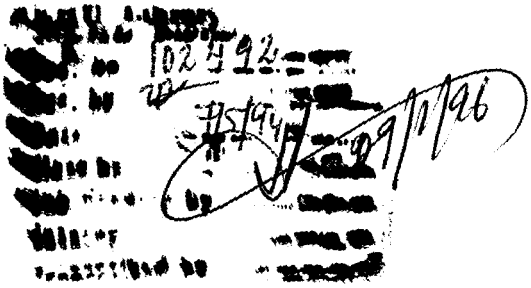
# ECOLOGY OF GAP PHASE REGENERATION IN A SUBTROPICAL BROADLEAVED CLIMAX FOREST OF MEGHALAYA

By

PRATHIMA RAO

THESIS SUBMITTED IN FULFILMENT OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN BOTANY


NORTH-EASTERN HILL UNIVERSITY
SHILLONG, INDIA
1992



Gram : NEHU
Phone (office) : 23390

# North-Eastern Hill University

DEPARTMENT OF BOTANY

School of Life Sciences
SHILLONG 793 014, INDIA

Dr. H. N. Pandey
Reader

I certify that the thesis entitled "Ecology of gap phase regeneration in a subtropical broadleaved climax forest of Meghalaya" submitted by Ms. Prathima Rao, for the degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong, embodies the record of original investigation by her under my supervision. She has been duly registered and the thesis presented is worthy of being considered for the award of the Ph.D. Degree. The work has not been submitted for any degree of any other University.

Shillong
The 17th February 1992.

Supervisor

Forwarded
17.2.92

## ACKNOWLEDGMENTS

I express my heartfelt gratitude to my teacher Dr. H.N. Pandey, Department of Botany, North-Eastern Hill University, Shillong for his able guidance, keen interest and constant encouragement throughout the course of this study. I am also sincerely grateful to Professor R.S. Tripathi for his valuable suggestions and encouragement.

I am grateful to Professor Y.S. Chauhan, Head, Department of Botany for providing necessary laboratory facilities. I am also grateful to Professor R.R. Mishra for providing necessary facilities during his tenure as Head, Department of Botany.

I wish to offer my warmest thanks to Mr. S.K. Barik and Ms. Jahnaba Misra who at every stage of the study rendered invaluable help.

The completion of this study is largely due to the help and support received from my lab mates: Dr. A.K. Das, Dr. M.L. Khan, Dr.(Ms) B. Wankhar, Dr.(Mrs) A. Laloo, Dr. G. Pradhan, Ms. S. Ryn-jah, Mr. L. Boral, Ms. T. Lyngdoh, Mr. D. Dutta, Mr. Umashankar, Mr. U.K. Sahoo and Mr. S. Dasgupta.

Thanks are also due to my friends Suman, Banita, Seema, Dhruv, Maitreyee, Subhashini and Nora for their unconditional help in innumerable ways.

To my parents, sister and brother, who perceived that this work was worth doing, and gave me wonderful encouragement and support.

Financial support received from the Council of Scientifc and Industrial Research, New Delhi in the form of Junior and Senior Research Fellowships is gratefully acknowledged.

Shillong
The 17th February, 1992.

Prathima Rao

# TABLE OF CONTENTS

# 1 GENERAL INTRODUCTION

The infinite variety of forests cover approximately 32% of the world's land surface in the alpine, temperate, subtropical and tropical climatic zones where the mean annual rainfall exceeds 85 cm. The distinctiveness of the forest ecosystem lies in the complexity of its structural and functional organization which yield stability and resiliency in the face of external disturbances and natural alterations of the system (Reichle 1974). The tropical rain forests which are stable only in a relative sense, show short-term changes as a result of natural catastrophies and human interventions (Richards 1986). The sheer bulk of energy-rich material they contain, coupled with continual increase by photosynthesis place tropical and subtropical forests in a unique position as far as world's natural resources are concerned.

Till recently forests have been regarded as a limitless natural resource, therefore very often over-exploited, causing rapid decline in their cover all over the globe. In particular, the destruction of tropical moist forests is taking place faster than the other ecobiomes (Myers 1987). The alarming rate of deforestation has led most countries with tropical forests to comply with the World Conservation Strategy (IUCN 1980) and protect at least 10% of their forest wealth in national parks and reserves. Destruction of tropical moist forests and realisation of their crucial importance for the entire biosphere, have probably aroused interest of scientists and ecologists around the world to undertake intensive study of the nature and functioning of this rich and productive yet fragile ecosystem.

Disturbance in climax communities have been viewed as forces that may bring instability to the system (Clements 1936) or increase the species diversity by preventing competitive exclusion by dominant species (Paine 1966, and Huston 1979). In the dense humid tropical forests, mild natural disturbances generated by treefalls play an important role in shaping the composition and organization of the community. When a tree falls, it creates a "canopy hole" or "chablis" wherein the process of forest rejuvenation, commonly known as "gap phase regeneration" takes

place. During this phase energy intake by the ecosystem considerably exceeds energy return to the environment and the net increase in biomass is rapid. Understanding of the gap disturbance regime and the tree replacement process in canopy gaps provide a better insight into the dynamics of closed canopy communities where these openings are the only means by which a tree can regenerate itself in the forest (Hubbell 1984, Hubbell and Foster 1986). Treefall gaps also play important role in maintaining species richness of the forest (Denslow 1980, Orians 1982). Thus a seemingly simple event of tree or branchfall actually sets in a series of complex changes in the closed canopy forests. This entire process is poorly understood and therefore forms one of the most important aspects of study in the humid tropical forest ecosystems of the world.

Successful natural regeneration of trees in a closed canopy forest greatly depends on creation of gaps in the continuous canopy either by treefalls or limbfalls. Immediately after creation, gaps are colonized by the propagules of surrounding plants and secondary succession progresses until a community similar to the original forest develops. Such a community dynamics is essential for the coexistence of both shade tolerant and shade intolerant species in the forest. Gap phase regeneration

encourages colonization of shade intolerant species and enhances the growth of suppressed shade tolerant species. This phase subsequently leads to the building phase that finally culminates into the mature forest. On account of this phenomenon, humid tropical forests have been visualised as spatial mosaics shifting through gap, building and mature phases (Whitmore 1989).

Treefall gaps vary in shape and size, show spatial heterogeneity and exhibit temporal variation in microclimatic and edaphic conditions. Thus they provide specialized regeneration niches (Grubb 1977) for different species in the species-rich humid tropical forest ecosystems. Species belonging to different regeneration guilds respond differently to th
the gaps of differe
their successful establishment de
tors, including their ability to exploit the resources available in gap-understorey mosaic of the forest.

Most of the studies on gap phase regeneration are confined to the tropical and temperate forests of the Western Hemisphere, particularly the forests on Barro Colorado Island, Panama, Ivory Coast and the Woodlands of North America. Studies pertaining to the patterns of regeneration in treefall gaps in the closed canopy tropical and subtropical forests of India is conspicuously lacking.

The subtropical wet hill broadleaved forests of Meghalaya which are similar to the evergreen oak forests of the Far East, represent the climax vegetation at higher altitudes of the state. They are under a state of degradation due to irrational human exploitation in the form of tree felling, shifting cultivation and overgrazing. In spite of these disturbances there still exists a few patches of undisturbed natural forest due to the religious beliefs of the local people. These forest stands have attained the status of "sacred groves". Natural tree regeneration in these space limited virgin forests is extremely slow and depends on canopy openings. Gap phase regeneration in these forests is poorly understood, although effect of canopy gaps on regeneration of trees in the disturbed stands of this forest have been carried out by Khan et al (1986), Khan et al (1987), Tripathi and Khan (1990), Rao et al (1990) and Khan and Tripathi (1991).

The present study was undertaken in an undisturbed broad-leaved forest stand at Mawphlang having the status of a "sacred grove" (locally known as "Law Lyngdoh"). The principal objectives of the study were (i) to carry out a detailed analysis of the floristic composition, tree population structure and other analytical community parameters to understand the forest structure, (ii) to study the causes of gap creation and their effects on forest micro-

environment and species diversity and (iii) to understand the regeneration behaviour of dominant trees in the tree-fall gaps. The results of the study carried out during 1988-1991 have been presented and discussed in this dissertation.

The first chapter of the thesis deals with the importance of gap phase regeneration in forests and sets out the objectives of the study. This is followed by the "Review of Literature" which presents the state of art of the subject. A brief description of the study site, its location, climate and geology has been dealt with in Chapter 3. This chapter also gives an account of community characteristics and analyses the tree population structure of the forest. Creation of gaps, their physical attributes and microenvironment in gaps and understorey have been discussed in Chapter 4. Chapter 5 deals with the micro-environmental variability along a gap size gradient in the forest. Among gaps as well as between gap and understorey variations in species diversity have also been discussed in this Chapter. The recruitment, survival and growth of naturally emerged seedlings of dominant tree species in gaps of different sizes and forest understorey have been analysed in Chapters 6 and 7. Chapter 8 discusses the effect of insect and rodent predation on seeds and seedlings of dominant tree species. A synthesis of the

results of the entire study is presented in a comprehensive manner in Chapter 9 which is followed by a summary of the work.

# 2 REVIEW OF LITERATURE

The idea that a tropical forest is a structural or floristic mosaic dates back to Aubreville's (1937) "mosaic theory of regeneration" (cited by Richards 1952). Since then several authors have emphasized that the tropical rain forests consist of patches of different stages of forest cycle manifesting the effects of past disturbances (Hladik 1982, Whitmore 1978, 1982, 1989). Disturbance initiates a set of cyclic changes in the forest which could be arbitrarily recognised as gap, building and mature phases (Watt 1947, Cousens 1974, Whitmore 1975, 1978, 1982, 1989). According to Boremann and Likens (1979) tropical forests represent the shifting mosaic of different sized patches cycling through gap, building and mature phases. Martinez-Ramos et al (1989) considered forests as dynamic mosaic of vegetation patches of different ages while Barden (1989) attributed the existing forest composition of old growth forests at Barro Colorado Island, Panama to the tree replacement process in canopy gaps.

The extent to which canopy gap dynamics may contribute to the mosaic structure of forest landscape has been discussed by Christensen and Franklin (1987). Dale et al (1986) reported various types of canopy disturbances and discussed their importance in controlling community dynamics. Runkle (1989) considered treefall gaps necessary for the establishment and growth of many forest trees, while Milthrope (1961) and Miles (1974) showed that in most closed canopied forests, regeneration is dependant upon the gaps in the community. Similarly Hartshorn (1980), Brokaw (1985b) and Denslow (1987) recognized the importance of canopy openings in the regeneration of forest trees. Importance of gap phase regeneration in influencing tree and forest architecture and forest composition have been discussed by Jones (1945), Whitmore (1975), Hartshorn (1978), Runkle (1981), Brokaw (1985a). Studies of Connell (1978) and Huston (1979) suggested that disturbances delay the process of competition exclusion among the species, while Strong (1977) attributed much of the high species diversity of some tropical forests to canopy gaps. Recent studies by Runkle (1990) and Denslow and Gomez Diaz (1990) show that gap habitats play an important role in tree regeneration in undisturbed forest community and an understanding of natural gap dynamics may be useful in the management of forest ecosystem by maintaining its biological diversity (Denslow and Spies 1990).

The first definition of gap was given by Oldeman (1978) who visualised it as a dumbbell shaped "chablis" - a French word denoting "the fall of a tree, the resulting damage and the fallen tree itself". Since then many authors have defined a gap as an area opened by tree or branch fall where the plants are not more than 2-3m in height (Brokaw 1982a, Lawton and Putz 1988). The gaps are generally created by rain or wind action. The role of rain in creation of gaps has been investigated by Rand (1976) and Brokaw (1982b) at Barro Colorado Island, Alexandre (1982) at Ivory Coast, Sarukhan (1978) at Los Tuxtlas, Mexico and Oldeman (1972) and Riera (1985) in French Guiana. Lawton (personal communication), however, found wind to be the primary cause of gap formation in the montane forest at Monte Verde, Costa Rica, while Webb (1985), Doyle (1981) considered cyclonic storms as a major factor in gap formation in the Australian forests. Dunn et al (1983) studied the effect of catastrophic wind disturbance in creation of treefall gaps in an old-growth hemlock-hardwood forest, at Wisconsin. The effect of small and large windthrows in shaping the structure of forests was studied by Oliver and Stephens (1977).

Oldeman (1978), Hartshorn (1978), Lawton and Dryer (1980), Lawton (1982) and Ashton et al (1984) linked treefalls to topography and soil characteristics. Wadsworth (1959)

and Vooren (1985) argued that edaphic and topographic differences may produce local variation in gap formation rates. Webb (1968) showed that the forests on unstable soil are likely to have different gap characteristics than the forests on more stable soils.

Differences in frequency distribution of gaps of different sizes at different sites may occur primarily due to variation in the pattern of treefalls. At Barro Colorado Island, Panama, Brokaw (1982b) related gap size to the size of falling trees and at San Carlos de Rio Negro, Venezuela, Uhl and Murphy (1981) attributed the small canopy openings to the slow growing small statured trees in the forest. Foster and Brokaw (1982) suggested that the fewer large gaps in the second growth forest than in the old growth forest at Barro Colorado could be due to the presence of few large canopy trees and Putz (1984) found that liana connections could raise the incidence of multiple treefalls in the forest. Species specific death of trees also affect gap size (Brokaw 1985a). Florence (1981) and Sanford et al (1986) studied the role of falling trees and branches in gap creation and their influence on gap size.

The size and frequency of recent gaps in mature and old hardwood forests have been analysed by Romme and

Martin (1982), Runkle (1982) and Naka (1987). Brokaw (1982a), Foster and Brokaw (1982), Uhl (1982) and Rollet (1983a) have reported that the turnover rate of gap creation in various tropical rain forests. Poore (1968) and Uhl and Murphy (1981) used data on gap size distribution and gap closure to estimate the gap turnover rate. Permanent plot data on tree mortality have also been used to estimate stand turnover rate by several workers Lang and Knight (1983), Leigh (1975), Lieberman et al (1985), Putz and Milton (1982) and Swain and Hall (1986) and usefulness of gap-based turnover rate as an index of stand dynamics has been emphasized by Runkle (1982). In a recent study Howe (1990) explored the implications of gap geometry for gap colonization by tree species in tropical forests.

Natural disturbance generated by tree or limb falls in tropical rain forests causes a great degree of spatial heterogeneity (Whitmore 1975, 1978, 1982, Brokaw 1982a, b, 1985, Martinez-Ramos 1985) both within and among the gaps making the gap phase regeneration a complex phenomenon within the forest. Findings of Orians (1982), Nunez Farifan Dirzo (1984) and McCarthy and Facelli (1990) show that small scale disturbances such as treefalls may significantly alter habitat heterogeneity and at certain frequencies and intensities it may affect community dynamics. Small scale spatial heterogeneity has also been regarded as

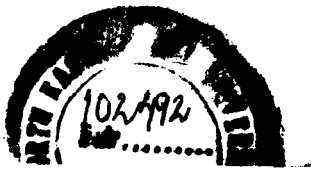
an important environmental factor, since it affects ecology and evolution of plants and animals (Strobeck 1974, Wilson 1980, Turkington and Aarsen 1984). Pickett and White (1985) argued that plant communities exhibit heterogeneity in composition and structure over spatial scales and dynamics and succession at these scales may control species composition and abundance within and between communities. Coley (1983a) and Dirzo (1984) suggested that spatial heterogeneity may promote heterogeneity of the biotic environment which may in turn affect the performance of the individuals in the gaps in tropical forests. Beatty (1984) studied the influence of microtopography and canopy species on spatial patterns of forest understorey plants and Beatty and Stone (1985) and Beatty and Sholes (1988) quantified the variety of soil microsites such as pits, root mats and soil mounds created by treefalls and concluded that the process of treefall creates long-term soil patterns and maintains microsite heterogeneity in forest communities. Lutz (1940), Stephens (1956), Lutz (1960), Stone (1975), and Brown (1976) reported that the uprooting of trees result in small scale variation in microtopography. Stephens (1956), Lyford and Maclean (1966) found that about 14-48% of the forest floor may be covered by the treefalls in the temperate areas. Brewer and Merritt (1978) studied the effects of soil disturbances in regeneration and Tripathi and Khan (1990) investigated the effects of microsite

characteristics on germination and seedling fitness in Quercus spp. Role of microsite characteristics in growth and survival of plants has also been studied by several workers (Rorison 1967, Mack and Harper 1977, Silverton 1981).

Most gap studies have focussed on the death and replacement on one or several canopy trees. Nevertheless the role of canopy gaps in maintaining tree species diversity is equally important (Bray 1956, Loucks 1970, Williamson 1975 and Runkle 1980). Connell (1978), Denslow (1980) and Orians (1982) in their studies emphasized the significance of spatial heterogeneity in maintaining species richness in the forest. Long-term effects of environmental variability in gaps in maintaining species diversity have been dealt with by Janzen (1970), Connell (1971), Grubb (1977), Chesson and Warner (1981) and Warner and Chesson (1985). Grubb (1977) outlined the general importance of regeneration niche in plant communities, while Ricklefs (1977), Connell (1978), Huston (1979), Denslow (1980) and Orians (1982) explicitly theorized that specialized gap phase regeneration requirements of species contribute to diversity of the forests. Hutchinson (1978) stressed the importance of microsite heterogeneity in understanding the concept of niche specialization. Collins and Good (1987) have dealt with the effect of habitat

heterogeneity on regeneration niche differentiation of tree seedlings.

In general canopy openings are characterized by increased resource availability to the plants inhabiting the lower strata of the forest community. The availability of environmental resources such as light, water, nutrients in the gaps is strongly influenced by a variety of physical and biological characteristics of the gap and surrounding vegetation. Within gap microenvironmental heterogeneity has been studied by Putz (1983), Beatty (1984), Christy and Mack (1984), Lawton and Putz (1988). Between gap variations in microclimatic conditions have been discussed by Lee (1978) and Denslow (1980). They argued that gap microclimatic conditions are the function of gap size. Canopy gaps are characterized by temporary increase in light availability (March and Skeen 1976, Canham 1984, 1988, Chazdon and Fetcher 1984a, b). Canham et al (1990) studied the impact of treefalls on light environment in five temperate and tropical forests. Poulson and Platt (1989) studied the influence of gap light regimes on canopy tree diversity. In addition to increased incident light levels, gap microclimate is generally characterized by lower humidity and higher temperature (Schulz 1960, Fetcher et al 1985). In some studies soil temperature was found to be higher in gaps than the surrounding understorey (Fetcher et al 1987), while in others (Vitousek and Dens-



low 1987, Uhl et al 1988, Becker et al 1988) higher soil moisture has been reported in the gaps. Apart from soil moisture, higher soil nutrients has been reported in gaps by Minckler et al (1973). Leaf litter besides being the chief source of available nutrients to plants, affects soil moisture and temperature of the forest floor (Hart et al 1962). Treefall debris also serves as a potential source of available nutrients and generates a nutrient pulse in gaps (Uhl et al 1982).

In the biological environment, effects of root competition and allelopathy have been studied in more detail. The former gradually decreases with the increase in gap size (Janos 1980) while the latter is more pronounced in gaps (Anaya 1976).

Treefall clearings are widely recognised as important precondition for the establishment and growth of rainforest tree species (Richards and Williamson 1975, Sarukhan 1978, Hartshorn 1980, Denslow 1980, Alexandre 1982, Brokaw 1985a and Clark and Clark 1987). Growth and survival of saplings in closed canopy forests depend on canopy openings (Bazzaz and Pickett 1980, Brokaw 1985, Martinez-Ramos 1985, Rollet 1983a,b and Whitmore 1978). Studies on seedling and sapling growth rates in gaps (Uhl 1982, Brokaw 1985b, 1987) and their growth responses in different light regimes (Bazzaz and Pickett 1980, Pearcy 1983, Chazdon 1986) suggests that

species show a distinct niche partitioning within the complex gap-understorey environmental mosaic in the forest. Brokaw (1985a) and Denslow (1987) concluded in their reviews that gaps in the forest canopies affect germination of seeds and growth and survival of plants in them. Murray et al (1988) and Vasquez-Yanes and Smith (1982) studied the role of canopy openings in influencing the germination the germination of certain tree species. Hartshorn (1980), Vaaquez-Yanes and Orozco-Segovia (1984), Fletcher et al (1983) and Chazdon and Pearcy (1986a,b) have stressed the importance of solar radiation and its effects on germination and behaviour of plants in gaps as compared to the forest understorey. Vegis (1965), Lang (1965) and Stokes (1965) have reviewed the literature on interactions between germination and environmental factors such as moisture tension, light and mineral nutrition. Janzen (1970), Connell (1971), Hubbell (1979, 1980) and Augspurger (1984b) studied the influence of seedling recruitment patterns on seed dispersal and distribution of adult plants. Howe and Smallwood (1982) examined the role of seed dispersal distance in species distribution within a forest. Orians (1982) postulated that germination and survival of seeds and seedlings should vary with gap microhabitat and gap size.

Canopy gaps have a positive effect on the survival and growth of tree seedlings. Performance of seedlings also

depend on resource availability and their physiological ability to efficiently use the higher level of resources present in gaps (Brokaw 1985b, Hladik and Blanc 1987). The importance of rapid growth rate for the exploitation of resources in the canopy gaps by tree species has been widely discussed (Marks 1975, Runkle 1981, Hibbs 1982, Canham and Marks 1985). Studies comparing the performance of juvenile plants in gaps and understorey are many (Clark and Clark 1987, Welden et al 1991). Augspurger (1984a,b,c), Howe et al (1985), Clark (1987) and Desteven (1988) have compared the performance of tree seedlings and saplings in gaps and understorey. Brokaw (1985b), Denslow (1987) and Whitmore (1989) emphasized on the importance of relationship between gap size and growth abilities in ecological differentiation of species. Leigh et al (1982) and Brokaw and Scheiner (1989) examined the effect of gap size on species abundance and growth. Popma and Bongers (1988) studied the effect of canopy gaps on growth of seedlings, while Denslow et al (1990) investigated the growth response of tropical shrubs to treefall gap environments. Uhl et al (1988) studied the vegetation dynamics in Amazonian treefall gaps. Lorimer (1981) studied survival and growth of understorey trees in oak forests and Canham (1988) investigated growth and canopy architecture of shade tolerant trees and their response to canopy gaps. Streng et al (1989) analysed dynamics of woody seedling in East

Texas Floodplain forests. Large amount of work has been done on the effect of natural forest disturbances on growth of suppressed tree seedlings and saplings (Marshall 1927, Ghent 1958, Wardle 1959, McQuilkin 1975, Oliver and Stephens 1977, Bormann and Likens 1979, Kohyama and Fujita 1981, Marquis and Bjorkbom 1982, Nakashizuka and Numata 1982, Platt and Hermann 1986). Lorimer (1989) studied the development of red maple understorey in northeastern oak forests of North America and Forcier (1975) studied the reproductive strategies of climax tree species. Pickett and Bazzaz (1976, 1978) and Werner and Platt (1976) have compared plant responses along gradients of resource availability. Schupp et al (1989) studied arrival and survival of tree species in treefall gaps. Lawton (1990) and Spies et al (1990) have monitored the effects of canopy gaps on seedling mortality and population dynamics of trees. Aide (1987), and Gartner (1989) considered mild disturbances as a cause of seedling mortality, while Denslow (1987) attributed seedling mortality to the gap understorey environmental mosaic.

Studies on the effect of microenvironmental factors on seedling survivorship and growth are limited (Streng et al 1989). Survivorship and fine scale habitat characteristics of tree seedling with regard to microenvironmental variations have been studied by Bazzaz and Pickett (1980), Aug-

spurger (1984a), Collins (1989). Burton and Mueller-Dombois (1984) and Connell et al (1984) have studied the effect of light on survival and growth of tree seedlings while Sorensen and Ferrel (1973) have investigated the role of temperature on the growth of juveniles. Fetcher et al (1987) on the basis of microclimatic measurements at seedling levels have suggested that temperature and relative humidity return to pre-gap levels within two years of treefall. Denslow (1980), Whitmore (1982), Canham and Marks (1985) and Veben (1985) reported that spatial variation in light is the most important factor which affects seedling performance in a forest.

The effect of soil moisture on the seedlings was studied by McLeod and Murphy (1977), Mueller-Dombois et al (1980), Schulte and Marshall (1983). A large number of workers have also evaluated the influence of soil nutrients on seedling establishment and growth (Campbell 1982, Rao and Singh 1985, Khan et al 1986, Khan et al 1987). Schulte and Marshall (1983) studied the effect of water stress on growth of pine seedlings and Bonner (1968), and Borger and Kozlowski (1972) reported that drought stress at early stages can impair seedling growth and development and may cause seedling mortality.

For most plants, mortality rates are highest in seed and seedling stages (Harper and White 1974, Cook 1979). Tree

seedling survival depends on both biotic and abiotic variables and their interactions within the forest. Among the biotic factors, disease and predation of seed and seedlings play a key role in seedling emergence and establishment (Schupp et al 1989). Study of seedling herbivory partly answers the question of what determines plant distribution and density (Harper 1969, 1977 and Janzen 1970). According to Brues (1946) herbivores together constitute a prime factor in regulating the abundance of all plants. Salisbury (1942), Janzen (1969, 1971) and Louda (1978) have proposed that predispersal seed predation by insects is a wide spread cause of plant mortality. Louda (1982, 1983) studied the effect of predispersal seed predation on seed production and seedling establishment, Desteven (1981) has analysed the extent of predispersal seed predation in forest trees. Ehrlich and Raven (1965, 1967), Whittaker (1972) and Louda (1978) have studied the response of exploited plant communities to seed predation. Schupp (1988) has studied seed and early seedling predation in forest understorey and treefall gaps. Janzen (1969), Connell (1971), Howe and Smallwood (1982) considered predation to have major effects on reproductive success of individuals and diversity of tree communities. Uhl et al (1988) and Platt and Herman (1986) suggested that species benefit from higher light in gaps if they avoid seed predation.

Herbivores can be a major cause of leaf loss in forests which in turn reduces assimilation rate and growth of plants, but plants show specific differences in susceptibility to the herbivory (Crawley 1983). Gibson et al (1987) and Coley and Aide (1991) reported that herbivores can influence competition between plants while results of Prins and Nell (1990) suggest that herbivory can lead to small scale disturbances of the soil needed by plants for germination. Aide and Zimmerman (1990) studied the patterns of insect herbivory in a neotropical liana. Clark and Clark (1985) studied the impact of herbivory and meristem damage on seedling dynamics and Schmid et al (1988) investigated the effect of insect herbivory on growth. Ed van der Meijden et al (1988), McNaughton (1983) and Rhoades (1985) have studied the various defense strategies adopted by plants in the struggle against herbivores. Alliende (1988) attempted to determine the reasons for differences in intensity of leaf predation in trees and Lloyd and Webb (1977) and Bullock (1984) suggested that in dioecious species phenology of flowering and nutritional value of tissues of two sexes might influence their acceptability to herbivores. Harper (1969), Handel (1976) and Maiorana (1981) demonstrated that leaf loss to herbivores may vary among plants in adjacent habitats. Burdon (1987) suggested that density and spatial distribution of individuals may also affect the degree

of infection by pathogens. Newbery and Foresta (1985) studied the herbivory and defense mechanism in pioneer, gap and understorey trees of tropical rain forests in French Guiana while Moore et al (1991) illustrated the differences in the vertical distribution of herbivory in oak trees. Feeny (1976), Rhoades and Cates (1976), Moran and Hamilton (1980) and Burdon (1987) showed that poor nutritional quality of foliage is a widespread anti-herbivore adaptation in forest trees.

Insect herbivores have been shown to have strong effects on plant reproductive success (Louda 1984, Marquis 1984, and Brown 1984), competitive ability (Bentley and Whittaker 1979, Windle and Franz 1979) and successional sequence of plant communities (Brown 1985, Bach 1990). Cates and Orians (1975), Sousa (1979), Coley (1980), Brawley and Adey (1981) and Lubchenco and Gaines (1981) have suggested that herbivores generally prefer early successional plants. Loss to insect herbivores varies along a spatial gradient and it can influence plant fitness (Harper 1969, Janzen 1971, Rausher and Feeny 1980, Parker and Root 1981). Differential herbivory has been reported across sun and shade gradients (Huffaker and Kennett 1959, Janzen 1975, Stanton 1975, Coley 1983a,b, Louda and Rodman 1983a,b, Louda et al 1987). Plant water stress has been hypothesized to be the mechanism underlying insect herbivory (White 1974,

1976, 1978) and increase in plant susceptibility to herbivores (Fennah 1965, Abdel Rahman 1973, Bjorkman et al 1981, Cates and Alexander 1982, Cox and McEvoy 1983). The effect of light environment and leaf age on leaf characteristics and herbivory rates have been investigated by Milton (1979), Rockwood and Glander (1979), Rausher (1981). Scriber and Slansky (1981), Coley (1983), and Coley and Aide (1991) have demonstrated that young leaves are preferred by herbivores. Coley (1980, 1983) has shown lower rates of herbivory on mature leaves and found that the leaf toughness was negatively related to the leaf damage, while Fetcher et al (1983) demonstrated leaf thickness to have a positive effect on foliage damage in tropical tree seedlings. Some studies show higher damage rates in light environment (Bigger 1981, Lincoln and Mooney 1984 and Harrison 1987), while others show higher damage in low light environments (Rice et al 1978). Lawton and McNeill (1979) and Price et al (1980) have reported relatively lower leaf predation in gaps but Newbery and Foresta (1988) have reported greater leaf area loss in the forest understorey. Mattson (1980), Caldwell et al (1981) have correlated the impacts of herbivory to the differences in composition of tissues consumed. Rhoades(1985) believed chemical mechanism to be one way of responding to herbivory. However, it is doubtful whether there is a single plant species which is completely protected by its defense against herbivory (McNaughton 1983).

The review of literature on various topics related to tree-fall gap, and growth and population behaviour of tree seedlings in forests, presented in the foregoing pages reveals that gap-phase regeneration - though a comparatively new area of study in forest ecology, has been mainly confined to the tropical rain forests of North America and neo tropical forests on Barro Colorado Island, Panama. Some work has been carried out in the temperate forests as well. However, there is a conspicuous lack of similar studies in the humid tropical forests of India.

# 3 STUDY SITE AND STRUCTURE OF MAWPHLANG FOREST

## STUDY SITE

### Location

The study was conducted in an undisturbed old growth subtropical broadleaved wet hill forest located at Mawphlang, 40 km south-west of Shillong (altitude 1900m, latitude 25°34'N, longitude 91°56'E) in Meghalaya, India (Fig.3.1).

### Climate

The climate of the area is monsoonic with an average annual rainfall of 2500mm, distributed over seven months of the year. The year can be divided into four seasons: (i) Spring (March to mid May), (ii) Rainy (mid May to September) (iii) Late rainy or Autumn (October to November) and (iv) Winter (December to February). The spring season is characterised by occasional showers and gradual increase in temperature over the preceding winter months. The spring is followed by rainy season during which 85% of the annual rainfall is received. The rain often continues upto the end of October, after which rainfall as well

Fig.3.1. Location of study site.

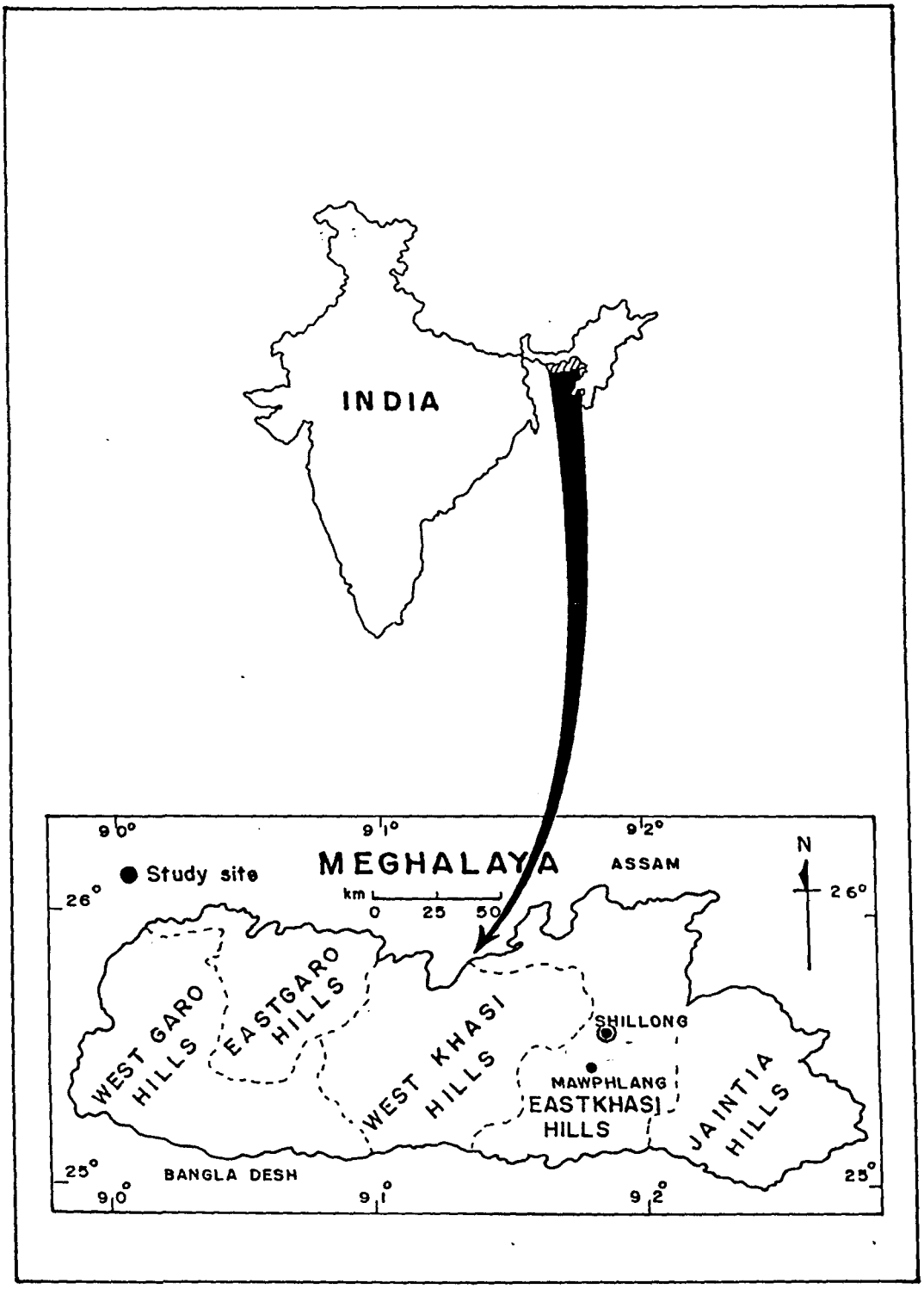
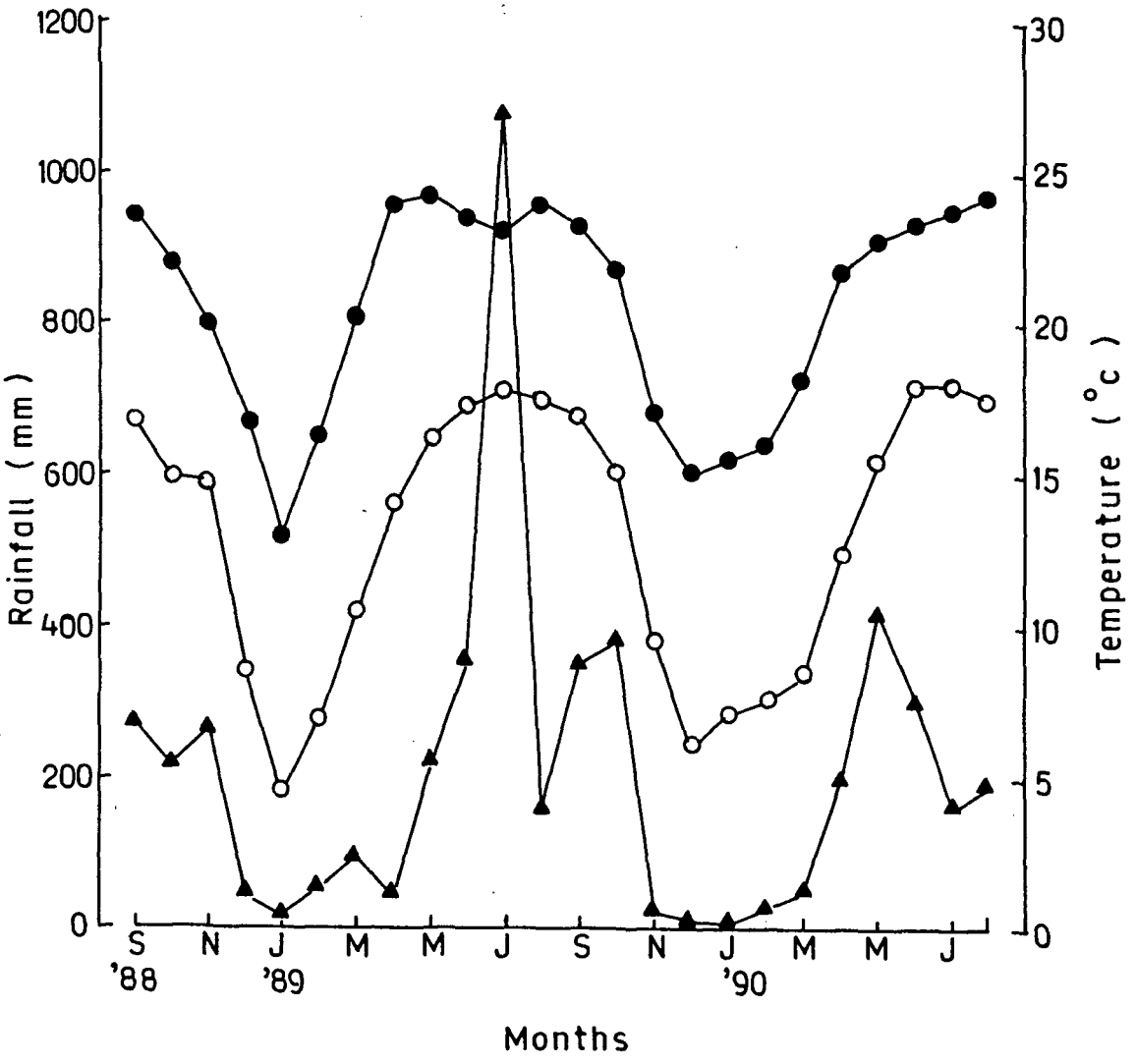

INDIA
MEGHALAYA
ASSAM
Study site
km
0 25 50
N
26°
25°
90°
91°
92°
WEST GARO HILLS
EASTGARO HILLS
WEST KHASI HILLS
SHILLONG
MAWPHLANG
EASTKHASI HILLS
JAINTIA HILLS
BANGLA DESH

Fig.3.2. Total monthly rainfall (▲), mean maximum (●) and minimum (o) temperature of the study site during the study period.


1200
1000
800
600
400
200
0
Rainfall (mm)
30
25
20
15
10
5
0
Temperature (°c)
S
N
J
M
M
J
S
N
J
M
M
J
'88
'89
'90
Months

as the temperature decline rather sharply. In the winter season the mean minimum temperature is 3°C, and the mean maximum is 16°C. Occasional rain and gusty winds lash out during this season. The days are usually clear, followed by frosty nights. The mean annual maximum and minimum temperatures are 22°C and 16°C, respectively (Fig 3.2).

