ECOLOGICAL STUDIES OF SOME IMPORTANT TREE SPECIES OF SUBTROPICAL HUMID FOREST OF MEGHALAYA

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

NORTH EASTERN HILL UNIVERSITY
SHILLONG – 793 022, INDIA

2004

NORTH EASTERN HILL UNIVERSITY

Department of Botany

November, 2004

I, Mr. Nripemo Odyuo, hereby declare that the subject matter of this thesis is the record of work done by me, that the contents of this thesis did not form basis of the award of any previous degree to me or to the best of my knowledge to anybody else, and that the thesis has not been submitted by me for any research degree in any University/Institute.

This is being submitted to the North-Eastern Hill University for the degree of Doctor of Philosophy in Botany.

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ACKNOWLEDGEMENT

This research work materialized due to the patience, constant monitoring and critical examination by Prof. H.N. Pandey, my supervisor, owing to his keen interest in the field of plant diversity and regeneration ecology of tree species, which will always be cherished with gratitude and fondness in my memory for days to come. His untiring enthusiasm and commitment to the field of forest ecology is commendable.

To Prof. R.S. Tripathi FNA, I owe him for his constant encouragement, valuable suggestions and help in many ways till the end of the study.

My senior lab mates Dr. Babu John, Dr. S. Dasgupta and Dr. Alemmeren Jamir were always there to rely on in times of need; I acknowledge their help and encouragement.

My sincere thanks goes to Prof. R.R. Mishra and Prof. H.N. Pandey, former Heads of Botany Department and Prof. A.K. Mishra, Head of Botany Department for providing laboratory facilities during the study.

My sincere thanks go to the faculty members of Botany Department for their cooperation and encouragement.

Dr. M. Sanjappa, Director, Botanical Survey of India, Kolkata – 1, gave kind permission to continue with the research work for which I thank him sincerely.

I thank Dr. (Mrs.) S. Phukan, Deputy Director, and my senior colleagues, Dr. A.A. Mao, Dr. B.K. Sinha and Mr. S.L. Abbas of Botanical Survey of India, Shillong for their cooperation during the writing of the thesis.

My friend Late Miss. Pearline constantly pushed me to put my best in the work. I thank her sincerely.

Dr. Krishna Upadhya was with me through thick and thin and without whose help this work would not have seen the light of day, I am grateful to him.

The help rendered by my lab mates Dr. Pynsakkhiat Law, Dr. O.P. Tripathi, Mr. Amit Biswas, Kanhaya Lal Chaudhury, John Lakadong Ms. Swapna Prabhu, V. Ralte, Bishwarupa Ghosh, Shairi Nongbri and Jenpuiru Kamei are acknowledged with thanks.

The patience and support in whatever way possible by my parents, brothers and sisters are gratefuly acknowledged.

My heartfelt thanks goes to all my friends and well wishers for their prayers and support.

I thank Mr. S. Kumar (Photographer), Bah Modin Kharbuli (Driver) and all the staff of Botany Department for their cooperation during the study.

Above all, I thank Almighty God for His grace, love and wisdom and giving me the strength to complete the thesis.

2/11/04

Shillong 1st November 2004. (Nripemo Odyuo)

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CHAPTER I
INTRODUCTION

Forests are complex and self-perpetuating system, which cover about 26.6 percent of the worlds' land area (Sharma et al. 1992). They are valuable natural resource that ameliorates environmental conditions and contribute to human welfare. A dense forest cover reduces soil erosion, regulates stream flow and heat budget of the area, and provides shelter to a wide variety of plant and animal species. Besides, influencing climate and edaphic processes, forests serve as an important source of food, fuel, fodder, medicine and many other things of economic and socio-cultural value for man and his domesticated animals. Human activities have always modified the forest environment, but the intensity and scale of forest use have increased many folds in the recent years. Everyone is benefited when forests are treated as a renewable resource, protected to preserve biodiversity, or transformed to support other economic activities on a sustainable basis. Conversely, destructive exploitation of forests has caused serious economic, social and environmental losses.

