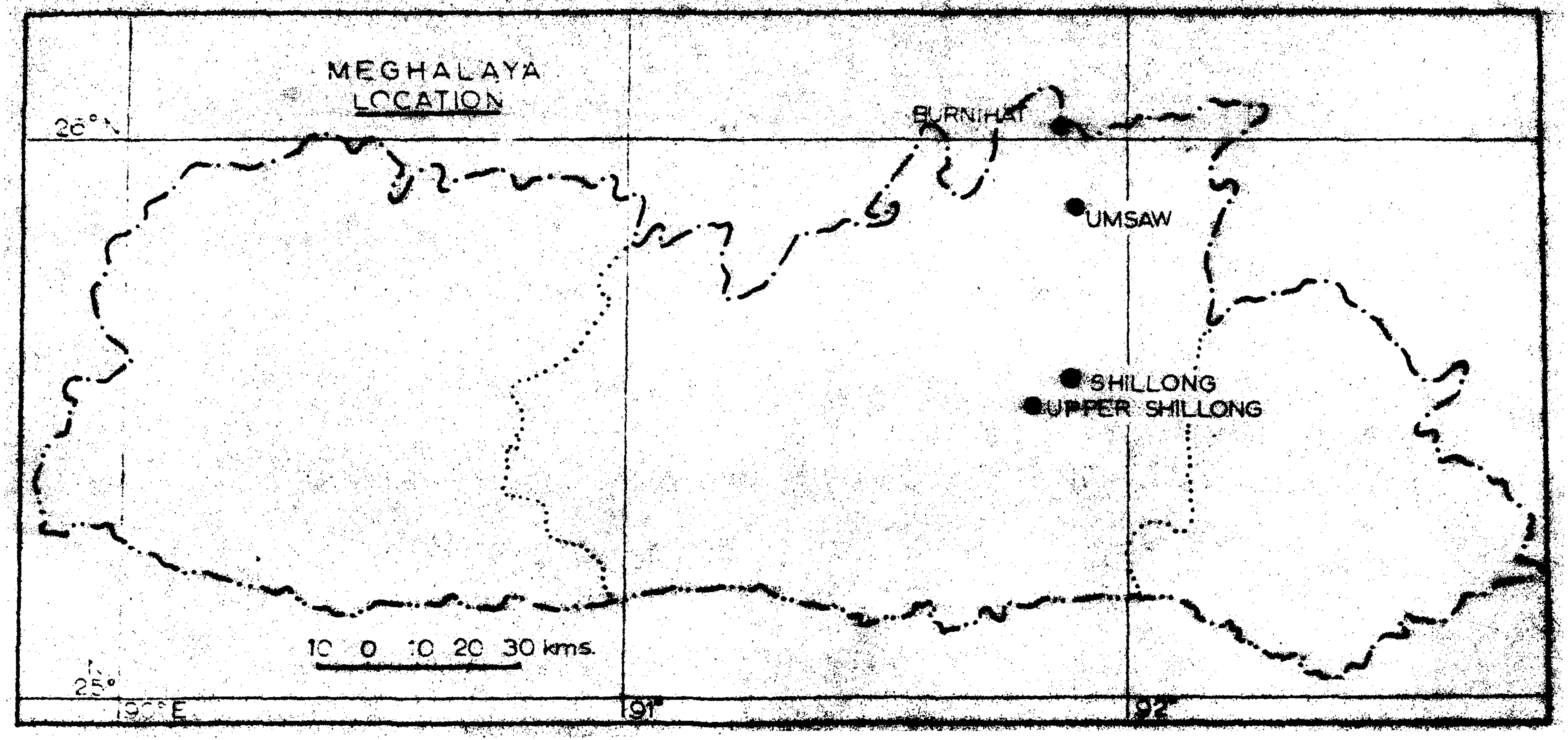
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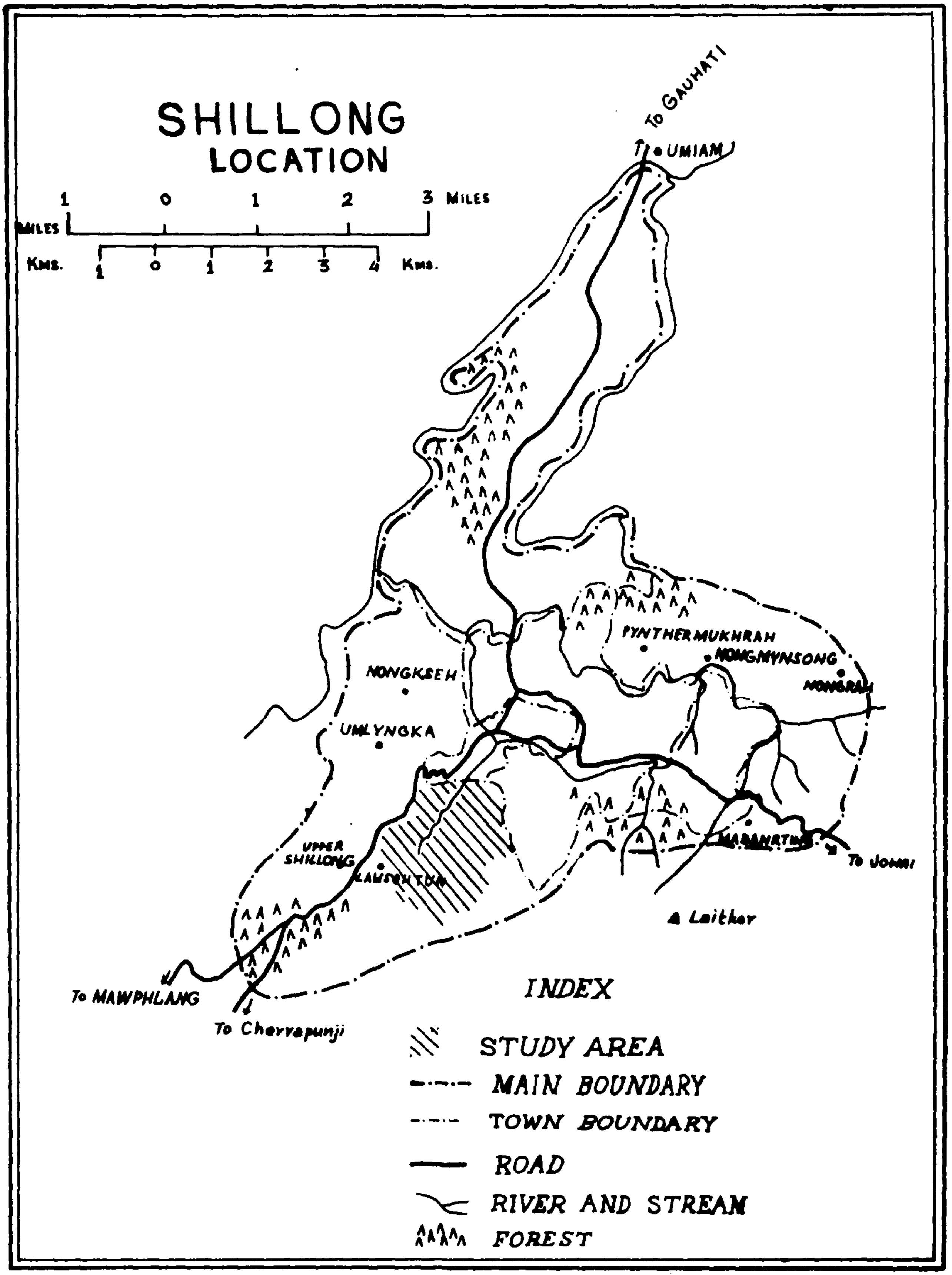
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UPPER SHILLONG
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PUBLICATIONS (PUBLISHED/ARISING OUT) OF THESIS