**Geology and Soil**

The Shillong plateau as described by Gansser (1964) is situated at an elevation of 1500m above the Brahmaputra valley and is made up largely of pre-cambrian rocks acutely folded and steeply dipping with an overturned fringe of Mesozoic and Tertiary sediments. A major portion of the plateau is formed by the Archean gneisses and granites. Sandstones, limestones and conglomerates with subordinate clays superimposed over these rocks also occur in the Shillong plateau (Zimba 1977).

The soils are derived from the underlying gneisses, schists and granites and are grouped under latosol (oxisol) type (Pascoe 1950). The soil in the Mawphlang forest is covered by a thick detrital layer composed of duff and litter which shows a dense network of fine roots of trees, shrubs and ground vegetation. The mineral soil in top layer (0-10 cm) is a loam and shows an acidic reaction (pH 5.6) and is rich in organic matter content (5.6%). The total nitrogen content of the soil is 0.28%.

## STRUCTURE OF MAWPHLANG FOREST

The climax formation of Meghalaya ranges from moist deciduous to subtropical broadleaved wet hill forests (Champion and Seth 1968). Both forest types are exposed to various kinds of biotic disturbances. In particular, the age-old shifting agriculture, which is still prevalent among the tribals of the area is the major cause of forest destruction in the state. Nevertheless a few patches of relict forests still exist almost in undisturbed condition due to religious beliefs of the people and are called as 'sacred groves'.

The subtropical evergreen wet hill forest at Mawphlang is a closed canopied sacred grove and represents the climax vegetation of the area (Plate 3.1). It covers an area of about 150 ha. The forest shows floristic affinity with those occupying lower elevation (1000-2000m) of Eastern Himalayas. The forest is dominated by Quercus griffithii H., Q. dealbata L., Q. glauca Thunb.,Bl and Schima khasiana Dyer. Symplocus chinensis and Daphne shillong Banerjee are important species among the shrubs. The plant species in the forest is distributed into four distinct strata - the canopy layer (average height 10m), sub-canopy layer (average height 3-10m), shrub layer and the ground vegetation. There is a heavy growth of a large number of epiphytic orchids, mosses, ferns and lianas in the forest (Plates. 3.2, 3.3).

Plate 3.1. An overview of the subtropical broadleaved forest at Mawphlang


Plate 3.2. A close up of the Mawphlang forest showing some of the dominant tree species. A. Quercus dealbata; B. Quercus griffithii; C. Schima khasiana.

Plate 3.3. Inside views of the Mawphlang forest.

## METHODS

The structure of forest vegetation was analysed in August 1988 prior to the commencement of tree regeneration studies in the forest. An area of 50 ha was demarcated and 25 quadrats each of 10m x 10m size were laid randomly to study tree and shrub components, while ground vegetation (herbaceous components, tree seedlings and saplings) was studied by laying 40 quadrats of 1m x 1m size. In case of tree species, three categories viz., seedlings (height <20cm), saplings (height 20-150cm and dbh < 10cm), and trees (dbh > 10cm) were recognised. The tree component was further divided into six diameter classes viz., 10-20, 21-30, 31-40, 41-50, 51-60 and 61-70cm. Density, frequency, abundance, basal cover and IVI of all the species were determined according to the methods given by Misra (1968). Species diversity of the forest was computed using Pielou's evenness index (e) (Pielou, 1966).

$$e = \frac{(n_i/N) \log (n_i/N)}{\log S}$$

where, $n_i$ is the IVI of individual species, N is the total IVI of all the species and S is the total number of species present.

Spatial distribution pattern was determined using applied Poisson distribution method followed by log normal (G) test

for goodness of fit (Poole 1974) and also by Whitford's index.

$$\text{Whitford's index} = \frac{\text{Abundance}}{\text{Frequency}}$$

Density-diameter curves were drawn for individual tree species as well as for the total tree species to depict the tree population structure in the forest.

## RESULTS AND DISCUSSION

### Floristic composition

The floristic composition of the forest is given in Table 3.1. Thirteen tree species were recorded in this forest, of which Quercus dealbata showed the highest IVI. Q. griffithii and Q. glauca were codominant, while Schima khasiana and R. arboreum were present in large numbers. Out of eleven shrub species present, Daphne shillong was the dominant followed by Baliospermum micrantha and Lindera pulcherrima. Thirteen herbaceous species and pteridophytes were recorded. Among the tree and shrub species relative abundance was more or less evenly distributed indicating high equitability or low dominance in these two components of the forest vegetation.

The species in the forest were distributed in four distinct strata. The canopy layer was mainly composed of Q. dealbata,

Table 3.1. Density (Plants $ha^{-1}$ ±S.E.) and importance value indices (IVI) of component species in the Mawphlang forest. Values in parentheses are species rating on the basis of IVI

| Species | Density | IVI |
|---|---|---|
| **Tree species** | | |
| Castonopsis kurzii (Hance) B. | 60 ± 2.2 | 17.21 (10) |
| Corylopsis himalayana Griff. | 40 ± 1.0 | 9.23 (13) |
| Exbucklandia populnea (Griff.) Br. | 80 ± 2.5 | 18.10 (8) |
| Ficus nerifolia Sm. | 40 ± 1.6 | 6.25 (14) |
| Manglietia insignis (Wall.) Bl. | 90 ± 3.5 | 23.61 (6) |
| Myrica esculenta Buch. Ham. | 70 ± 1.5 | 24.22 (5) |
| Prunus undulata Buch. Ham. | 90 ± 3.2 | 17.13 (11) |
| Quercus dealbata L. | 210 ± 2.8 | 50.17 (1) |
| Quercus glauca Thunb. | 90 ± 3.5 | 27.22 (3) |
| Quercus griffithii Hk. | 150 ± 4.5 | 31.11 (2) |
| Rhododendron arboreum Sm. | 90 ± 2.8 | 25.17 (4) |
| Schima khasiana Dyer. | 90 ± 2.3 | 21.21 (7) |
| Taxus baccata L. | 40 ± 3.4 | 11.62 (12) |
| Terminalia tomentosa | 60 ± 2.8 | 17.75 (4) |
| **Shrub species** | | |
| Ardisia chrispa (Thunb.) DC. | 40 ± 3.1 | 17.36 (9) |
| Baliospermum micrantha Muell Arg. | 50 ± 2.2 | 41.25 (2) |
| Camellia caduca C.B. Cl. | 20 ± 1.3 | 17.74 (8) |
| Daphne bhalve Buch.Ham. exd. Don. | 20 ± 1.3 | 16.92 (10) |
| Daphne shillong Banerjee | 100 ± 3.3 | 45.92 (1) |
| Eurya japonica Thumb. | 50 ± 2.2 | 30.93 (4) |
| Lindera pulcherrima Benth. | 90 ± 4.8 | 33.58 (3) |
| Mahonia pyenophylla (Fedde) Takeda | 40 ± 2.8 | 18.62 (7) |
| Symplocus chinensis | 70 ± 2.6 | 30.13 (5) |
| Viburnum foetidum Wall. | 30 ± 2.1 | 16.29 (11) |
| Viburnum sinensis Wall. | 50 ± 2.3 | 25.85 (6) |

Table 3.1. (Contd.)

| Species | Density | IVI |
|---|---|---|
| **Ground vegetation** (density x $10^3$) | | |
| Arundinella khasiana Nees. | 6 ± 0.3 | 15.06 |
| Brunella vulgaris Linn. | 4 ± 0.2 | 11.49 |
| Commelina sp. | 16 ± 0.8 | 14.50 |
| Cyanotis cristata Linn. | 4 ± 0.3 | 5.20 |
| Cyperus rotundus Linn. | 7 ± 0.2 | 18.22 |
| Dioscoria alata Linn. | 8 ± 0.3 | 14.14 |
| Drymeria cordeata Willd. | 21 ± 0.7 | 21.25 |
| Geranium sp. | 5 ± 0.3 | 8.32 |
| Gleichenia longissima Bl. | 45 ± 2.3 | 25.83 |
| Hypocharis radicata Linn. | 15 ± 0.7 | 15.39 |
| Lycopodium clavatum | 11 ± 0.7 | 13.57 |
| Oxalis crinata | 25 ± 1.3 | 17.71 |
| Plantago major Linn. | 36 ± 1.7 | 25.45 |
| Polygonum sp. | 6 ± 0.3 | 7.94 |
| Potentilla blanda | 7 ± 0.5 | 17.73 |
| Ranunculus diffusus DC. | 12 ± 0.5 | 15.15 |
| Rubia cordifolia Linn. | 8 ± 0.5 | 11.93 |
| Rubus sp. | 9 ± 0.6 | 9.82 |
| Selaginella sp. | 29 ± 1.8 | 18.74 |

S. khasiana and M. esculenta. Besides these species, trees of Q. griffithii, Q. glauca and M. insignis were also present in this layer. The sub-canopy layer was composed of Exbucklandia populnea, Prunus undulata and R. arboreum. The shrub layer was dominated by D. shillong. The ground vegetation was mainly composed of herbaceous species and some pteridophytes. The seedlings and saplings of Q. dealbata, Q. griffithii and S. khasiana were abundant on the forest floor (Table 3.2). Seedlings of Taxus baccata, the only conifer in the forest, were also found in large numbers.

**Tree phenology**

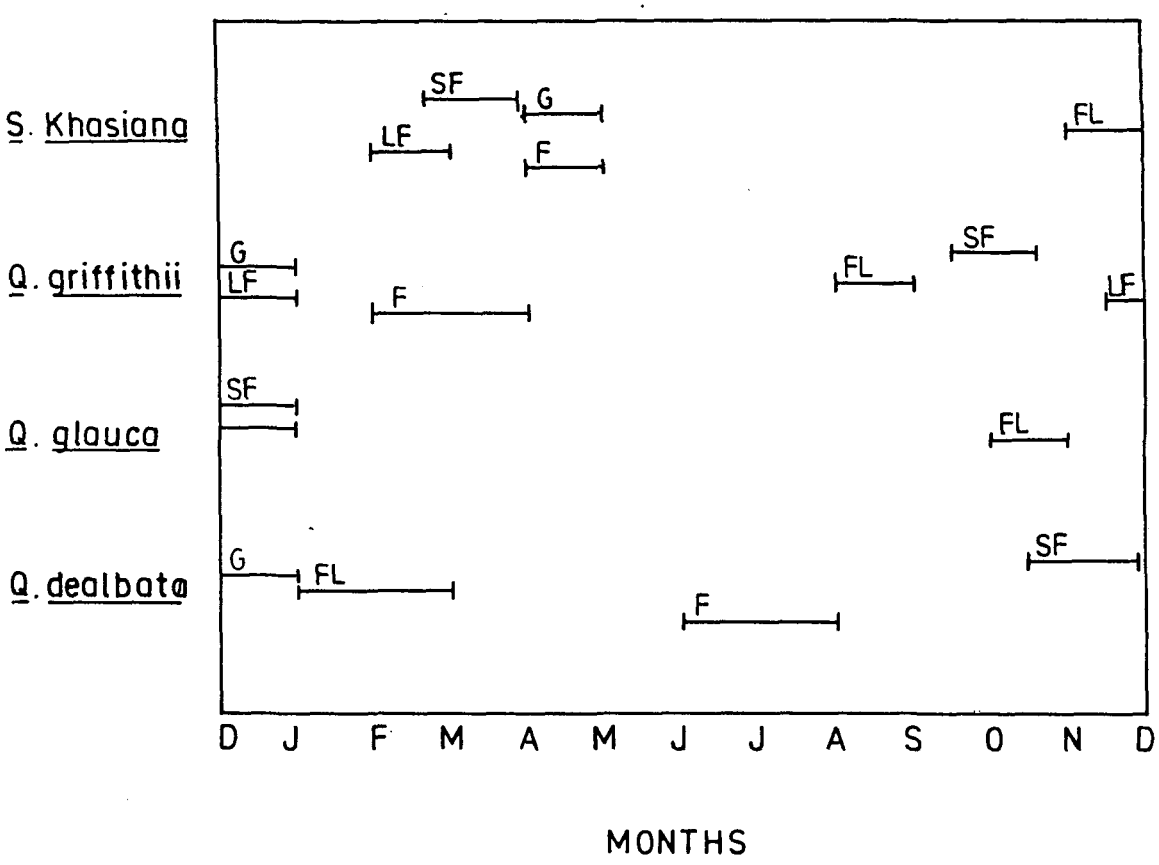
The phenological behaviour of Q. dealbata, Q. glauca, Q. griffithii and S. khasiana, the four dominant tree species of the forest, has been depicted in Fig.3.3. The period of seed fall in the three oak species ranged from mid September to mid December. In case of S. khasiana the seed fall occured during February and March. The seeds of the Quercus spp. germinated during December and January, whereas germination in S. khasiana took place between March to May. The three Quercus species differed in the flowering time. Q. dealbata flowered during January to March, Q. griffithii between February to April and Q. glauca in October. Trees of S. khasiana flowered in November and December. Out of the four tree species studied, Q. dealbata and

Table 3.2. Density of tree seedlings (Plants $ha^{-1}x10^3$ ± S.E.) and saplings (Plants $ha^{-1}$ ± S.E.) during peak growth period (August-September, 1988) in the Mawphlang forest.

| Species | Seedling | Sapling |
|---|---|---|
| *Castonopsis kurzii* | - | 20 ± 2.0 |
| *Exbucklandia populnea* | - | 20 ± 2.0 |
| *Prunus undulata* | - | 30 ± 2.1 |
| *Quercus dealbata* | 32 ± 1.12 | 40 ± 2.2 |
| *Quercus griffithii* | 12 ± 0.8 | 60 ± 3.4 |
| *Rhododendron arboreum* | 4 ± 0.22 | - |
| *Schima khasiana* | 9 ± 0.69 | 40 ± 3.1 |
| *Taxus baccata* | 23 ± 1.42 | - |

Dashes indicate species absence

Fig.3.3. Phenology of dominant tree species in the Mawphlang forest (Seedfall-SF; Germination-G; Flowering -FL; Leaffall-LF; Flushing-F).


S. Khasiana
Q. griffithii
Q. glauca
Q. dealbata
SF
G
LF
F
FL
SF
G
LF
F
FL
LF
SF
FL
G
FL
F
SF
D J F M A M J J A S O N D
MONTHS

Q. glauca are evergreen. Q. griffithii is a deciduous species showing complete leaf fall during mid November to January. S. khasiana is a semi-deciduous species, which partially sheds its leaves during February. In Q. griffithii the new flush of leaves was observed between February to April, while flushing in S. khasiana occured before leaf fall, during November to mid December. Q. dealbata showed leaf flush during June to August, and Q. glauca trees flushed during October and November. A more detailed account of foliage dynamics of these species has been discussed in Chapter 7.

**Species diversity and spatial distribution**

Table 3.3 shows the species diversity and spatial distribution pattern of trees, shrubs and herbs in the forest. Species diversity of the forest is high for all the three components as compared to the disturbed stand of the forest (Rao et al 1990). In terms of species richness, the subtropical forest at Mawphlang having a total of 43 species, may be considered relatively species poor as compared to other tropical forests of the world (Brokaw 1985, Whitmore 1972, Foster and Brokaw 1982). However, with respect to species composition and diversity this forest is comparable to the Lucidophyll forest or East Asian Evergreen Oak Forests of the Far East (Kira 1977, 1978, 1991).

Table 3.3.Pielou's evenness index (e) and spatial distribution pattern of trees, shrubs and herbs in the Mawphlang forest.

| Vegetation component | Species evenness index | Distribution (%) | | |
|---|---|---|---|---|
| | | Regular | Random | Contagious |
| Trees | 0.98 | 38 | 54 | 8 |
| Shrubs | 0.97 | - | 64 | 56 |
| Herbs | 1.02 | - | - | 100 |

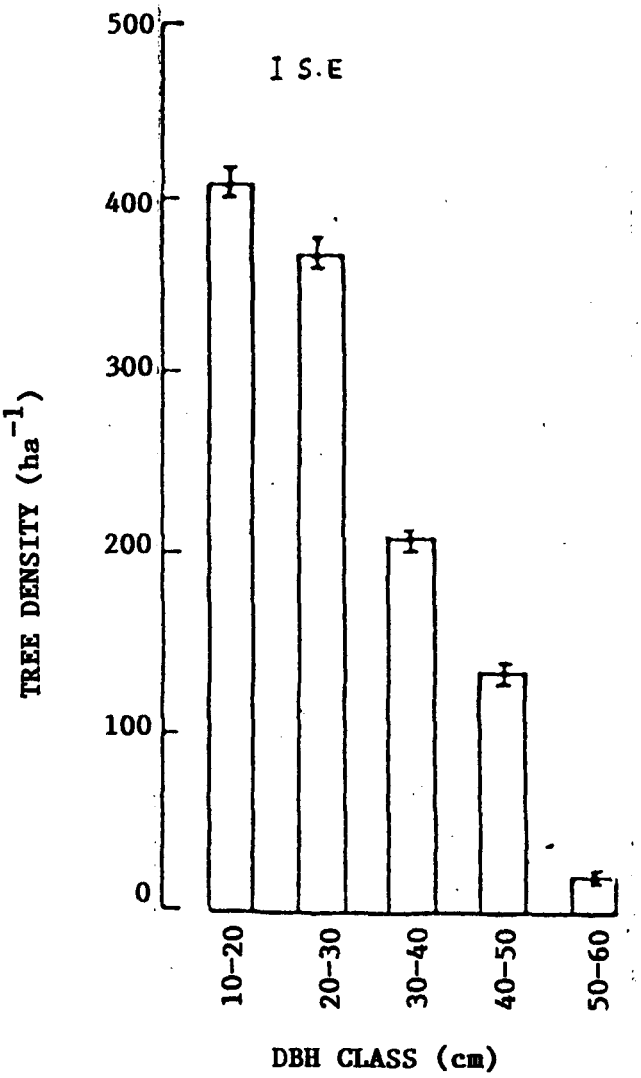
The spatial distribution pattern as depicted by the poisson statistic and Whitford's A/F ratio indicates that 54% tree species were randomly distributed, 38% were regularly distributed and 8% were contagiously distributed in the forest. None of the shrub species showed regular distribution. They were either randomly or contagiously distributed. All the herb species showed contagious or patchy distribution pattern which was strongly related to the canopy gaps.

**Density-diameter distribution of tree species**

Density-diameter distribution of trees has been often used to represent the population structure of forests (Saxena et al 1984, Khan et al 1987, Newton & Smith 1988). Configuration and slope of the curves have been correlated with the age structure of stands, successional status of forests (Goff & West 1975, Saxena et al 1984) and degree of tolerance to shade (UNESCO/UNEP/FAO 1978). In the Mawphlang forest tree density was high in lower dbh classes and low in higher dbh classes (Fig.3.4) and the forest showed an overall straight line relationship between density and diameter. The negative exponential curve obtained for the forest is similar to the findings of Schmeiz and Lindsey (1965) for uneven aged mixed stands of old growth forests in Indiana.

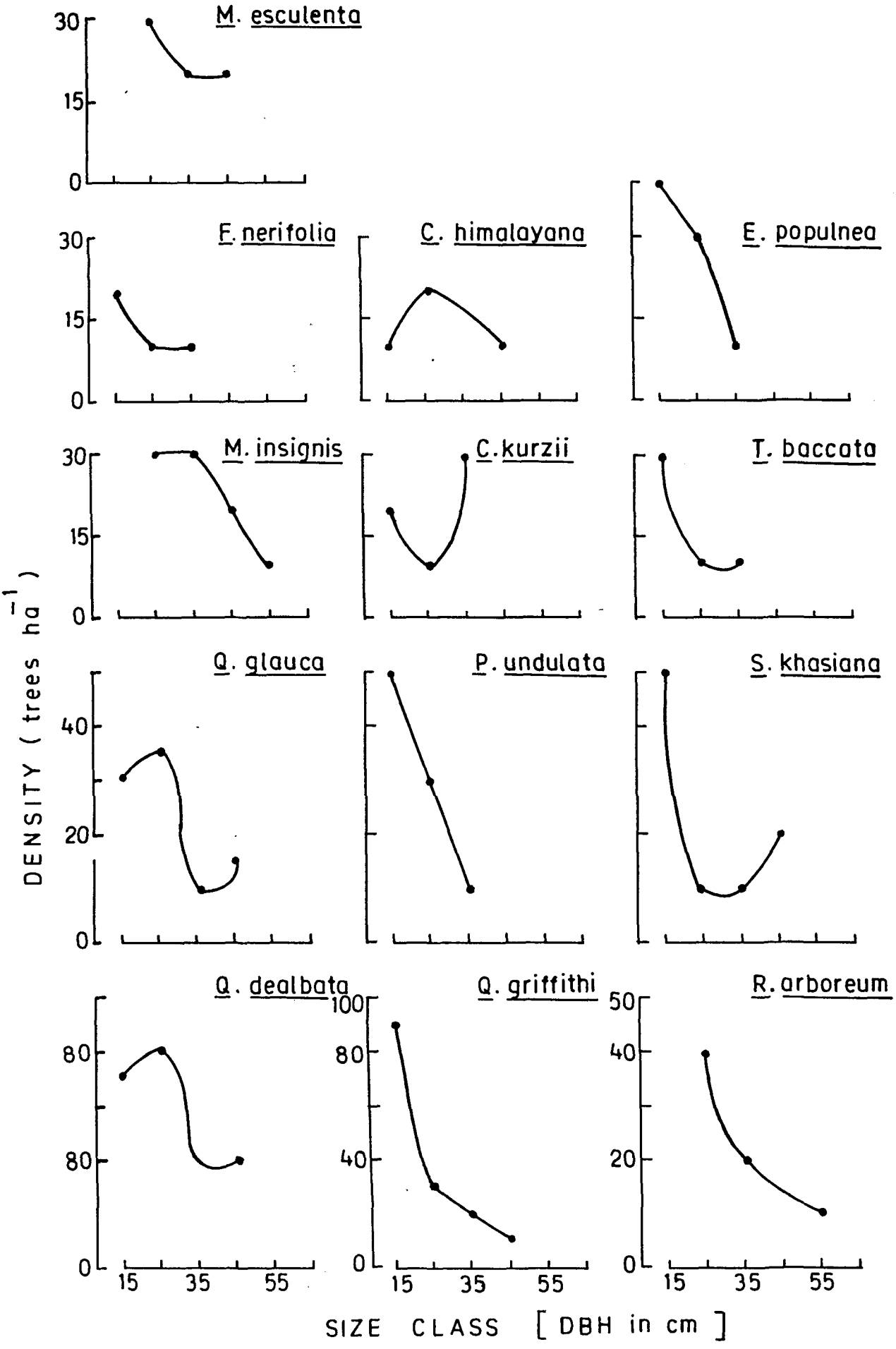
The density-diameter distribution in the population of

Fig.3.4. Density-diameter distribution of trees in the Mawphlang forest.


500
400
300
200
100
0
I S.E
TREE DENSITY (ha$^{-1}$)
10-20
20-30
30-40
40-50
50-60
DBH CLASS (cm)

individual species is shown in Fig 3.5. It indicates a marked variation in the shape of curves for different species. Q. dealbata and Q. glauca showed a rotated sigmoid curve with a plateau near the intermediate diameter region. R. arboreum, Q. griffithii, M. esculenta, S. khasiana, T. baccata and F. nerifolia showed reverse J-shaped curves, while M. insignis showed a bimodal mound type distribution. C. kurzii showed a J-shaped curve (peak being at intermediate diameter class) and Corylopsis himalayana showed a normal distribution. P. undulata and E. populnea had a typical mixed stand character of negative exponential type (Schmeiz and Lindsey 1965). A normal distribution curve shows preponderance of individuals in the intermediate girth classes. According to Benton and Werner (1977) the population is on the way to extinction if such a trend continues. Similarly a plateau in a rotated sigmoid curve can be explained on the basis of lower mortality rate (Saxena et al 1984) across the larger diameter classes as interpretted by Wet et al (1981). Occurence of reverse J-shaped curves in shade intolerant pioneer species such as S. khasiana and M. esculenta indicates predominance of lower diameter classes, which may be attributed to lower mortality in these classes and stunted growth due to dense overhead canopy of other species. Occurence of bimodal mound shaped curve in M. insignis appears to be species specific, while the J-shaped curve represents the typical behaviour of species in a climax forest.

Fig.3.5. Density-diameter distribution curves of different tree species in the Mawphlang forest.


M. esculenta
F. nerifolia
C. himalayana
E. populnea
M. insignis
C. kurzii
T. baccata
Q. glauca
P. undulata
S. khasiana
Q. dealbata
Q. griffithi
R. arboreum
DENSITY ( trees ha$^{-1}$ )
SIZE CLASS [ DBH in cm ]

# 4 TREEFALL GAPS

Forests have been considered as floristic mosaics of different ages, the structure and composition of which are determined by endogenous disturbances (White 1979, Pickett and White 1985, Martinez-Ramos et al. 1989). These disturbances result in a discontinuity in the forest canopy and create a spatial heterogeneity on the forest floor, providing a variety of microsites. Such a microsite mosaic could be important in maintaining species population in a forest community. In closed canopied forests small scale disturbances such as tree falls create 'light gaps' and initiate a chain of events known as "gap phase regeneration" which result in the replacement of previously existing trees by new ones (Whitmore 1975, Brokaw 1985a). Tree replacement in canopy gaps are the only means by which most tree species maintain themselves in a climax forest (Hubbell and Foster 1986) and can account for the existing composition of the forest.

Structural complexities make a gap difficult to define, as falling trees do not create clearly delimiting holes in the forest canopy. Oldeman (1978) visualised a gap as a dumbbell shaped "Chablis" - a French word which means "the fall of a tree, the resulting damage, and the fallen tree itself". In nature an ideal dumbbell shaped gap is infrequent and a wide range of variability in the shape of gaps is often encountered. Most workers have defined a gap as an area opened by tree or branch falls where the plants are not more than 2-3 m in height (Brokaw 1982a, Lawton and Putz 1988).

The importance of frequency and size of treefall gaps on the forest composition has been emphasized by many workers (Runkle 1982, Brokaw 1987). The nature of gap creation (Runkle 1985, Nakashizuka and Numata 1982) and the microenvironmental heterogeneity within the gaps (Putz 1983, Beatty 1984, Lawton and Putz 1988) are also considered important characteristics of treefall gaps which influence growth and establishment of tree species.

This chapter describes the creation of gaps, microsite heterogeneity therein and other physical attributes of treefall gaps in the subtropical broadleaved forest at Mawphlang. It also discusses how microenvironmental factors such as photon flux density, relative humidity, air temperature, soil moisture and litter depth changes with the creation of gaps in the forest.

## METHODS

The forest was surveyed in August, 1988 and an experimental area of about 50 ha was demarcated for intensive study of treefall gaps (Fig.4.1). A gap was considered as an "opening in the forest extending down through all foliage levels to an average height of 2 m above ground (Brokaw 1982a) (Plate 4.1). All the gaps larger than 20 $m^2$, originating from either single or multiple tree falls or branch falls were identified. Gap area was estimated by mapping the gaps to the scale. In each gap the distance from the gap centre to the gap margin was measured at 45° intervals around the gap. The approximate gap margins were then sketched onto a scaled drawing. Based on these drawings the gaps were then grouped into 5 categories depending on their shape. The area of the gaps of different shapes were then calculated using the following formulae

(a) Elliptical gap:

$$A = \pi ab$$

(b) Trapezoid gap:

$$A = \tfrac{1}{2} (a+b) h$$

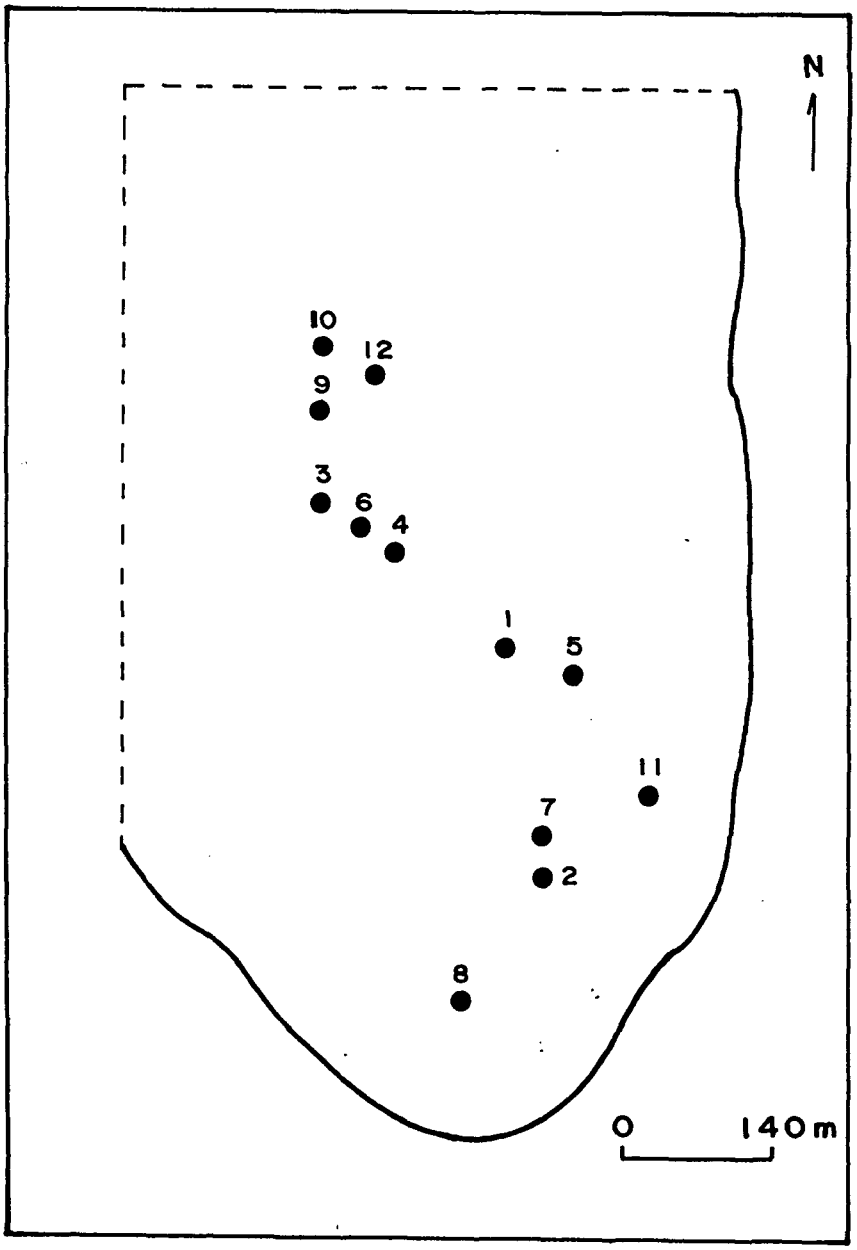
(c) Circular gap:

$$A = \pi r^2$$

(d) Dumbbell shaped gap:

$$A = \tfrac{1}{2} (a+b) h \times 2$$

Fig.4.1. Map of the experimental site in the forest at Mawphlang showing scale drawing of 50 hectare plot and approximate location of treefall gaps. Gaps in the map are numbered in ascending order of their size.


N
10
12
9
3
6
4
1
5
11
7
2
8
0
140m

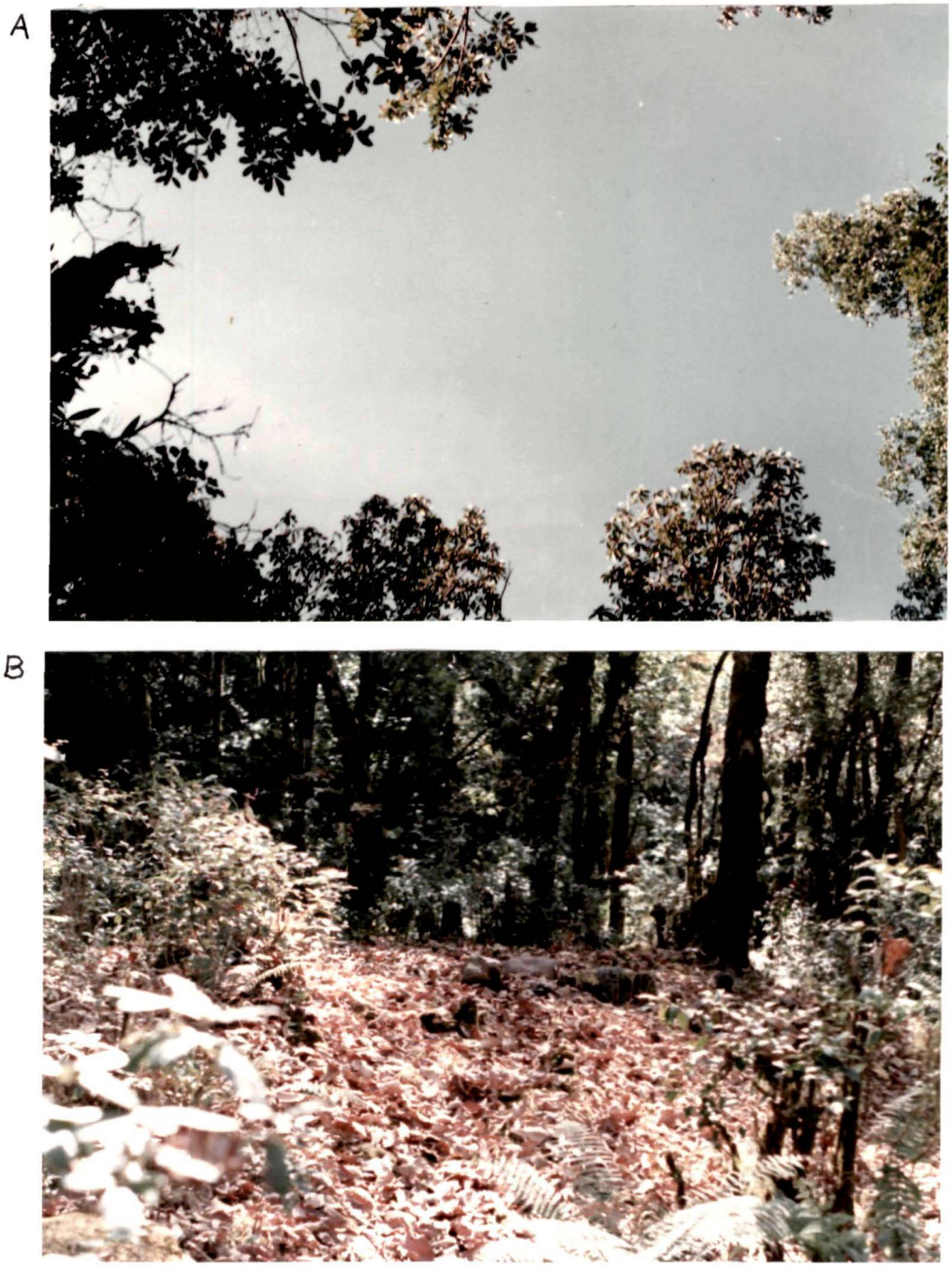



Plate. 4.1. A. Canopy opening in the Mawphlang forest.
B. Forest floor of a treefall gap.

(e) Quadrangular gaps:

$$A = 2\,(l \times b)$$

On the basis of enquiry from the local people, remnants of fallen trees and successional stages of vegetation in the gaps, all gaps in the study area were grouped in three age classes, viz., < 5, 5-10 and >10 years old. Slope angle and orientation of each gap were measured with a clinometer. Other physical characteristics related to post treefall debris were also recorded in each gap.

Since the microclimate in the gap is directly influenced by the surrounding trees and their height, Lorey's mean height ($h_L$) (Lorey 1878 cited by Evert 1964) of different trees was computed as follows:

$$h_L = \frac{\sum_{i=1}^{z} n_i g_i h_i}{\sum_{i=1}^{z} n_i g_i}$$

where, $n_i$ is the number of trees in a diameter class and $g_i$ and $h_i$ are the average basal area and height of the trees, respectively in a diameter class.

The microenvironment of the gaps and the surrounding forest understorey were studied at monthly intervals for a period of two years (August, 1988 - August, 1990). The climatic and edaphic variables were measured in the centre of the

gaps and at five points in the surrounding forest understorey, 5 m away from the gap-edge at 1200 Hrs. The photon flux density was measured at ground level using an infrared $CO_2$ gas analyser (ADC, London) with PAR sensor as an accessory. The relative humidity and air temperature were measured at ground level using a hygrometer and a thermometer respectively. Soil temperature and soil moisture content were measured down to 10 cm depth using a soil thermometer and a digital moisture meter (OSK-2800, Tokyo), respectively. The litter depth was determined by line intercept method (Mueller-Dombois and Ellenberg 1974). The monthly variation in microenvironmental variables in the gaps and understorey was analysed using two-way ANOVA. For the comparison of microenvironment of gaps with understorey, the values of microenvironmental variables of 5 medium sized gaps (107 $m^2$ to 215 $m^2$) were averaged.

## RESULTS

### Physical features of gaps

Heavy rain and wind are the proximate agents that create most gaps in this forest. Of the total gaps opened, 67% were caused by uprooting of trees or snapping off of the bole (Plate 4.2). About 8% of the gap openings could be attributed to man-induced fire and rest to the branch fall or to the death of old trees. Considering the area of individual


Plate. 4.2. Gap creation due to uprooting of trees (A) and snapping off of the bole (B).

gap and its probable mode of origin, it was found that about 58% of the total number of gaps was formed from the falling of a single tree, while 17% were the result of multiple tree falls and 25% could be ascribed to the fall of branches, often strangulated with lianas. On area basis, multiple treefall gaps occupied about 55% of the total gap area (3040 $m^2$) in the forest stand (Table 4.1).

Of the total gaps created by rain and wind, 44% were located on the slopes. Gaps on steep slopes ( $\geq 60°$) was bigger than those on gentle slopes or on level topography (Table 4.1). The dumbbell-shaped gaps were most common (gap nos. 3, 4, 6, 9, 10, 12) followed by elliptical (gap nos. 1, 2) and quadrangular (gap nos. 5, 6) shapes. Circular and trapezium shapes were infrequent. Different microsites like root mats, mounds and pits (sensu Beatty & Stone 1986) were also observed within the gaps (Table 4.1)(Plate 4.3,4.2).

Mean gap size, number of gaps per hectare and percentage gap area (sensu Brokaw 1985a) were 253.5 $m^2$, 0.24 and 0.6, respectively. The proportional distribution of area and number in different gap size classes shows that the less common large gaps covered more total area than the more frequent small ones (Fig. 4.2).