Depletion of forest is most serious in the tropics, where about 2.5 billion people depend on the natural resources for economic and environmental goods and services (Rowe et al. 1992). The effect of human activities on species diversity has attracted the attention of ecologist both from theoretical and applied standpoints (Stapanian *et al* 1997). The most important cause of biodiversity loss in the tropics is shifting cultivation and logging for timber based industries (Richards 1996). It has been estimated that every hour

2-5 species are being lost from the tropical forests alone. Timber species are inevitably the first choice to be selectively logged from rich tropical forests, often illegally by 'tree poachers' and by unlicensed local people. Given that population densities of many of the tree species are often very low, selective logging can easily cause local extinction, only trees in the most remote and inaccessible parts are likely to survive. Substantial reduction in forest cover is also caused by fuel wood extraction, since nearly 3 billion people worldwide depend on wood, primarily on natural forests and trees outside forest areas, as their main or only source of household energy (Rowe et. al. 1992). Shifting cultivation is probably the most important cause of deforestation, which is practiced everywhere in the tropics and subtropics (Richards 1996).

Meghalaya with a geographical area 22429 sq. km has about 15633 sq. km of forest cover (FSI 1999). Out of the estimated 17000 flowering plants in India (Khoshoo 1995) the state has 3128 plant species including 1173 endemic species (Khan et al. 1997). Though the state occupies only 0.7% of the total land area of India, it harbours about 21% of all the flowering plant species.

During 1987-1997, the state lost 854 sq. km (5.4%) of the forest cover (FSI 1987; 1997; Tiwari et al. 1999). For a small state like Meghalaya, this figure is alarmingly large area. The main causes of depletion of forest cover in the state are logging for timber trade and fuel wood, and continued practice of shifting cultivation.

The mature forests in Meghalaya are found mainly in the form of Biosphere Reserves, National Parks, Wild Life Sanctuaries and Sacred Groves. Out of these, the local tribes maintain the sacred groves. The protection of small patches of forest as sacred

groves or tree species as sacred trees is an ancient ethos of the people all over the world. Although such practices became extinct in most parts of the world, basically due to changes in the religious beliefs of the people and their resource use patterns during recent times. Sacred groves and sacred trees continue to be of much importance in religion, culture and resource use systems in many parts of India (Chandran and Gadgil 1998). Sacred groves are ecologically and genetically very important. They are the abodes of rare, endemic and endangered species of flora and fauna. Besides, they serve the function of preserving the genetic diversity of even common species. The increasing human population, along with the deteriorating religious faith, has led to the relentless exploitation of these vegetational sanctities in the recent past (Nair et al. 1997).

In order to understand the co-existence of tree species in the tropical forests, attempts have focused on biotic interactions and specialized regeneration requirements of the tree species (Grubb 1977; Denslow 1980 1987). The success of tree regeneration in a forest is determined by successful completion of several events in the tree's life cycle, such as seed production and dispersal to safe sites, germination and seedling emergence and establishment and onward growth (Barik et al. 1996).

Disturbances such as gap formation, herbivory, landslides, and logging affect the abundance and composition of the seedlings in the forest understorey (Benitez-Malvido 1998) and therefore play an important role in tree regeneration process. Increasing interest in the development and management of mixed plantations, uneven-aged stands and natural forests has made it imperative to understand the regeneration process that ensures maintenance of the community structure and ecosystem stability (Moravie et. al. 1997).

Studies on forest regeneration following canopy gap formation or large-scale disturbances such as wind throw and timber harvest show that seedlings and saplings established before disturbance make a significant, if not, dominant, contribution to future stand composition (Brokaw 1985; Ashton 1990; Marquis et al. 1992; Morin 1994). Gaps increase environmental heterogeneity of forest in several ways (Runkle et al. 1995), and provide suitable regeneration niches for several tree species (Grubb 1977). Gaps in vegetation are local sites where additional resources, both above- and below-ground, have become available due to the absence of the resident plant. As a consequence, the increased resources allow neighbours or new recruits located in and around the gap to grow, survive and reproduce better than outside (Conell et al. 1997). Gap-phase regeneration of trees occurs when canopy gaps are filled with the growth of previously suppressed or newly colonizing saplings. This process has important effects on forest architecture, forest composition, and tree population dynamics (Jones 1945; Whitmore 1975; Hartshorn 1978; Runkle 1981; Brokaw 1985). In fact mature forests have been described as shifting mosaics of different-sized patches cycling through gap, building and mature phases (Watt 1947; Whitmore 1975; Oldeman 1978; Borman and Likens 1979). The mosaic concept suggests that to interpret forest composition and dynamics one must study regrowth in gaps of different sizes.