(a) Full papers

1. Temperature responses to seed germination in two closely related tree species of *Schima* Reinw. *Current Science* 50, 416-418 (1981).

2. Germination behaviour of seeds of *Alnus nepalensis* Don. *National Academy Science Letters*. Vol.4, No.2, (1981) (In Press).

3. An analysis of architecture and growth pattern of *Schima* species. *Biotropica* (Accepted).

4. Growth strategy of trees related to successional status:

   I. Architecture and extension growth

5. II. Leaf dynamics

   Forest Ecology& Management (submitted)

6. Seasonal adaptation of trees in a sub-tropical montane humid evergreen forest of north-east India.

   I. General phenological patterns.

7. II. Pattern of Litter production.

   Oecologia generalis (submitted)

8. Seed germination & Seedling establishment of two closely related tree species of *Schima*. *Proceedings Indian National Science Academy* (submitted).

(b) Abstracts of papers presented

1. Population variation in seed germination of *Schima wallichii*. 67th Indian Science Congress, Calcutta (1980).

2. Growth strategy and architecture related to productivity. 3rd All India Botanical Conference, Lucknow. (1980).

3. Growth pattern of young *Schima khasiana* trees 68th Indian Science Congress, Varanasi (1981).

4. Architecture and growth pattern of trees: applications for Social forestry. Seminar on Productivity in forestry operations. Organized by National Productivity Council, Shillong (1981).