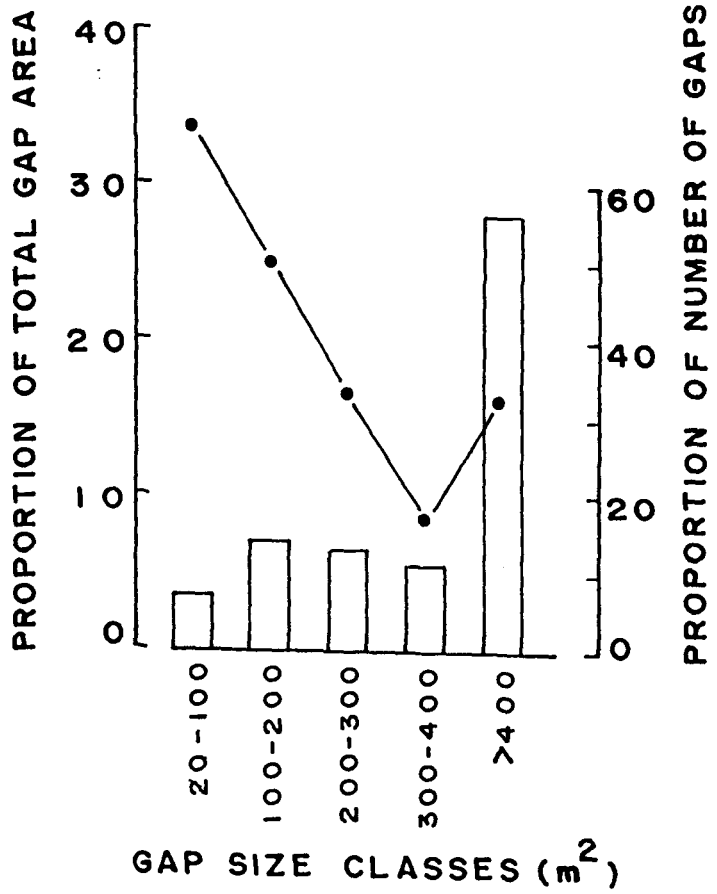
Table 4.1. **Physical features and microsite heterogeneity of the treefall gaps in the sub-tropical broadleaved forest at Mawphlang.**

| Gap Number | Area ($m^2$) | No. of tree falls | Probable cause | Topography | Microsite heterogeneity |
|---|---|---|---|---|---|
| * 1. | 34.3 | Single | Branch fall | Level surface | Branch fall debris |
| † 2. | 36.3 | Single | Tree fall | Level surface | Root mats |
| † 3. | 61.0 | Single | Natural death | Level surface | Dead tree trunk |
| † 4. | 79.5 | Single | Tree fall | Level surface | Pits |
| † 5. | 107.1 | Double | Wind | Level surface | Broken stump and stony surface |
| † 6. | 131.5 | Single | Tree fall | 36° South | Pits |
| † 7. | 157.5 | Single | Wind | Level surface | Broken stump |
| † 8. | 210.0 | Single | Tree fall | 26° South | Root mats and mounds |
| † 9. | 215.0 | Double | Tree fall | 30° South West | Soil mounds |
| * 10. | 335.0 | Single | Fire | Level surface | Burnt tree remnants |
| **11. | 723.5 | Multiple | Natural, wind, rain | Level surface | Decaying log |
| **12. | 950.0 | Multiple | Unknown | 60° West | No tree remnants |

NOTE : Estimated age of gaps: * 3-4 yrs; † 5-10 yrs; ** 10 yrs.

Plate. 4.3. Microsite heterogeneity in gaps showing root mats.

Fig.4.2. Distribution (%) of gap area (line) and number (bar) in five size classes of gaps in the Mawphlang forest.


PROPORTION OF TOTAL GAP AREA
40
30
20
10
0
60
40
20
0
PROPORTION OF NUMBER OF GAPS
20-100
100-200
200-300
300-400
>400
GAP SIZE CLASSES (m²)

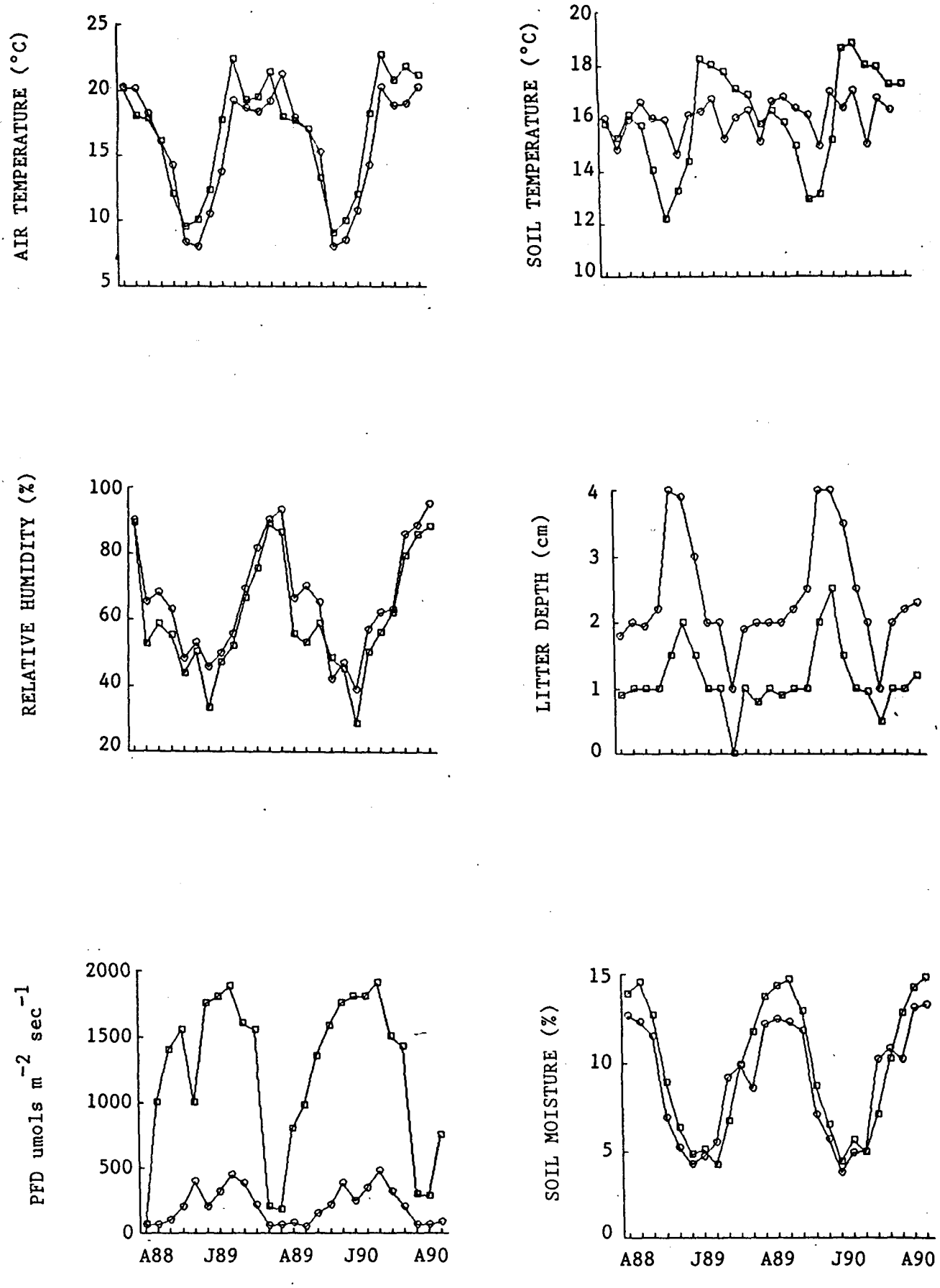
**Microenvironment in gaps vs understorey**

Mean monthly values of climatic and edaphic variables in the gaps and forest understorey shown in Fig.4.3 indicate that photon flux density in the gaps was significantly higher ($P < 0.01$) than the understorey except during the peak rainy season (June-August). Relative humidity and litter depth were significantly higher ($P < 0.01$) in the understorey throughout the year. Soil and air temperatures were higher in the gaps than in the surrounding understorey throughout the year except during winter season. The difference was, however, not significant. Soil moisture did not vary significantly between gaps and understorey although the values were higher in the gaps during a major part of the year (Fig.4.3). Soil moisture showed a significant negative correlation with litter depth in the gaps ($r=-0.53$; $P < 0.05$) and forest understorey ($r=-0.72$; P 0.01). Soil temperature in the gaps was negatively correlated to litter depth ($r=-0.75$ $P < 0.01$) and photon flux density ($r=-0.50$; $P < 0.05$).

## DISCUSSION

Heavy rain often associated with high velocity wind during the wet season is an important factor that creates treefall gaps in different forests (Oldeman 1972, Falinski 1978, Brokaw 1982b). In the Mawphlang forest, heavy precipitation

Fig.4.3. Monthly variation in microenvironmental factors in gaps (o) and forest understorey (□).


AIR TEMPERATURE (°C)
25
20
15
10
5
SOIL TEMPERATURE (°C)
20
18
16
14
12
10
RELATIVE HUMIDITY (%)
100
80
60
40
20
LITTER DEPTH (cm)
4
3
2
1
0
PFD umols m -2 sec -1
2000
1500
1000
500
0
SOIL MOISTURE (%)
15
10
5
0
A88
J89
A89
J90
A90
MONTHS

during rainy season and high wind speed during February seem to create gaps, since human activities were minimum here due to its sacred grove status. The number of gaps per hectare and percent gap area are low compared to other forests (see Brokaw 1985a). Mean gap size in this forest is higher than that reported by Brokaw (1982b) in Barro Colorado Island forest and lower than the French Guiana forest studied by Mutoji-a-Kazadi (1977) (cited by Torquebian 1981). Presence of a few large gaps in the Mawphlang forest is in conformity with the findings of Brokaw (1982a) in BCI forest and Lawton and Putz (1988) in Elfin forest of Monteverde, Costa Rica. However, unlike the BCI forest, proportional area of large gaps was more than the smaller ones in this forest. The biggest gap, having 31% of total gap area, was formed on a steep slope (60°) where the vegetation was relatively sparse and the soil was unstable.

Seasonal variation in all the six microenvironmental variables was similar in both gaps and understorey. As far as the difference between gaps and understorey is concerned it was prominent in photon flux density, litter depth and soil temperature. The overhead canopy caused about 83% reduction in solar radiation on the forest floor in the understorey region. The reduction was minimum (60%) in the peak period of rainy season (June-July) when the sky is overcast with multilayered clouds. Conversely the

difference was maximum (79%) during early spring (February-March) when the sky is clear and some of the tree species in the forest shed their leaves (Fig 3.3). Litter depth was generally higher in the understorey, and the difference between gaps and understorey was maximum during winter (January-February) and the minimum during early rainy season. These periods correspond to the periods of litter fall and decay, respectively. Thickness of litter layer in the gaps was affected by gap size, surrounding vegetation and topography (Tables 4.1, 4.2). Results suggest that soil temperature in gaps was influenced more by litter depth than by solar radiation. During the period of rapid decomposition (April-September) when the amount of litter was reduced considerably, soil temperature was more than rest of the year. Litter depth also influenced soil moisture regime in the gaps and understorey region of the forest.

The seasonal changes in microenvironmental factors along a gap size gradient has been discussed in the ensuing chapter where an attempt has been made to evaluate the effect of gap area on gap microenvironment.

Table 4.2. Species composition and Lorey's mean tree height (m) of the vegetation surrounding different gaps in the Mawphlang forest.

| Gap Number | Surrounding tree species | Lorey's tree height |
|---|---|---|
| 1. | Q. dealbata | 8.54 |
| 2. | M. insignis, Q. dealbata, Q. glauca | 9.40 |
| 3. | Q. dealbata, Q. glauca, S. khasiana | 12.90 |
| 4. | Q. dealbata, Q. glauca | 10.20 |
| 5. | M. insignis, P. undulata, Q. griffithii, S. khasiana | 10.10 |
| 6. | M. insignis, Q. dealbata, S. khasiana, M. esculenta | 9.80 |
| 7. | Q. griffithii | 10.60 |
| 8. | Q. dealbata, S. khasiana | 13.00 |
| 9. | M. insignis, Q. dealbata, Q. glauca | 10.20 |
| 10. | M. insignis, Q. dealbata, S. khasiana | 9.30 |
| 11. | M. insignis, Q. dealbata, T. baccata | 9.30 |
| 12. | C. kurzii, Q. glauca, S. khasiana | 10.60 |

# 5 MICROENVIRONMENT AND SPECIES DIVERSITY IN TREEFALL GAPS

An understanding of canopy tree replacement processes in treefall gaps provides a better insight into the much debated question of whether or not a forest community tends to maintain an equilibrium in its species composition (Hubbell 1984). Treefall gaps with diverse physical features and microenvironmental heterogeneity offer specialized regeneration niches for tree species in close canopied forests. Even within a gap, temporal and spatial differences in light, moisture and temperature regimes and spatial heterogeneity caused by root, bole and crown zones, create a number of potential regeneration microsites. Such heterogeneities have been considered by many workers to be of fundamental importance in the maintenance and promotion of high tree diversity in tropical forest communities (Connell 1978, Denslow 1980). Brokaw (1982b, 1985a, Denslow (1980), Hartshorn (1978, 1980) and Whitmore (1974) have independantly argued that gap size is a critical variable for the recruitment and establishment of different species.

Brokaw (1985b) reported a positive relationship between gap size and colonization of pioneer or shade intolerant tree species in the neotropical forests at Barro Colorado Island (BCI), Panama.

The role of gaps in the maintenance of species diversity in the climax subtropical broadleaved forests is poorly understood. It is also not clear as to what extent the gap disturbance regime and microenvironmental heterogeneity in the gaps are responsible for offering specialized regeneration niches to different plant species in these forests. In this chapter data related to certain important microenvironmental variables such as photon flux density, relative humidity and soil moisture and species diversity ($\alpha$- and $\beta$-diversity) in treefall gaps and understorey region of the Mawphlang forest have been presented. These results are discussed to explain among gaps as well as between gap and understorey variations in species diversity. Seasonal variation in microenvironmental conditions along gap size gradient has also been discussed.

## METHODS

The microenvironmental variables such as photon flux density, relative humidity, air temperature, soil moisture, soil temperature and litter depth were studied at monthly intervals in the gaps and understorey according to the methods described in Chapter 4. These data were used to

study the seasonal variation in microenvironment along a gap size gradient.

Species composition of the gaps and forest understorey was studied in the beginning of the study in August, 1988 and after a period of two years in August, 1990. The total number of tree seedlings (height $\leq$ 20 cm) and shrubby plants was counted and their basal cover was measured in each of the twelve gaps. Density and basal cover of the herbs were determined by laying 2-10 quadrats of 1m x 1m size depending on the size of the gap. In the understorey region surrounding each gap, density and basal cover of tree seedlings, shrubs and herbs were also determined. For this purpose, twelve quadrats, 10m x 10m size for tree seedlings and shrubs and 1m x 1m size for herbs, were laid 5m away from the gap edge.

Species similarity for gaps and understorey was measured by using presence/absence data for herbs, shrubs and tree seedlings according to Sørensen similarity index (Sørensen, 1948)

$$IS_s = \frac{2C}{a + b} \times 100$$

where, a is the number of species present in the gaps, b is the number of species found in the understorey and c is the number of species common to both gaps and understorey.

Species diversity in the gaps and understorey was determined by using Pielou's evenness index (Pielou 1966), taking relative density and basal cover values together as an index of abundance.

Species diversity in the gaps and understorey has been discussed on the basis of $\alpha$- and $\beta$-diversity (Brokaw and Scheiner 1989, Whittaker 1972). $\alpha$-diversity refers to the mean number of species per gap and $\beta$-diversity is the mean similarity among gaps. These indices were also computed for the understorey vegetation adjacent to each gap. $\alpha$-and $\beta$-diversities of tree seedlings and shrubs were calculated on the basis of per sampling plot whose area (100 $m^2$) is close to the minimum gap area (157 $m^2$) which contained 87% of the total species content of all the gaps. For the computation of $\beta$-diversity, gap similarity matrices for herbs, shrubs and tree seedlings were seperately prepared using Spatz's similarity index (Spatz, 1970). In the similarity matrix,

$$\alpha_{ij} = R \times \frac{M_c}{M_i + M_j + M_c} \times 100$$

where, R is the sum of the fractions obtained by the division of smaller abundance values of species common to both i and j gaps/plots by that of the greater and finally dividing the resulting fraction by the total number of

species in the two (i and j) gaps, $M_i$ is the total abundance of all species occuring only in i gap, $M_j$ is the total abundance of all species occuring only in j gap and $M_c$ is the total abundance of all species common to both i and j gaps.

*The seasonal variation in microenvironmental variables* was analysed using two-way ANOVA. The technique of Principal Component Analysis (Poole 1974) was applied to the six microenvironmental factors to obtain Principal Component I and II which together accounted for about 92% of the total variation in the microenvironmental factors among the twelve gaps (Table 5.1). These two variables were used to analyse the variability in species diversity and density of tree seedlings among the gaps. In order to examine the relationship between gap size and species composition, Principal Component Analysis was used to ordinate the gaps by taking total number of individuals of shade tolerant and shade intolerant tree species as the two variables. The combined species co-ordinates in each gap were used to ordinate the gaps.

## RESULTS

### Gap microenvironment

Among the six microenvironmental variables studied, only

Table 5.1. Principal component of microenvironmental factors, tree seedling density and total species diversity in twelve treefall gaps in the sub-tropical broadleaved forest at Mawphlang.

| Gap area ($m^2$) | Principal Component-1 * | Principal Component-2 ** | Tree seedling density ($ha^{-1}$) | Total species diversity(e) |
|---|---|---|---|---|
| 34.3 | - 7.173 | - 1.260 | 2621 | 1.10 |
| 36.3 | - 7.841 | - 0.528 | 1651 | 0.98 |
| 61.0 | - 3.261 | - 0.008 | 1967 | 1.02 |
| 79.5 | - 3.083 | 1.099 | 1761 | 1.40 |
| 107.1 | - 1.415 | 0.953 | 747 | 1.36 |
| 131.5 | 0.570 | 0.685 | 836 | 0.80 |
| 157.5 | 0.025 | 0.381 | 380 | 0.82 |
| 210.0 | - 0.397 | 0.153 | 475 | 0.90 |
| 215.0 | 3.245 | - 0.546 | 140 | 0.80 |
| 335.0 | 4.962 | 0.190 | 538 | 0.70 |
| 723.5 | 7.283 | - 0.299 | 995 | 0.86 |
| 950.0 | 7.084 | - 0.899 | 211 | 0.80 |

* Eigen value = 4.778 ; Accounts for ca 80% of total variation

** Eigen value = 0.690 ; Accounts for ca 12% of total variation

photon flux density, relative humidity and soil moisture varied significantly ($P < 0.01$) among the gaps and the seasons (Fig.5.1). Relative humidity was highest in the rainy season and lowest in the winter season. It did not vary significantly among gaps. Photon flux density increased with increase in gap size in all the four seasons; the increase being most prominent during the winter and least prominent during rainy season. Seasonal variation in soil moisture was similar to relative humidity.

Principal Component I of microenvironmental variables showed a significant positive correlation with gap size ($r = 0.831$; $P < 0.001$). Relationship between gap size (A) and the First Principal Component (Y) of microenvironmental variables depicted in Fig.5.2a yielded the following relationship:

$$Y = 0.014\ A - 3.68\ (r^2=0.69)$$

**Species diversity in gaps and understorey**

Table 5.2 gives an inventory of tree seedlings, shrubs and herbaceous species in gaps and understorey in the forest. All the tree species were common to both gaps and understorey, except for M. esculenta which was exclusive to the gaps. Q. dealbata, S. khasiana and T. baccata were found in most of the gaps. None of the shrub species showed restricted distribution, either to gaps or to the

Fig.5.1. Photon flux density, relative humidity and soil moisture content as a function of gap area in different seasons |Rainy (●); Autumn (△); Winter (◐); Spring (○)|.

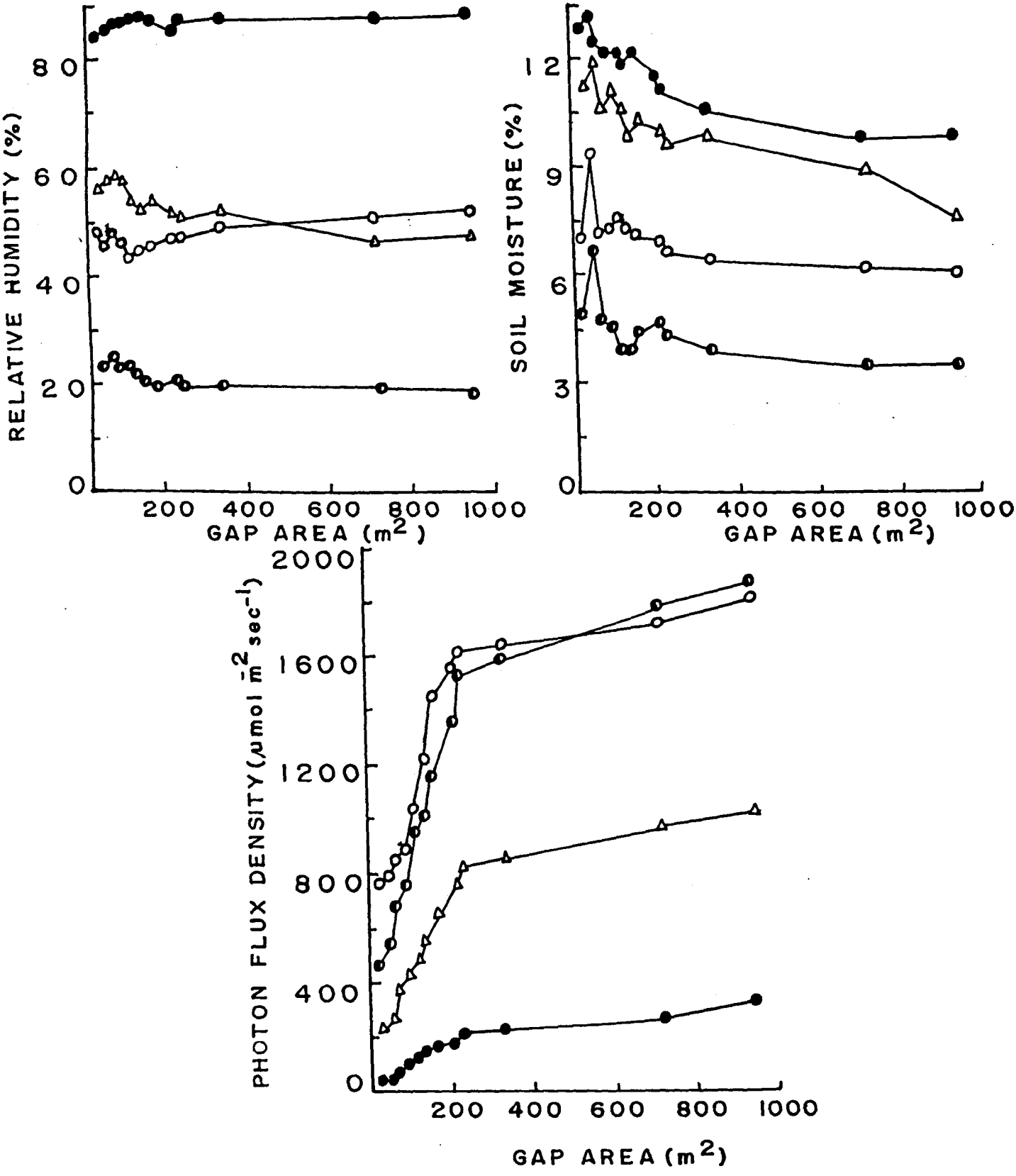

RELATIVE HUMIDITY (%)
0
20
40
60
80
200
400
600
800
1000
GAP AREA (m2)
SOIL MOISTURE (%)
0
3
6
9
12
200
400
600
800
1000
GAP AREA (m2)
PHOTON FLUX DENSITY (μmol m-2 sec-1)
0
400
800
1200
1600
2000
200
400
600
800
1000
GAP AREA (m2)

Fig.5.2. Relationship between (a) gap area and Principal Component-I of microenvironmental factors, (b) gap area and cumulative number of species, and (c) density of tree seedlings and Principal Component-I of microenvironmental factors.

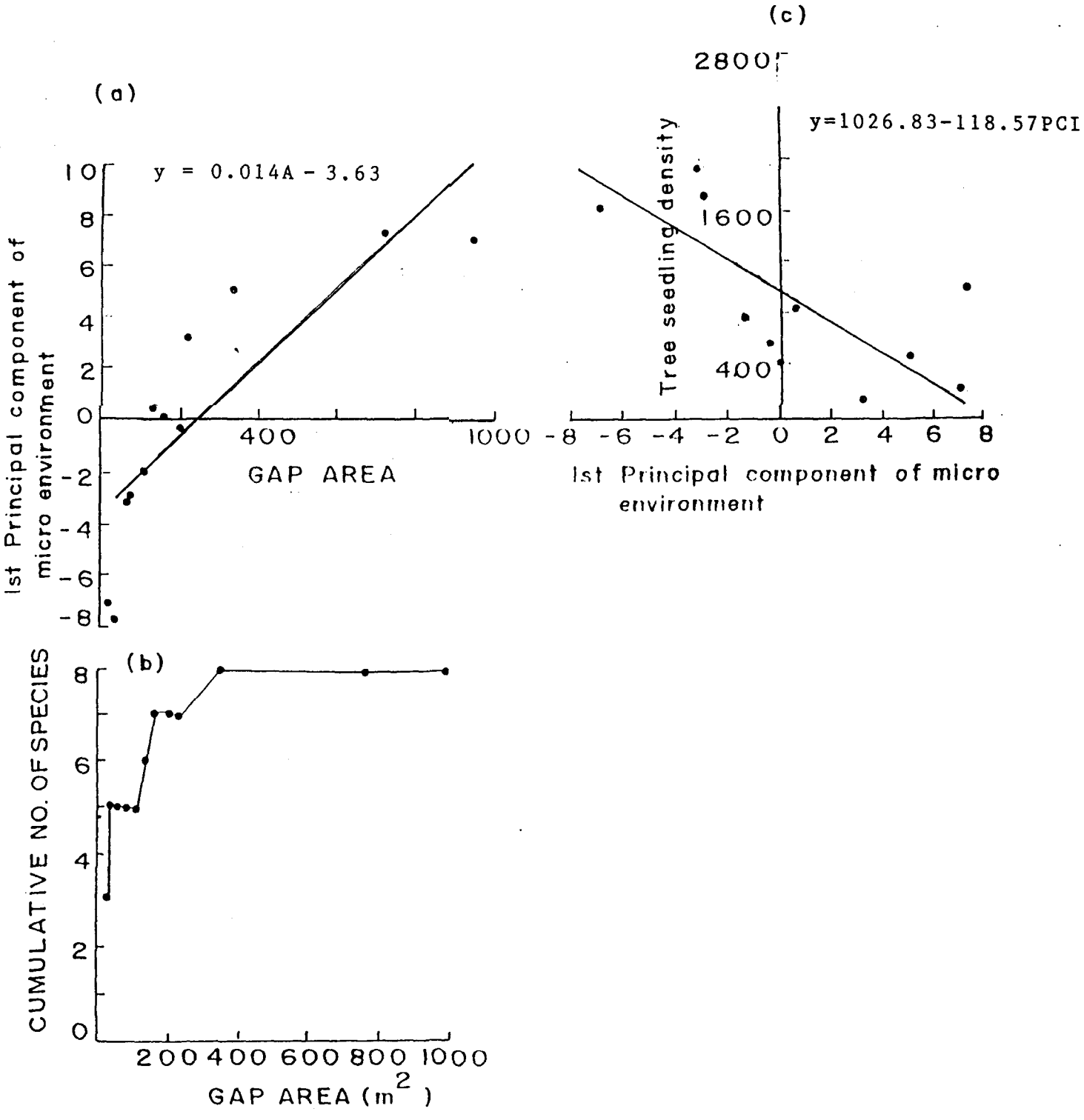

(a)
y = 0.014A - 3.63
1st Principal component of micro environment
GAP AREA
(b)
CUMULATIVE NO. OF SPECIES
GAP AREA (m2)
(c)
y=1026.83-118.57PCI
Tree seedling density
1st Principal component of micro environment

Table 5.2. **Species composition in treefall gaps and forest understorey in the subtropical broadleaved forest at Mawphlang.**

| Species | Gap Number | | | | | | | | | | | | Understorey |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | |
| **TREES** | | | | | | | | | | | | | |
| Castonopsis kurzii (Hance) B. | - | - | - | - | - | - | - | - | + | - | - | - | + |
| Corylopsis himalayana Griff. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Exbucklandia populnea (Griff.) Br. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Ficus nerifolia Sm. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Manglietia insignis (Wall.) Bl. | - | - | - | - | - | + | - | - | + | + | - | + | + |
| Myrica esculenta Buch. Ham. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Prunus undulata Buch. Ham. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Quercus dealbata L. | + | + | - | + | + | + | + | + | - | + | + | + | + |
| Quercus glauca Thunb. | - | - | - | - | - | - | - | + | - | + | - | + | + |
| Quercus griffithii HK. | - | - | - | - | - | - | + | - | - | - | + | - | + |
| Rhododendron arboreum Sm. | + | - | - | - | - | - | - | - | - | - | + | - | + |
| Schima khasiana Dyer. | + | - | - | - | + | + | - | - | + | + | + | - | + |
| Taxus baccata L. | - | + | + | + | - | + | + | - | - | - | + | - | + |
| Terminalia sp. | - | + | - | - | - | - | - | + | - | - | - | - | + |
| **SHRUBS** | | | | | | | | | | | | | |
| Ardisia crispa (Thumb.) DC. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Baliospermum micrantha Muell Arg. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Camellia caduca C.B. Cl. | + | - | - | - | - | + | - | - | - | + | + | + | + |

Table 5.2. (Contd.)

| Species | Gap Number | | | | | | | | | | | | Understorey |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | |
| Daphne shillong Banerjee | - | + | - | - | - | - | + | + | + | - | + | + | + |
| Eurya japonica Thumb. | - | - | + | - | + | - | - | - | - | + | + | + | + |
| Lindera pulcherrima Benth. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Manoma pygnophylla (Fedde) Takeda | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Symplocus chinensis | - | - | - | - | - | - | - | + | - | - | + | + | + |
| Viburnum foetidum Wall. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Viburnum sinensis Wall. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| **HERBS** | | | | | | | | | | | | | |
| Arundinella khasiana Nees. | + | + | + | + | + | + | + | + | + | + | + | + | - |
| Brunella vulgaris Linn. | + | - | - | + | + | + | + | + | + | + | + | + | + |
| Commelina sp. | + | + | + | + | + | + | - | + | + | - | + | + | - |
| Cyanotis cristata Linn. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Cyperus rotundus Linn. | + | + | + | + | + | + | + | + | + | + | - | + | - |
| Dioscoria alata Linn. | + | + | + | + | + | + | + | + | + | + | + | + | - |
| Drymaria cordata Willd. | + | + | + | + | - | + | - | + | - | - | + | + | - |
| Geranium sp. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Gliechenia longissima Bl. | - | + | + | + | + | + | + | + | - | + | - | - | - |
| Hypocharis radicata Linn. | + | - | + | - | + | - | + | + | + | - | + | + | + |
| Lycopodium clavatum | + | + | - | + | + | + | - | + | + | - | + | + | + |
| Oxalis crinata | + | + | + | + | + | - | + | - | + | - | + | + | + |
| Plantago major Linn. | + | + | + | + | + | - | + | - | + | + | + | + | - |
| Polygonum sp. | - | - | + | - | + | - | + | - | + | - | + | + | + |
| Potentilla blanda | + | - | - | - | + | - | - | - | - | - | + | + | - |

**Table 5.2. (Contd.)**

| Species | Gap Number | | | | | | | | | | | | Under-storey |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | |
| Rannunculus diffusus Dc. | - | + | - | + | - | - | - | - | - | + | + | + | + |
| Rubia cordifolia Linn. | + | - | + | + | - | + | + | + | - | + | - | + | - |
| Rubus sp. | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Selaginella sp. | - | + | + | - | + | - | + | - | + | - | + | + | - |

(+) Presence, (-) Absence

forest understorey. Many of the herbaceous species like A. khasiana, B. vulgaris and D. cordata were present only in the gaps and others like C. cristata, Geranium sp. and Rubus sp. were confined exclusively to the understorey region.

All the three components i.e. trees, shrubs and herbs showed high diversity in the understorey. The composition of tree species was very much similar ($Is_s$ -93%) between gaps and understorey. The composition of shrubs and herb components was less similar ($Is_s$ $\leq$ 54%) between the two habitats in the forest (Table 5.3).

In the gaps, $\alpha$-diversity was highest for the herbs and lowest for the shrubs (Table 5.4). All the three components showed an increase in $\alpha$-diversity in August, 1990 as compared to the values in August, 1988. Shrubs having the highest $\beta$-diversity value, showed greater similarity among the gaps than the other two components. $\beta$-diversity for tree seedlings was the least among the gaps. After a period of two years, $\beta$-diversity of herbs and tree seedlings increased; increase was maximum for the tree seedlings. $\alpha$-diversity for the shrubs, however, declined during the same period (Table 5.4).

In the understorey, $\alpha$-diversity was highest for the shrubs and lowest for the herbs. Here the tree species showed the

Table 5.3. Species diversity (e) and total stem density (plants $ha^{-1}$) in treefall gaps and forest understorey and index of species similarity between the two habitats in the Mawphlang forest.

| Vegetation Components | Sampling time | Gaps | | Understorey | | Similarity index(%) |
|---|---|---|---|---|---|---|
| | | Species Diversity | Density | Species Diversity | Density | |
| Herbs* | August 1988 | 0.90 | 1649 ± 0.5 | 1.00 | 17.1 ± 0.3 | 53.8 |
| | August 1990 | 0.89 | 1118 ± 0.9 | 0.96 | 55.85 ± 0.6 | |
| Shrubs | August 1988 | 0.90 | 151 ± 4.1 | 1.00 | 560 ± 7.9 | 53.3 |
| | August 1990 | 0.91 | 350 ± 7.4 | 0.93 | 510 ± 9.2 | |
| Tree seedlings | August 1988 | 0.80 | 1056 ± 21.7 | 0.86 | 2160 ± 346.1 | 93.3 |
| | August 1990 | 0.92 | 1266 ± 32.8 | 0.94 | 3408 ± 312.2 | |

* Density values are x $10^3$ ; ± S.E.

Table 5.4. $\alpha$ and $\beta$ diversities of different vegetation components in the gaps and adjacent forest understorey.

| Vegetation components | Sampling time | $\alpha$-diversity | | $\beta$-diversity | |
|---|---|---|---|---|---|
| | | Gaps | Understorey | Gaps | Understorey |
| Herbs | August 1988 | 11.5 | 1.6 | 16.7 | 2.5 |
| | August 1990 | 12.9 | 2.1 | 17.6 | 2.7 |
| Shrubs | August 1988 | 1.6 | 3.2 | 17.8 | 3.8 |
| | August 1990 | 1.8 | 3.7 | 13.2 | 5.3 |
| Tree seedlings | August 1988 | 2.9 | 1.8 | 10.2 | 12.5 |
| | August 1990 | 3.3 | 2.6 | 10.0 | 10.4 |

highest $\alpha$-diversity followed by herbs and shrubs. All the three components showed an increase in $\alpha$- and $\beta$-diversities in August, 1990. The only exception was the $\alpha$-diversity of the tree seedlings which showed a decline after a period of two years.

Total species diversity was negatively correlated with Principal Component I of the microenvironmental factors ($r = -0.57$; $P<0.05$). Total species diversity (Y) in gaps yielded the following relationship with gap area (A) and the two Principal Components of microenvironment (PC I and PC II):

$$Y = 0.81 + 0.0006\ A - 0.05\ PC\ I + 0.20\ PC\ II\ (r^2=0.60)$$

**Density and importance value of tree seedlings along the gap size gradient**

Analysis of similarity matrix based on Spatz's index showed variable trends (Table 5.5a & b). In August, 1988 similarity between gap nos. 3 and 9 was zero and they were dissimilar to most of the gaps in the forest stand. However, in August. 1990 gap nos. 5 and 9 were dissimilar to most of the gaps. Gap nos 2 and 8 showed maximum (51%) similarity in August, 1988, while gap nos. 2 and 4 were found to be most similar (55%) in August, 1990. In both the years similarity of tree seedlings among the gaps was lower than

Table 5.5. Similarity matrix for tree seedlings among twelve treefall gaps (a) in August, 1988 and (b) in August, 1990.

(a)

| Gap number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | 15.4 | 0 | 2.1 | 24.7 | 8.9 | 8.0 | 19.3 | 0 | 6.8 | 14.7 | 5.6 |
| 2 | 15.4 | | 1.7 | 9.2 | 11.1 | 15.3 | 29.4 | 50.5 | 0 | 2.4 | 9.8 | 5.6 |
| 3 | 0 | 1.7 | | 39.9 | 0 | 1.0 | 1.7 | 0 | 0 | 0 | 2.9 | 0 |
| 4 | 2.1 | 9.2 | 39.9 | | 2.9 | 9.3 | 10.5 | 2.8 | 0 | 2.3 | 11.0 | 2.4 |
| 5 | 24.7 | 11.1 | 0 | 2.9 | | 24.2 | 11.8 | 14.8 | 0 | 18.1 | 15.2 | 8.1 |
| 6 | 8.9 | 15.3 | 1.0 | 9.3 | 24.2 | | 14.4 | 4.5 | 4.7 | 43.9 | 23.7 | 23.3 |
| 7 | 8.0 | 29.4 | 1.7 | 10.5 | 11.8 | 14.4 | | 10.0 | 0 | 2.7 | 28.2 | 6.7 |
| 8 | 19.3 | 50.5 | 0 | 2.8 | 14.8 | 4.5 | 10.0 | | 0 | 2.9 | 3.8 | 7.0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 4.7 | 0 | 0 | | 6.2 | 0 | 7.9 |
| 10 | 6.8 | 2.4 | 0 | 2.3 | 18.1 | 43.9 | 2.7 | 2.9 | 6.2 | | 10.1 | 46.2 |
| 11 | 14.7 | 9.8 | 2.9 | 11.0 | 15.2 | 23.7 | 28.2 | 3.8 | 0 | 10.1 | | 4.2 |
| 12 | 5.6 | 5.6 | 0 | 2.4 | 8.1 | 23.3 | 6.7 | 7.0 | 7.9 | 46.2 | 4.2 | |
| Mean Similarity | 9.6 | 13.7 | 4.3 | 8.4 | 11.9 | 15.7 | 11.2 | 10.5 | 1.7 | 12.9 | 11.2 | 10.7 |

Contd.

(b)

| Gap number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | - | 6.80 | 0 | 11.46 | 3.32 | 2.35 | 9.79 | 10.01 | 0 | 33.13 | 12.75 | 30.75 |
| 2 | 6.80 | - | 12.54 | 58.56 | 6.59 | 10.56 | 12.18 | 26.12 | 0 | 16.44 | 10.46 | 23.13 |
| 3 | 0 | 2.54 | - | 5.61 | 0 | 16.78 | 19.88 | 0 | 32.04 | 11.30 | 14.53 | 2.87 |
| 4 | 11.46 | 58.56 | 5.61 | - | 8.26 | 15.15 | 5.25 | 18.67 | 0 | 13.51 | 13.92 | 24.11 |
| 5 | 3.32 | 6.59 | 0 | 8.26 | - | 5.25 | 0 | 6.92 | 0 | 7.85 | 0 | 14.71 |
| 6 | 2.35 | 10.56 | 16.78 | 15.15 | 5.25 | - | 10.25 | 7.83 | 5.13 | 29.72 | 36.67 | 17.91 |
| 7 | 9.79 | 12.18 | 19.88 | 5.25 | 0 | 10.25 | - | 17.46 | 0 | 11.79 | 30.41 | 6.92 |
| 8 | 10.01 | 26.12 | 0 | 18.67 | 6.92 | 7.83 | 17.46 | - | 0 | 9.44 | 6.92 | 17.23 |
| 9 | 0 | 0 | 32.04 | 0 | 0 | 5.13 | 0 | 0 | - | 12.92 | 0 | 3.62 |
| 10 | 33.13 | 16.44 | 11.30 | 13.51 | 7.85 | 29.72 | 11.79 | 9.44 | 12.92 | - | 9.95 | 37.19 |
| 11 | 12.75 | 10.46 | 14.53 | 13.92 | 0 | 36.67 | 30.41 | 6.92 | 0 | 9.95 | - | 10.61 |
| 12 | 30.75 | 23.13 | 2.87 | 24.11 | 14.71 | 17.91 | 6.97 | 17.23 | 3.62 | 37.19 | 10.61 | - |
| Mean Similarity | 11.67 | 16.98 | 10.50 | 14.95 | 4.81 | 13.42 | 11.27 | 10.96 | 4.88 | 17.57 | 13.29 | 17.19 |

between their respective adjacent understories (Table 5.6a & b).