Light is a major determinant of seedling growth in gaps (Read et al. 1983), providing nearly all the required carbon and chemical energy (Bjorkman 1981). When newly germinated seedlings are in competition with established plants, they are at a competitive disadvantageous position because established plants are already fully

exploiting the soil profile and foliar energy. Root competition has usually been shown to be more important than shoot competition, both in even-aged stands (Wilson 1988) and between established and establishing tree species (Jeangros and Nosberger 1990). The shoot competition is mainly for light, whereas root competition is for nutrients and water. Several investigators have studied the competition for nutrients (Weldin and Jilman 1993; Snaydon and Howe 1986). Wilson (1988) and have reported that root competition influences plant dry matter production more than does shoot competition.

The success of tree regeneration in a forest is determined by successful completion of several events in the tree life cycle such as seed production and its dispersal to safe sites, germination and seedling emergence, establishment and onward growth (Barik et al. 1996). Seedling establishment and juvenile growth are critical periods in the life cycle of perennial species. Morphological and physiological attributes during these periods are important factors, which determine ecological relationships such as competition, invasion and dominance of species (Kramer et al. 1996).

Recently, number of ecological studies have been carried out in the primary forest of the northeast India to understand the structure, function and regeneration status of these forests (Rao *et al* 1997; Jamir 2000; Law 2002; Tripathi 2001; Upadhaya 2002; Upadhaya et al. 2003).

However, detailed studies on seed and seedling ecology of humid subtropical forest species are limited. Therefore the present study was undertaken to investigate the seed and seedling ecology of three important tree species viz. *Podocarpus neriifolia, Acer*

laevigatum and *Syzygium tetragonum* of subtropical semi-evergreen forest of northeast India with emphasis on the following aspects:

(i) Effect of light and temperature on seed germination

(ii) Role of light and soil water and nutrient levels on seedling growth

(iii) Nutrients concentration, accumulation and their use efficiency under different light and soil water and nutrient levels.

CHAPTER II
REVIEW OF LITERATURE

The economic development of many developing countries of the world is closely linked with the exploitation of tropical forests. Increasing demand for the forest resources from within the region as well as from the developed world are important causes of destruction of tropical forests in many parts of the world. Mounting pressure on forested areas due to rapid population growth for agriculture, livestock grazing, fuelwood and other domestic humans needs often end in over-exploitation of tropical forest. Utilization of forests for economic growth has led to faster rate of deforestation in many developing countries of the humid tropics. It is ironic that the very process of deforestation carried out in the name of development is responsible for the steady erosion of the natural resources base and life-support system of the forest dwellers.

Tropical forests have received much attention in recent years because of their species richness (Whitmore 1984), high standing biomass (Brunig 1983) and greater productivity (Jordan 1983). These forests also act as the major carbon sink (Lugo 1992). However, the structure, composition and functioning of forests undergo changes as a natural process or on account of human and livestock intervention. As a result, there occurs lot of spatial and temporal variation in the species richness, composition and productivity.

The loss of biodiversity is irreversible and has attracted the interest of a number of ecologists from both theoretical and applied standpoints (Stapanian et al. 1997). Earlier, human impacts were restricted in time and space and therefore, deforested clearings usually regenerated to a level close to the original community. Impact of human

disturbance on tropical rain forests has changed in pace and scale through time leading to biodiversity loss. The most important causes of biodiversity loss in the tropics is shifting cultivation and logging for timber-based industries (Richards 1996).

Understanding of the dynamics of the forest is helpful to increase the productivity, to maintain species composition, to limit the financial inputs and to develop prescription for silvicultural operations (Oliver 1990).

Phenology is the study of periodically occurring phenomena in relation to climate and seasonal cycle. It is an important adaptive trait of plant species since it determines the duration and timing of the growing season as well as the period of reproduction (Lechowiez 1984; Hanninen 1990; Reich et al. 1992; Kikizawa 1998). Leith (1970) and Leith and Radford (1971) have discussed the concepts and significance of phenological studies. The seasonal periodicity and sequential patterning of the phenological activity differs from one species to another. Several factors, which govern the phenology of the flowering plants, determine the reproductive success of the plant species. Among these factors, the time, frequency, and duration of the flowering period are obviously of great importance.

Phenological study deals with vegetative and reproductive phases corresponding to seasonal changes of a particular area and determines the degree of reproductive synchrony with other plant species (Rathcke 1988 a, b). Synchrony among species might be advantageous to them as the presence of one species may facilitate the frequency of the visit of pollinators and therefore enhance fruit/seed set in another species (Thompson 1980, 1982; Rathcke and Lacey 1985). Phenological study is important in plant

management and afforestation, honey analysis, floral biology, estimation of reproductivity and regeneration (Mulik and Bhosale 1989). Flowering phenology differs from species to species in accordance with the ecosystems they associates, thereby suggesting that specific patterns of flowering phenology may be characteristic of specific ecosystem types (Pojar 1974; Heinrich 1976).