TEMPERATURE RESPONSES TO SEED GERMINATION IN TWO CLOSELY RELATED TREE SPECIES OF *SCHIMA*, REINW

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A number of studies on germination ecology of species are available wherein germination requirements are closely related to their adaptation and distribution pattern in space[1-3] and in time[4]. Temperature requirement is one such factor which has received considerable attention[4-6]. However this aspect of the problem in relation to adaptive strategy of tree species has not received much attention[7]. The present study is concerned with temperature responses of the seeds of *Schima khasiana*, Dyer and *S. wallichii*, Choisy, two closely related and economically important timber tree species of north-east India, which are also extensively distributed in Meghalaya, on an altitudinal basis. The former is restricted to higher elevations (1600 to 1900 m), whereas the latter occurs at lower elevations (300 to 1600 m).

Seeds of *S. khasiana* and *S. wallichii* were collected from upper Shillong (1800 m) and Mawlai (1500 m) respectively during February March 1978, which were separated out from fruits by air drying. Germination

TABLE I

Germination total (%) (with S.E. values) for S. khasiana *and* S. wallichii *at different temperature regimes*

Species	Constant temperatures (° C)						Alternating temperatures (° C)	
	10	15	20	25	30	35	25/20	25/15
S. khasiana	10±2·3	55±2·7	46±3·6	44±2·9	42±2·2	0	45±5·5	46±2·3
S. wallichii	0	37±4·3	48±6·0	48±6·8	33±4·1	20±7·5	50±4·6	48±4·1

TABLE II

Germination values (with S.E.) for S. khasiana *and* S. wallichii

Species	Constant temperatures (° C)						Alternating temperatures (° C)	
	10	15	20	25	30	35	25/20	25/15
S. khasiana	0·32±0·12	12·08±0·9	6·08±0·9	8·66±1·7	3·41±0·43	0	2·36±1·18	3·82±0·58
S. wallichii	0	6·34±1·6	9·4±2·0	8·83±1·6	4·06±0·5	3·23±2·0	10·95±2·2	2·36±1·18

tests were performed, at a given temperature in incubators, on fresh seeds between moist filter papers. Only alternating temperature regimes received 14 hour light period at the time of higher temperature in the cycle. Fifty seeds in four replicates were used for all treatments.

Table I shows that seeds of both the species could germinate well over a wide range of temperatures, though the germination of *S. khasiana* was poor at 10° C and no germination occurs for *S. wallichii* at this temperature. At constant temperature regimes, while *S. khasiana* gave optimum germination at 15° C, that for *S. wallichii* occurred at 20 and 25° C. The two alternating temperature regimes did not have any favourable effect on the germination of *S. khasiana*, whereas the germination of *S. wallichii* improved slightly at 25/20° C alternating temperature regime compared to that at a constant 20 or 25° C. Further the range of temperature at which at least some germination occurred varied for the two species, *S. khasiana* having a range of 10 to 30° C and *S. wallichii* with a range of 15° to 35° C.

Germination values are given in Table II which are indices of germinability combining speed and completeness of germination, and are calculated using the formula PV × MDG where PV represents peak value of germination and MDG represents mean daily germination[8]. This is a better indicator of germination behaviour of the species concerned. *S. khasiana* gave maximum value at a constant temperature of 15° C. It is significant that the values at alternating temperature regimes for *S. khasiana* were extremely low though the final germination total was fairly good as seen from Table I. This is due to very low mean daily germination at alternating temperature regimes compared to that at constant temperatures of 20 or 25° C, where also the final germination total is more or less similar. *S. wallichii*, on the other hand, gave maximum germination value at 20° C followed by 25° C constant. It is significant that much better germination value was observed for this species at an alternating temperature of 25/20° C.

These results indicate that the two species are closely adapted to their altitudinal restriction at least as far as temperature response to seed germination is concerned. Thus, *S. khasiana* exclusively found at higher elevations tends to germinate better at lower temperatures and *S. wallichii* from lower elevations responds better to comparatively higher temperatures. Though such studies are lacking in this country, particularly on tree adaptation, similar conclusions have been made on some temperate trees like *Pinus contorta*[9], *P. sylvestris*[10] and *Acer negundo*[11].

This study was supported through a research grant from the Department of Science and Technology, Government of India.

July 9, 1980.

1. Koller, D., Mayer, A. M., Peljakoff-Mayber, A. and Klein, S., *Annu. Rev. Plant Physiol.*, 1962, **13**, 437.
2. Ramakrishnan, P. S., In *Biology of Land Plants* (ed. V. Puri *et al.*), Sarita Prakashan, Meerut, 1972, p. 344.
3. Thompson, P. A., In *Taxonomy and Ecology* (ed. V. H. Heywood), Academic Press, New York, 1973, p. 93.
4. Kapoor, P. and Ramakrishnan, P. S., *Curr. Sci.*, 1973, **42**, 838.
5. Thompson, K., Grime, J. P. and Mason, G., *Nature*, 1977, **267**, 147.
6. Thompson, P. A., *Ibid.*, 1970, **225**, 827.
7. Kozlowski, T. T., *Growth and Development of Trees*, Vol. I, Academic Press, New York, 1971.
8. Czabator, F. J., *For. Sci.*, 1962, **8**, 386.
9. Haasis, F. W. and Thrupp, A. C., *Ecology*, 1931, **12**, 728.
10. Kamra, S. K. and Simak, M., *Stud. For. Suec.*, 1968, **62**, 1.
11. Williams, R. D. and Winstead, J. E., *Trans. Kentucky Acad. Sci.*, 1972, **33**, 43. ✓