The cummulative number of species increased upto a gap size of 335 $m^2$ and then remained constant (Fig.5.2b).

Density of tree seedlings (Y) in gaps was negatively correlated with the first Principal Component of the Microenvironment ($r= -0.748$; $P < 0.01$) and showed the following relationship (Fig.5.2c):

$$Y = 1026.8 - 118.6 \text{ PC I} \quad (r^2=0.64)$$

Dominance was more or less equatably distributed among the three species in the larger gaps than in the smaller gaps where 70-80% dominance was concentrated in one species (Fig.5.3). The shade tolerant Quercus spp., in particular, Q. dealbata dominated the smaller gaps except for gap no 5 where T. baccata was dominant. The larger gaps were dominated by shade intolerant pioneers like M. esculenta and S. khasiana which showed low dominance or complete absence in most of the smaller gaps. Q. dealbata, however, was found to be dominant in some of the larger gaps as well (Fig.5.3). Tree species richness in the larger gaps with level topography (gap nos. 10 and 11) was higher than the smaller gaps as well as the largest gap (gap no. 12) situated on the steep slope (Table 4.1).

Table 5.6. **Similarity matrix for tree seedlings in forest understorey (a) in August, 1988 and (b) in August, 1990.**

**(a)**

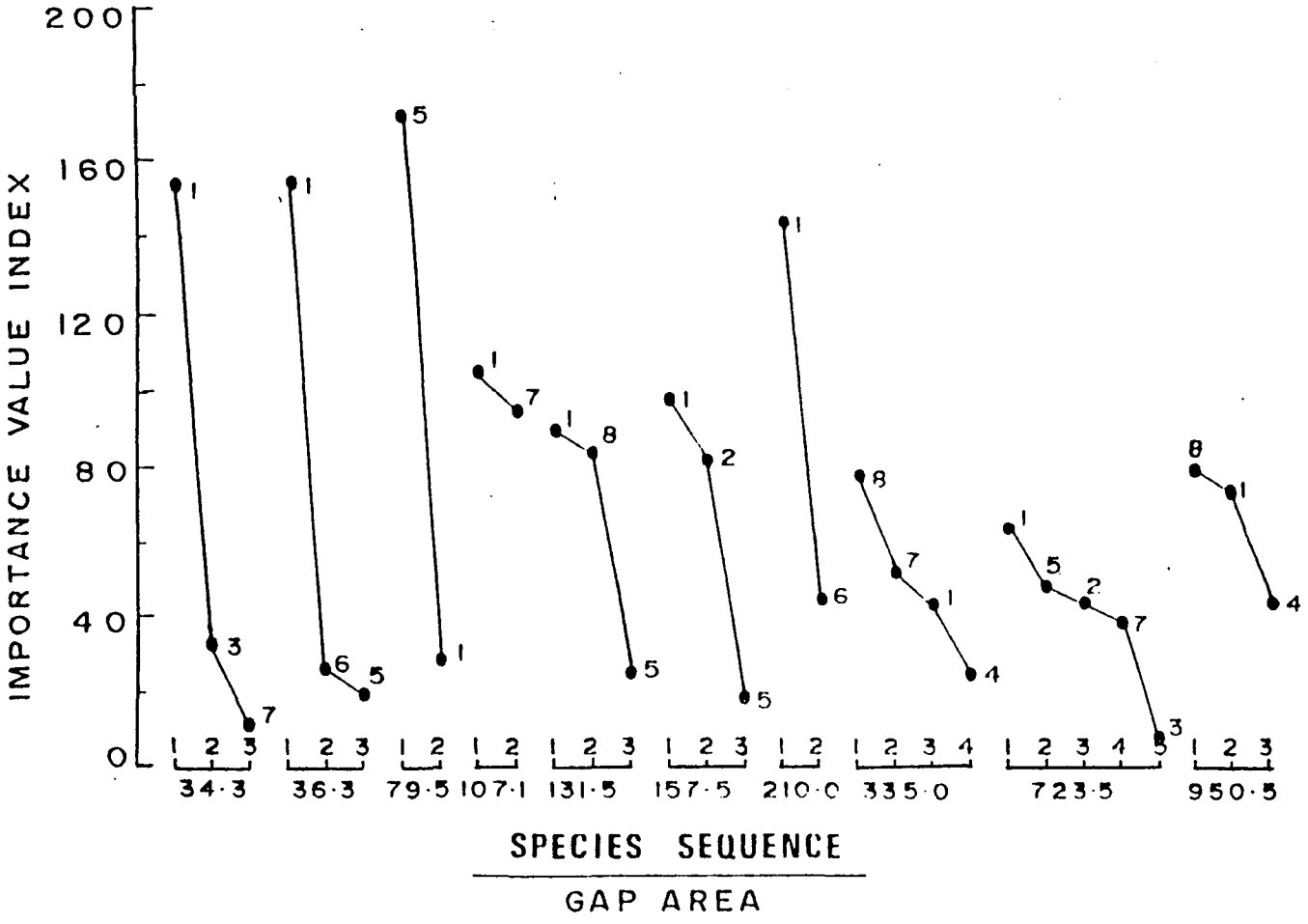
| Gap Number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | 14.5 | 23.5 | 16.7 | 7.0 | 11.7 | 4.8 | 36.2 | 0 | 17.6 | 0 | 24.3 |
| 2 | 14.5 | | 8.7 | 10.1 | 0 | 11.4 | 6.3 | 39.3 | 10.0 | 10.5 | 6.6 | 60.9 |
| 3 | 23.5 | 8.7 | | 18.8 | 0 | 53.7 | 0 | 11.2 | 0.9 | 40.8 | 4.3 | 23.8 |
| 4 | 16.7 | 10.1 | 18.8 | | 4.3 | 36.7 | 1.1 | 8.6 | 1.5 | 15.0 | 0 | 17.0 |
| 5 | 7.0 | 0 | 0 | 4.3 | | 2.3 | 25.0 | 5.5 | 2.8 | 0 | 0 | 0 |
| 6 | 11.7 | 11.4 | 53.7 | 36.7 | 2.3 | | 3.0 | 10.0 | 8.4 | 25.3 | 3.6 | 15.6 |
| 7 | 4.8 | 6.3 | 0 | 1.1 | 25.0 | 3.0 | | 17.8 | 23.5 | 0 | 6.1 | 5.9 |
| 8 | 36.2 | 39.3 | 11.2 | 8.6 | 5.5 | 10.0 | 17.8 | | 1.8 | 9.0 | 2.2 | 57.8 |
| 9 | 0 | 10.0 | 0.9 | 1.5 | 2.8 | 8.4 | 23.5 | 1.8 | | 0.7 | 13.1 | 4.3 |
| 10 | 17.6 | 10.5 | 40.8 | 15.0 | 0 | 25.3 | 0 | 9.0 | 0.7 | | 7.2 | 14.3 |
| 11 | 0 | 6.6 | 4.3 | 0 | 0 | 3.6 | 6.1 | 2.2 | 13.1 | 7.2 | | 5.8 |
| 12 | 24.3 | 60.9 | 23.8 | 17.0 | 0 | 15.6 | 5.9 | 57.8 | 4.3 | 14.3 | 5.8 | |
| Mean Similarity | 14.2 | 16.2 | 16.9 | 11.8 | 4.3 | 16.5 | 8.5 | 17.2 | 6.1 | 12.8 | 4.4 | 20.9 |

Contd.

(b)

| Gap Number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | - | 0.1648 | 0 | 0.2385 | 0.0217 | 0.0589 | 0.1893 | 0.0540 | 0.4053 | 0.0265 | 0.0460 | 0.0627 |
| 2 | 0.1648 | - | 0.050 | 0.5174 | 0.017 | 0.0551 | 0.0330 | 0.2415 | 0.0272 | 0.2464 | 0.1992 | 0.2187 |
| 3 | 0 | 0.050 | 0 | 0.045 | 0 | 0 | 0 | 0.1006 | 0 | 0.1619 | 0.1519 | 0 |
| 4 | 0.2385 | 0.5174 | 0.045 | - | 0 | 0.2581 | 0.0783 | 0.3432 | 0.0707 | 0.1679 | 0.4135 | 0.3359 |
| 5 | 0.0217 | 0.017 | 0 | 0 | - | 0 | 0 | 0 | 0.0508 | 0.0442 | 0 | 0 |
| 6 | 0.0589 | 0.0551 | 0 | 0.2581 | 0 | - | 0 | 0.2624 | 0 | 0.0345 | 0 | 0.1584 |
| 7 | 0.1893 | 0.0330 | 0 | 0.0783 | 0 | 0 | - | 0 | 0.4652 | 0 | 0.1666 | 0.1858 |
| 8 | 0.0540 | 0.2415 | 0.1006 | 0.3432 | 0 | 0.2624 | 0 | - | 0 | 0.2087 | 0.3152 | 0.1237 |
| 9 | 0.4053 | 0.0272 | 0 | 0.0707 | 0.0508 | 0 | 0.4652 | 0 | - | 0 | 0.0766 | 0.0744 |
| 10 | 0.0265 | 0.2464 | 0.1699 | 0.1679 | 0.0442 | 0.0345 | 0 | 0.2087 | 0 | - | 0.0431 | 0.0341 |
| 11 | 0.0460 | 0.1992 | 0.1519 | 0.4135 | 0 | 0 | 0.1666 | 0.3152 | 0.0766 | 0.0431 | - | 0.1674 |
| 12 | 0.0627 | 0.2187 | 0 | 0.3359 | 0 | 0.1584 | 0.1858 | 0.1237 | 0.0744 | 0.0341 | 0.1674 | - |
| Mean Similarity | 0.1152 | 0.1609 | 0.0470 | 0.2244 | 0.0112 | 0.0752 | 0.1017 | 0.1499 | 0.1064 | 0.0887 | 0.1436 | 0.1237 |

Fig.5.3. Rank-abundance curves showing the relative abundance of tree species in the gaps. Species are ranked from most abundant on the left to the least abundant on the right. Gaps with only one species have not been drawn. Key to species number: 1. Q. dealbata; 2. Q. griffithii; 3. R. arboreum; 4. Q. glauca; 5. T. baccata; 6. T. tomentosa; 7. S. khasiana; 8. M. esculenta.

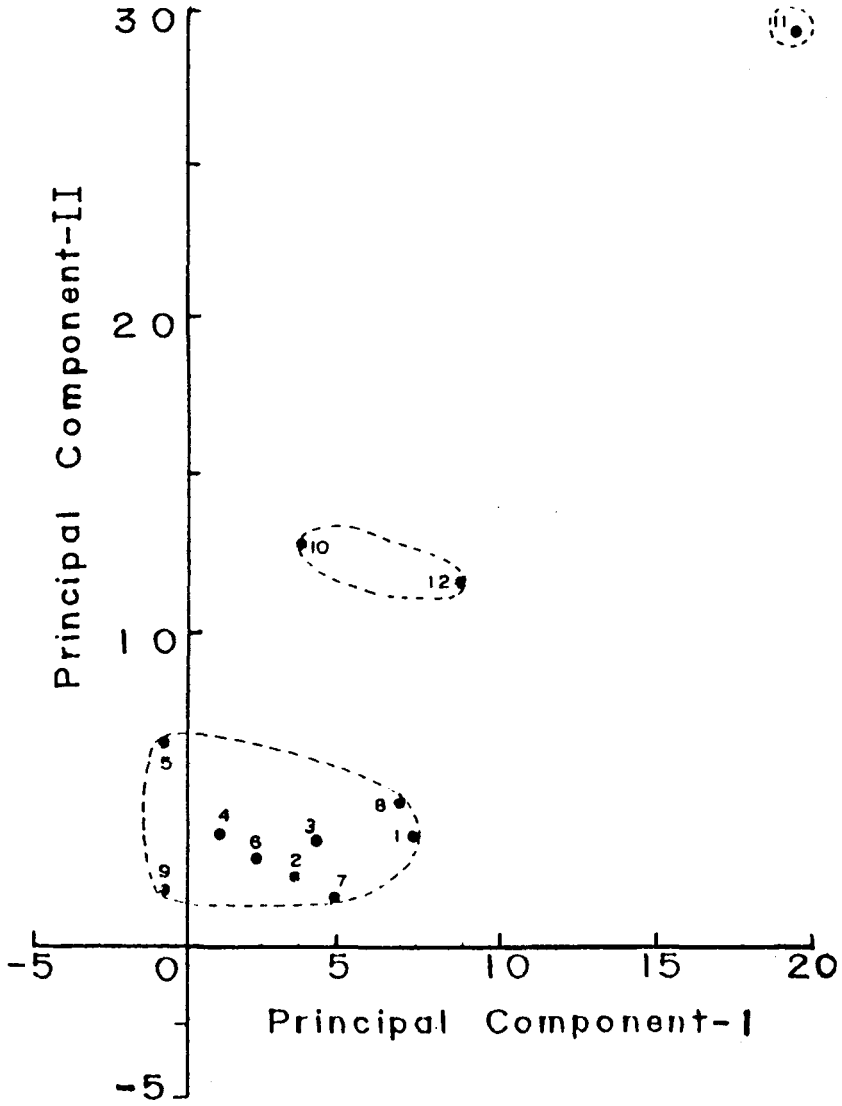

IMPORTANCE VALUE INDEX
200
160
120
80
40
0
1 2 3
1 2 3
1 2
1 2
1 2 3
1 2 3
1 2
1 2 3 4
1 2 3 4 5
1 2 3
34·3
36·3
79·5
107·1
131·5
157·5
210·0
335·0
723·5
950·5
SPECIES SEQUENCE
GAP AREA

Ordination of gaps on the basis of Principal Component Analysis of the shade tolerant and shade intolerant species resulted into the clustering of the twelve gaps into three distinct groups (Fig.5.4). The smaller gaps (gap nos. 1 to 9) comprised the first cluster, while the second cluster included two of the large gaps (gap nos. 10 and 12). Gap no. 11 formed a group of its own.

## DISCUSSION

The treefall gaps in the Mawphlang forest showed marked seasonal variation in the photon flux density, relative humidity and soil moisture content. Photon flux density and soil moisture also varied along the gap size gradient. The increase in photon flux density in the winter months may be attributed to the clear cloudless sky and to the leaf fall pattern of some tree species like Q. griffithii and S. khasiana. These trees shed their leaves totally or partially during winter and early spring whereby canopy of the trees surrounding the gaps become sparse and solar radiation is markedly increased on the forest floor. The seasonal variation in relative humidity and soil moisture content in the gaps is inversely related to the photon flux density which is influenced by the degree of canopy opening. Therefore these two variables were maximum during rainy season when the sky is overcast with

Fig.5.4. Ordination of gaps on the basis of Principal Component Analysis of shade tolerant and shade intolerant species.


30
20
10
-5
0
5
10
15
20
Principal Component-II
Principal Component-I
11
10
12
5
4
6
3
8
1
2
9
7

clouds and the photon flux density is at a minimum. Reduction in soil moisture along the gap size gradient may be attributed to relatively higher irradiance and soil temperature, both of which could enhance evaporation losses. This, however, does not agree with the findings of Lee (1978) who predicted higher soil moisture in larger gaps. Principal Component Analysis showed a marked influence of gap area on its microenvironment. At the same time Principal Component I and II of microenvironmental factors were related to the density of tree seedlings as well as total species diversity in the gaps. Thus it may be concluded that the size of the gaps played an important role in determining the species diversity and regulating tree seedling density therein.

Several workers (Harper et al 1961, Struick and Curtis 1962, Bratton 1976, Falinski 1978) have emphasized the role of fine scale heterogeneity in affecting species richness in gaps. Beatty (1984) reported that in maple beech forest of Eastern New York some understorey species are exclusively present in pits, mounds or in undisturbed soil pits. Beatty and Sholes (1988) suggested that microsite heterogeneity helps in maintaining species richness of the forest through spatial segregation of competing species.

Results presented in the foregoing pages indicate that

none of the species was exclusively present in any particular microsite observed in the gap. Thus the species distribution pattern observed in the subtropical broad-leaved forest at Mawphlang does not confirm the findings of Beatty (1984).

Rank abundance curves indicate that shade tolerant species Q. dealbata was dominant in the small gaps and the shade intolerant pioneers S. khasiana and M. esculenta were important in the larger gaps. This is the probable reason why smaller gaps having higher density of shade tolerant species like Q. dealbata, Q. glauca and Q. griffithii clustered into one group, while the larger gaps having comparatively higher density of shade intolerant species like S. khasiana and M. esculenta constituted another cluster. Gap no 11 contained shade tolerant and shade intolerant species in more or less equal proportion and therefore it formed a distinct group of its own.

$\alpha$-diversity for the trees is low in the Mawphlang forest than other species rich tropical forests (Brokaw and Scheiner 1989). However, higher $\alpha$-diversity in the gaps than in the adjacent understorey clearly suggests that gaps provide favourable conditions for regeneration of certain species, presumably the shade intolerant ones which need greater light intensity for their successful

establishment. Very low seedling density of S. khasiana and absence of M. esculenta in the understorey region could be due to poor light conditions. Such shade intolerant species require gap openings for their establishment. Higher $\alpha$-diversity in the gaps may therefore be attributed to the presence of these species.

$\beta$-diversity shows the mean similarity among gaps and measures the extent of species replacement or biotic change along environmental gradients (Whittaker 1972, Brokaw and Scheiner 1989). It also reflects the extent of similarity and habitat diversity among the gaps. An increase in $\beta$-diversity during a period of two years indicates that gaps become more similar with passage of time. Since $\beta$-diversity is dependant on species composition and their abundance, increase in similarity among gaps may be attributed to the colonization by some new species like R. arboreum and T. tomentosa, particularly in the smaller gaps and to the increase in abundance of already existing species.

# 6 RECRUITMENT AND SURVIVAL OF TREE SEEDLINGS IN GAPS AND UNDERSTOREY

Disturbance influences the dynamics of tree populations in the forest by altering its microenvironment (McCarthy and Facelli 1990). Since the juveniles are highly vulnerable to adverse microenvironmental conditions, any change in light, temperature and moisture regimes as well as other physico-chemical and biological characteristics of the forest floor may have a marked influence on the recruitment and survival of different species in the forest. Treefall gap which is considered as a disturbance of small magnitude in the forest creates new habitats and alters the existing ones, thereby offering oppurtunities for niche differentiation among different tree species. Thus the canopy opening plays an important role in shaping the composition and organisation of forest community.

The survival pattern of tree seedlings varies between gaps and understorey (Clark and Clark 1987, Welden et al. 1991). It has also been shown that the survivorship diff-

ers significantly along a gap size gradient (Brokaw 1985). The differential population response to the gap size gradient could be due to variation in microenvironmental factors along the gradient and differences in the ability of different tree species to use the available resources in the gaps (Denslow 1980). Accordingly, species belonging to different regeneration guilds (Grubb 1977) specialize in different portions of the size gradient. Brokaw (1985) studied the regeneration behaviour of primary and pioneer tree species along a gap size gradient in Barro Colorado Island, Panama and concluded that light demanding pioneers establish successfully in larger gaps, while primary species were indifferent to gap size in terms of their recruitment and survival. The recruitment and population dynamics of tree seedlings in forest understorey and treefall gaps in the tropical and temperate forests have been studied in different parts of the world (Fox 1977, Denslow 1980, Ricklef 1985). The effect of environmental factors on the tree seedling survivorship and population dynamics have been studied by Streng et al. (1989). However, studied dealing with the population behaviour of tree species in the gaps and in forest understorey in the subtropical forests are lacking. Moreover, studies analysing the causes of seedling mortality in these forests have not been carried out as yet. The identification of those microenvironmental factors which influence seedling survi-

val will not only provide an insight into factors regulating the gap phase regeneration in the forest, but it would also give a clue for the adoption of correct silvicultural practices for reforestation of large sized gaps.

The present chapter analyses the recruitment and survival of naturally emerged seedlings of dominant tree species in gaps of different sizes and examines their germination and population behaviour in gaps and adjoining understorey of the forest. An attempt has also been made to identify the microenvironmental factors that are crucial for seedling mortality of different tree species in the forest.

## METHODS

The twelve treefall gaps described in Chapter 4 were classified arbitrarily into three size classes. Gaps having an area more than 700 $m^2$ were designated as large gaps, the gaps between 150 and 700 $m^2$ size were placed under the category of medium gaps and those having an area less than 150 $m^2$ were termed as small gaps (Table 4.1).

All the newly recruited individuals of Q. dealbata, Q. griffithii and Q. glauca (height < 7.0 cm), S. khasiana (height<3.0 cm), T. tomentosa (height<6 cm) and M. esculenta (height < 5 cm) were labelled using wax coated waterproof

labels in August, 1988. The seedlings of S. khasiana were at 2-3 leaf stage while those of other species were at 3-5 leaf stage (Plate 6.1, 6.2, 6.3).

In order to study the seedling dynamics in the understorey region, 10 permanent quadrats of 10m x 10m size were randomly laid adjacent to the gaps and all the seedlings of the six tree species in each quadrat were marked in the similar fashion. Survival of the tagged seedlings was monitored at monthly intervals until August, 1990. There was no significant variation in the tree seedling populations and mortality was restricted only to the winter season in all the species studied. Therefore, the data for the months of August, November, February and May were considered as the representatives of the rainy, autumn, winter and spring seasons, respectively. Since the seedling population of all the species showed a more or less stable age distribution, i.e. the seedlings were in the same age groups, the age specific mortality rate (qx) was calculated on a monthly basis using the life table of the seedling populations (Chaughley 1977) according to the following formula:

$$qx = dx/lx$$

where, lx is the initial number of individuals in the population and dx is the number of individuals that died during the one month period.

A

B

Plate 6.1. Naturally emerged seedlings on the forest floor. A. Q. dealbata; B. Q. griffithii.


Plate 6.2. Naturally emerged seedlings on the forest floor. A. Q. glauca; B. S. khasiana.

A

B

Plate 6.3. Naturally emerged seedlings on the forest floor. A. M. esculenta; B. T. tomentosa.

The different microenvironmental factors such as photon flux density, relative humidity, air temperature, soil moisture, soil temperature and litter depth were studied at monthly interval in the twelve gaps and the forest understorey according to the methods described in Chapter 4. The data for small gaps is the mean of gap nos 1 to 4, for medium gaps, it is the mean of gap nos. 5 to 10 and for the large gaps it is the average of gap nos. 11 and 12 (Table 4.1). The data was statistically analysed using 3-way ANOVA to study the effect of gap size and seasonal and yearly variations on each microenvironmental variable.

The influence of microenvironmental factors on seedling mortality was studied by computing partial correlation coefficients (Zar 1974). Multiple regression models were proposed for different species to establish the age specific mortality rate in a given set of microenvironmental factors (Zar 1974).

In order to explain the exceptionally low seedling recruitment in this forest as compared to other forests situated elsewhere, an experiment was designed to study the germination percentage of seeds of four tree species on the forest floor under natural conditions. Twenty plots, each of 1m x 1m size were established both in gaps and understorey between October, 1989 and February, 1990 depending on the time of seedfall of different species

(Fig.3.1). Twenty five seeds of each species were sown in each plot and germination was monitored at 15 day interval upto 3 months, after which period no further germination was observed even under laboratory conditions.

## RESULTS

### Seed germination in gaps and understorey

In general, germination was low in all the four species but it was still lower (20-30%) in case of oak species as compared to S. khasiana (40-50%). The effect of gap size on germination percentage was prominent only in case of S. khasiana and Q. dealbata, which showed better germination in the gaps than in the understorey (Fig.6.1).

### Seedling recruitment

Results of seedling recruitment in the gaps and understorey during August, 1988 furnished in Table 6.1 clearly indicate that the species differed in their seedling recruitment pattern in the forest. In the understorey, seedling of Q. dealbata were most abundant, followed in descending order by Q. glauca, Q. griffithii, S. khasiana and T. tomentosa. Seedlings of M. esculenta could not be found in the understorey. In the gaps, seedling density of M. esculenta, Q. dealbata, Q. glauca and T. tomentosa

Fig.6.1. Germination behaviour of Q. dealbata (QD), Q. glauca (QGL), Q. griffithii (QG) and S. khasiana (SK) in gaps and understorey in the Mawphlang forest.

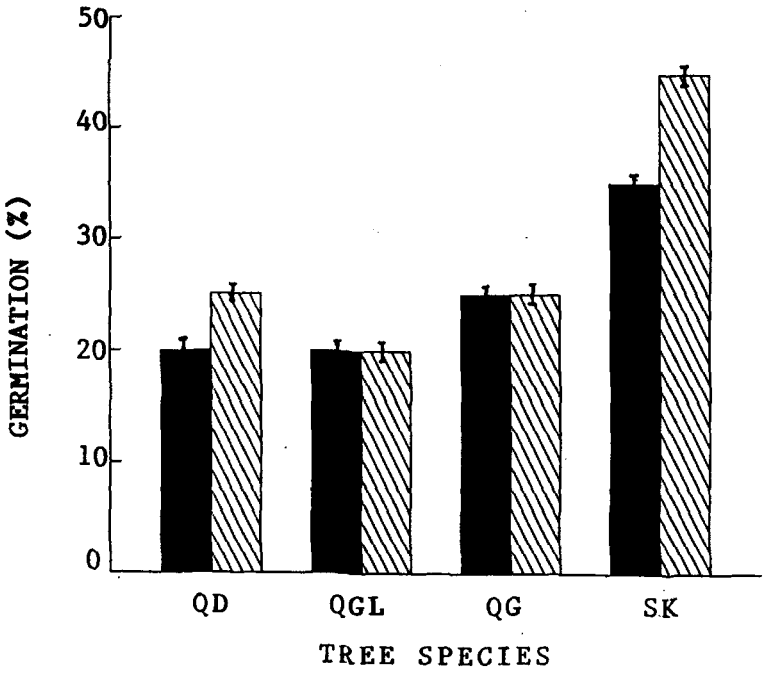

50
40
30
20
10
0
GERMINATION (%)
QD
QGL
QG
SK
TREE SPECIES

Table 6.1 **Tree seedling recruitment (plants $ha^{-1}$) in the gaps and understorey during August 1988.**

| Species | Understorey | Small gaps | Medium gaps | Large gaps |
|---|---|---|---|---|
| Myrica esculenta | - | 140 | 40 | 40 |
| Quercus dealbata | 720 | 840 | 180 | 140 |
| Quercus glauca | 570 | 170 | 30 | 60 |
| Quercus griffithii | 250 | - | 40 | 70 |
| Schima khasiana | 120 | 150 | 200 | 150 |
| Terminalia tomentosa | 80 | 130 | 20 | 30 |

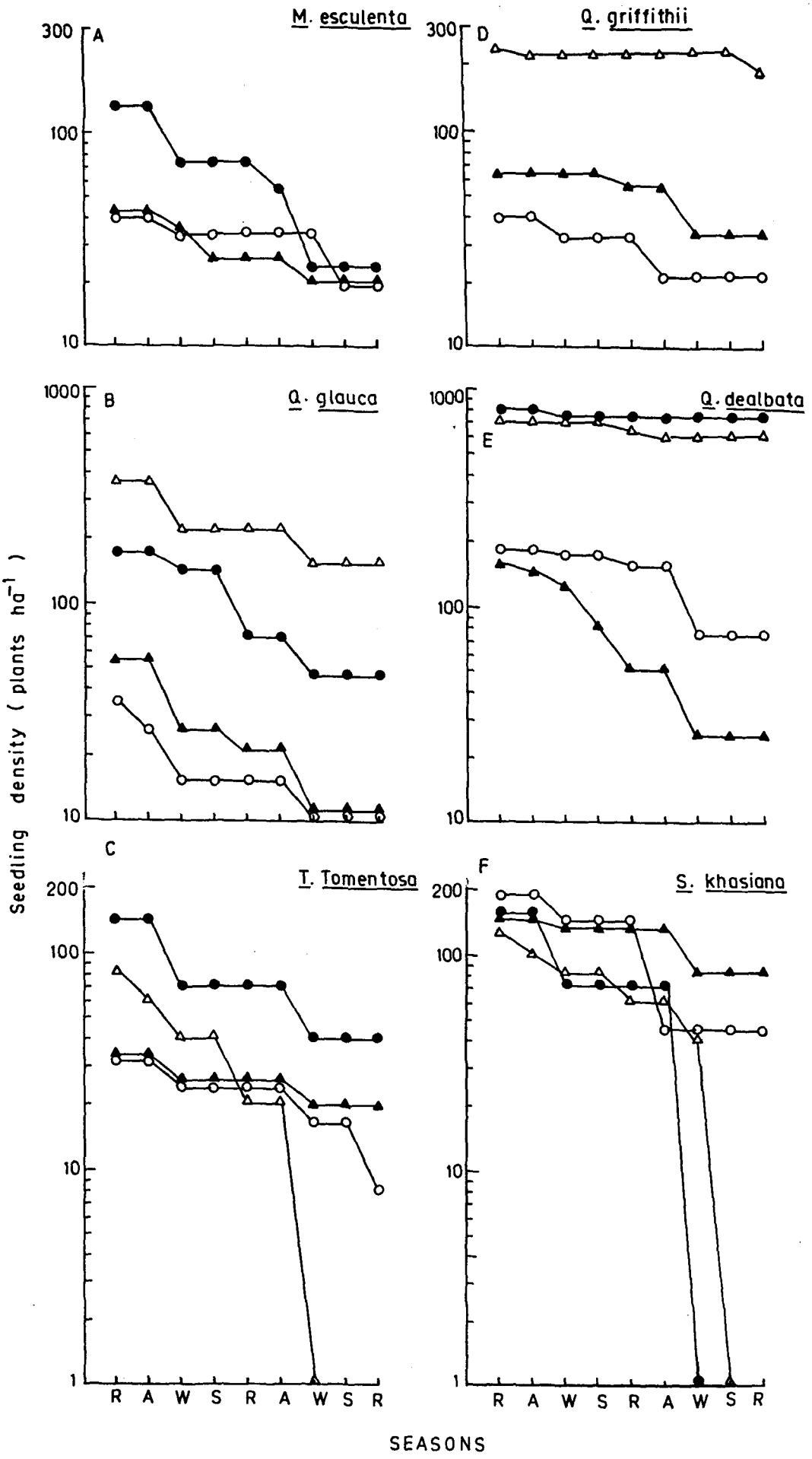
Dashes indicate species absence.

gradually declined with increasing gap size. In this respect Q. griffithii and S. khasiana did not show any definite trend. The small gaps were dominated by the seedlings of Q. dealbata, while in the medium and large gaps S. khasiana was more abundant. The seedlings of M. esculenta and T. tomentosa were abundant in the small gaps. Total tree seedling recruitment (plants $ha^{-1}$) sharply declined from 1430 in the small gaps to 510 in medium sized gaps and then remained unaffected by further increase in gap area.

**Population dynamics**

As depicted in Fig.6.2, inspite of the large variation in seedling recruitment of S. khasiana, M. esculenta and T. tomentosa in gaps of different sizes, they exhibited a similar mortality pattern. The shape of the survivorship curves of these species in the understorey was similar to the gaps. All of them showed high mortality during winter, in both first and second year of seedling growth (Fig.6.2). This was particularly true for S. khasiana in the understorey and in the small gaps where 100% mortality was observed during the second year of growth (Table 6.2). The three oak species showed much lower mortality, in both gaps and understorey in comparison to other species. In these species also mortality occurred only during winter (Fig.6.2). Seedling mortality in case of Q. griffithii and

Fig.6.2. Survivorship curves of six tree seedlings in understorey (△) and small (●), medium (○) and large (▲) gaps.


M. esculenta
A
300
100
10
Q. griffithii
D
300
100
10
Q. glauca
B
1000
100
10
Q. dealbata
E
1000
100
10
T. Tomentosa
C
200
100
10
1
S. khasiana
F
200
100
10
1
R A W S R A W S R
R A W S R A W S R
Seedling density ( plants ha$^{-1}$ )
SEASONS

Q. glauca was negligible in the understorey and small gaps. No mortality was observed in Q. dealbata in the understorey and small gaps. Seedling mortality declined in all the species during second year of growth (Table 6.2).

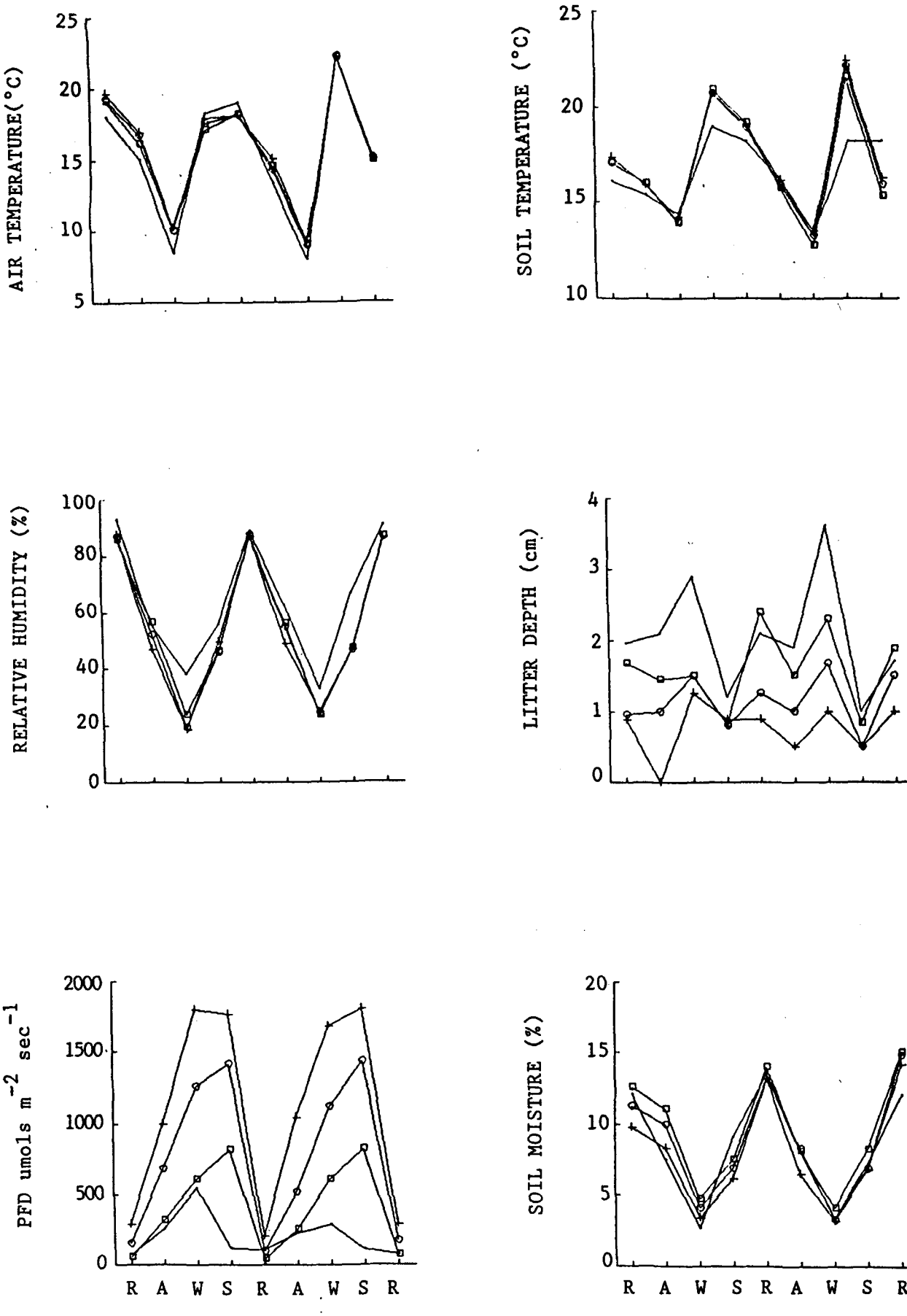
**Microenvironment in gaps and understorey**

**Climatic variables:** Photon flux density differed significantly ($P < 0.01$) among the gaps as well as between gaps and understorey. The seasonal variation in photon flux density both in gaps and understorey was also sinificant ($P < 0.01$). Relative humidity and air temperature did not vary significantly among the three gap sizes and forest understorey but seasonal variation in these factors was found to be significant ($P < 0.01$). Photon flux density which was maximum in the large gaps, declined with the decrease in gap size and it was minimum in the forest understorey. Forest floor received maximum radiation during winter and minimum during rainy season. The reverse was true in case of relative humidity and air temperature (Fig.6.3). The small gaps received 50% more solar radiation than the forest understorey, while it was 75% and 82% higher in the medium and large gaps, respectively. Relative humidity decreased in the range of 12% in small gaps to 15% in large gaps. Air temperature did not vary more than 7% among the gaps and understorey.

Table 6.2. **Mortality (%) of seedlings of six tree species in gaps and understorey.**

| Species | Understorey | | Small gaps | | Medium gaps | | Large gaps | |
|---|---|---|---|---|---|---|---|---|
| | Aug'88 -Aug89 | Aug'89 -Aug90 | Aug'88 -Aug89 | Aug'89 -Aug90 | Aug'88 -Aug89 | Aug'89 -Aug90 | Aug'88 -Aug89 | Aug'89 -Aug90 |
| Schima khasiana | 68 | 100 | 50 | 100 | 27 | 68 | 4 | 39 |
| Myrica esculenta | - | - | 44 | 64 | 19 | 38 | 13 | 20 |
| Terminalia tomentosa | 75 | 100 | 50 | 42 | 25 | 66 | 20 | 25 |
| Quercus dealbata | 11 | 0 | 11 | 0 | 16 | 48 | 65 | 51 |
| Quercus griffithii | 8 | 25 | - | - | 19 | 36 | 20 | 37 |
| Quercus glauca | 42 | 32 | 59 | 33 | 56 | 33 | 63 | 50 |

Fig.6.3. Seasonal variation in microclimatic and edaphic variables in the understorey (-●-) and small (-□-), medium (-○-) and large (+) gaps.


AIR TEMPERATURE(°C)
25
20
15
10
5
SOIL TEMPERATURE (°C)
25
20
15
10
RELATIVE HUMIDITY (%)
100
80
60
40
20
0
LITTER DEPTH (cm)
4
3
2
1
0
PFD umols m$^{-2}$ sec$^{-1}$
2000
1500
1000
500
0
SOIL MOISTURE (%)
20
15
10
5
0
R A W S R A W S R
R A W S R A W S R
SEASONS

**Edaphic variables:** Of the three edaphic variables studied, soil moisture and litter depth significantly varied ($P<0.01$) in different seasons, among the gaps and between gaps and understorey. However, differences among the gaps were more prominent in case of litter depth. Soil temperature did not vary among the gaps and understorey. Peak soil moisture was recorded during rainy season and trough was seen during winter season (Fig.6.3). Litter depth was significantly higher ($P < 0.01$) in the understorey than in the gaps throughout the year. On a seasonal basis highest litter accumulation was recorded during winter and lowest during rainy season (Fig.6.3). The thickness of litter layer, as compared to forest understorey, showed 22% reduction in the small gaps, 46% in the medium gaps and 61% in the large gaps. In the small gaps soil moisture was 11% more than the understorey, while the medium and large gaps registered about 4% decrease in their soil moisture contents.