Generally three environmental factors viz., photoperiod, temperature and moisture trigger the phenological process in the plants (Rathcke and Lacey 1985). These three factors are considered responsible for breaking bud dormancy and initiating developmental activity. Once set in motion this process advances as a function of temperature, day length, or a combination of the two.

Seasonal rhythm of flowering and fruiting are not only important from plant species reproduction point of view, but also it has a strong relation with the periodicity of the related faunal diversity such as 'mobile links' (Gilbert 1980). The flowering and fruiting phenology is an important characteristic feature of the tropical trees (Ashton 1969; Frankie et al. 1974; Richards 1996; Stranghetti 1997). In most cases flowering is reported to occur at the end of hot and dry season (Corlett 1993; Stranghetti 1997). Shukla and Ramakrishnan (1982) made phonological observations on 122 tree species in a subtropical humid forest and found that in majority of the species flushing started towards the end of the dry season, the degree and period of leaflessness varying with the species. For most of the species, flowering coincided with leaflessness. Proportionately more overstorey species flowered during the dry season, while wet season flowering was more characteristic of

understorey species. A majority of the species produced fleshy fruits during the wet season. Fruits, produced during the dry season, were mostly dry.

Study on phenological patterns of plants are important for germplasm conservation (Thompson 1980), as well as for better understanding of the ecological adaptations of individual species and its interactions with physical environment. The duration of different phenophases determines supply of specific resources such as pollen, nectar, fruit and seeds.

SEED CHARACTERISTICS

Tree regeneration by seed is a critical and frequently studied component of forest succession (Grubb 1977; Harcombe et al. 1982; Augspurger 1984; Streng et al. 1989; Schupp 1990; De Steven 1991a, b; Gill and Marks 1991). The success of tree regeneration in a forest is determined by successful completion of several events in the tree life cycle such as seed production and its dispersal to safe sites, germination and seedling emergence, establishment and onward growth (Barik et al. 1996). These events serve as a bottleneck that restricts regeneration of a particular species (Jones et al. 1994). Seeds are the basic raw materials for silvicultural research on native species and for forest management, reforestation and breeding programs (Ramos and Zanon 1984).

Seed production of trees are limited by various extrinsic factors such as resource availability, pollination failure, predation on flowers, fruits and leaves, and by climatic conditions, as well as by intrinsic factors such as age and size of the plant and its genetic constitution (Winn and Werner 1987).

Seed dispersal determines spatial arrangement and physical environment of seeds from which the next cohort of seedlings will emerge (Wenny 2000). Howe and Smallwood (1982) suggested that two possible advantages of seed dispersal are (i) to colonise new areas and (ii) to escape high mortality rates due to agents associated with the current population location.

The role of seed size and weight in seedling performance has received considerable attention (Howe and Richter 1982; Foster and Janson 1985; Tripathi and Khan 1990; Bonfil 1998). The wide differences in seed mass among species have been regarded as an important aspect of reproductive strategy (Grubb 1996). Seed mass plays a key role in the establishment of plant in its juvenile phase of life cycle especially under conditions of scare resources (Grubb and Coomes 1997; Grubb and Burslem 1998). Foster (1986) listed several potential advantages of large seeds of moist tropical trees and argued that large seed reserves might be used for the construction of large amount of photosynthetic tissue to maintain a positive net energy balance, or might also allow quick seedling growth for reaching higher light intensity strata. The differences in seed mass have been related to the ecological conditions in which plants establish. The species growing in open habitats have been reported to have lower seed mass than those in more closed habitats (Foster and Janson 1985; Mazer 1989). Large seeded species have an advantage in competitive environments (Gross 1984) and when seedlings experience defoliation (Armstrong and Westoby 1993), shade (Laishman and Westoby 1994) or moisture stress (Baker 1972).

In a given species, seeds of variable sizes may behave differently, for instance, germination percentage of large seeds may be higher than those of small seeds (Tripathi and Khan 1990; Khan and Uma Shankar 2001), or small seed may germinate to higher percentage than large seeds (Marshell 1986), or germination may be independent of seed size (Perez-Garcia et al. 1995). Within a species, heavier seeds may take lesser time for germination than lighter seeds (Dunlop and Barnett 1983; Barik et al.1996). Even lighter seeds may germinate earlier than the heavier seeds (Murali 1997; Khan et al. 1999) or germination time may not be dependent on seed weight (Perez-Garcia et al. 1995).