PINJORIAPOLLIS, A NEW FOSSIL POLLEN FROM THE PINJOR FORMATION (UPPER SIWALIK) EXPOSED NEAR CHANDIGARH

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3RD ALL INDIA BOTANICAL CONFERENCE, SYMPOSIUM II. UTILIZATION OF PLANTS AS ENERGY RESOURCES

SII.6 GROWTH STRATEGY AND ARCHITECTURE OF TREES RELATED TO PRODUCTIVITY

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Pattern of growth and architecture build-up of early successional (*Schima wallichii, S. Khasiana and Alnus nepalensis*) and late successional (*Manglietia insignis*, and *Quercus dealbata*) tree species were studied in a subtropical humid mountain forest at Shillong peak (altitude, 1900 m). Early successional tree species have indeterminate pattern of shoot growth, prolonged growth period, much more extension growth and leaf production than the late successional ones. The latter are with determinate growth pattern, make small amount of extension growth and confined the active growth mainly for a brief period of the growing season. The early successional species exhibit more frequent rhythms of shoot extension, branching and leaf production (becoming continuous growth in case of *Alnus nepalensis*) than the late successional species with single determinate flush of extension as well as branch and leaf production (production of lamma shoots or additional flush of shoot growth in response to favourable climatic conditions have been considered as special cases of basic determinate scheme). Branches are produced through Syllepsis-axillary buds grow into branches without a rest period in early successional tree species, conferring an advantage for having more frequency of branching. Late successional species, on the other hand produce branches prolaptically—axillary buds undergoing a period of rest. The early successional species, however, can produce prolaptic branches if main axis is disturbed which is a common feature in the region due to slash and burn agriculture. Early successional species tend to maintain a higher, narrower crown at a given diameter (correlative growth processes) than late successional trees which have longer, wider and deeper crown. Growth in the former tends to emphasize height growth in order to attain a superior competitive position while in the latter it emphasizes lateral growth. Consequently, branches of early successional tree species are more vertical at all canopy positions than the late successional trees. The leaf angles in late successional species in general is more near to horizontal than the early successional ones which have its leaves dispersed into several layers (multilayer) with sun leaves placed vertically and shade leaves to near horizontally.

The fast and prolonged indeterminate pattern of growth, multilayered distribution of leaves and branching pattern related to light interception strategy equips the early successional species to grow and occupy the ecological niche through *exploitive strategy*. On the other hand, the late successional species with determinate shoot growth pattern and consequent predictable shading of leaves (*monolayer*) as well as spreading crown are suited for *conservative strategy* of late successional environments. The significance of these results for exploiting forest resources of the north eastern region for timber and energy resources are discussed.

67th Session of Indian Science Congress

II. ECOLOGY AND PHYTOGEOGRAPHY

235. Population variation in seed germination of *Schima wallichii*, Choisy

RAM BOOJH & P. S. RAMAKRISHNAN, Shillong.

The germination behaviour of seeds of *Schima wallichii*, Choisy from different populations ranging from 300 to 1800 m elevations was studied under controlled environmental conditions. The higher elevation population showed maximum percentage germination at 15°C. Germination at the alternating temperature was reduced but the difference was not significant. Percentage germination value decreased significantly at higher temperatures. Lower elevation populations germinated maximum at 20°C, but also exhibited their adaptability to wide ranging temperatures. Thus there exists a correlation between the temperature requirement and the natural distribution of the populations.

68th Session of Indian Science Congress

305. Pattern of shoot growth in young *Schima Khasiana*, Dyer, trees.

RAM BOOJH and P. S RAMAKRISHNAN, Shillong.

The growth pattern of six year open grown *Schima khasiana*, an early successional timber tree species was studied at Shillong peak (altitude : 1900 m.). The growth starts with rapid extension of shoot and expansion of leaves in April. A single orthrotropic, sylleptic whorl of branches are produced on the main axis, from the axillaries of the current season, in May. This pattern is repeated on branches also. The radial growth starts and ceases later than extension growth, and this may be hormonal. Leaf production is triggered just at the begining of rains and leaf fall in drier months, which corresponds to seasonal climatic events. The species achieves much of height growth and leaf production throughout the growing season (April to October), which equipes it to occupy the ecological niche as an early successional and exploitive strategist species.