**Relationship between age specific mortality rate of seedlings and microenvironment**

In order to determine the most critical factor among the six environmental variables studied for seedling mortality in the forest, the age specific mortality rate of a particular species in the gaps and forest understorey was correlated with different microenvironmental variables.

The partial correlation coefficients 'r' thus obtained were compared and the highest significant value was considered to be the most influential factor for seedling mortality (Table 6.3).

Results indicate that for S. khasiana photon flux density is most important in the understorey region, while soil moisture is important in the small gaps. Relative humidity is most effective in medium and large gaps. Relative humidity is also important for seedling mortality of M. esculenta and T. tomentosa both in gaps and understorey. Age specific mortality of Quercus species in the understorey and large gaps was strongly related to relative humidity and photon flux density in the medium gaps. In the small gaps soil moisture was more important for Q. dealbata while litter depth, air temperature and soil temperature played a key role in influencing mortality of Q. glauca (Table 6.3).

The multiple regression models showing relationship between microenvironmental variables and age specific mortality rate have been proposed in Table 6.4.

## DISCUSSION

The differential germination response of tree species to canopy openings in the Mawphlang forest is in confor-

Table 6.3. Partial correlation coefficient (r) between age specific mortality (qx) of tree seedlings and environmental variables in understorey (US) and small (SG), medium (MG) and large (LG) gaps in the forest.

| Tree species | Forest stand | Microenvironmental variables | | | | | | n |
|---|---|---|---|---|---|---|---|---|
| | | Relative humidity(%) | PFD | Air temp(°C) | Soil Moisture(%) | Soil temp(°C) | Litter depth(cm) | |
| Schima khasiana | US | 0.139 | 0.737** | 0.455 | 0.252 | 0.251 | 0.478 | 21 |
| | SG | 0.208 | 0.347 | 0.344 | 0.562* | 0.069 | 0.288 | 23 |
| | MG | 0.609** | 0.594** | 0.371 | 0.052 | 0.308 | 0.205 | 24 |
| | LG | 0.594** | 0.199 | 0.307 | 0.332 | 0.388 | 0.011 | 24 |
| Myrica esculenta | US | - | - | - | - | - | - | - |
| | SG | 0.462* | 0.225* | 0.275 | 0.533* | 0.207 | 0.163 | 24 |
| | MG | 0.604** | 0.621** | 0.314 | 0.182 | 0.207 | 0.019 | 24 |
| | LG | 0.605** | 0.216 | 0.329 | 0.415 | 0.412 | 0.131 | 24 |
| Terminalia tomentosa | US | 0.147 | 0.387 | 0.586* | 0.128 | 0.258 | 0.143 | 18 |
| | SG | 0.510* | 0.313 | 0.408 | 0.670** | 0.032 | 0.598** | 24 |
| | MG | 0.717** | 0.534* | 0.445* | 0.356 | 0.531* | 0.530* | 24 |
| | LG | 0.657** | 0.117 | 0.409* | 0.329 | 0.357 | 0.380 | 24 |
| Quercus dealbata | US | 0.493* | 0.152 | 0.206 | 0.247 | 0.417 | 0.102 | 24 |
| | SG | 0.252 | 0.079 | 0.242 | 0.598** | 0.104 | 0.521 | 24 |
| | MG | 0.422* | 0.643** | 0.236 | 0.262 | 0.295 | 0.193 | 24 |
| | LG | 0.595** | 0.194 | 0.318 | 0.367 | 0.426 | 0.007 | 24 |
| Quercus griffithii | US | 0.018 | 0.361 | 0.226 | 0.228 | 0.064 | 0.426 | 24 |
| | SG | - | - | - | - | - | - | - |
| | MG | 0.586** | 0.690** | 0.442* | 0.027 | 0.420* | 0.412 | 24 |
| | LG | 0.600** | 0.166 | 0.326 | 0.282 | 0.336 | 0.073 | 24 |
| Quercus glauca | US | 0.658** | 0.274 | 0.094 | 0.190 | 0.190 | 0.019 | 24 |
| | SG | 0.035 | 0.260 | 0.168 | 0.418 | 0.556** | 0.638** | 24 |
| | MG | 0.609** | 0.418* | 0.348 | 0.272 | 0.317 | 0.221 | 24 |
| | LG | 0.617** | 0.162 | 0.315 | 0.430* | 0.340 | 0.187 | 24 |

* significant at $P<0.05$; ** significant at $P<0.01$

Table 6.4. **Multiple regression models showing relationships of age specific mortality of tree seedlings (qx) with microenvironmental variables in the understorey (US) and small (SG), medium (MG) and large (LG) gaps in the forest.**

| Species | Forest stand | Constant | Microenvironmental variables | | | | | | $R^2$ | n |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | RH | PFD | AT | SM | ST | LD | | |
| Schima khasiana | US | 0.687 | NS | -0.0025** | NS | NS | NS | NS | 0.725 | 21 |
| | SG | 0.192 | NS | NS | NS | 0.060* | NS | NS | 0.505 | 23 |
| | MG | -1.290 | NS | NS | -0.047* | 0.081** | 0.081** | 0.283** | 0.772 | 24 |
| | LG | 0.137 | NS | NS | -0.024* | NS | NS | -0.150* | 0.421 | 24 |
| Myrica esculenta | US | - | - | - | - | - | - | - | - | - |
| | SG | 0.185 | 0.006* | NS | NS | 0.046* | NS | NS | 0.380 | 24 |
| | MG | -0.141 | NS | NS | NS | NS | NS | NS | 0.478 | 24 |
| | LG | 0.157 | NS | NS | NS | NS | NS | NS | 0.363 | 24 |
| Terminalia tomentosa | US | 2.857 | NS | NS | -0.209* | NS | NS | NS | 0.532 | 18 |
| | SG | 0.929 | 0.005* | NS | NS | 0.055** | NS | 0.240 | 0.551 | 24 |
| | MG | 0.751 | 0.009* | 0.003 | NS | 0.0005* | NS | 0.317** | 0.627 | 24 |
| | LG | 3.089 | -1.487** | NS | 0.156** | -0.001* | -0.171** | NS | 0.771 | 24 |
| Quercus dealbata | US | -0.296 | 0.001 | NS | NS | NS | NS | -0.296* | 0.730 | 24 |
| | SG | 0.149 | NS | NS | 0.011** | NS | NS | -0.046* | 0.442 | 24 |
| | MG | 0.917 | NS | 0.0002 | -0.053 | NS | NS | -0.292 | 0.696 | 24 |
| | LG | 0.405 | NS | NS | NS | NS | NS | NS | 0.233 | 24 |
| Quercus griffithii | US | -0.0781 | NS | NS | NS | NS | NS | NS | 0.530 | 24 |
| | SG | - | - | - | - | - | - | - | - | - |
| | MG | -0.655 | NS | NS | NS | NS | NS | 0.158** | 0.746 | 24 |
| | LG | 0.440 | NS | NS | -0.038 | NS | 0.042* | -0.253* | 0.521 | 24 |
| Quercus glauca | US | 0.376 | -0.006 | NS | NS | NS | NS | NS | 0.561 | 24 |
| | SG | 0.304 | NS | NS | -0.059** | NS | 0.054* | -0.218** | 0.534 | 24 |
| | MG | 0.995 | NS | NS | 0.047* | NS | NS | -0.298** | 0.690 | 24 |
| | LG | 0.494 | NS | NS | 0.036* | NS | NS | NS | 0.581 | 24 |

* Significant at $P<0.05$
** Significant at $P<0.01$
NS Not Significant

mity with the findings of Brokaw (1985) and Denslow (1987) who concluded that gaps in forest canopies significantly affect germination of seeds and survival of plants therein. Murray (1988) also observed significantly higher germination success under gap conditions than under close canopy in three neotropical tree species. Vazquez-Yanes and Smith (1982) also observed similar germination response to canopy openings in seeds of Cecropia insignis. Relatively higher temperature in gaps and larger exposure to solar radiation may be the cause of better germination of certain species like S. khasiana and Q. dealbata in the gaps. Q. glauca and Q. griffithii which did not show any difference in germination in gaps and understorey, seem to have no specific temperature and light requirements. However, their lower seedling population density in the gaps than the adjacent understorey could be attributed to low seed input in the gaps due to the presence of fewer trees of these species in the periphery (Table 4.1) and higher seed predation (Chapter 8). A significant positive correlation between seedling density of S. khasiana and gap size ($r=0.69$; $P<0.01$) clearly shows a gap-dependant regeneration behaviour of this species. Such a colonization behaviour was also observed by Brokaw (1987) in 3 shade intolerant pioneer species at BCI, Panama. In case of T. tomentosa and M. esculenta small gaps seemed to have provided more favourable conditions than either larger

gaps or understorey. The gap size specificity exhibited by certain species might be due to favourable niches for their seedling establishment. Similar gap size specificity by different tree species has been observed by Ricklefs (1977), Florence (1981) and Orians (1982), who have attributed this response as a manifestation of niche partitioning among the species.

The importance of gap phase regeneration in maintaining structure of the tropical forests and its role in forest dynamics and composition have been emphasized by a large number of workers (Richards 1952, Schulz 1960, Whitmore 1975, Streng 1986, Hartshorn 1978, Oldeman 1978, Hubbel 1979, Denslow 1980, Alexandre 1982, Pickett 1983, Bazzaz 1984, Brokaw 1985, Martinez-Ramos 1985). Openings in the forest canopy considerably affects the life history of important species. A large number of species show better survival in gaps than in the understorey (Brokaw 1985b, Welden et al.1991). Augspurger (1984) has used the survival and growth rate of seedlings in shade as an index for shade tolerance. In the Mawphlang forest, species like S. khasiana, M. esculenta and T. tomentosa show better survival along the increasing gap size gradient and therefore may be called as shade intolerant species. On the other hand the three species of Quercus which were indifferent to gap creation as far as their seedling survival is concerned, may be termed as shade tolerant.

The importance of soil moisture (McLeod and Murphy 1977, Mueller-Dombois et al. 1980, Schulte and Marshall 1983), light (Howard 1973, Bazzaz and Pickett 1980, Augspurger 1984, Burton and Mueller-Dombois 1984, Connell et al. 1984), temperature (Sorensen and Ferrel 1973) and litter depth (Collins and Good 1987 ) in regulating tree seedling survival in tropical forests have been repeatedly emphasized. The main cause of peak mortality of tree seedlings during winter in the Mawphlang forest appears to be the low temperature and high soil moisture stress due to very low rainfall and high evapo-transpiration losses.

The detrimental effects of soil moisture stress in the survival of tree seedlings has also been reported by McLeod and Murphy (1977). Since the gap microenvironment varies along a gap size gradient and different species have different requirements, seed germination and seedling establishment of a particular species in understorey or in gaps depend on their niche specialization. Results presented in the foregoing pages indicate a partitioning of niches among different tree species in the forest.

# TREE SEEDLING GROWTH IN GAPS AND UNDERSTOREY

The importance of gap phase regeneration in maintaining species diversity in forest is well established. Regeneration in gaps involves colonization by new species and growth of hitherto suppressed seedlings and saplings. Most tropical trees depend on gaps for their successful regeneration (Hartshorn 1980, Whitmore 1984) and they show ecological differentiation in growth response to canopy openings (Ricklefs 1977, Connell 1978, Whitmore 1982, Pickett 1983, Brokaw 1985a). Most species are in some sense gap dependant since they positively respond to the locally enhanced light levels in the canopy openings. The canopy gaps created by treefalls, a major source of environmental heterogeneity in the close-canopied forest (Denslow 1980, Brokaw 1985a), are important for growth and reproduction of many forest trees (Richards and Williams 1975, Hartshorn 1980, Clark and Clark,

1987b). Gap microclimate is generally characterized by low humidity and high light intensity, temperature and soil moisture (Denslow et al 1990). The extent to which this increase in light and temperature and soil moisture regimes affects seedling growth depends on its physiological ability to utilize these resources. The effect of canopy gaps on the growth of tree seedlings in the tropical rain forests have been studied by Popma and Bongers (1988), Uhl et al (1988), Canham (1988) and Denslow et al (1990). Brokaw (1985b) and Denslow (1987) have emphasized the importance of relationship between gap size and growth abilities of tree species in determining the structure and composition of tropical forests, while Leigh et al (1982) and Brokaw and Scheiner (1989) have examined the effect of gap size on growth of tree species. However, only a few workers have compared the performance of tree juveniles in the gaps and understorey (Clark and Clark 1987). Such studies on tree seedling performance in gaps and understorey are completely lacking in India. Further, the effect of gap induced changes in forest microenvironment on the growth of tree seedlings is also not well understood.

The growth response of seedlings of dominant tree species in gaps of different sizes and in the forest understorey studied in the Mawphlang forest has been presented in

this chapter. The influence of various microenvironmental factors on the growth performance of the seedlings has also been assessed.

## METHODS

Growth performance of the tagged tree seedlings in the small, medium and large gaps and in the ten permanent quadrats in the understorey (cf. Chapter 6) were studied from August, 1988 to August, 1990. Various growth parameters such as shoot length, number of leaves, total leaf area and stem diameter of all seedlings were measured at monthly intervals. Leaf area was measured by a portable leaf area meter (LICOR, USA) and the stem diameter was measured just above the ground level with the help of a screw gauge. All the parameters were expressed on per seedling basis. By using these data, growth functions such as relative shoot growth rate (RSGR) and leaf area index (LAI) were computed according to the methods described by Combs *et al* (1985).

$$RSGR = \frac{\ln h_2 - \ln h_1}{t_2 - t_1}$$

where, t is the time in months, $h_1$ is the shoot length at time $t_1$ and $h_2$ is the shoot length at time $t_2$.

$$LAI = \frac{\text{Total surface area of leaves}}{\text{Ground area covered by seedling canopy}}$$

Since growth in shoot length and leaf area was very slow, RSGR and LAI were calculated on seasonal basis. Thus the values of August, November, February and May were taken as representatives of growth during rainy, autumn, winter and spring seasons, respectively.

The effects of photon flux density, relative humidity, soil moisture, air temperature, soil temperature and litter depth on growth behaviour of seedlings were studied by computing partial correlation coefficients. In order to simplify the analyses, the four growth parameters described above were combined into a synthetic measure of growth using Principal Component Analysis (Poole 1974). The first Principal Component (PC I) explained about 75% variance among the four growth parameters of the seedlings in gaps and understorey. Thereafter partial correlation coefficients (r) were computed between PC I of growth and microenvironmental variables. Multiple regression models were proposed for the different species to estimate the growth response of seedlings in a given set of microenvironmental factors (Zarr 1974).

# RESULTS

## Growth

Relative shoot growth rate of three Quercus species was higher in the forest understorey than in the gaps but S. khasiana, M. esculenta and T. tomentosa seedlings showed better growth in the medium and large gaps (Fig.7.1). In general, all species showed maximum RSGR during rainy season. Basal area of all tree seedlings increased with time both in gaps and forest understorey (Fig.7.2). Difference in basal area along understorey-gap size gradient was prominent in case of M. esculenta, Q. griffithii, Q. glauca and T. tomentosa. In Q. glauca it was higher in the understorey and small gaps while in Q. griffithii the seedlings inhabiting understorey and medium gaps had higher basal area than those in large gaps. Basal area of M. esculenta seedlings was negatively related to gap size, but in T. tomentosa it was higher in the small gaps. In case of Q. dealbata and S. khasiana the trend was not clear (Fig.7.2).

## Foliage dynamics

Figure 7.3 shows the foliage dynamics of tree seedlings in the Mawphlang forest. The behaviour of Q. glauca and Q. dealbata was similar, both having long leaf blade expansion period extending from May to February. In these

Fig.7.1. Relative shoot growth rate of tree seedlings in understorey (■) and small (▨), medium (▩), and large (▨) gaps during Autumn (A), Winter (W), Spring (S) and Rainy (R) seasons.

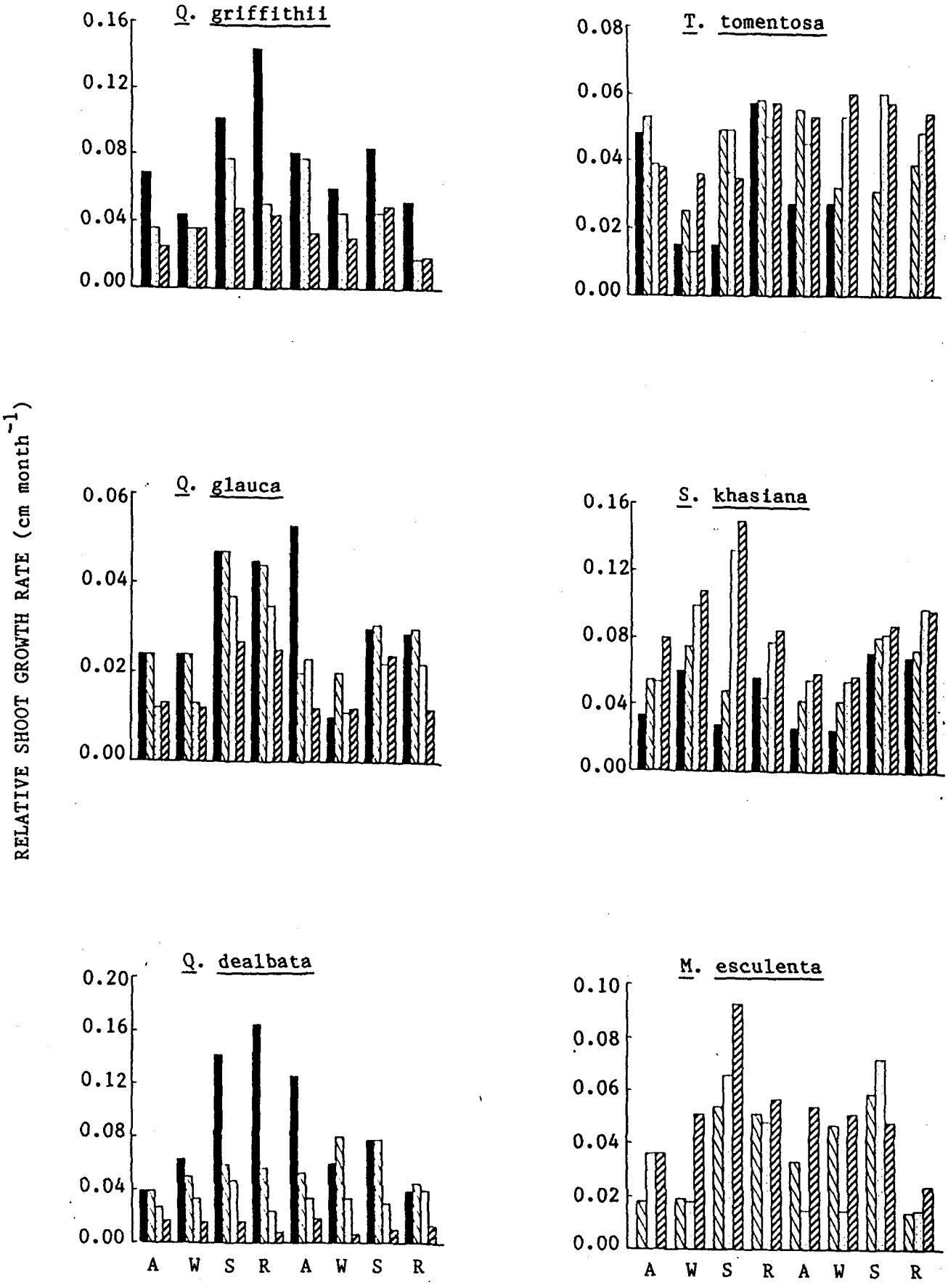

Q. griffithii
0.16
0.12
0.08
0.04
0.00
T. tomentosa
0.08
0.06
0.04
0.02
0.00
Q. glauca
0.06
0.04
0.02
0.00
S. khasiana
0.16
0.12
0.08
0.04
0.00
Q. dealbata
0.20
0.16
0.12
0.08
0.04
0.00
M. esculenta
0.10
0.08
0.06
0.04
0.02
0.00
A W S R A W S R
SEASONS
RELATIVE SHOOT GROWTH RATE (cm month$^{-1}$)

Fig.7.2. Seasonal increase in basal area of tree seedlings during two years of growth in understorey (-•-) and small (-□-), medium (-○-) and large ( + ) gaps. [ Autumn (A); Winter (W); Spring (S); Rainy (R) ].

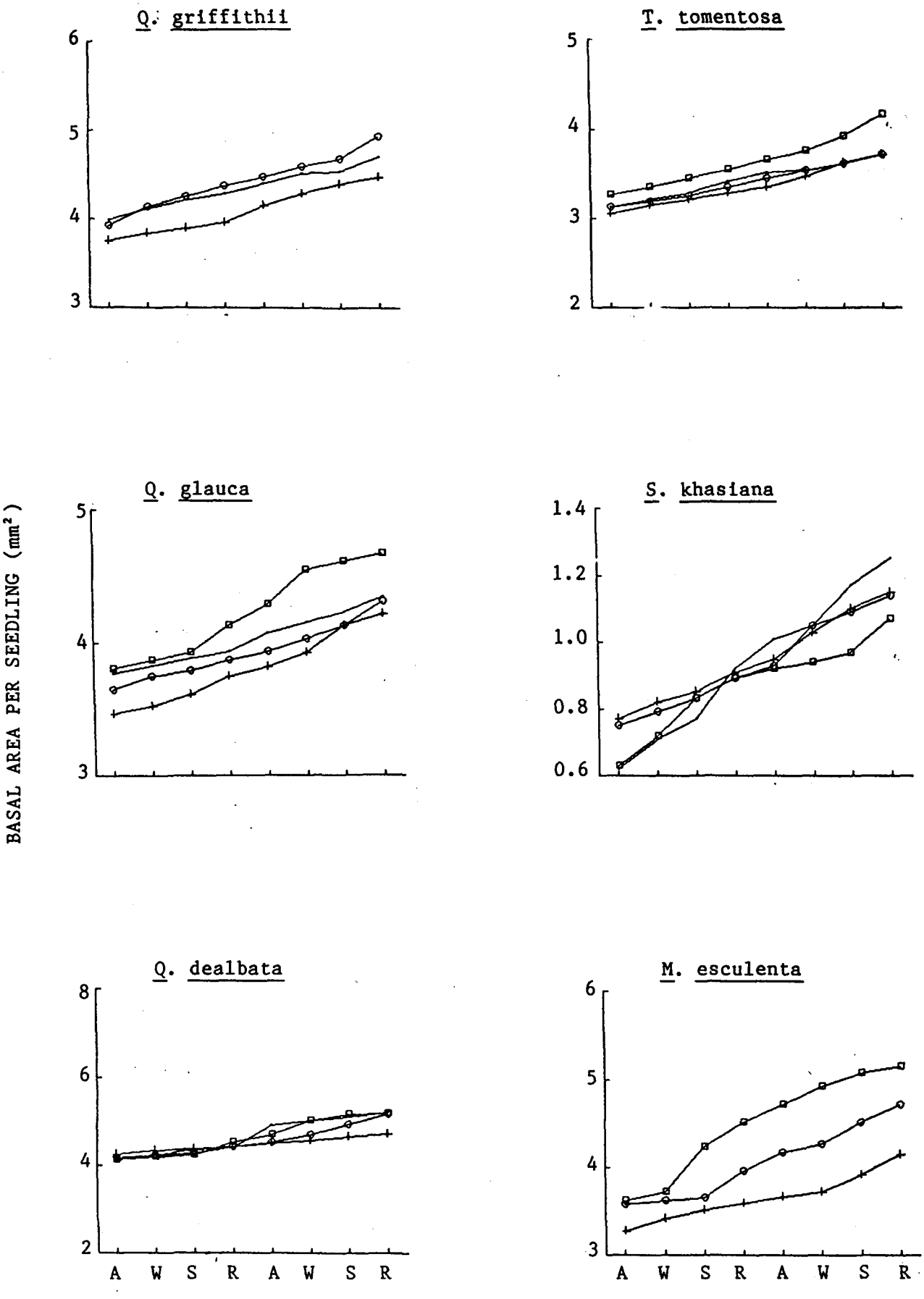
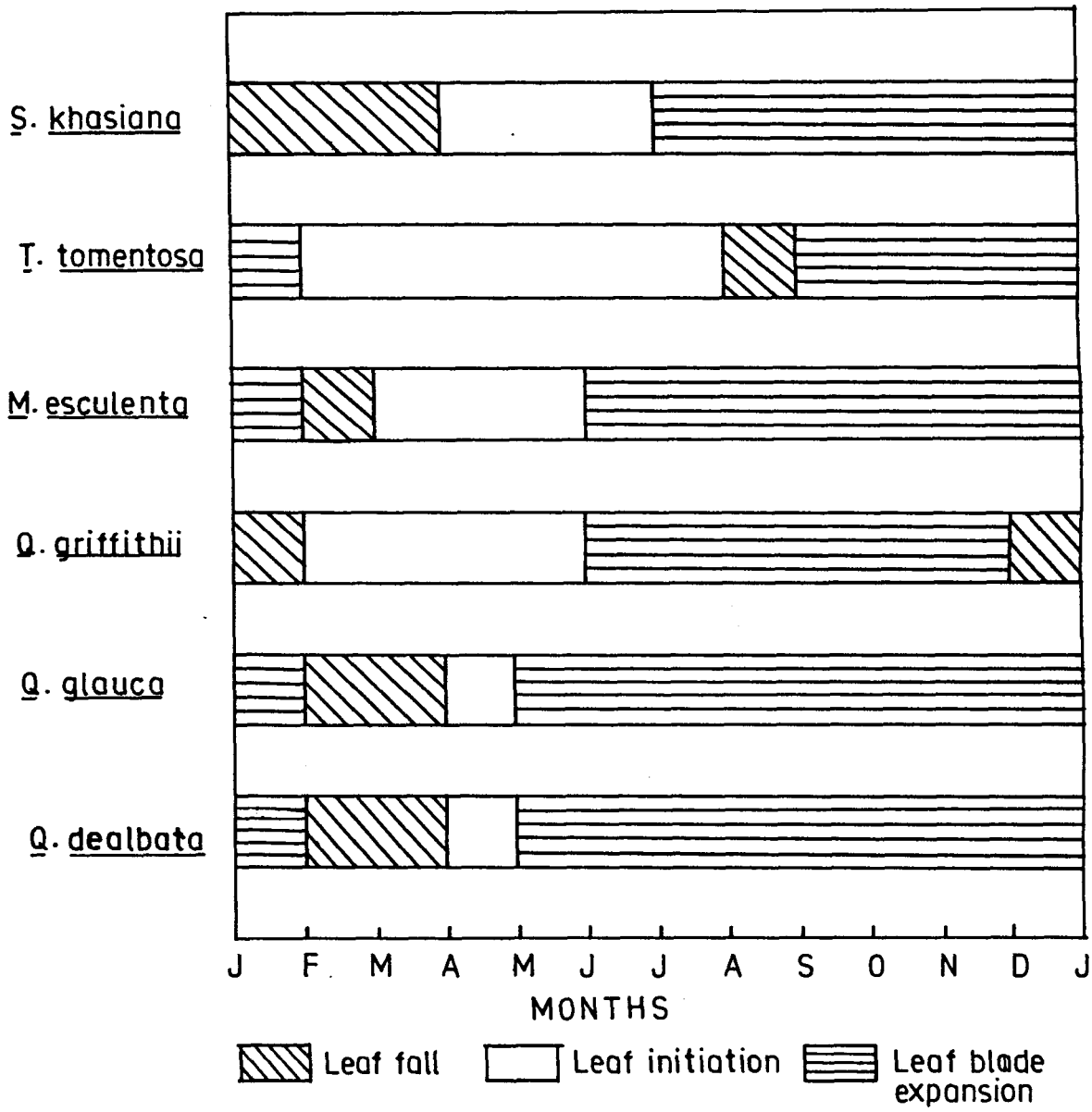

Q. griffithii
T. tomentosa
Q. glauca
S. khasiana
Q. dealbata
M. esculenta
BASAL AREA PER SEEDLING (mm²)
A W S R A W S R
SEASONS

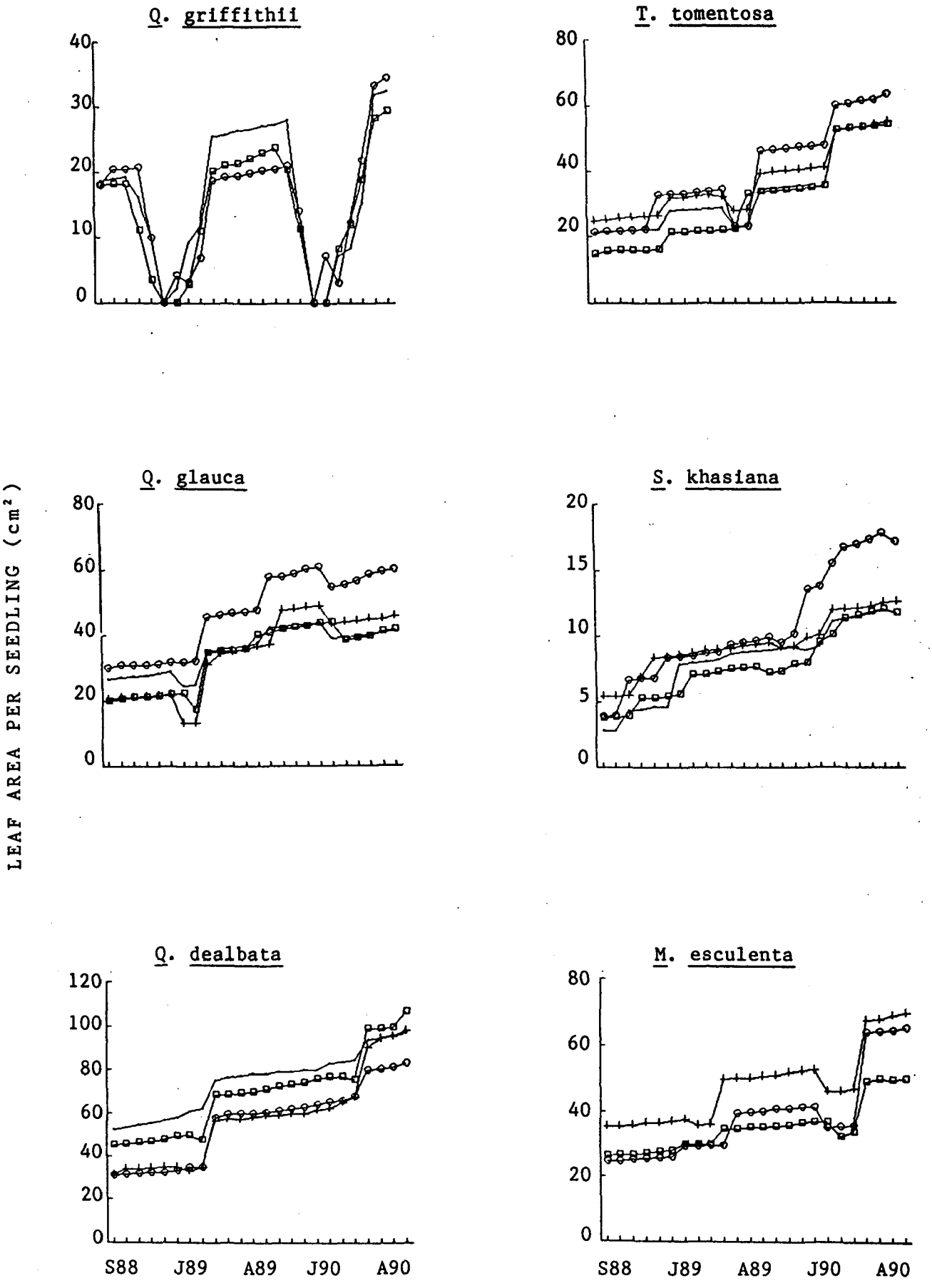
Fig.7.3. Foliage dynamics of tree species in the Mawphlang forest.


S. khasiana
T. tomentosa
M. esculenta
Q. griffithii
Q. glauca
Q. dealbata
J F M A M J J A S O N D J
MONTHS
Leaf fall
Leaf initiation
Leaf blade expansion

species leaf initiation occurs between April and May. Both the species show partial leaf shedding during spring (February to April). Q. griffithii is a deciduous species and leaf shedding is complete between December and February. New leaves appear during spring and early rainy season (March to July), and expansion of leaf blade takes place between June and December. Leaf blade expansion in M. esculenta extends from June to February. Leaf initiation in these two species takes place between May and June and February and August, respectively. Leaf fall in these species lasted for a brief period during winter. S. khasiana, a semi-deciduous species, partially sheds its leaves between January and April. Leaf initiation is observed between April and July and blade expansion occurs during July to January.

In general, leaf area per seedling increased with time. Q. griffithii and Q. dealbata showed maximum leaf area in the understorey, while other species showed higher values in large and medium sized gaps (Fig.7.4). Seasonality in foliage dynamics influenced the photosynthetic surface of seedlings as is clearly evident from the fall and rise of leaf area curves during different months of the year. The deciduous nature of Q. griffithii was responsible for the drop in leaf area to zero during winter. Among the other two Quercus spp, leaf shedding was prominent only in

Fig.7.4. Changes in total leaf area of tree seedlings during two years of growth in understorey (-●-) and small (-□-), medium (-○-), and large ( + ) gaps.


Q. griffithii
T. tomentosa
Q. glauca
S. khasiana
Q. dealbata
M. esculenta
LEAF AREA PER SEEDLING (cm²)
S88
J89
A89
J90
A90
M O N T H S

case of Q. glauca. Seasonality in leaf area of M. esculenta and T. tomentosa was observed only during the second year of their growth. S. khasiana showed a gradual rise in leaf area during two years of study. In this semi-deciduous species, seasonality was not prominent due to overlapping of leaf fall and leaf initiation periods. In all species the period of sudden increase in leaf area corresponds to the period of leaf initiation (Fig.7.4).

Leaf area index (LAI) of Q. dealbata and Q. griffithii was maximum in the understorey and minimum in the large gap. In case of Q. glauca and T. tomentosa it was higher in the medium sized gaps. S. khasiana and M. esculenta had highest LAI in the large gaps and lowest in the small gaps (Fig.7.5).

**Relationship between seedling growth and microenvironment**

The influence of various microenvironmental variables on seedling growth was evaluated by comparing significant ($P < 0.05$) values of partial correlation coefficients 'r' between PC I of growth and climatic and edaphic variables. These values are represented through a bar diagram in Fig.7.6.

Results indicate that growth of all species except M. esculenta in forest understorey was significantly affected

Fig.7.5. Leaf area index of tree seedlings in understorey (■) and small (▧), medium (▩) and large (▨) gaps during Autumn (A), Winter (W), Spring (S) and Rainy (R) seasons.

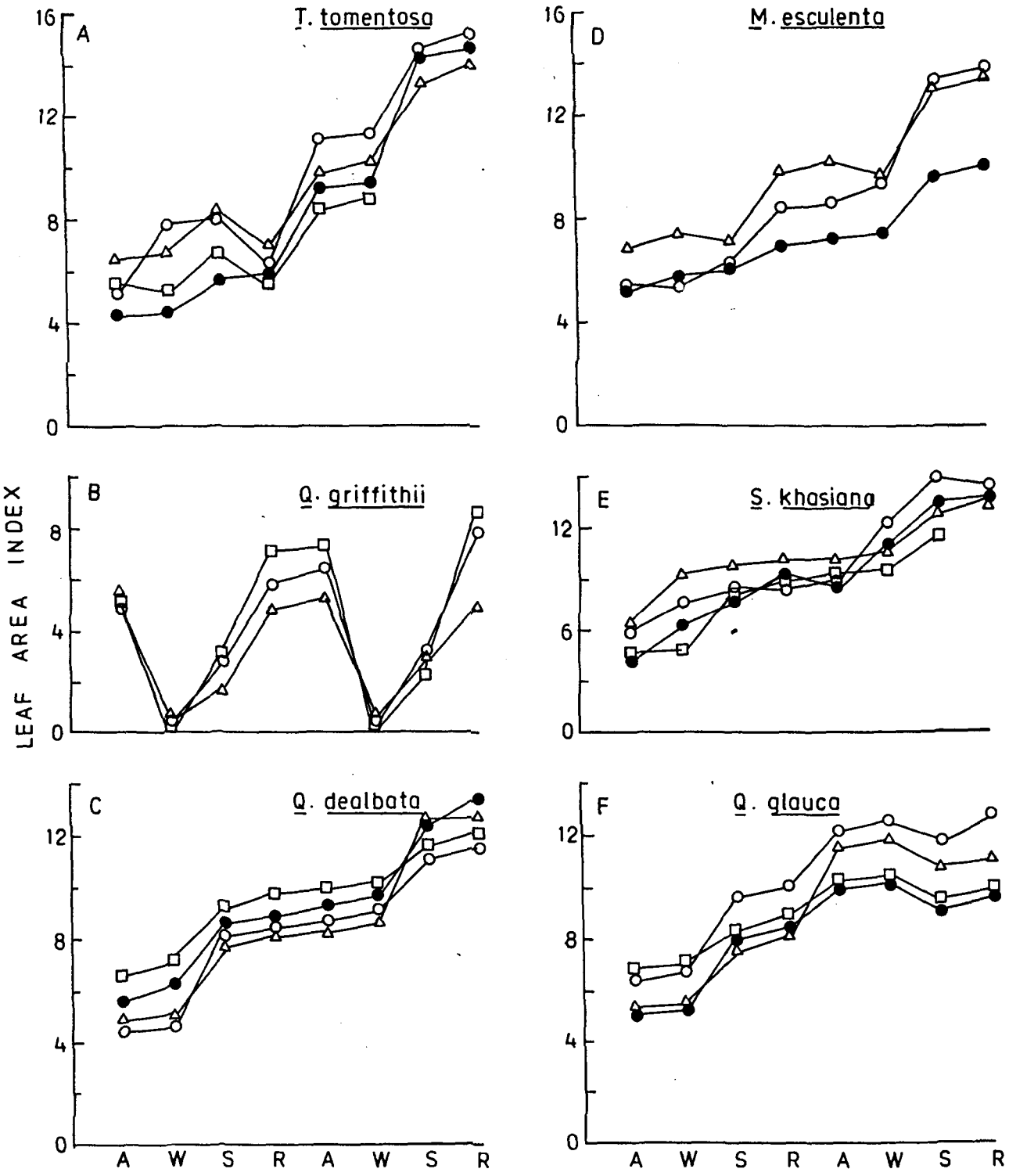
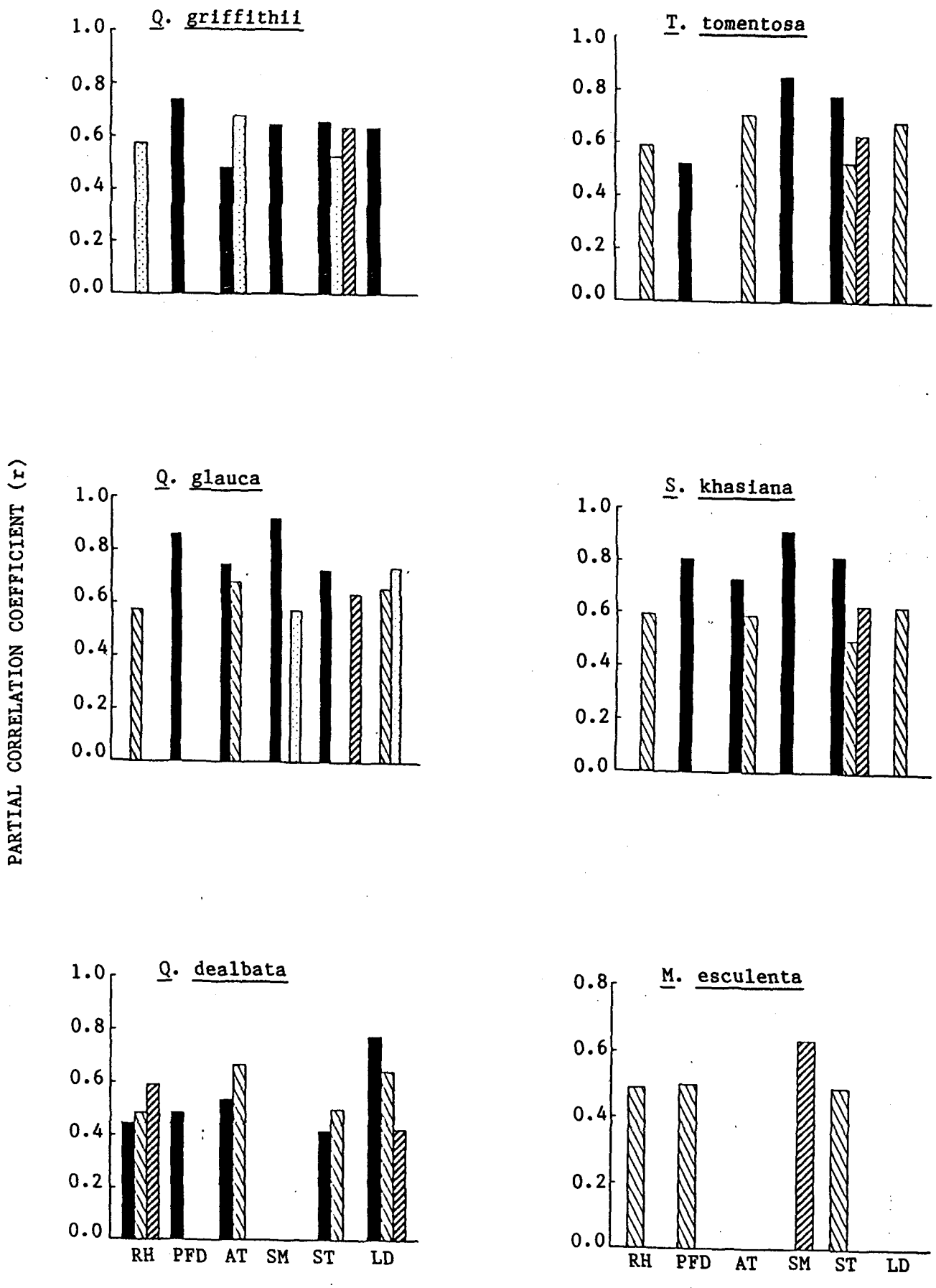

A
T. tomentosa
D
M. esculenta
B
Q. griffithii
E
S. khasiana
C
Q. dealbata
F
Q. glauca
LEAF AREA INDEX
SEASONS
A W S R A W S R

Fig.7.6. Partial correlation coefficients (r) between Principal Component-I of the growth parameters of tree seedlings and six microenvironmental variables in understorey (■) and small (▧), medium (▩) and large (▨) gaps. The values represented in the figure are significant at $P < 0.05$ (RH - relative humidity; PFD-photon flux density; AT-air temperature; SM-soil moisture; ST-soil temperature; LD-litter depth).