Westoby et al. (1996) reported that large seeded species establish better in shade, under drought, when buried beneath soil or litter and in established vegetation. Large seed mass might be an advantage in nutrient-poor soils (Stock et al. 1990). It has been shown that large-seeded species tend to survive longer in absence of soil nutrients (Jurado and Westoby 1992) and their early growth may be less affected by the level of soil nutrients (Milberg and Lamont 1997). Under nutrient-poor conditions, high re-translocation of mineral nutrients from the cotyledons during growth probably enables large seeded species to produce large seedlings. This was confirmed by the fact that the seedling mass of the small-seeded species was greatly increased by even small amounts of added nutrients (Milberg et al. 1998). Their study showed that the influence of seed mass on seedling growth decreased with increasing nutrient availability in soil, indicating that it is only under extremely nutrient-impoverished situations that seed mass exerts a large influence on seedling performance. Latham (1992) reported maximum response to added nutrients in

the smallest-seeded species during a study on six North American tree species grown for 4 months.

Young seedlings from large seeds are more likely to tolerate adverse conditions (Milberg et al. 1998). Westoby et al. (1996) suggested that the various benefits of large seed could have a single underlying mechanism i.e., the 'reserve effect'. Thus extra metabolic resources in large seeds could support unpredictable levels of carbon deficits caused by droughts, shade or herbivory. Under this scenario, large seededness would only be beneficial in hazards that are fitful and temporary, and where there is some chance of conditions to improve after a while (Milberg et al. 1998).

Milberg et al. (1998) showed that within two woody families larger seeds contain more N, P and K, much of which is translocated to the young seedling, and produce larger seedlings at a diminishing rate in nutrient-impoverished soil. In contrast, smaller seeds produce seedlings that respond to nutrient addition so that they may catch up with seedlings of the larger seeded species.

Seeds of most plant species can be stored for short periods without affecting their viability, but they gradually lose viability during storage. Palma et al. (1995) stored *Acacia senegal* seeds at room temperature for two, three and five years. They found that as the age of seeds increased their germination percentage decreased, and concluded that age of the seeds has a great impact on their germination. Pradhan (2000) also reported similar result in the case of *Alder nepalensis*, where irrespective of mode of seed storage, germination vigour decreased exponentially with increasing time and reached at the lowest value after 395 days.

Seeds are generally classified as orthodox or recalcitrant with respect to their storage behaviour (Roberts 1973). Orthodox seeds can be safely dried to low moisture content (<10%) and stored at low temperature for many years without significant loss of viability. The recalcitrant seeds are sensitive to both moisture loss as well as low temperature. Hay and Proberts (1995) defined desiccation tolerance as the ability of seed to germinate following drying. Desiccation down to 5% moisture content increased the longevity of *Azadirachta indica* seeds and they were tolerant to desiccation even down to 3.2% moisture content without significant loss in viability (Nayal et al. 2000). Prichard (1991) reported that damage begins in recalcitrant seed embryos at much higher moisture content than that proposed by Roberts (1973); embryos of *Quercus rubra* were damaged when moisture content was still over 40%.

Orthodox seeds commonly undergo a period of desiccation prior to shedding from the tree, but recalcitrant-seeded species do not have this final maturation drying stage in their evolutionary strategy and are thus vulnerable to moisture loss (Connor and Bonner 2001). This susceptibility makes any useful period of seed storage for many recalcitrant seeded species very short. Forest tree genera with recalcitrant seeds are abundantly found in the tropics but are less common in the temperate zone (Connor and Bonner 2001). Some temperate tree genera such as *Castanea* (Jaynes 1969; Pritchard and Manger 1990), *Quercus* (Bonner and Vozzo 1987), *Aesculus* and some *Acer* species (Bonner 1990) have recalcitrant seeds.

Many hypotheses have been proposed to explain the physiological basis of recalcitrance. Theories concerning changes in membrane and storage lipids and physical

disruption of seed membranes have been proposed by several workers (Flood and Sinclair 1981; Seewaldt et al. 1981; Priestly and Leopold 1983). Changes in seed proteins and carbohydrates, and the complexities of water properties in seeds have been explored, with varying degrees of success (Roberts 1973; Farrant et al. 1985, 1988; Pammenter et al. 1991; Wesley-Smith et al. 1992). Pammenter et al. (1994) and Berjak and Pammenter (1997) recognized the damage caused by aberrant metabolic processes while seeds are in hydrated storage or as water is lost. Thus, while much progress has been made in understanding the nature of recalcitrance, the storage of some recalcitrant tree seed over a long period is yet an insurmountable problem (Connor and Bonner 2001).