Q. griffithii
T. tomentosa
Q. glauca
S. khasiana
Q. dealbata
M. esculenta
1.0
0.8
0.6
0.4
0.2
0.0
RH
PFD
AT
SM
ST
LD
PARTIAL CORRELATION COEFFICIENT (r)
MICRO ENVIRONMENT

by photon flux density. For M. esculenta this factor was important in small gaps; in the large gaps soil moisture was found to be important. Relative humidity was important in small gaps for the seedlings of S. khasiana, M. esculenta, T. tomentosa, Q. dealbata and Q. glauca. It influenced the growth of Q. griffithii and Q. dealbata in medium and large gaps, respectively. In the understorey, growth of S. khasiana, T. tomentosa and Q. glauca was strongly related to soil moisture. Seedlings of Q. griffithii were also affected by the soil moisture in the understorey, although the relationship was less significant. Soil and air temperature and litter depth seemed to influence growth of most species in the understorey and small gaps.

The multiple regression equations showing the relationship between PC I of growth and the microenvironmental factors have been given in Table 7.1.

## DISCUSSION

Differential growth response of tree species in different micro-habitats in the forest has an important bearing on their spatial and temporal distribution patterns. Small scale disturbances like treefalls have been shown to

Table 7.1. Multiple regression equations showing relationship of PC I of growth with microenvironmental factors in the understorey (US), small (SG), medium and large (LG) gaps.

| Species | Forest stand | Constant | Microenvironmental variables | | | | | | $R^2$ | n |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | RH | PFD | AT | SM | ST | LD | | |
| Schima khasiana | US | -18.213 | NS | -0.163** | NS | -2.163** | 2.165** | NS | 0.843 | 21 |
| | SG | -17.109 | -0.112** | NS | -1.108** | NS | 1.238* | 5.418** | 0.725 | 23 |
| | MG | -10.990 | NS | NS | NS | NS | NS | -0.307** | 0.284 | 24 |
| | LG | -18.434 | NS | NS | NS | NS | 1.858** | -0.140** | 0.457 | - |
| M. esculenta | US | - | - | - | - | - | - | - | - | 24 |
| | SG | - 1.691 | -0.125** | NS | NS | NS | 1.653* | NS | 0.501 | 24 |
| | MG | - 7.887 | NS | NS | NS | NS | NS | NS | 0.269 | 24 |
| | LG | -18.92 | NS | NS | NS | NS | 1.879** | NS | 0.485 | 24 |
| T. tomentosa | US | -14.307 | NS | -0.070* | NS | -3.601** | 4.103** | NS | 0.897 | 18 |
| | SG | -17.395 | -0.116** | NS | -1.168** | NS | 1.178* | 5.783** | 0.746 | 24 |
| | MG | -10.623 | NS | NS | NS | NS | NS | NS | 0.349 | 24 |
| | LG | -12.522 | NS | NS | NS | NS | 1.306** | NS | 0.442 | 24 |
| Q. dealbata | US | -27.024 | -0.21* | 0.008* | 0.458* | NS | NS | 2.308** | 0.775 | 24 |
| | SG | -17.865 | -0.082* | NS | -0.972** | NS | 1.1015* | 4.820** | 0.706 | 24 |
| | MG | - 7.711 | NS | NS | NS | NS | NS | NS | 0.274 | 24 |
| | LG | - 9.213 | 0.111* | NS | NS | NS | NS | 0.061* | 0.481 | 24 |
| Q. griffithii | US | -12.417 | NS | -0.012** | 0.425* | -0.643** | 0.929** | 2.067** | 0.913 | 24 |
| | SG | - | - | - | - | - | - | - | - | - |
| | MG | 7.515 | NS | NS | NS | -0.888** | NS | -2.16* | 0.840 | 24 |
| | LG | - 7.956 | NS | NS | NS | NS | 0.912** | NS | 0.440 | 24 |
| Q. glauca | US | 9.465 | NS | 0.030** | 1.504** | -3.153** | 1.948** | NS | 0.930 | 24 |
| | SG | -15.538 | -0.121** | NS | -1.169** | NS | NS | 5.868** | 0.703 | 24 |
| | MG | 0.995 | NS | NS | NS | -0.047** | NS | -0.298** | 0.690 | 24 |
| | LG | -17.730 | NS | NS | NS | NS | 1.849** | -0.231** | 0.450 | 24 |

* Significant at $P<0.05$
** Significant at $P<0.01$
NS Not significant

influence habitat heterogeneity (Orians 1982, Nunez Farifan and Dirzo 1988, McCarthy and Facelli 1990) which in turn affect the performance of individuals in the gaps (Dirzo 1988). The results of this study indicate that the species differed in their growth responses to gaps and understorey conditions. Seedlings of S. khasiana, M. esculenta and T. tomentosa showed better growth in medium and large gaps, while the three oak species showed little response to canopy openings and registered higher shoot growth rate in the understorey region. This is in accordance with the results of Brokaw (1985b) who found higher height growth rates in the gaps for pioneer species than the primary species, but does not support the findings of Augspurger (1984b) and Popma and Bongers (1988) who reported enhanced growth for all species in gaps. Spatial variation in light among gaps and understorey and its effect on tree growth has been extensively studied (Denslow 1980, Whitmore 1982, Brokaw 1985 and Canham and Marks 1985).

Simultaneous increase in LAI and shoot growth rates of different species in various micro-habitats does not agree with the findings of Canham (1988), who reported an increase in LAI in sugar maple saplings without any significant increase in shoot length. Based on the growth response of seedlings to the increased light intensity along the increasing gap size gradient, S. khasiana and

M. esculenta which showed maximum growth in the large gaps may be classified under the shade intolerant or gap phase species, while Q. dealbata, Q. griffithii and Q. glauca may be termed as shade tolerant or mature phase species. T. tomentosa seedlings whose performance was better in the small and medium gaps may be regarded as a species occupying an intermediate position between shade tolerant and shade intolerant species distributed along the understorey-gap size gradient in the forest.

The role of soil moisture in influencing growth of seedlings has also been studied by McLeod and Murphy (1977) and Mueller Dombois (1980). Leaf litter, apart from being the chief source of nutrients, also affects soil moisture and temperature of the forest floor (Hart et al 1962 Campbell 1982 ), thereby indirectly affects seedling growth by enhancing availability of soil moisture and nutrients. In this forest peak seedling growth during rainy season could be attributed to the increased availability of nutrients due to rapid decomposition of litter on the forest floor and also to the higher moisture content of the soil.

Thus the differential growth response of seedlings of different tree species to almost same set of microenvironmental conditions that varied along the gap size gradient

may be a species specific attribute which influence the physiological ability of plant for efficient utilization of environmental resources.

# 8 SEED AND SEEDLING HERBIVORY IN GAPS AND UNDERSTOREY

Survival and growth of tree juveniles in forest are determined by a large number of biotic and abiotic factors of forest microenvironment. Among the biotic factors plant-pathogen interactions and seed and seedling predation are considered more important (Schupp 1989). Many workers have suggested that predispersal seed predation play an important role in determining the reproductive success of forest trees (Janzen 1979, Louda 1978, 1983, Desteven 1981, Uhl et al. 1988). Leaf loss to herbivory, particularly during seedling stage, is a major factor that determines the growth and survival of plant species. Loss to insect herbivory may vary among the individuals of a population, between different species (Harper 1969, Maiorana 1981, Crawley 1983) and also along an environmental gradient (Janzen 1971, Bach 1983, Burdon 1987). Light and soil moisture induced plant water stress has been hypothesized

to be the mechanism underlying insect outbreaks (White 1978, Louda and Rodman 1983b, Louda et al 1987). Increased light intensity and soil moisture stress cause physiological changes in trees that render them susceptible to insect attack (Mattson 1980, Bjorkman et al 1981, Cates and Alexander 1982). In addition to the array of environmental factors that effect the susceptibility of the host to herbivore attack, leaf age and leaf quality also influence herbivore feeding behaviour (Scriber and Slansky 1981, Corre 1983). Poor nutritional quality of foliage is a possible anti-herbivore adaptation in forest trees (Feeny 1976, Rhoades 1985).

Since the structure and density of overhead canopy influence the understorey environment in the forest, creation of gaps may indirectly affect the pattern of seedling herbivory by altering the microenvironment. Newbery and Foresta (1985) and Uhl et al (1988) have studied the tree seedling response to herbivores in the gaps and understorey of tropical and temperate forests. Intensity of predation has also been shown to vary between the persistant and pioneer species (Newbery and Foresta 1985). Studies describing plant-herbivore interaction in the forests of N.E. India are limited (Khan and Tripathi 1991).

This chapter analyses the effect of insect herbivory on seed and seedlings of dominant trees in the Mawphlang

forest. The extent of pre- and post-dispersal seed predation have been studied in three oak species and intensity of seedling defoliation has been assessed in six tree species growing in the gaps and understorey. The effect of light environment and soil moisture on herbivore damage along a gap size gradient has also been analysed to explain the role of sun-shade gradient in influencing the leaf damage of the tree seedlings.

## METHODS

Seed production by Q. dealbata, Q. griffithii, Q. glauca and S. khasiana was estimated for marked trees in the forest. Ten trees of Q. dealbata and Q. griffithii and five trees of Q. glauca and S. khasiana in each of the three dbh classes viz. 10-20 cm, 20-30 cm and 30-40 cm, were marked for the study. While selecting the tree, effort was made to ensure that no other tree of the same species was present in a radius of 35-40 m. Seed production per tree ($S_p$) for the three oak species was estimated in 1988, 1989 and 1990 and for S. khasiana in 1989, 1990 and 1991 using the following formula:

$$S_p = T_b \times T_{sb} \times T_i \times T_a$$

where $T_b$ is the number of main branches per tree, $T_{sb}$ is

the number of subbranches per main branch, $T_i$ is the number of infloresence per subbranch and $T_a$ is the average number of acorns (in case of Quercus spp.) or seeds (in S. khasiana) per infloresence. The data was statistically analysed using 2-way ANOVA to study the yearly variation and effect of dbh class on seed production.

Seed predation by insects and rodents in oak species was studied at pre- and post-dispersal stages during 1989 and 1990. Predation in S. khasiana could not be studied because of light and wind dispersed nature of seeds. In case of the oak species, 5 seed traps of 1m x 1m size were randomly laid under each tree and the seeds collected in these traps were counted after the period of seed fall was over. The seeds in the seed traps were catagorized into 3 groups viz. insect damaged, partially rodent damaged and intact (Plate 8.1). Based on the number of seeds per trap and area of canopy cover, total number of seeds in the various categories under the tree canopy were calculated. Per tree pre-dispersal seed loss to rodents ($SL_r$) was calculated as follows:

$$SL_r = S_p - S_{fl}$$

where, $S_p$ is the total seed production per tree and $S_{fl}$ is the number of seeds present under the tree canopy.

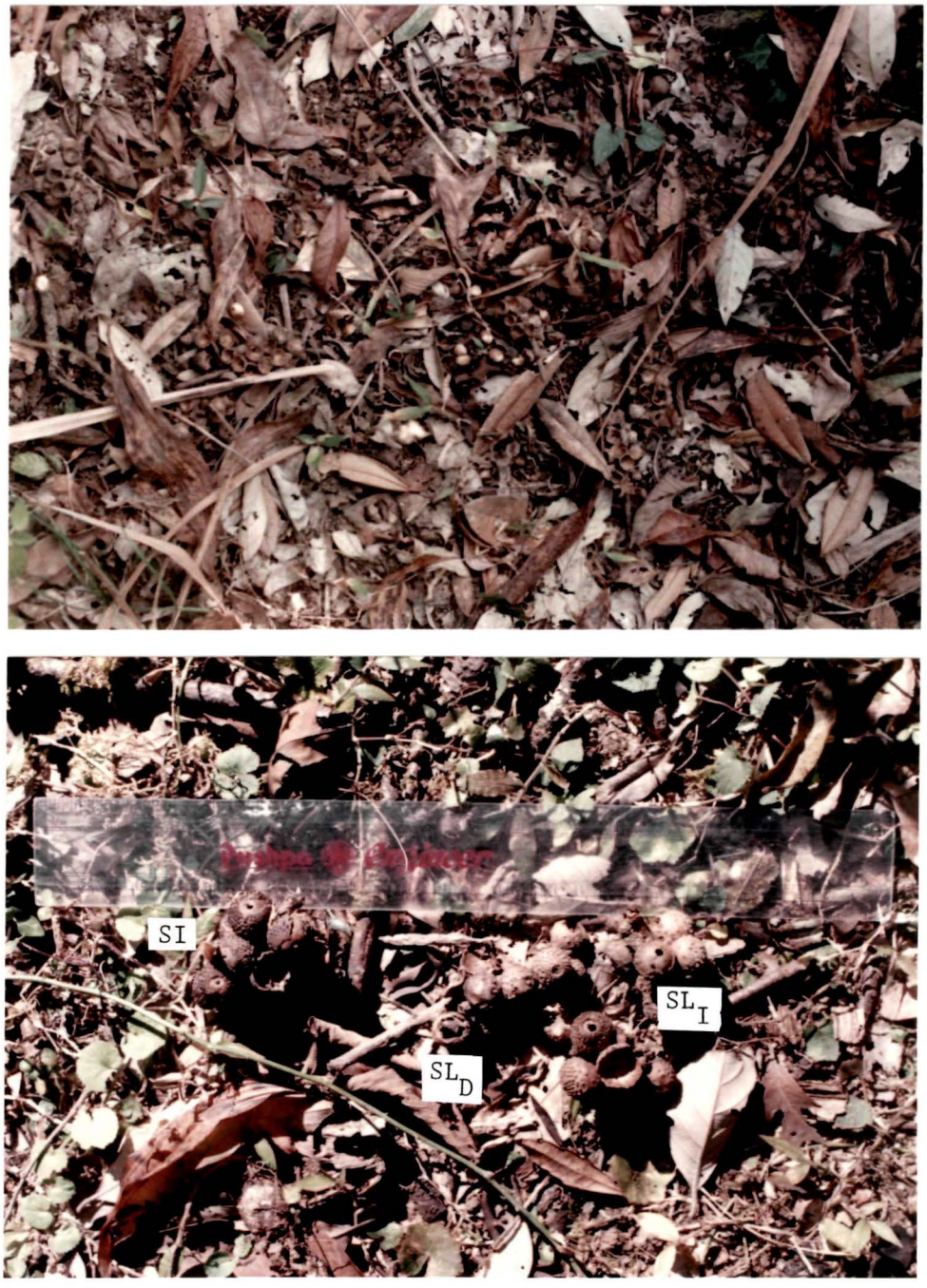



Plate 8.1. Intact and predated oak seeds on the forest floor. SI-Intact seeds; $SL_D$-Rodent predated; $SL_I$-Insect predated.

Total seed loss before dispersal was then estimated as follows:

$$SL = SL_r + SL_i + SL_d$$

where, SL is the total pre-dispersal seed loss per tree, $SL_i$ is the seed damaged by insects and $SL_d$ is the number of seeds partially damaged by the rodents.

The intact seeds (SI) were left in the seed traps and their fate was observed after 3 months to estimate the post-dispersal seed predation. Post-dispersal seed loss was calculated as follows:

$$SL_{(pd)} = SI - [SI_{(pd)} + SG]$$

where, $SL_{(pd)}$ is the post-dispersal seed loss, SI is the number of intact seeds on the forest floor after seed fall, $SI_{(pd)}$ is the number of rotten seeds on the forest floor 3 months after seed fall and SG is the number of germinated seeds. The pre- and post-dispersal seed losses were expressed as percentages of total seed production and total number of intact seeds on forest floor after seed fall, respectively.

The studies on seedling herbivory were conducted in the twelve treefall gaps classified into three size classes

and in the ten permanent quadrats in the understorey as described in Chapter 6. All the tagged tree seedlings in these sampling units were carefully examined for leaf damage and only the predated seedlings were considered for the study. Total leaf area and the area of damaged portion per seedling were measured from August, 1990 at three months interval and the percentage of leaf area damaged per seedling was calculated. A portable leaf area meter (Licor, USA) was used to estimate the leaf area. The data recorded during August, November, February and May were considered representatives of rainy, autumn, winter and spring seasons, respectively. Depending on the extent of leaf damage the seedlings were classified into eight leaf damage classes viz. 20-30%, 31-40%, 41-50%, 51-60%, 61-70%, 71-80%, 81-90% and 91-100%.

Correlation coefficients (r) between peak leaf damage and photon flux density and soil moisture during the corresponding period (autumn) were calculated in order to study the effect of these two microenvironmental factors on seedling herbivory.

## RESULTS

### Seed production

Seed production significantly varied ($P < 0.01$) between the

years and dbh classes in all the four species (Fig.8.1). Seed production was minimum in Q. dealbata and maximum in Q. glauca and Q. griffithii. In Q. dealbata seed production was maximum in 1990 and minimum in 1988. Q. glauca and Q. griffithii showed highest production in 1988 and lowest in 1990. Seed production increased with increase in dbh in all the four species. S. khasiana produced more seeds during 1990 than during 1991 in all the three dbh classes.

**Seed predation**

Seed predation by rodents and insects during pre- and post-dispersal periods in oak species was estimated during 1988 and 1989. At pre-dispersal stage, percentage of seed predation was low (52-66%) in Q. dealbata and high (90-95%) in Q. glauca and Q. griffithii. But during post-dispersal stage predation was very high (96-98%) in all the species (Table 8.1). In general, seed predation was more during 1990 than 1991.

**Patterns of leaf herbivory**

All the six species showed maximum leaf damage during autumn and minimum during spring. The proportion of leaf damage was minimum in the understorey and it increased with increase in gap area (Fig.8.2). The shade tolerant oak species were found to be more susceptible to leaf

Fig.8.1. Year wise variation in seed production of trees in three DBH classes of four species in the Mawphlang forest. 1988 (▨), 1989 (▭), 1990 (▩), 1991 (■).

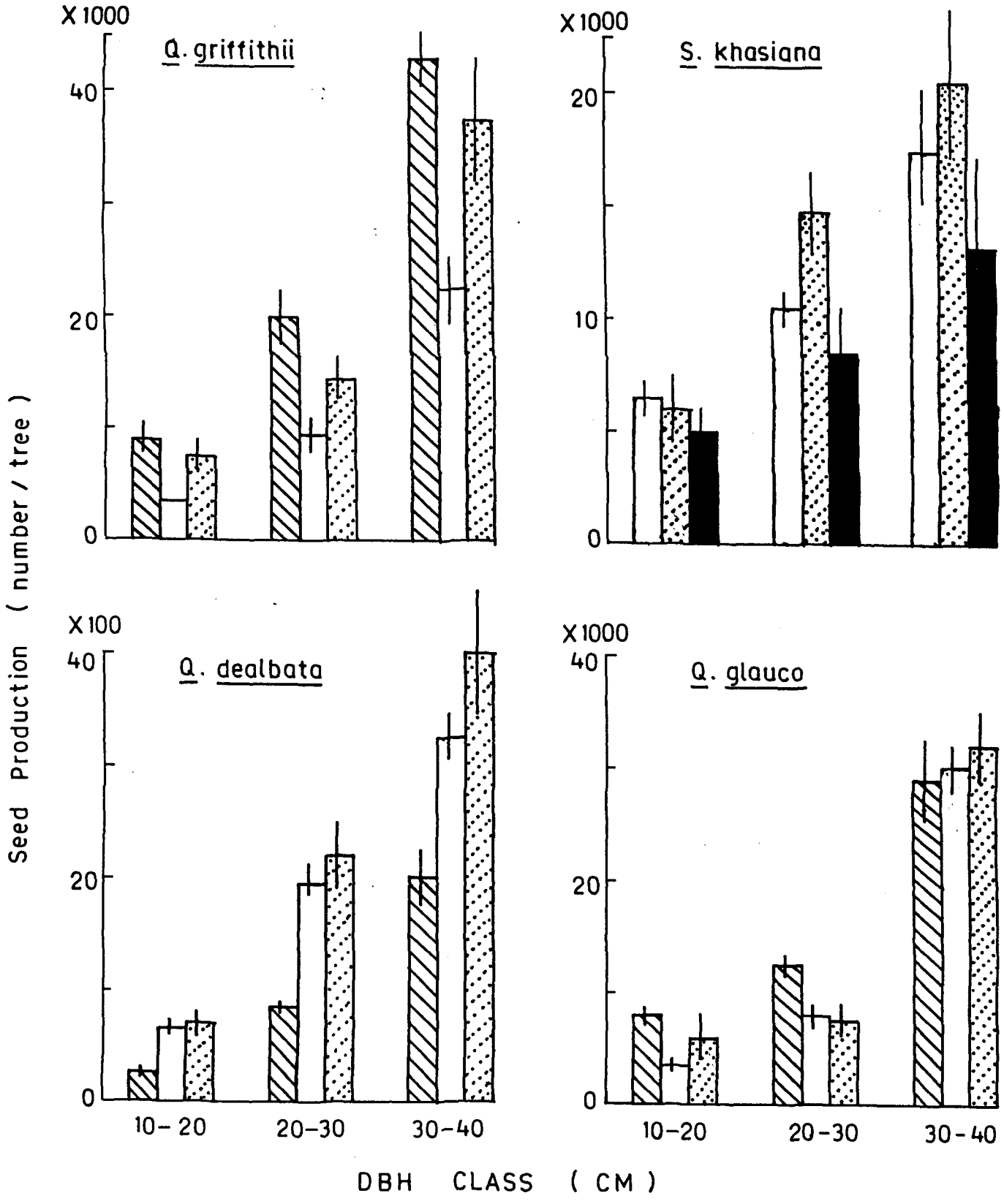
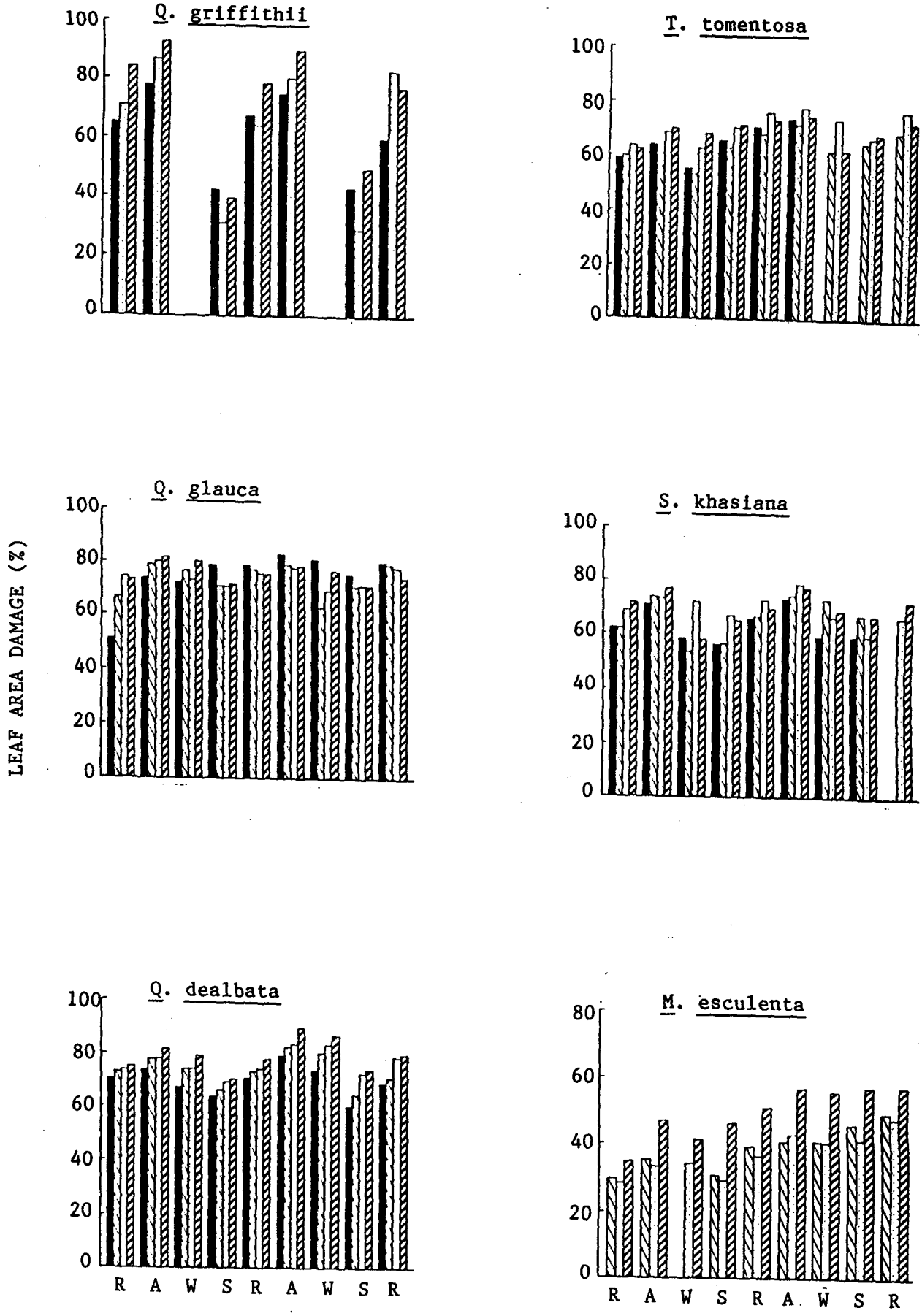

X 1000
Q. griffithii
40
20
0
X 1000
S. khasiana
20
10
0
X 100
Q. dealbata
40
20
0
X 1000
Q. glauco
40
20
0
10-20
20-30
30-40
10-20
20-30
30-40
Seed Production ( number / tree )
DBH CLASS ( CM )

Table 8.1. **Pre dispersal seed predation (% of total production) and post dispersal seed predation (% of freshly fallen intact seeds under the tree canopy) of three oak species by insects and rodents during 1989 and 1990 in the Mawphlang forest.**

| Tree species | Predation (%) | | | |
|---|---|---|---|---|
| | Pre-dispersal period | | Post-dispersal period | |
| | 1989 | 1990 | 1989 | 1990 |
| Quercus dealbata | 52.46 ± 3.03 | 65.87 ± 4.29 | 97.0 ± 11.4 | 95.61 ± 0.28 |
| Quercus glauca | 90.48 ± 1.13 | 94.06 ± 1.05 | 98.56 ± 0.18 | 98.82 ± 0.22 |
| Quercus griffithii | 93.72 ± 2.05 | 95.35 ± 0.79 | 97.88 ± 0.32 | 98.21 ± 0.19 |

± S.E.

Fig.8.2. Seasonal variation in leaf area damage (per cent of total leaf area per seedling) by insect herbivory in understorey (■) and small (▧), medium (▩) and large (▨) gaps during Rainy (R), Autumn (A), Winter (W) and Spring (S) seasons.


Q. griffithii
T. tomentosa
Q. glauca
S. khasiana
Q. dealbata
M. esculenta
LEAF AREA DAMAGE (%)
100
80
60
40
20
0
R A W S R A W S R
SEASONS

herbivory than the shade intolerant S. khasiana. Seedlings of M. esculenta were least predated. Figures 8.3 and 8.4 show the distribution of seedlings into different damage classes in gaps and understorey. In case of Q. dealbata highest number of damaged seedlings was found in the medium gaps and lowest in the large gaps. However, the number of plants belonging to higher leaf damage class was more in the large gaps (Fig.8.3). Q. glauca and Q. griffithii showed maximum loss in the understorey and large gaps. In general, percentage of leaf damage was more during 1990, but the number of affected seedlings was less than the preceding year (Figs. 8.3 and 8.4).

Among the shade intolerant species, the proportion of leaf damage per seedling was maximum in S. khasiana. The number of damaged seedlings was also higher in this species. In this case maximum damage of about 82% was observed during autumn in the large gaps, values being more during first year of the study. But M. esculenta and T. tomentosa showed higher damage during 1991 than 1990. These species showed highest damage in large and medium sized gaps (Fig.8.4).

Table 8.2 gives the correlation coefficients between two important microenvironmental variables (photon flux density and soil moisture) and percentage leaf damage along a gap size gradient for six tree species. Photon

Fig.8.3. Seasonal variation in frequency distribution of seedlings into different classes (1. 20-30; 2. 30-40; 3. 40-50; 4. 50-60; 5. 60-70; 6. 70-80; 7. 80-90; 8. 90-100%) based on leaf damage (per cent of leaf area damaged per seedling) in gaps and understorey during 1988-89 (-) and 89-90 (---). Rainy (R), Autumn (A), Winter (w), Spring (S).

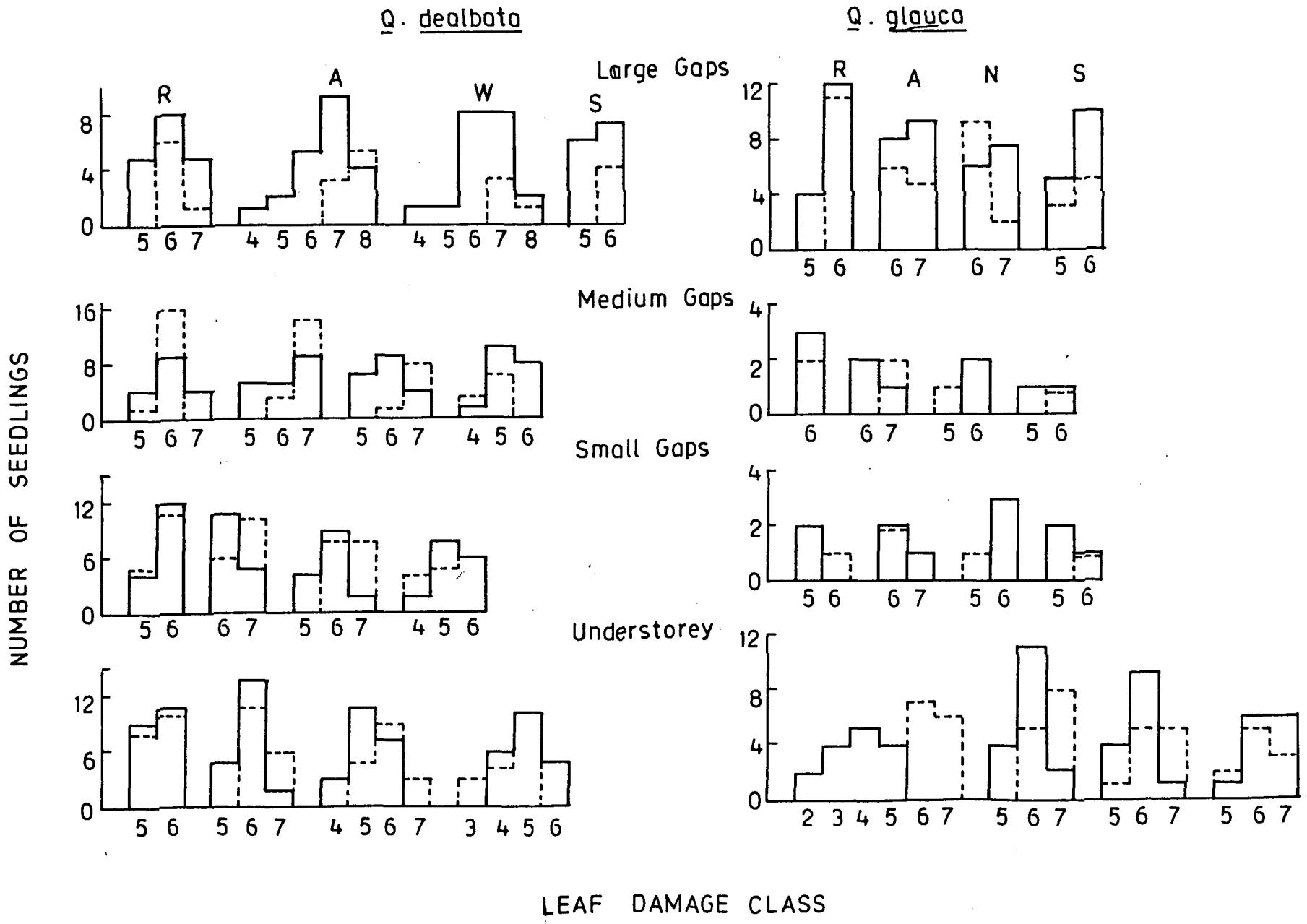

Q. dealbata
Q. glauca
Large Gaps
Medium Gaps
Small Gaps
Understorey
R
A
W
S
N
NUMBER OF SEEDLINGS
LEAF DAMAGE CLASS

Fig.8.4. Seasonal variation in frequency distribution of seedlings into different classes (1. 20-30; 2. 30-40; 3. 40-50; 4. 50-60; 5. 60-70; 6. 70-80; 7. 80-90; 8. 90-100%) based on leaf damage (per cent of leaf area damaged per seedling) in gaps and understorey during 1988-89 (-) and 89-90 (---). Rainy (R), Autumn (A), Winter (W), Spring (S).

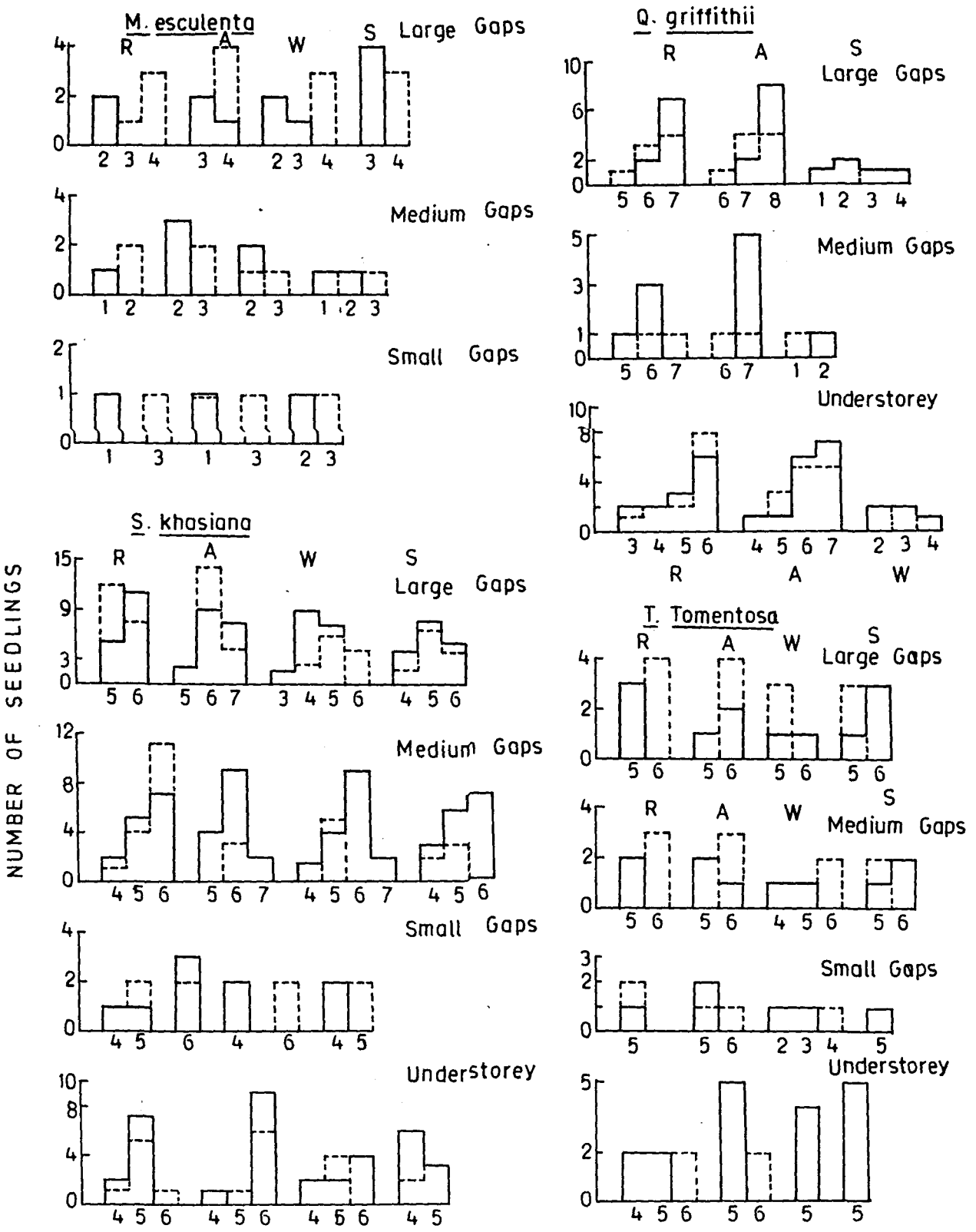

M. esculenta
R
A
W
S
Large Gaps
Medium Gaps
Small Gaps
Understorey
Q. griffithii
S. khasiana
T. Tomentosa
NUMBER OF SEEDLINGS
LEAF DAMAGE CLASS

Table 8.2. **Correlation coefficient 'r' between percent leaf damage and Photon flux density and soil moisture during peak season of leaf predation (autumn) along a gap size gradient.**

| Tree species | Pearson's Correlation coefficient 'r' | | n |
|---|---|---|---|
| | Photon Flux Density | Soil moisture (%) | |
| M. esculenta | 0.541* | -0.807** | 24 |
| Q. dealbata | 0.425* | -0.895** | 26 |
| Q. glauca | 0.490* | -0.885** | 26 |
| Q. griffithii | 0.907** | -0.237 | 18 |
| S. khasiana | 0.630** | -0.577* | 26 |
| T. tomentosa | 0.253 | -0.885** | 26 |

* Significant at $P<0.01$

** Significant at $P<0.001$

flux density showed a significant positive correlation with leaf damage in all species except T. tomentosa. Conversely, soil moisture was negatively correlated with leaf damage in all except Q. griffithii. Herbivory in Q. griffithii and S. khasiana was more strongly correlated to the light environment in the gaps, while in Q. dealbata, Q. glauca, T. tomentosa and M. esculenta it was influenced more by the soil moisture regime than the solar irradiance.

## DISCUSSION

Composition of seed rain is one of the best ways of predicting the composition of species colonizing in the gaps or in the forest as a whole. The consequences of seed rain on forest floor would ultimately depend on the fate of seeds which may either be predated or be dispersed to 'safe sites' and germinate to contribute to the population of seedlings occupying gaps and understorey of the forest (Denslow and Gomez Diaz 1990). Results presented so far indicate that in spite of marked yearly variation in seed production in all the four species studied, total seed output per tree was generally high. For instance, high seed predation both at the pre- and post-dispersal stages in all the three oak species could be one of the many factors responsible for their low

seedling recruitment in this forest (Table 6.1). Louda (1983) also showed that seed predation was a critical factor limiting the seedling recruitment in case of Haplopappus venetius. Findings of many other workers also suggest that pre-dispersal seed predation could be a major cause of plant mortality (Salisbury 1942, Janzen 1971 and Harper 1971). Thus lower pre-dispersal seed predation in Q. dealbata may account for its higher seedling population than Q. glauca and Q. griffithii in both gaps and understorey (Table 6.1). Total seed loss to predation ranged from 91% in Q. dealbata to 98% in Q. griffithii and Q. glauca. Less than 1% of the seeds produced in Q. dealbata germinated, while the germination percentage was still lower in Q. glauca and Q. griffithii (0.03%). The rest of the seeds were either found to be rotten or presumably dispersed. The exceptionally low seed germination and consequently low tree seedling recruitment as discussed in Chapter 6, further corroborates that seed predation strongly limits the seedling establishment in this forest forest.

Insect herbivores were found to be the primary cause of leaf damage in this forest. Higher damage in shade tolerant oak species than in shade intolerant species in gaps and understorey does not conform with the findings of Feeny (1976) and Rhoades and Cates (1976) who showed

that slow growing primary species defend their foliage by increased production of tanins which reduce the palatability of the leaves to predators. The increase in percent leaf damage along the increasing gap size gradient could be related to the increase in photon flux density along the gradient. This assumption finds support from the findings of Bigger 1981, Lincoln and Mooney 1984, and Harrison 1987 who reported that increased light may increase damage rates by herbivores.

Decline in water content in surface soil due to high light intensity in gaps, leading to greater evaporation losses may be another reason for increased levels of herbivory in gaps as has been discussed by Fennah (1965), Louda (1983) and White (1978). Significant negative correlation between leaf damage in most of the species studied and soil moisture in the gaps and understorey also lend support to the argument that variation in the plant water relations across the sun-shade gradients existing between gaps and understorey may account for the differential response of plants to herbivore damage.

# 9 GENERAL DISCUSSION

The conditions in a climax broadleaved forest are intensely inimical for the recruitment and growth of new individuals who have to compete with the established plants for essential resources. Canopy gaps created by treefalls provide favourable conditions for the growth of tree seedlings and in most closed canopied forests tree regeneration is dependant upon the occurence of gaps in the community (Milthrope 1961, Miles 1974). An understanding of tree replacement process in treefall gaps also provides a better insight into its role in promoting high species diversity (Connell 1978, Denslow 1980) and maintaining an equilibrium in species composition (Hubbell 1984) in the forest communities.

Gap openings may be of any size and can arise naturally either by the death of individual trees or by shedding of a branch. Gaps are also created by the action of rain, storm and wind which uproot the trees or snap off the branches (Oldeman 1972, Doyle 1981, Brokaw 1982b and Dunn et al. 1982). unstable soil and topography are also known to promote gap creation in the forests (Webb 1968, Oldeman 1978, Hartshorn 1978, Putz and Milton 1982, Lawton 1982). In the Mawphlang forest, heavy precipitation during rainy season and high wind speed during spring are the most proximate agents to gap creation. These factors have created single and multiple treefall gaps which vary in shape and size. Dumbbell-shaped gaps were most common, while circular and trapezium shapes were infrequent. The size of the gaps varied between 34 $m^2$ and 950 $m^2$. On the basis of mean gap size, the gaps studied in the Mawphlang forest may be put under intermediate category in the range reported by Brokaw (1982a) and Mutoji-a-Kazadi (1977) (cited by Torquebian 1981) from other tropical forests of the world. The proportional area of infrequent large gaps was found to be more than the frequently occurring smaller gaps. Different microsites such as root mats, mounds and pits were also observed in the gaps, but none of the tree species were found to be exclusive to any of these microsites as have been reported by many workers (Beatty 1984, Beatty and Stone 1985, Beatty and Sholes 1988).

Canopy openings have been shown to alter many aspects of forest understorey microenvironment, which in turn influence the species diversity in the forest. Lee (1978) has reported that spatial and temporal microenvironmental heterogeneity produced by the treefalls increases with gap size. Denslow (1980), Hartshorn (1978, 1980) and Brokaw (1982b, 1985a) have argued that gap size is also a critical variable for the recruitment and establishment of different species.

Results of this study indicate that among the six microenvironmental variables studied, only photon flux density and soil moisture varied significantly along the gap size gradient. PC I obtained from Principal Component Analysis of the six microenvironmental variables was positively correlated with gap area, while tree seedling density and species diversity were negatively related to PC I, thereby indicating an important role of gap size in determining the species diversity and regulating tree seedling density in gaps.

The effect of gap size on the abundance of different tree seedlings was analysed with the help of rank abundance curves. These curves showed that shade tolerant species Q. dealbata was dominant in the small gaps while the shade intolerant pioneers S. khasiana and M. esculenta were abundant in the larger gaps which also had higher

species richness. Ordination of gaps on the basis of Principal Component Analysis of shade tolerant and shade intolerant species in gaps resulted into clustering of the twelve gaps into three distinct groups. The smaller gaps having higher density of shade tolerant species forming one group (gap nos. 1 to 9), while the larger gaps with higher density of shade intolerant species constituting another cluster (gap nos. 10 and 12). Gap no. 11 with shade tolerant and shade intolerant species in equal proportions formed a group of its own.

Species diversity in the gaps and understorey has been discussed on the basis of $\alpha$- and $\beta$-diversities. $\alpha$-diversity, the mean number of species per gap or sampling unit, is low in the Mawphlang forest in comparison to other tropical forests of the world (Brokaw and Scheiner 1989). In this forest, $\alpha$-diversity of trees is higher in the gaps than in the adjacent understorey, suggesting that gaps provide favourable conditions for growth and establishment of a number of species which require greater light intensity. $\beta$-diversity which measures the extent of species replacement along environmental gradients and reflects the extent of similarity among the gaps (Whittaker 1972, Brokaw and Scheiner 1989) was lower for the tree seedlings than the herbs and shrubs. In this forest, $\beta$-diversity for the tree seedlings is lower than that in BCI forest studied by Brokaw and Scheiner (1989).

Distance of parent trees from the gaps, their seed dispersal mechanism and gap size specificity of some tree species might have contributed to the lower β-diversity. Nevertheless, its increasing trend over a period of two years suggests that the gaps tend to become more similar with the passage of time. The increase may be attributed to the incresed abundance of certain species new to gaps and also to the increase in abundance of those which were already present in the gaps.

Treefalls create new habitats and alter the existing ones, thereby offering specialized regeneration niches for a number of species which exploit them for better growth and survival in gaps than in the understorey (Brokaw 1985b and Welden et al. 1991). One of the important effects of gap creation is the change in the microenvironment of the forest floor which markedly influence the growth and survival of juveniles of different tree species. In general, gaps are characterized by an increase in light intensity and availability of other resources. The extent to which the seedlings utilize these resources for their growth and establishment is a species specific character (Denslow 1980). Even after the seedlings have established in the gaps, their ultimate success depends on their ability to reach canopy status. Results of the study in Mawphlang forest indicate that the process of tree regeneration is very slow and gaps are essential

for the establishment of pioneer species like S. khasiana, M. esculenta and T. tomentosa which show better seed germination in gaps. Relatively higher temperature in gaps and longer exposure to solar radiation might be the cause of better germination of these species. Q. dealbata, a shade tolerant species also showed enhanced germination in gaps than the forest understorey. Germination behaviour of tree species also was reflected on their seedling recruitment patterns. Density of S. khasiana showed a significant positive correlation with gap size thereby indicating a gap dependant regeneration behaviour. Q. dealbata showed high seedling density both in gaps and understorey. Q. glauca and Q. griffithii showed higher recruitment in the understorey, while M. esculenta and T. tomentosa seemed to prefer small and medium sized gaps. However, in general, seedling recruitment of the dominant species in this forest was very low (30-720/ha). inspite of high seed production (3662-42,856 seeds/tree).

The consequences of seed rain on the forest floor ultimately depends on the fate of the seeds which are either predated or dispersed to 'safe sites'. The fate of the seeds produced by the three oak species in this forest was studied during 1989 and 1990. The results summarised in the flow diagrams (Fig.9.1 and 9.2) indicate that in spite of yearly variation in the total seed output, the percentage of seeds that germinated and contributed

to the seedling population in the forest was similar during both the years. Importance of seed predation in limited seedling recruitment has been discussed by Louda (1983) and Schupp (1988). High seed predation both at pre- and post-dispersal stages in all the three oak species could be one of the factors responsible for their extremely low germination and seedling recruitment in the forest. Among the three oak species, lower pre-dispersal predation and high germination (0.6%) in Q. dealbata may account for its higher seedling population in the gaps and understorey. Conversely, higher pre-dispersal percentage and lower germination of seeds (0.03%) in case of Q. glauca and Q. griffithii were responsible for their lower recruitment both in the gaps and understorey (Fig.9.1 and 9.2). The other three species, S. khasiana, M. esculenta and T. tomentosa showed large variation in recruitment pattern in gaps of different sizes but exhibited a similar mortality pattern by registering high mortality during winter, both in the 1st and 2nd year of seedling growth. In case of S. khasiana, 100% mortality was observed in the understorey and small gaps. Seedling mortality in case of the oak species was negligible. Peak mortality during winter appears to be due to low temperature and high soil moisture stress caused by low rainfall and high evapo-transpiration losses.

Fig.9.1. Fate of seeds produced by three oak species in the Mawphlang forest during 1989. All values are on per tree basis.

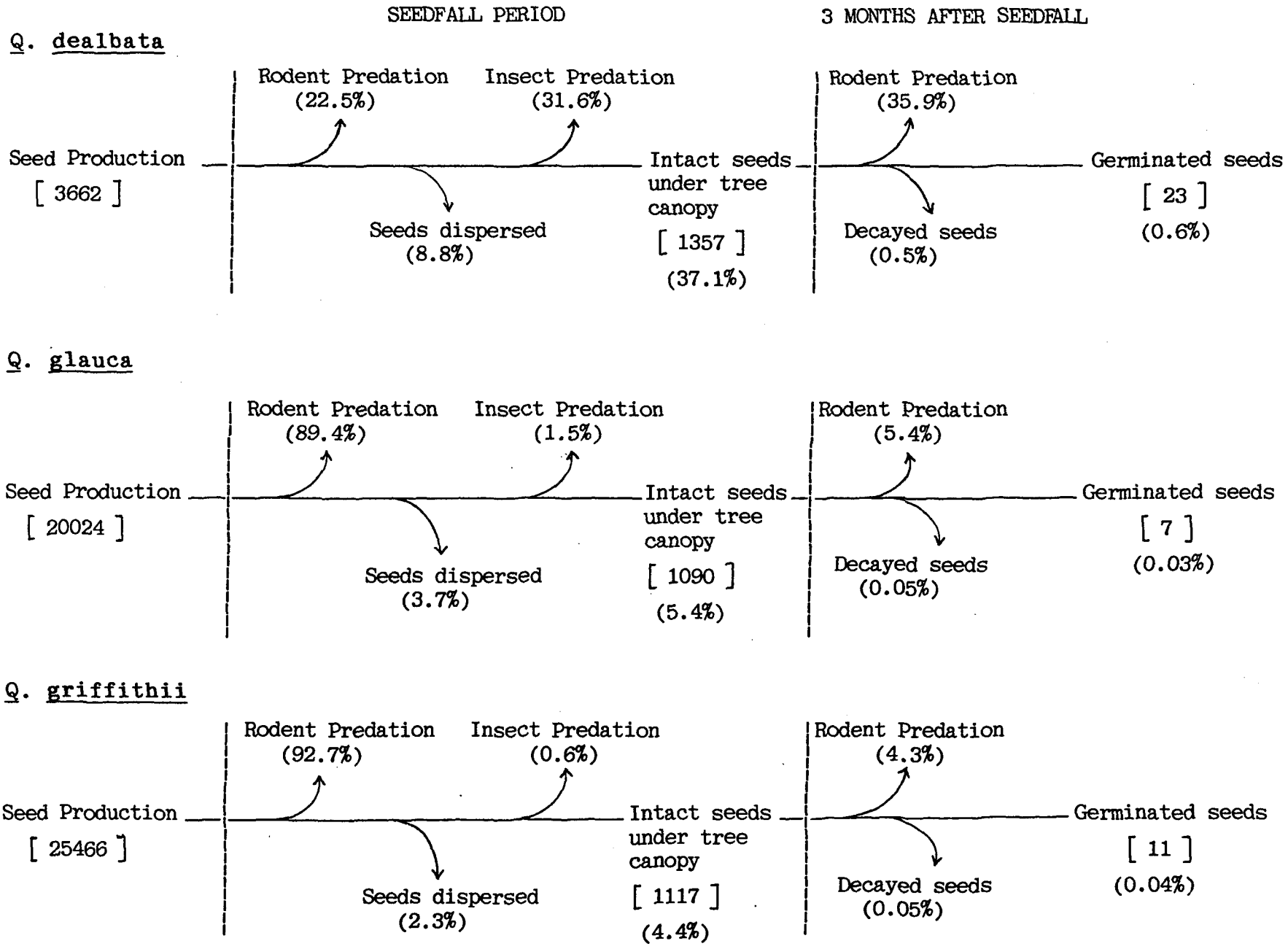
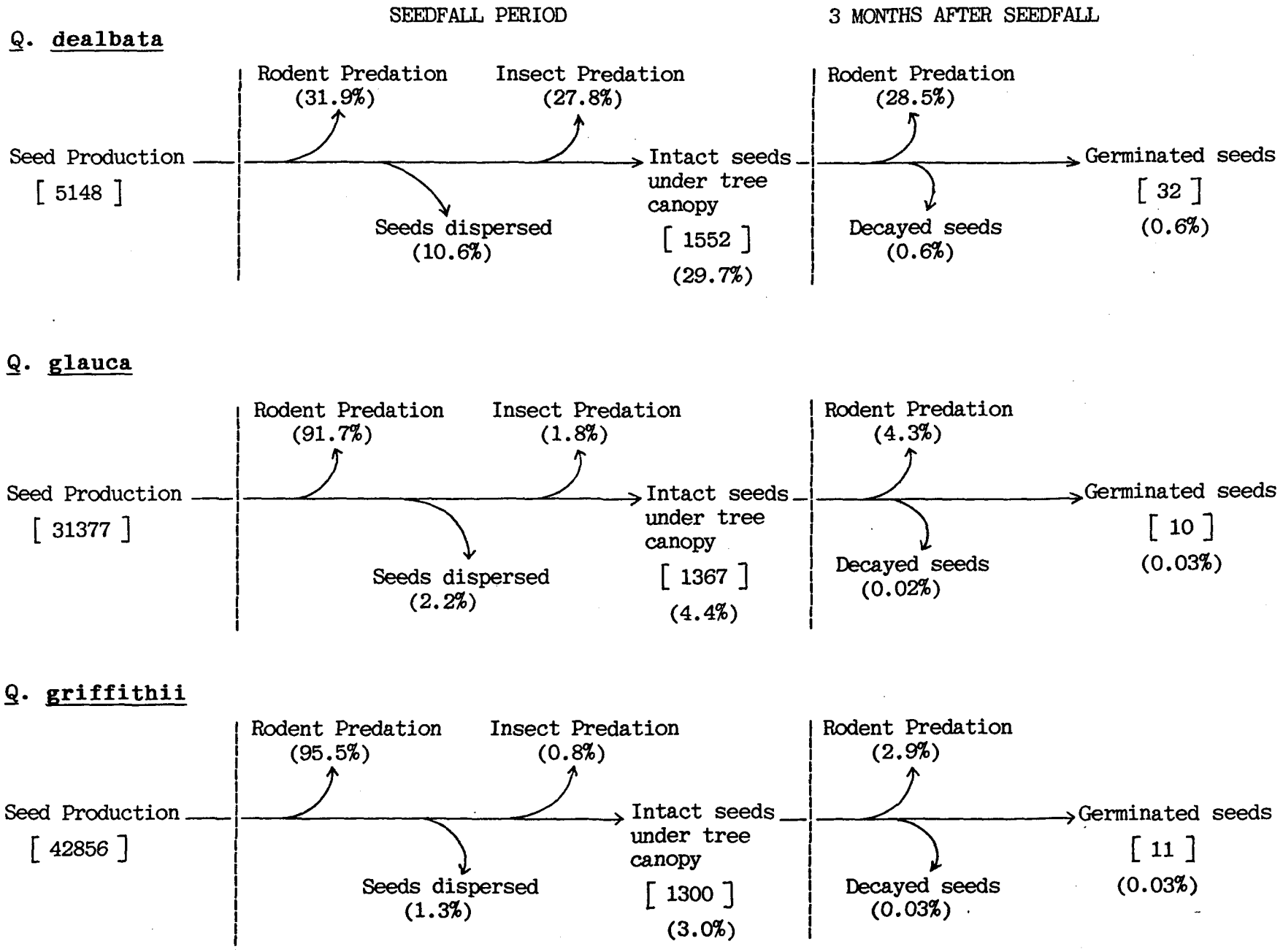

SEEDFALL PERIOD
3 MONTHS AFTER SEEDFALL
Q. dealbata
Rodent Predation (22.5%)
Insect Predation (31.6%)
Seed Production [ 3662 ]
Seeds dispersed (8.8%)
Intact seeds under tree canopy [ 1357 ] (37.1%)
Rodent Predation (35.9%)
Decayed seeds (0.5%)
Germinated seeds [ 23 ] (0.6%)
Q. glauca
Rodent Predation (89.4%)
Insect Predation (1.5%)
Seed Production [ 20024 ]
Seeds dispersed (3.7%)
Intact seeds under tree canopy [ 1090 ] (5.4%)
Rodent Predation (5.4%)
Decayed seeds (0.05%)
Germinated seeds [ 7 ] (0.03%)
Q. griffithii
Rodent Predation (92.7%)
Insect Predation (0.6%)
Seed Production [ 25466 ]
Seeds dispersed (2.3%)
Intact seeds under tree canopy [ 1117 ] (4.4%)
Rodent Predation (4.3%)
Decayed seeds (0.05%)
Germinated seeds [ 11 ] (0.04%)

Fig.9.2. Fate of seeds produced by three oak species in the Mawphlang forest during 1990. All values are on per tree basis.


SEEDFALL PERIOD
3 MONTHS AFTER SEEDFALL
Q. dealbata
Rodent Predation (31.9%)
Insect Predation (27.8%)
Seed Production [ 5148 ]
Seeds dispersed (10.6%)
Intact seeds under tree canopy [ 1552 ] (29.7%)
Rodent Predation (28.5%)
Decayed seeds (0.6%)
Germinated seeds [ 32 ] (0.6%)
Q. glauca
Rodent Predation (91.7%)
Insect Predation (1.8%)
Seed Production [ 31377 ]
Seeds dispersed (2.2%)
Intact seeds under tree canopy [ 1367 ] (4.4%)
Rodent Predation (4.3%)
Decayed seeds (0.02%)
Germinated seeds [ 10 ] (0.03%)
Q. griffithii
Rodent Predation (95.5%)
Insect Predation (0.8%)
Seed Production [ 42856 ]
Seeds dispersed (1.3%)
Intact seeds under tree canopy [ 1300 ] (3.0%)
Rodent Predation (2.9%)
Decayed seeds (0.03%)
Germinated seeds [ 11 ] (0.03%)

The growth response of tree seedlings in different micro-habitats of the forest was similar to their survival pattern. S. khasiana and M. esculenta showed higher growth rate in the large gaps, while the three oak species performed better in the understorey region. Seedlings of T. tomentosa showed best growth in the small and medium sized gaps. Peak seedling growth during rainy season may be attributed to the favourable temperature and edaphic conditions including availability of different mineral elements as a result of rapid decomposition of litter on the forest floor. The gap size specificity with respect to survival and growth exhibited by different species may be a manifestation of niche partitioning among these species. Similar response by different species has also been observed by Ricklefs (1977), Florence (1991), Orians (1982) and Brokaw (1985a, b).

Augspurger (1984) has used the survival and growth rate of seedlings in shade as an index of shade tolerance. Several other workers (Martinez-Ramos 1985, Popma and Bongers 1988 and Canham 1988) have also reported similar ecological differentiation among species and have classified them according to their degree of shade tolerance. The response of the six tree species to canopy openings differed distinctly in the Mawphlang forest. Species like S. khasiana and M. esculenta performed better along

the increasing gap size gradient, while the three Quercus species were indifferent to gap creation as far as their survival was concerned and they showed better growth in the understorey. T. tomentosa which showed best growth in the small and medium gaps seem to occupy an intermediate position in this gradient of shade tolerance.

Seed and seedling predation and plant-pathogen interactions are important biotic factors that regulate the dynamics of tree seedling populations in a forest. the interactive influence of biotic and abiotic factors on seedling performance is evident from the patterns of leaf damage in gaps and understorey. Increased herbivore damage along the gap size gradient could be related to the increase in photon flux density and other related changes in atmosphere and soil along the gradient. Differential response of plants to herbivores across the sun-shade gradient that exists between gaps and understorey is further corroborated by the significant negative correlation between leaf damage and soil moisture content.

Thus canopy openings due to treefall may be considered as an important precondition for the establishment and growth of tree species in the Mawphlang forest. Since gap environment is highly heterogeneous and dynamic due to the interplay of a number of biotic and abiotic factors. The gap size strongly influences its environmental conditions

which are highly dynamic and heterogeneous. Success of tree seedlings occupying different niches in the gap-understorey environmental mosaic depend on favourable light and soil moisture conditions and the extent of damage caused to seed and seedlings by insect and rodent predators in the forest.

# SUMMARY

The present study of gap phase regeneration, conducted in a broadleaved subtropical forest at Mawphlang, 30 km south-west of Shillong, Meghalaya, deals with the community characteristics, physical features of treefall gaps and their influence on microenvironment and species diversity of the forest. It also examines the growth and population behaviour of naturally recruited seedlings of dominant tree species in treefall gaps within the forest.

The forest stand at Mawphlang representing the relict climax vegetation of the area, is dense and evergreen with trees not exceeding 20 m in height. The canopy layer is mainly composed of Quercus dealbata L., Quercus griffithii Hk., Quercus glauca Thunb., Schima khasiana Dyer, Myrica esculenta Buch.Ham, and Manglietia insignis (Wall)Bl. The sub-canopy layer (3-10 m height) shows abundance of Exbucklandia populnea (Griff) Br., Prunus undulata Buch.Ham. and Rhododendron arboreum Sm. The shrub layer is dominated

by Daphne shillong Banerjee and Baliospermum micrantha Muell Arg. The ground vegetation is mainly composed of herbaceous species and some pteridophytes. The seedlings and saplings of Q. dealbata, Q. griffithii and S. khasiana are abundantly found on the forest floor. In terms of species richness, the forest is relatively poor than other humid tropical forests, but it is comparable to the subtropical or warm temperate forests of the Far East.

The tree density was high in lower dbh (10-20 cm; 20-30 cm) classes and low in higher dbh (40-50 cm; 50-60 cm) classes and the tree population of the forest showed an overall straight line relationship between density and diameter. Density-diameter curves of individual species showed a marked variation in shape, ranging from sigmoid to bimodal and reverse J-shaped.

All treefall gaps larger than 20 $m^2$ were identified in an experimental area of about 50 ha. Shape, size and various other physical characteristics related to topography and post treefall debris were studied in each of the twelve identified gap. Dumbbell shaped gaps were most common followed by elliptical and quadrangular gaps. The size of the gaps varied between 34 $m^2$ to 950 $m^2$.

Photon flux density, relative humidity, air temperature, soil moisture, soil temperature and litter depth were

monitored at monthly intervals for two years in gaps and understorey. Photon flux density was higher (about 70%) and relative humidity was lower (15%) in gaps than in the surrounding understorey. Litter layer was relatively thin in the gaps throughout the year. Seasonal as well as among gap variations were significant only for photon flux density, relative humidity and soil moisture content. Photon flux density was maximum during winter and minimum during rainy season and it increased with increase in gap area. Relative humidity and soil moisture content, however, decreased along the increasing gap size gradient. Both of them showed peak during rainy season and minimum value during winter season. The technique of Principal Component Analysis was applied to the six microenvironmental variables and PC I and PC II were obtained. They together accounted for 92% (PC I 80%; PC II 12%) of the total variation in the microenvironmental factors. PC I of microenvironment was positively correlated with gap area.

The number of tree species (seedlings) in the gap increased with an increase in its size. Likewise equatibility of dominance among the species also increased from the smaller to larger gaps. Tree seedling density and total species diversity in the gaps was negatively correlated to the Principal Component I of microenvironmental variables. Gaps were ordinated into groups on the basis of Principal

Component Analysis of the shade tolerant and shade intolerant tree species. The smaller gaps (gap nos. 1 to 9) with higher density of shade tolerant species formed one cluster and the large gaps (gap nos. 10 and 12) having a comparatively higher density of shade intolerant species constituted another cluster. Gap no. 11 with more or less equal proportion of shade tolerant and shade intolerant species formed a distinct group of its own.

$\alpha$-diversity, the mean number of species per gap, for tree seedlings was higher in the gaps than in the understorey. $\beta$-diversity which shows the mean similarity among the gaps was lower for tree seedlings than for herbs and shrubs. $\alpha$-diversity for tree seedlings, shrubs and herbs and $\beta$-diversity for tree seedlings increased between August, 1988 and August, 1990 suggesting that the gaps became more similar after a period of two years in their species composition.

Seed production per tree in four dominant tree species, Q. dealbata, Q. glauca, Q. griffithii and S. khasiana ranged between 3662 in Q. dealbata and 42,856 in Q. griffithii. Recruitment of naturally emerged seedlings of these species as well as M. esculenta and T. tomentosa was low in this forest. In the understorey Q. dealbata seedlings were most abundant followed by Q. glauca, Q. griffithii,

S. khasiana and T. tomentosa in descending order. Q. dealbata seedlings were also abundant in the small gaps, while in the medium and large gaps S. khasiana was more abundant. Total tree seedling recruitment (plants $ha^{-1}$) sharply declined from 1430 in the small gaps to 510 in the medium gaps. Further increase in gap area did not influence the density of recruited seedlings.

Survival and growth of the seedlings recruited in the gaps and understorey were monitored from August, 1988 to August, 1990. Seedlings of S. khasiana, T. tomentosa and M. esculenta registered high mortality during winter due mainly to low temperature and high soil moisture stress created by low rainfall and high evapo-transpiration losses. Mortality was negligible in the oak species.

S. khasiana and M. esculenta showed higher shoot growth rate in the large gaps, while the three oak species performed better in the understorey. T. tomentosa showed best growth in the small and medium sized gaps. Peak seedling growth during rainy season in all the species is attributed to the favourable temperature and edaphic conditions of the forest floor.

Seed and seedling predation influenced the performance of the tree seedlings in this forest. High seed predation both at the pre- and post-dispersal stages in the three

oak species could be one of the reasons for their poor germination and low seedling recruitment in the forest. Total seed loss to predation ranged from 91% in Q. dealbata to 98% in Q. griffithii and Q. glauca.

Seedlings of all the six tree species showed maximum leaf area damage (85-95%) during autumn. The proportion of damaged leaf area per seedling also increased along the gap size gradient. The shade tolerant oak species were more susceptible to leaf damage than the shade intolerant species.

Thus it may be concluded that the creation of treefall gaps in the oak forest at Mawphlang brings about a marked change in the forest microenvironment by significantly increasing the solar radiation which triggers off a series of changes in atmospheric and edaphic conditions in the gaps. Size of the gap also plays an important role in influencing its microenvironment. Species with different regeneration guilds tend to occupy the newy created niches causing a change in species diversity between gaps and understorey as well as along the increasing gap size gradient. Recruitment of tree seedlings of oak species is adversely affected by pre- and post-dispersal predation of seeds by insects and rodents. Growth and population behaviour of infinitively small proportion (0.03-0.5% of total seed production) of naturally recruited seedlings in

gaps and understorey is further regulated by sharp seasonal variation in certain climatic variables and the activity of insect herbivores which damage as high as 71% of the recruited seedlings in the population.

# REFERENCES

Abdel Rahman, A.A. 1973. Effects of moisture stress on plants. Phyton. **15**: 67-86.

Aide, T.M. 1987. Limbfalls: a major cause of sapling mortality for tropical forest plants. Biotropica. 19: 284-285.

Aide, T.M. & J.S. Zimmerman. 1990. Patterns of insect herbivory, growth and survivorship in juveniles in a neotropical liana. Ecology. **71**: 1412-1421.

Alexandre, D.Y. 1982. Aspects de la regeneration naturelle en foret dense de cote-D'Ivorie. Caondollea. 32: 579-588.

Alliende, M.C. 1988. Demographic studies of a dioecious tree. II. The distribution of leaf predation within and between trees. J.Ecol. 77: 1048-1058.

Anaya, L.A.L. 1976. Consideraciones sobre el potencial alelopatico de la vegetacion secundaria. In: Regeneracion des Selvas. pp. 428-446.

Ashton, P.S., Y.Y. Gan & F.W. Robertson. 1984. Electrophoretic and morphological comparisons in ten rain forests species of Shorea (Dipterocarpaceae). Bot.J.Linn.Soc. 89: 293-304.

Augspurger, C.K. 1984a. Light requirements of neotropical tree seedlings: a comparitive study of growth and survival. J.Ecol. **72**: 777-796.

Augspurger, C.K. 1984b. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density and light conditions. Oecologia. 61: 211-217.

Augspurger, C.K. 1984c. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps and pathogens. Ecology 65: 1705-1712.

Bach, C. 1990. Plant successional stage and insect herbivory: flea beetles on sand-dunes willow. Ecology. 71: 598-609.

Barden, L.N. 1989. Repeatability in forest gap research: studies in Great Smoky Mountains. Ecology. 70: 558-559.

Bazzaz, F.A. 1984. Demographic consequences of plant physiological traits: some case studies. In: R. Dirzo and J. Sarukhan, (Editors)

Perspectives in Plant Population Ecology. Sinauer Associates Inc., Sunderland, MA. pp. 324-346.

Bazzaz, F.A. & S.T.A. Pickett. 1980. The physiological ecology of tropical succession: a comparative review. Ann.Rev.Ecol.Syst. 11: 287-310.

Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial pattern of forest understorey plants. Ecology. 65: 1406-1419.

Beatty, S.W. & O.D.V. Sholes. 1988. Leaf litter effect on plant species composition of deciduous forest treefall pits. Can.J.For.Res. 18: 553-559.

Beatty, S.W. & E.L. Stone. 1986. The variety of soil microsites created by treefalls. Can.J.For.Res. 16: 539-548.

Becker, P., P.E. Rabenold, J.R. Idol & A.P. Smith. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. J.Trop.Ecol. 4: 173-184.

Bentley, S. and J.B. Whittaker. 1979. Effects of grazing by chrysomelid beetle, Gastrophysa viridula, on competition between Rumex obtusifolia and R. crispus. J.Ecol. 67: 79-90.

Benton, A.H. & W.E. Werner Jr. 1976. Field Biology and Ecology. McGraw-Hill New York. pp. 564.

Bigger, M. 1981. Observations on the insect fauna of shaded and unshaded Amelonado cocoa. Bull.Entom.Res. 71: 107-119.

Bjorkman, O., S.B. Powles, D.C. Fork & G.Oquist. 1981. Interactions between high irradiance and water stress on photosynthetic reactions. Year Book, Carnegie Inst.Wash. 80: 57-59.

Bonner, F.T. 1968. Water uptake and germination of red oak acorns. Bot.Gaz.(Chicago). 129: 83-85.

Borger, G.A. & T.T. Kozlowski. 1972. Effects of water deficits on first periderms and xylem development in Fraxinus pennsylvanica. Can. J.For.Res. 2: 144-151.

Bormann, F.H. & G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, USA.

Brawley, S.H. and W.H. Adey. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. Marine Biology. 61: 167-177.

Bray, W.L. 1956. Gap phase replacement in a maple-basswood forest. Ecology. 37: 598-600.

Brewer, R. & P.G. Merritt. 1978. Windthrow and tree replacement in a climax beech-maple forest. Oikos. 30: 149-152.

Brokaw, N.V.L. 1982a. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica. 11: 158-160.

Brokaw, N.V.L. 1982b. Treefalls: frequency, timing, and consequence In: E.G. Leigh, Jr., A.S. Rand and D.W. Windsor, (Editors), The Ecology of a tropical forest: seasonal rhythms and long term changes. Smithsonian Institute Press, Washington, D.C., USA. pp. 101-108.

Brokaw, N.V.L. 1985a. Treefalls, regrowth and community structure in tropical forests. In: S.T.A. Pickett and P.S. White, (Editors), The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp.53-69.

Brokaw, N.V.L. 1985b. Gap-phase regeneration in a tropical forest. Ecology. 66: 682-687.

Brokaw, N.V.L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. J.Ecol. 75: 9-19.

Brokaw, N.V.L. & S.M. Scheiner. 1989. Species composition in gaps and structure of a tropical forest. Ecology. 70: 538-541.

Brown, J.L. 1976. Etude de la perturbation des horizons du sol par un arbre qui se renverse et de son impact sur la pedogenese. Can.J. Soil Sci. 57: 173-186.

Brown, V.K. 1984. Secondary succession insect-plant relationships. Bioscience. 34: 710-716.

Brown, V.K. 1985. Insect herbivores and plant succession. Oikos. 44: 17-22.

Brues, C.T. 1946. Insect Dietary. Harvard University Press, Cambridge, Mass.

Bullock, S.H. 1984. Biomass and nutrient allocation in a neotropical dioecious palm. Oecologia. 63: 426-428.

Burdon, J.J. 1987. Diseases and Plant Population Biology. Cambridge University Press, Cambridge.

Burton, P.J. & D. Mueller-Dombois. 1984. Response of Metrosidros polymorpha seedlings to experimental canopy. Ecology. 65: 779-791.

Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Noveak & R.S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid Agropyron bunch grasses. Oecologia. 50: 14-24.

Campbell, T.E. 1982. Imbibition, desiccation and reimbibition effects on light requirements for germinating southern pine seeds. For. Sci. 28: 539-543.

Canham, C.D. 1984. Canopy recruitment in shade tolerant trees: the response of Acer saccharum and Fagus grandiflora to canopy openings. Ph.D. thesis, Cornell University, Ithaca, NY.

Canham, C.D. & P.L.Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth. In: S.T.A. Pickett and P. White, The ecology of natural disturbance and patch dynamics. Academic Press, Orlando. pp.197-216.

Canham, C.D. 1988. Growth and canopy architecture of shade tolerant trees: the response to canopy gaps. Ecology. 69(3): 786-795.

Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies & P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can.J.For.Res. 20: 620-631.

Cates, R.G. & G.H. Orians. 1975. Successional status and the palatability of plants to generalized herbivores. Ecology. 56: 410-418.

Cates, R.G. & H. Alexander. 1982. Host resistance and susceptibility. In: J.B. Mitton and K.B. Sturgeon, (Editors), Bark beetles of North America and conifers, ecology and evolution. Univ. Texas Press, Austin.

Champion, H.G. & S.K. Seth. 1968. A revised survey of the forest types of India. Govt. India Publ. Delhi. pp.251-267.

Chaugley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, New York, USA.

Chazdon, R.L. 1986. Light variations and carbon gain in rain forest understorey plants. Adv.Ecol.Res. 18: 1-63.

Chazdon, R.L. & N. Fetcher. 1984a. Light environments of tropical forests. In: E. Medina, H.A. Mooney and C. Vasquez-Yanes, (Editors), Physiological ecology of plants in the wet tropics. Dr. W. Junk, Boston, Massachusetts, USA, pp.27-36.

Chazdon, R.L. & N. Fetcher. 1984b. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. J.Ecol. 72: 553-564.

Chazdon, R.L. & R.W. Pearcy. 1986a. Photosynthetic responses to light variation in rainforest understorey species. I. Induction under constant and fluctuating light conditions. Oecologia. 69: 524-531.

Chazdon, R.L. & R.W. Pearcy. 1986b. Photosynthetic responses to light variation in rainforest understorey species. II. Carbon gain and photosynthetic efficiency during sunflecks. Oecologia. 69: 524-531.

Chesson, P.L. & R.R. Warner. 1981. Environmental variation promotes coexistence in lottery competitive systems. Am.Nat. 117: 923-943.

Christensen, N.L. & J.F. Franklin. 1987. Small scale disturbance in forest ecosystems: a review of a workshop on forest gaps. Bull. Eco.Soc.Am. 68: 51-53.

Christy, E.J. & R.N. Mack. 1984. Variation in demography of juvenile Tsuga heterophylla across the substratum mosaic. J.Ecol. 72: 75-91.

Clark, D.A. & D.B. Clark. 1987a. Temporal and environmental patterns of reproduction in Zamia skinneri a tropical rain forest cycad. J.Ecol. 75: 135-150.

Clark, D.A. & D.B. Clark. 1987b. Analisis de la regeneracion de árboles del dosel en bosque muy humedo tropical: aspectes teoreticos y practicos. In: D.A. Clark, R. Dirzo and N. Fetcher, (Editors), Ecologia y ecophysiologia de plantas en los bosques mesoamericanos. Revista de Biologia Tropical. 35 (Supplemento), pp.41-54.