SEED GERMINATION

The seeds of tropical rain-forest trees show large interspecific variation in time taken to germinate. In a sample of 330 species of the forests of Malaysia, 65% of species germinated within 20 weeks of sowing fresh seed in a lightly shaded nursery. The remaining 35% of the species that took longer than 20 weeks to germinate often had hard, thick seed coats or endocarps around the seed (Ng 1980). A number of factors can cause delayed germination in tropical rain-forest tree seeds (Vazquez-Yanes and Orozco-Segovia 1993). These include low water content of seed at maturity, presence of a hard seed coat, small size and early stage of development of the embryo and the presence of chemical germination inhibitors. Rapid germinators tend to have high seed water content at maturity and soft seed coats. Many such species are difficult to store. They lose viability if dried and germinate if stored at high water content (Turner 2001).

Several studies carried out at different temperature regimes have shown thermal dependence of seed germination and have revealed temperature limits for optimum germination in many species (Labouriau and Osborn 1984; Jacobsen and Bach 1998). For instance 22-27^{0}C for *Catharanthus roseus* (Cardoso 1999), 17 to 27.2^{0}C for *Eucalyptus grandis* (Souza and Cardoso 2000), 25^{0}C for *Moringa stenopetala* (Teketay 1995), 20-30^{0}C for *Trema micrantha* (Castellani and Aguiar 2001) and 25^{0}C for *Atriplex semibaccata* (De Villiers et al. 1994).

The ability of some species to remain dormant in shade and germinate only in direct sunlight has been recognized as a characteristic uniting a group of tropical tree species of similar ecology. Swaine and Whitmore (1988) used this as a key character to define 'pioneer' species. These are the fast-growing, shade-intolerant species typically found only in gaps or on other early successional sites in the forest. The shade-tolerant species have germination that is generally not dependent on the degree of shading. Swaine and Whitmore (1988) referred to these species as 'non-pioneers'. Dependence on light for germination is correlated with seed size. Germination in darkness declines progressively as seed size decreases (Grime et al. 1981). In a germination experiment under 90%, 52% and 28% of full light, Khan and Uma Shankar (2001) reported best germination of *Quercus semiserrata* under 52% light. Raich and Gong (1990) investigated the germination of 43 Malaysian tree species in clearing, gap and forest understorey sites with 60%, 40% and 1.2% of full-sun respectively. Only seven species germinated equally well at all sites. In the clearing, 16 species showed low germination rate, or failed completely; 22 species germinated at higher rates in the understorey than the clearing and 12 species germinated

better in one or other of the open sites than they did in the understorey. Some species showed poor germination in the understorey, but did so readily when these seeds were transferred to the clearing. The clearing conditions killed seeds of a number of species. Raich and Gong (1990) concluded that a clear dichotomy of species on germination response to light was not easy to discern. Similar picture also emerged from a study of 19 tree species from tropical West Africa (Kyereh et al. 1999). Only three species germinated in significantly lower proportions in complete darkness than under light treatment and only one species responded to variation in R: FR radiation. All species showed some germination in forest understorey conditions. The sample included several species that were strongly light-demanding such as *Ceiba pentandra* and *Ricinodendron heudelotii*.

NUTRIENTS AND DRY-MATTER ALLOCATION IN SEEDLING

The growth rate of seedling is closely related to N status in many species (Hirose 1988; Ingestad and Agren 1988). Furthermore, as small plants are less likely to survive during winter than larger ones, survival could be positively correlated with seedling N accumulation and growth rate (Walters and Reich 1996). Factors such as irradiance (Dale and Causton 1992), light quality (Aphalo and Lehto 1997) and allelopathy (Nilsson 1993) have shown to affect N economy. Karlsson (1987) demonstrated that leaf nitrogen concentration differs between species growing on soils with equal concentrations of total nitrogen, suggesting an individualistic response of species to fertilization.

The rate of nutrient absorption depends upon concentration in the external solution, since nutrient status of plants declines as the concentration of a given nutrient declines at the root surface (El-Ghonemy et al. 1978). Nitrogen, phosphorus and potassium are so dilute in the soil solution that mass flow of soil water to meet the transpiration losses provides only a small part of the total plant requirement (Chapin 1980). Once within the shoot, mobile nutrients such as nitrogen, phosphorus and potassium move preferentially to sites of greatest merestematic activity or 'sink strength' as determined by growth form and growth stage (Watson 1963; Langer 1966; McIntyre 1977). Of the mobile elements, nitrogen generally has greatest effect on growth, affecting cell number and cell size; phosphorus has similar but less pronounced effects and potassium has least effect on growth, affecting mainly cell size (Watson 1963; Langer 1966).

Chapin (1980) studied the seasonal movement of nutrients in different growth forms in Alaskan tundra and observed that the two morphologically distinct populations were most similar to each other and all the deciduous species were more similar to one another than the evergreen shrubs. The deciduous species showed relatively high concentration of N, P and K in the leaves, and it changed with season while evergreen species showed low concentration of nutrients. Such a difference between evergreen and deciduous species has been reported from temperate species (Schlisinger and Chabot 1977) and tropical species (Cornelissen et al. 1998; Guo Ke and Werger 1999).

The relationship between foliar nutrient concentration and mean soil fertility has been reported differently by different researchers world over. Boerner (1984) in *Quercus*

prinus L. and *Q. alba* L. and Boerner (1985) in *Hammamelis virginiana* L. showed that foliar nutrient concentration is directly proportional to mean soil fertility, whereas research on *Acer rubrum* and *Fagus grandifolia* (Boerner 1984), *Cornus florida* (Kost and Boerner 1985) and *Viburnum acerifolium* L. (Minoletti and Boerner 1994) failed to support this hypothesis.

Changes in the relative abundance of plants along a soil fertility gradient suggest that nutrient supply might be exerting a direct influence on plant growth, survival or reproductive output at one or more life history stages (Gunatilleke et al. 1997).

In deciduous species nutrient translocation into leaves occurs when conditions are least favorable for nutrient uptake from soil, indicating the importance of nutrient storage, particularly in the belowground parts. In these species seasonal variation in nutrient (N,P,K) concentration suggest depletion and removal of stored resources; not observed in evergreen species. Some deciduous species are known to support leaf production primarily with nutrient stored in belowground parts. Both seasonal stability and small belowground biomass of evergreen species suggest that nutrients storage in belowground part in winter is limited. Evergreen-dominated heath tundra typically has smaller proportion of biomass belowground (30-40%) than the deciduous tundra (75-85%) as reported by Tyler et al. (1973) and presumably has less belowground nutrient storage. This strategy of nutrient reserves of evergreen species places them in a position vulnerable to herbivores (Rhoades and Cates 1976).

Abrahamson and Gadgil (1982) suggested that during future studies on mineral element allocation one should be careful to compare the plant materials of the same age or

state as older leaves are known to accumulate much less phosphate than younger leaves and to export N and P as they aged.

Species adaptability and their successful establishment in different environment can be predicted by studying relative apportionment of biomass or energy (MacArthur and Wilson 1967; Gadgil and Solbrig 1972; Abrahamson 1975). Such study is also important in assessing the adaptive potential of tropical trees occupying different ecological niches in a forest community (Ramakrishnan 1978). Studies on biomass and nutrient allocation are mostly available for the herbaceous species. Similar studies on tree seedlings and saplings have been carried out by Chapin et al. (1980), Shukla and Ramakrishnan (1984), Agren (1988), Santa Regina et al. (1997), Hughes et al. (1999) and Niinemets (2001).

Shukla and Ramakrishnan (1984) studied productivity and biomass allocation of two early successional (*Duabanga Sonneratioides* and *Anthocephalus cadamba*) and two late successional (*Dillenia pentagyna* and *Artocarpus chaplasha*) tree species of moist tropical forest. Their studies suggest that the former tend to maximize allocation to the shoot system at the expense of root system in order to produce canopy as rapidly as possible to exploit higher light intensity available in early successional communities. The late successional species which grow under low light regime, on the other hand, showed a higher allocation to roots. Early successional species have greater root biomass concentration to a depth of 20cm in soil profile. Though this may offer poor physical support to the shoot system, it probably provides enough absorptive surface to exploit nutrient and water particularly at disturbed sites (Marks and Borman 1972; Marks 1975). On the other hand, more uniform distribution of roots through soil profile in late

successional species and higher proportion of total biomass to roots at depths greater than 20cm may reflect their ability to draw nutrients from deeper layers of soil over a long period of time (Shukla and Ramakrishnan 1984). Thus the study on allocation of biomass and nutrient in tree species can highlight their adaptive strategy and explain the functional position of the tree species with respect to competition for light, energy and nutrients.