Clark, D.B. & D.A. Clark. 1985. Seedling dynamics of a tropical tree: Impacts of herbivory and meristem damage. Ecology. 66: 1884-1892.

Clements, F.E. 1936. Nature and structure of the climax. J. Ecol. 24: 252-284.

Coley, P.D. 1980. Effects of leaf age and plant life history patterns on herbivory. Nature (Lond.) 284: 545-546.

Coley, P.D. 1983a. Intraspecific variation in herbivory on two tropical tree species. Ecology. 64: 426-433.

Coley, P.D. 1983b. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol.Monog. 53: 209-233.

Coley, P.D. & T.M. Aide. 1991. A comparison of herbivory and plant defenses in temperate and tropical broadleaved forests. In: P.W. Price, T.M. Lewinsohn, W.W. Benson and G.W. Fernandes, (Editors), Herbivory: tropical and temperate perspectives. John Wiley & Sons, New York, New York, USA.

Collins, S.L. & R.E. Good. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest. Oikos. 48: 89-98.

Collins, S.L. 1989. Habitat relationships and survivorships of tree seedlings in hemlock-hardwood forest. Can.J.Bot. 68: 790-797.

Cook, R.E. 1979. Patterns of juvenile mortality and recruitment in plants. In: O.T. Solbrig, S. Jain, G.B. Johnson and R.H. Raven, (Editors), Topics in Plant Population Biology. Columbia University

Press, New York. pp. 207-231.

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: P.J. den Boer and G.R. Gradwell, (Editors), Dynamics of Populations. PUDOC, Wageningen, The Netherlands. pp. 289-312.

Connell, J.H. 1987. Diversity in tropical rain forest and coral reefs. Science. 199: 1302-1310.

Connell, J.H., J.H. Tracey & L.J. Webb. 1984. Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. Ecol.Monog. 54: 141-164.

Corre, W.J. 1983. Growth and morphogenesis of sun and shade plants. I. The influence of light intensity. Acta.Bot.Neer. 32: 49-62.

Coombs, J., D.U. Hall, S.P. Long & J.M.O. Scurlock (Editors). 1985. Techniques in Bioproductivity and Photosynthesis. Pergamon Press.

Cousen, J.E. 1974. An introduction to woodland ecology. Oliver and Boyd, Edinburgh, Scotland.

Cox, C.S. & P.B. McEvoy. 1983. Effect of summer moisture stress on the capacity of tansy ragwork (Senecio jacobaea) to compensate for defoliation by the cinnabar moth (Tyria jacobaeae). J.Appl. Ecol. 20: 225-234.

Crawley, M.J. 1983. Herbivory: the dynamics of animal-plant interactions. University of California Press, Berkley, California, USA.

Curtis, J.T. 1959. Vegetation of Wisconsin. University of Wisconsin Press, Madison.

Dale, V.H., M.Hemstrom & J. Franklin. 1986. Modeling the long term effects of disturbances on forest succession, Olympic Peninsula, Washington. Can.J.For.Res. 16: 56-67.

Denslow, J.S. 1980. Gap partitioning among tropical rain forest trees. Biotropica. 12 (Supplement): 47-55.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. Ann.Rev.Ecol.Syst. 18: 431-451.

Denslow, J.S. & A.E. Gomez Diaz. 1990. Seed rain to treefall gaps in a neotropical rain forest. Can.J.For.Res. 20: 642-648.

Denslow, J.S. & T. Spies. 1990. Canopy gaps in forest ecosystems: an introduction. Can.J.For.Res. 20: 619.

Denslow, J.S., J.C. Schultz & P.M. Vitousek. 1990. Growth response of tropical shrubs to treefall gap environments. Ecology. 71: 165-179.

Desteven, D. 1981. Abundance and survival of a seed infesting weevil, Pseudanthonomous hamamelidis (Coleoptera: Curculimidae), on its variable-fruiting host plant, witch-hazel (Eamamelis virginiana). Ecol.Entom. 6: 387-391.

Desteven, D. 1988. Light-gaps and long-term seedling performance of a neotropical canopy tree (Dipteryx panamensis, Leguminosae). J.Trop.Ecol. 4: 407-411.

Doyle, T.W. 1981. The role of disturbance in the gap dynamics of a montane rainforest: an application of a tropical forest succession model. In: D.C. West, H.H. Shugart and D.B. Bolkin, (Editors), Forest Succession: Concepts and Applications. Springer-Verlag, New York. pp.56-73.

Dunn, C.P., G.R. Guntenspergen & J.R. Dorney. 1983. Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. Can.J.Bot. 61: 211-217.

Dirzo, R. 1984. Herbivory: a phytocentric overview. In: R. Dirzo and J. Sarukhan, (Editors), Perspectives on plant population ecology. Sinauer, Sunderland, Massachusetts, USA. pp.141-165.

Ed Vander Meijden, M. Wijn & H.J. Verkar. 1988. Defense and regrowth, alternative plant strategies in the struggle against herbivores. Oikos. 51: 355-363.

Ehrlich, P.R. & P.H. Raven. 1965. Butterflies and plants: a study in coevolution. Evolution. 18: 586-608.

Ehrlich, P.R. & P.H. Raven. 1967. Butterflies and plants. Scientific American. 216: 105-113.

Evert, F. 1964. *Components of stand volume and its increment.* J.For. 62: 810-813.

Falinski, J.B. 1978. Uprooted trees, their distribution and influence in the primeval forest biotope. Vegetatio. 38: 175-183.

Feeny, P. 1976. Plant apparency and chemical defence. Recent Adv.Phytochem. 10: 1-40.

Fennah, R.O. 1965. The influence of environmental stress on the Cacao tree in determining feeding sites of Cacao thrips, Selenothrips rubricinetus (Giard), on leaves and pods. Bull.Entemol.Res. 56: 333-349.

Fetcher, N., B.R. Strain & S.F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology and water relations of seedlings of two species of tropical trees. Oecologia. 58: 314-319.

Fetcher, N., S.F. Oberbauer, G. Roja & B.R. Strain. 1987. Effects of light regime on photosynthesis and growth in seedlings of tropical rain forest trees. Rev.Biol.Trop. 35: 97-110.

Fetcher, N., S.F. Oberbauer & B.R. Strain. 1985. Vegetation effects on microclimate in lowland tropical forest in Costa Rica. Int.J. Biometeor. 29: 145-155.

Florence, J. 1981. Chablis et sylirgenese dans une foret dense humide sempervirente du Gabon. Ph.D. Thesis, Universite Louis Pasteur de Strasbourg, France.

Forcier, R.T.T. 1975. Reproductive strategies and the cooccurence of climax tree species. Science. 189: 808-810.

Foster, R.B. & N.V.L.Brokaw. 1982. Structure and history of the vegetation of Barro Colorado Island. In: E.G. Leigh, Jr., A.S. Rand and D.M. Windsor, (Editors), The Ecology of a Tropical Forest. Smithsonian Institution Press, Washington, D.C. pp. 67-81.

Fox, J.F. 1977. Alteration and coexistence of tree species. Am.Nat. 111: 69-89.

Fujita, T.T. 1978. Manual of down-burst identification for Project NIMROD. SMRP Research Paper No.156. University of Chicago, Chicago.

Gartner, B.L. 1989. Breakage and regrowth of Piper species in rain forest understorey. Biotropica. 21: 303-307.

Ghent, A.W. 1958. Studies of regeneration in forest stands devastated by the spruce budworms. II. Age, height, growth and related studies of balsam fir seedlings. For.Sci. 4: 135-146.

Gibson, C.W.D., V.K. Brown & M. Jepsen. 1987. Relationships between the effects of insect herbivory and sheep grazing on seasonal changes in an early successional plant community. Oecologia. 71: 245-253.

Gansser, A. 1964. Geology of the Himalayas. A volume in the regional geographical series edited by L.U. de Sitter. Inter Science Publishers - a division of John Wiley & Sons. Inc.

Goff, F.G. & D.C. West. 1975. Canopy-understorey interaction effects on forest population structure. For.Sci. 21: 98-108.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of regeneration niche. Biol.Rev.Cambridge Philos.Soc. 52: 312-335.

Handel, S.N. 1976. Population ecology of three woodland Carex species. Dissertation. Cornell University. Ithaca, New York, USA.

Harper, J.L. 1969. The role of predation in vegetation diversity. Brookhaven Symposium in Biology. 22: 48-62.

Harper, J.L. 1977. The population biology of plants. Academic Press, New York, New York, USA.

Harper, J.L. & J. White. 1974. The demography of plants. Ann.Rev.Ecol. Syst. 5: 419-463.

Harper, J.L., J.N. Clatworthy, I.H. McNaughton & G.R. Sagar. 1961. Evolution and Ecology of closely related species living in the same area. Evolution (Lawrence, Kans). 15: 209-227.

Harrison, S. 1987. Treefall gaps versus forest understorey as environments for a defoliating moth on a tropical forest shrub. Oecologia. 72: 65-68.

Hart, G.E., Jr., R.E. Leonard & R.S. Pierce. 1962. Leaf fall, humus depth and soil frost in a northern hardwood forest. USDA For.Serv. Northeast.For.Exp.Stn.Res. Note No.1131.

Hartshorn, G.S. 1978. Treefalls and tropical forest dynamics. In: P.B. Tomlinson and M.H. Zimmermann, (Editors), Tropical trees as living systems. Cambridge University Press, New York, New York, USA. pp. 617-638.

Hartshorn, G.S. 1980. Neotropical forest dynamics. Biotropica. 12: 23-30.

Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. Can.J.For. Res. 12: 522-527.

Hladik, A. & P. Blanc. 1987. Croissance des plantes en Sous-Bois de foret dense humide (Makokou, Gabon). La Terre et La Vie. 42: 209-234.

Howe, H.F. & J. Smallwood. 1982. Ecology of seed dispersal. Am.Rev. Ecol.Syst. 13: 201-228.

Howe, H.F. 1990. Habitat implications of gap geometry in tropical forests. Oikos. 59(1): 141-144.

Howe, H.F., E.W. Schupp & L.C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (Virola surinamensis). Ecology. 66: 781-789.

Hubbell, S.P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science. 203: 1299-1309.

Hubbell, S.P. 1984. Methodologies for the study of the origin and maintenance of tree diversity in tropical rain forest. In: G. Maury-Lechou, G.M. Hadley and Y. Younes, (Editors), The significance of species diversity in tropical forest ecosystems. Biology International (IUBS), pp. 8-13.

Hubbell, S.P. & R.B. Foster. 1986. Canopy gaps and the dynamics of a neotropical forest. In: M.J. Crawley, (Editors), Plant Ecology. Blackwell Scientific Publications, Oxford, pp. 77-96.

Huffaker, C.B. & C.E. Kennett. 1959. A ten-year study of vegetational changes associated with biological control of Klamath weed. J.Range Manage. 12: 69-82.

Huston, M. 1979. A general hypothesis of species diversity. Am.Nat. 113: 81-101.

Hutchinson, G.E. 1978. An introduction to population ecology. Yale University Press. New Haven. CT.

IUCN. 1980. World conservation strategy, IUCN, Gland, Switzerland.

Janos, D.P. 1980. Vesicular-arbuscular mycorrhizae affects lowland tropical rain forest plant growth. Ecology. 61: 151-162.

Janzen, D.H. 1969. Seed eaters versus seed size, number, toxicity and dispersal. Evolution. 23: 1-27.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forest. Am.Nat. 104: 501-528.

Janzen, D.H. 1971. Seed predation by animals. Ann.Rev.Ecol.Syst. 2: 465-492.

Janzen, D.H. 1975. Intra- and interhabitat variations in Guazuma ulmifolia (Sterculariaceae) seed predation by Ambiycerus cistelinus (Bruchidae) in Costa Rica. Ecology. 56: 1009-1013.

Jones, E.W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. New Phytologist. 44: 130-138.

Khan, M.L. & R.S. Tripathi. 1986. Tree regeneration in a disturbed subtropical wet hill forest of north-east India: Effect of stump diameter and height on sprouting of four tree species. For.Ecol. Manage. 17: 199-209.

Khan, M.L., J.P.N. Rai & R.S. Tripathi. 1986. Regeneration and survival of tree seedlings and sprouts in tropical deciduous and subtropical forests of Meghalaya, India. For.Ecol.Manage. 14: 293-304.

Khan, M.L., J.P.N. Rai & R.S. Tripathi. 1987. Population structure of

some tree species on disturbed and protected subtropical forests of north-east India. Acta Oecol./Oecol.Appl. 8: 247-255.

Khan, M.L. & R.S. Tripathi. 1991. Seedling survival and growth of early and late successional tree species as affected by insect herbivory and pathogen attack in sub-tropical humid forest stands of north-east India. Acta Oecologica. 12: 569-579.

Kira, T. 1977. Forest vegetation of Japan. Shidei & Kira, 1-9. Univ. Tokyo Press, Tokyo.

Kira, T. 1978. Introduction. Kira et al.(1978), 1-7.

Kira, T. 1991. Forest ecosystems of East and Southeast Asia in a Global Perspective. Ecol.Res. 6: 185-200.

Kohyama, T. & N. Fujita. 1981. Studies on the Abies population of Mt. Shimagare. I. Survivorship curve. Botanical Magazine of Tokyo. 94: 55-68.

Lang, A. 1965. Effects of some internal and external conditions on seed germination. In: W. Ruhland, (Editor), Encyclopedia of Plant Physiology; Vol. 15/2, Springer-Verlag, Berlin, Heidelberg and New York. pp. 848-893.

Lang, G.E. & D.H. Knight. 1983. Tree growth, mortality, recruitment and canopy gap formation during a 10-year period in a tropical moist forest. Ecology. 64: 1075-1080.

Lawton R.O. 1982. Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. Am.J.Bot. 69: 1204-1230.

Lawton, R.O. & F.F. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology. 69: 764-777.

Lawton, J.H. & S. McNeill. 1979. Between the devil and the deep sea: On the problem of being a herbivore. In: R.M. Anderson, B.O. Tuner and L.R. Taylor, (Editors), Population dynamics. Blackwell, Oxford. pp. 223-244.

Lawton, R.O., R.O. Lawton & V. Dryer. 1980. The vegetation of the Monteverde cloud forest reserve. Brenesia. 18: 31-46.

ment of a shrub, Haplopappus venetus (Asteraceae), along a climatic gradient. Ecology. 64: 511-521.

Louda, S.M. & J.E. Rodman. 1983a. Ecological patterns in the glucosinolate content of a native crucifer under field conditions. Acta Oecologica, Oecologica generalis. 7: 37-53.

Louda, S.M. & J.E. Rodman. 1983b. Variation in glucosinolate concentration in relation to habitat and insect herbivory for the native crucifer, Cardamine cordifolia (bitter cress). Biochem.Syst.Ecol. 11: 199-208.

Louda, S.M. 1984. Herbivore effect on stature, fruiting and leaf dynamics of a native crucifer. Ecology. 65: 1379-1386.

Louda, S.M., N. Huntly & P.M. Dixon. 1987. Insect herbivory across a sun/shade gradient: response to experimentally-induced in situ plant stress. Acta Oecologica, Oecologica generalis. 8: 357-363.

Lubchenco, J. & S.D. Gaines. 1981. A unified approach to marine plant herbivore interactions. I. Populations and communities. Ann.Rev. Ecol.Syst. 12: 405-437.

Lutz, H.J. 1940. Disturbance of forest soil resulting from the uprooting of trees. Bull.Yale Univ.Sch.of Forestry. No.45.

Lutz, H.J. 1960. Movement of rocks by uprooting of forest trees. Am.J. Sci. 258: 752-756.

Lyford, W.H. & D.W. Maclean. 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. Harvard Forest Paper No.15.

Mack, R.N. & J.L. Harper. 1977. Interference in dune animals: spatial pattern and neighbourhood effects. J.Ecol. 65: 345-363.

Maiorana, V.C. 1981. Herbivory in sun and shade. Biol.J.Linn.Soc. 15: 151-156.

Marks, P.L. 1975. On the relation between extension growth and successional status of deciduous trees on the north-eastern United States. Bull.Tor.Bot.Club. 102: 172-177.

Lawton, R.O. 1990. Canopy gaps and light penetration into a wind-exposed tropical lower montane rain forest. Can.J.For.Res. 20: 659-667.

Lee, R. 1978. Forest microclimatology. Columbia University Press, New York.

Leigh, E.G. 1975. Structure and climate in tropical rain forest. Ann. Rev.Ecol.Syst. 6: 67-86.

Leigh, E.G., Jr., A.S. Rand & D.M. Windsor. 1982. The ecology of a tropical forest: seasonal rhythms and long term changes. Smithsonian Institute Press, Washington, D.C., USA.

Lieberman, D., M. Lieberman, G. Hartshorn and R. Peratta. 1985. Growth rates and age-size relationships of lowland tropical wet forest trees in Costa Rica. J.Trop.Ecol. 1: 97-109.

Lincoln, D.E. & H.A. Mooney. 1984. Herbivory on Diplacus aurantiacus shrubs in sun and shade. Oecologia. 64: 173-176.

Lloyd, D.G. & C.J. Webb. 1977. Secondary sex characters in seed plants. Bot.Rev. 43: 177-216.

Lorimer, C.G. 1989. Survival and growth of understorey trees in oak forests of the Hudson Highlands, New York. Can.J.For.Res. 11: 689-695.

Lorimer, C.G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology. 70: 565-567.

Loucks, O.L. 1970. Evolution of diversity, efficiency and community stability. Am.Zool. 10: 17-25.

Louda, S.M. 1978. A test of predispersal seed predation in the population dynamics of Haplopappus (Asteraceae). Ph.D. thesis. The University of California, Riverside, California and San Diego State University, San Diego, California.

Louda, S.M. 1982. Limitation of the recruitment of the shrub Haplopappus squarrosus (Asteraceae) by flower-feeding and insect-feeding insects. J.Ecol. 70: 43-54.

Louda, S.M. 1983. Seed predation and seedling mortality in the recruit-

March, W.J. & J.N. Skeen. 1976. Global radiation beneath the canopy and n a clearing of a suburban hardwood forest. Agric.Meteor. 16: 321-327.

Marquis, R.J. 1984. Leaf herbivores decrease fitness of a tropical plant. Science. 226: 537-539.

Marquis, D.A. & J.C. Bjorkbom. 1982. Guidelines for evaluating regeneration before and after clearcutting Allengheny hardwoods. U.S. For.Ser.Res. Note NE-307.

Marshall, R. 1927. The growth of hemlock before and after release from suppression. Harvard For.Bulletin Number 11. Petersham, Massachusetts, USA.

Martinez-Ramos, M. 1985. Claros, historia de vida de los arboles tropicales y la regeneracion natural de las selvas atlas perennifolias. Regeneracion de Selvas II (Ed. by A. Gomez-Popma & S.del Amo). Compania Editorial, Mexico City.

Martinez-Ramos, M.R., E. Alvarez-Buylla and J. Sarukhan. 1989. Tree demography and gap dynamics in a tropical rain forest. Ecology. 70: 555-558.

Martinez-Ramos, M., E. Alvarez-Buylla, J. Sarukhan & D. Pinero. 1988. Treefall age determination and gap dynamics in a tropical forest. J.Ecol. 76: 700-716.

Mattson, W.J., Jr. 1980. Herbivory in relation to plant nitrogen content. Ann.Rev.Ecol.Syst. 11: 119-161.

McCarthy, B.C. & J.M. Facelli. 1990. Microdisturbances in oldfields and forests: implications for woody seedling establishment. Oikos.58:55-60.

McLeod, K.W. & P.G. Murphy. 1977. Establishment of Ptelea trifoliata on lake Michigan sand dunes. Am.Mid.Nat. 97: 350-362.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos. 40: 329-336.

McQuilkin, R.A. 1975. Growth of four types of white oak reproduction after clearcutting in the Missouri Ozarks. U.S.For.Ser.Res.Pap. NC-116.

Miles, J. 1974. Effects of experimental interference with stand structure on establishment of seedlings in callunetum. J.Ecol. 62: 675-687.

Milthrope, F.L. 1961. Mechanisms in biological competition, SEB Symposium 15, Cambridge University Press, Cambridge.

Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. Am.Nat. 114: 362-378.

Minckler, L.S., J.D. Woerheide & R.C. Schlesinger. 1973. Light, soil moisture and tree reproduction in hardwood forest openings. U.S. For.Serv.Res.Pap. NC-89.

Misra, R. 1968. Ecology work book. Oxford Publishing Company, Calcutta.

Moore, R., S. Warrington & J.B. Whittaker. 1991. Herbivory by insects on oak trees in pure stands compared with paired mixtures. J.Appl. Ecol. 28: 290-304.

Moran, N. & W.D. Hamilton. 1980. Low Nutritive Quality as Defense against herbivores. J.Theor.Biol. 86: 247-254.

Mueller-Dombois, D. & H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, Inc., New York.

Mueller-Dombois, D., J.D. Jacobi, R.G. Cooray & N. Balakrishnan. 1980. Ohia rainforest study: Ecological investigations of the Ohia dieback problem in Hawaii. Miscellaneous Publications, 183. Hawaii Institute of Tropical Agriculture and Human Resources, Honolulu, Hawaii, USA.

Murray, K.G. 1988. Avian seed dispersal of three neotropical gap-dependant plants. Ecol.Monogr. 58: 271-298.

Myers, N. 1987. The extinction spasm impending: Synergisms at work. Cons.Biol. 1: 14-21.

Nakashizuka, T. & M. Numata. 1982. Regeneration process of climax beech forests. I. Structure of the beech forest with the undergrowth of Sasa. Jap.J.Ecol. 32: 57-67.

Newbery, D.M. & H. de Foresta. 1985. Herbivory and defense in pioneer, gap and understorey trees of tropical rain forests in French Guiana. Biotropica. 17: 238-244.

Newton, P.F. & V.G. Smith. 1988. Diameter distributional trends within mixed Black-spruce/Balsam-fir and pure Black-spruce stand types. For.Ecol.Manage. 25: 123-138.

Nunez-Farfan, J. & R. Dirzo. 1988. Within-gap heterogeneity and seedling performance in a Mexican tropical forest. Oikos. 51: 274-284.

Oldeman, R.A.A. 1972. L'architecture de la vegetation ripicole forestiere des fleuves et criques guyanias. Adansonia (New Series) 12: 253-265.

Oldeman, R.A.A. 1978. Architecture and energy exchange of dicotyledonous trees in the forest. In: P.B. Tomlinson and M.H. Zimmerman. (Editors), Tropical trees as living systems. Cambridge University Press, Cambridge, England.

Oliver, C.D. & E.P. Stephens. 1977. Reconstruction of a mixed species forest in central New York. Soil Sci. 88: 107-111.

Orians, G.H. 1982. The influence of treefalls in tropical forests on tree species richness. Trop.Ecol. 23: 255-279.

Paine, R.T. 1966. Food web complexity and species diversity. Am.Nat. **100**: 65-75.

Pandey, A.M. & J.S. Singh. 1985. Mechanism of ecosystem recovery. A case study from Kumaun Himalaya. Recr.Revege.Res. 3: 271-292.

Parker, M.A. & R.B. Root. 1981. Insect herbivores limit the habitat distribution of a native composite Machaeranthera canescens. Ecology. **62**: 1390-1391.

Pascoe, E.H. 1950. A manual of the geology of India and Burma. G.S.I., New Delhi.

Pearcy, R.H. 1983. The light environment and growth of $C_3$ and $C_4$ tree species in the understorey of a Hawaiian forest. Oecologia. 58: 19-25.

Pickett, S.T.A. 1983. Differential adaptation of tropical species to canopy gaps and its role in community dynamics. Trop.Ecol. 24: 68-84.

Pickett, S.T.A. & F.A. Bazzaz. 1978. Organization of an assemblage of early successional species on a soil moisture gradient. Ecology. 59: 1248-1255.

Pickett, S.T.A. & P.S. White, (Editors). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. J.Theo.Biol. 13: 131-144.

Platt, W.J. & S.M. Hermann. 1986. Relationships between dispersal syndrome and characteristics of populations of trees in a mixed-species forest. pp. 309-321. In: A. Estrada and T.H. Flemings, (Editors). Frugivores and seed dispersal. Dr. W. Junk, Dordrecht, The Netherlands.

Poore, M.E.D. 1968. Studies in Malaysian rain forest. I. The forest on triassic sediments on Jengka Forest Reserve. J.Ecol. 56: 143-196.

Popma, J. & F. Bongers. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. Oecologia. 75: 625-632.

Poulson, J.L. & W.J. Platt. 1989. Gap light regimes influence canopy tree diversity. Ecology. 70: 553-555.

Price, P.W., C.E. Bouton, P. Gross, B.A. McPherson, J.N. Thompson & A.E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Ann. Rev. Ecol. Syst. 11: 41-65.

Prins, A.H. & H.W. Nell. 1990. Positive and negative effects of herbivory on the population dynamics of Senecio jacobaea L. and Cynoglossum officinale L. Oecologia. 83: 325-332.

Putz, F.E. & K. Milton. 1982. Tree mortality rates on Barro Colorado Island. In: E.G. Leigh, Jr., A.S. Rand and D.M. Windsor, (Editors) The Ecology of a Neotropical Forest: Seasonal Rhythms and Long-term changes. Washington, DC: Smithsonian Inst.

Putz, F.E. 1983. Treefall pits and mounds, buried seeds and the importance of soil disturbance to pioneer trees on Barro Colorado Tsland, Panama. Ecology. 64: 1069-1074.

Putz, F.E. 1984. How trees avoid and shed lianas. Biotropica. 16: 19-23.

Rand, A.S. 1976. Number of treefalls per month. In: D.M. Windsor (Editor), Environmental Monitoring and Baseline Data from the Isthmus of Panama. Smithsonian Institution, Vol.IV. pp.134.

Rao, P., S.K. Barik, H.N. Pandey & R.S. Tripathi. 1990. Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient. Vegetatio. 88: 151-162.

Rao, P.B. & S.P. Singh. 1985. Response breadths on environmental gradients of germination and seedling growth in two dominant forest tree species of Central Himalaya. Ann.Bot. 56: 783-794.

Rausher, M.D. 1981. Host plant selection by Battus philenor butterflies: the roles of predation, nutrition and plant chemistry. Ecol. Monogr. 5: 1-20.

Rausher, M.D. & P. Feeny. 1980. Herbivory, plant density and plant reproductive success: the effect of Battus philenor on Aristolochia reticulata. Ecology. 61: 905-917.

Reichle, D.E. (Editor). 1974. Forest Ecosystem. McGraw-Hill Year book Science and Technology. pp. 196-201.

Rhoades, D.F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. Am.Nat. 125: 205-238.

Rhodes, D.F. & R.G. Cates. 1976. Towards a general theory of plant antiherbivore chemistry. Rec.Adv.Phytochem. 10: 168-213.

Rice, R.L., D.E. Lincoln & J.H. Langenheim. 1978. Palatability of a monoterpenoid compositional types of Satureja douglassi to a generalist molluscan herbivore Ariochmax dolichophallus. Biochem. Syst.Ecol. 6: 45-53.

Richards, P.W. 1952. The Tropical Rain Forest. Cambridge University Press, London and New York.

Richards, P.W. 1986. The nature of tropical forest ecosystems. In: Nicholas Polunin, (Editor), Eco.Theo.App. John Wiley & Sons Ltd.

Richards, P. & G.B. Williamson. 1975. Treefalls and patterns of understorey species in a wet lowland tropical forest. Ecology. 56: 1226-1229.

Ricklefs, R.E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. Am.Nat. 111: 376-381.

Riera, B. 1985. Importance des bultes de deracinement dans la regeneration forestiere en Guyane Francaise. Rev.

Rockwood, L.L. & K.E. Glander. 1979. Howling monkeys and leaf cutting ants: comparative foraging in a tropical deciduous forest. Biotropica. 11: 1-10.

Rollet, B. 1983a. La regeneration naturelle dans les trouees. Rev.Bios. et.Forets.Trop. 201: 3-34.

Rollet, B. 1983b. La regeneration naturelle dans les trouees. Part II. Rev.Bios.et.Forets.Trop. 202: 18-34.

Romme, W.H. & W.H. Martin. 1982. Natural disturbance by tree falls in old growth mixed mesophytic forest: Lilley Cornett Woods, Kentucky. In: R.N. Mueller (Editor), Proceedings of the Central Hardwood Conference. IV. University of Kentucky, Lexington, Kentucky, USA.

Rorison, I.H. 1967. A seedling bioassay on some soils in the Sheffield area. J.Ecol. 55: 725-741.

Runkle, J.R. 1981. Gap regeneration in some old growth forests of the Eastern United States. Ecology. 62: 1041-1051.

Runkle, J.R. 1982. Pattern of disturbance in some old-growth mesic forests of eastern North America. Ecology. 63: 1533-1546.

Runkle, J.R. 1985. Disturbance regime in temperate forests. In: S.T.A. Pickett and P.S. White, (Editors). The ecology of natural disturbance and patch dynamics. S.T.A. Pickett and P.S. White. Academic Press, New York. pp.17-33.

Runkle, J.R. 1989. Synchrony of regeneration, gaps and latitudinal differences in tree species diversity. Ecology. 70: 546-547.

Runkle, J.R. 1990. Gap dynamics in a Ohio Acer-Fagus forest and speculations on the geography of disturbance. Can.J.For.Res. 20: 632-641.

Salisbury, E. 1942. The reproductive capacity of plants. Bell, London.

Sanford, R.I. Jr, H.E. Braker & G.S. Hartshorn. 1986. Canopy openings in a primary neotropical forest. J.Trop.Ecol. 2: 277-282.

Sarukhan, J. 1978. Studies on the demography of tropical trees. In: P.B. Tomlinson and M. Zimmerman, (Editors). Tropical Trees as Living Systems. Cambridge University Press, Cambridge, England. pp.163-184.

Saxena, A.K., S.P. Singh & J.S. Singh. 1984. Population structure of forests of Kumaun Himalaya: implications for management. J.Environ.Manage. 19: 307-324.

Schmeiz, D.A. & A.A. Lindsey. 1965. Size-class structure of old-growth forests in Indiana. For.Sci. 11: 258-264.

Schmid, B., G.M. Puttick, K.H. Burgess & F.A. Bazzaz. 1988. Clonal integration and effects of simulated herbivory in old-field perennials.

Schulte, P.J. & P.E. Marshall. 1983. Growth and water relations of black locust and pine seedlings exposed to controlled water stress. Can.J.For.Res. 13: 334-338.

Schulz, J.P. 1960. Ecological studies on Rain Forest in Northern Suriname. Verhandelingen der koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde, Tweed Reeks, Deel 53(1), Amsterdam.

Schupp, E.W. 1988. Seed and early seedling predation in the forest understorey and in treefall gaps. Oikos. 51: 71-78.

Schupp, E.W., H.F. Howe, C.K. Augspurger & D.J. Levey. 1989. Arrival and survival in tropical treefall gaps. Ecology. 70: 562-564.

Silverton, J.W. 1981. Micro-spatial heterogeneity and seedling demography in species-rich grasslands. New Phytol. 88: 117-128.

Scriber, J.M. & F. Slansky. 1981. The nutritional ecology of immature insects. Ann.Rev.Entom. 26: 183-211.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Det.Kong.Danske Vidensk, Selsk Biology Skr.(Copenhagen) 5: 1-34.

Sorensen, F.C. & W.K. Ferrell. 1973. Photosynthesis and growth of Douglar fir seedlings when grown in different environments. Can.J. Bot. 51: 1689-1698.

Sousa, W.P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49: 227-254.

Spatz, G. 1970. Pflazangesellschaften, Leistungen und Leistungs potential von Allgquer Alpweiden in Abhangigkeit von Standort und Bewirtschaftung. Dissertation (Dr.Agr.) Tech.Univ. Munich.

Spies, T.A., J.F. Franklin & M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Can.J.For.Res. 20: 649-658.

Stanton, N.L. 1975. Herbivore pressure on two types of tropical forests. Biotropica. 7: 8-11.

Stearns, F.W. 1949. Ninety years change in a northern hardwood forest in Wisconsin. Ecology. 30: 350-358.

Stephens, E.P. 1956. The uprooting of trees: a forest process. Soil Sci.Soc.Am.Proc. 20: 113-116.

Stoeckeler, J.H. & G. Arbogast. 1955. Forest management lessons from a 1949 windstorm in northern Wisconsin and Upper Michigan. U.S.Dep. Agric.For.Serv. Lake States for Exp.Stn. Paper No.34.

Stokes, P. 1965. Temperature and seed dormancy. In: W. Ruhland (Editor). Encyclopedia of Plant Physiology. Vol.15/2, Springer-Verlag, Berlin, Heidelberg and New York. pp. 746-803.

Stone, E.L. 1975. Windthrow influences on spatial heterogeneity in a forest soil. Fidg.Anst.Forstl.Versuchswes.Mutt. 51: 176-184.

Streng, D.R. 1986. Patterns of seedfall and seedling establishment in an East Texas river flood plain forest: the contribution of seedling dynamics to species coexistence. Dissertation, Rice University, Houston, Texas, USA.

Streng, D.R., J.S. Glitzenstein & P.A. Harcombe. 1989. Woody seedling dynamics of an east Texas flood plain forest. Ecol.Monogr. 59: 177-204.

Strobeck, C. 1974. Sufficient conditions for polymorphism with niches and mating groups. Am.Nat. 108: 152-156.

Strong, D.R. 1977. Epiphyte loads, treefalls and perennial forest disruption: a mechanism for maintaining higher tree species richness in tropics without animals. J.Biogeogr. 4: 215-218.

Struick, G.J. & J.T. Curtis. 1962. Herb distribution in an Acer-Saccharum forest. Am.Midl.Nat. 68: 285-296.

Swain, M.D. & J.B. Hall. 1986. Forest structure and dynamics. In: G.W. Lawson (Editor), Plant Ecology in West Africa. Wiley, New York. pp.47-93.

Torquebian, E. 1981. Analyse architecturale de la foret de les Tuxtlas (Veracruz). Mexique. Ph.D. thesis, Universite des Sciences.

Tripathi, R.S. & M.L. Khan. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two

species of Quercus in a subtropical wet hill forest. Oikos. 57: 289-296.

Troedsson, T. & W.H. Lyford. 1973. Biological disturbance and small-scale spatial variation in a forested soil near Garpenberg, Sweden. Stud.For.Suec. No.109.

Turkington, R. & L.W. Aarsen. 1984. Local-scale differentiation as a result of competitive interactions. In: R. Dirzo and J. Sarukhan, (Editors), Perspectives on plant population ecology. Sinauer, Sunderland, MA. pp.107-127.

Uhl, C. 1982. Tree dynamics in a species rich Tierra Furnie forest in Amazonia, Venezuela. Acta.Cienc.Ven. 33: 72-77.

Uhl, C., K. Clark, N. Dezzeo & P. Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology. 69(3): 751-763.

Uhl, C. & P.G. Murphy. 1981. Composition, structure and regeneration of tierra firme forest in the Amazon Basin of Venezuela. Trop. Ecol. 22: 219-237.

UNESCO/UNEP/FAO. 1978. Tropical forest ecosystem: A state-of-knowledge report. Paris: UNESCO.

Vazquez-Yanes, C. & A. Orozco-Seguia. 1984. Ecophysiology of seed germination in the tropical humid tropics of the world: a review. In: E. Medina, H.A. Mooney and C. Vazquez-Yanes, (Editors), Physiological ecology of plants in the wet tropics. Dr.W. Junk, Dordrecht, The Netherlands.

Vazquez-Yanes, C. & H. Smith. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer Cecropia obtusifolia and Piper auritum and its ecological significance. New Phytol. 92: 477-485.

Veblen, T.T. 1985. Forest development in tree-fall gaps in the temperate rain forests of Chile. Nat.Geogr.Res. 1: 162-183.

Vegis, A. 1965. Ruhezustande bei hoheren Pflanzen, Induktion, Verlauf und Beendigung: Ubersicht Terminologie, allgemeine Probleme. In: W. Ruhland (Editor), Handbuch der Pflanzen-physiologie, Vol.15/2.

Springer-Verlag, berlin, Heidelberg and New York.

Vitousek, P.M. & J.S. Denslow. 1987. Nitrogen and phosphorus availability in treefall gaps. J.Ecol. 74: 1167-1178.

Vooren, A.P. 1985. Patterns in Tree and Branchfall in West African Rain Forest Wageningen: Wageningen Agric.Univ.Dept. Silviculture.

Wadsworth, F. & G.Englerth. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. Carib. Forest. 20: 38-50.

Wardle, P. 1959. The regeneration of Fraxinus excelsior in woods with a field layer of Mercurialis perennis. J.Ecol. 47: 483-497.

Warner, R.R. & P.L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to storage effect. Am.Nat. 125: 769-787.

Watt, A.S. 1947. Pattern and process in the plant community. J.Ecol. 35: 1-22.

Webb, L.J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, North Queensland. Aust.J.Bot. 6: 220-228.

Webb, L.J. 1968. Environmental relationships of the structural types of Australian rain forest vegetation. Ecology. 49: 296-311.

Welden, C.W., S.W. Hewett, S.P. Hubbell & R.B. Foster. 1991. Sapling survival, growth and recruitment: Relationship to canopy height in a neotropical forest. Ecology. 72(1): 35-90.

Werner, P.A. & W.J. Platt. 1976. Ecological relationships of co-occuring golden rods (Solidago: Compositae). Am.Nat. 110: 959-971.

West, D.C., H.H. Shugart, Jr. & J.W. Ranney. 1981. Population structure of forest over a large area. For.Sci. 27: 701-710.

White, P.S. 1979. Pattern, process and natural disturbance in vegetation. Bot.Rev. 45: 229-299.

White, T.C.R. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special referance to populations of Selidosema sauvis in a plantation of Pinus radiata in New Zealand. Oecologia. 16: 279-301.

White, T.C.R. 1976. Weather, food and plagues of locusts. Oecologia. 22: 119-134.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia. 33: 71-86.

Whitmore, T.C. 1974. Change with time and the role of cyclones in tropical rain forest on Kelom bangara, Solomon Islands. Common wealth Forestry Institute Paper No.46. University of Oxford, Oxford, England.

Whitmore, T.C. 1975. Tropical Rainforests of the Far East. Clarendon Press, Oxford, England.

Whitmore, T.C. 1978. Gaps in the forest canopy. In: P.B. Tomlinson and M.H. Zimmerman (Editors), Tropical Trees as Living Systems. Cambridge Univ. Press, Cambridge, England. pp.639-655.

Whitmore, T.C. 1982. On pattern and process in forests. In: E.J. Newman (Editor), The Plant Community as a Working Mechanism. Blackwell, Oxford, England. pp. 45-57.

Whitmore, T.C. 1989. Canopy gaps and the two major groups of forest trees. Ecology. 70: 536-538.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon. 21: 213-251.

Whittaker, R.H. 1977. Evolution of species diversity in land communities. Evol.Biol. 10: 1-67.

Williamson, G.B. 1975. Pattern and seral composition in an old growth beech-maple forest. Ecology. 56: 727-731.

Wilson, D.S. 1980. The natural selection of population and communities. The Benjamin/Cummings Publ.Co. California.

Wilson, M.V. & A. Shmida. 1984. Measuring $\alpha$-diversity with presence-absence data. J.Ecol. 72: 1055-1064.

Windle, P.N. & E.H. Franz. 1979. Effects of insect parasitism on plant competition: green bugs and barley. Ecology. 60: 521-529.

Zar, J.H. 1974. Biostatistical analysis. Prentice Hall, Inc., Engelwood Cliff, NJ.

Zimba, D.T. 1977. Geography of Meghalaya. Standard Printing Press, Gauhati.