Studies on plant biomass allocation help explain the interaction between different abiotic factors and the adaptive strategies of the plants in the ecosystem. Allocation of above and belowground biomass across elevation regime shows a decrease, more from low- to mid-elevation than from mid- to low-elevation. Species showed a decline in height and leaf number with increase in elevation, higher dry mass at low and mid elevation sites compared to that of higher elevation and higher biomass of single leaf at mid elevation than at higher elevation (Gunatilleke et al. 1998).

Variation in dry mass allocation between plant parts is a potential mechanism of species differentiation along resource gradient (Smith and Huston 1989). Plants which grow on nutrient poor soils distribute a greater proportion of dry mass to roots, while plants of nutrient-rich soils show greater plasticity in dry mass distribution in response to variation in nutrient supply (Chapin 1980). In response to low nutrient availabilities, reserves are allocated to root at the expense of shoot growth (Chapin 1980). A 100 - fold drop in availability of a limiting nutrient may cause 1.5 to 12 fold increase in root:shoot ratio, depending upon species and initial growth conditions (Davidson 1969; Brewster et al. 1975; Christie and Moorby 1975).

Guo Ke and Werger (1999) in their study on seedlings of evergreen (*Cyclobalanopsis multinervis*) and deciduous (*Quercus aliena* var *acuteserrata*) oak species found that evergreen species allocated proportionally more biomass to leaves than the deciduous trees. They reported that leaf biomass ratio of evergreen species was about twice that of deciduous species, while the root mass ratio of evergreen seedling was about two third of that in deciduous species. Shoot: root ratio was higher in evergreen seedlings as compared to the deciduous species. Cornelisssen et al. (1998) studied the growth of eight woody species from British Isles and northern Spain and showed that deciduous species grew consistently faster than evergreen species, which indicated that mean relative growth rate was closely related to leaf area ratio and specific leaf area. Studies on chir pine (*Pinus roxburghii*) and banj oak (*Quercus leucotrichophora*), the early and late successional species, respectively, in central Himalaya along light gradient, revealed that the root: shoot ratio was generally higher for late successional species, and it increased with the increase in light intensity while the early successional species showed a reverse allocation pattern (Bargali and Singh 1995).

Studies on reproductive efforts of plants (Agren 1988) revealed that biomass and nutrients are not necessarily distributed in equivalent ways and allocation of nutrients may provide a better measure of reproductive effort than allocation of biomass. Reekie and Bazzaz (1987) argued that carbon because of its energetic role in plants tends to integrate the allocation pattern of other nutrients as well, and therefore, can be used as common currency to assess allocation pattern.

The brief review of literature presented in the foregoing pages clearly indicates that ecological studies on important tree species of humid subtropical forest of northeast India are limited. The present study was undertaken to study germination and seedling behaviour of three tree species in gap (light) and forest understorey (shade) conditions as well as under different soil water and nutrient treatments.

CHAPTER III
STUDY SITE, MATERIALS AND METHODOLOGY

The field study was carried out in two sacred groves (viz. Urkhla and Khloo Langdoh located at Jowai town (latitude 25^0 26' 32" N, longitude 92^0 12'E, altitude 1200-1300 m asl), representing subtropical semi-evergreen broad-leaved forest (Champion and Seth 1968) and in the net-house of the Department of Botany, North Eastern Hill University, Shillong (latitude 25^0 34' N, longitude 91^0 45' E, altitude 1450 m asl). The sacred groves are located ca. 64 km from Shillong, the capital of Meghalaya (Fig. 3.1).

The two sacred groves Urkhla and Khloo Langdoh are located within a radius of 1km in Jowai town. Khloo Langdoh is surrounded by human habitation and Urkhla is situated in the outskirts of Jowai town on the north and northeast facing slopes of a hill and is almost double the size of Khloo Langdoh and more dense. A major part of this grove is on steep slope (Table 3.1). The floristic composition of these two sacred groves gives an impression that the two groves might have been one in the past, which got fragmented due to human interference (Jamir 2000).

Table 3.1. Physiographic characters of the sacred groves.

Name of the sacred grove	Area ha.(approx.)	Direction of slope	Angle of slope
Urkhla	12	East Northeast	$20\text{-}30^0$ $>40^0$
Khloo Langdoh	7	East	$10\text{-}30^0$

Geology

Jowai falls in the formation of Jaintia series/Disang series, which are made up of Sylhet sandstone consisting of sedimentary structures like wedge and festoon type of

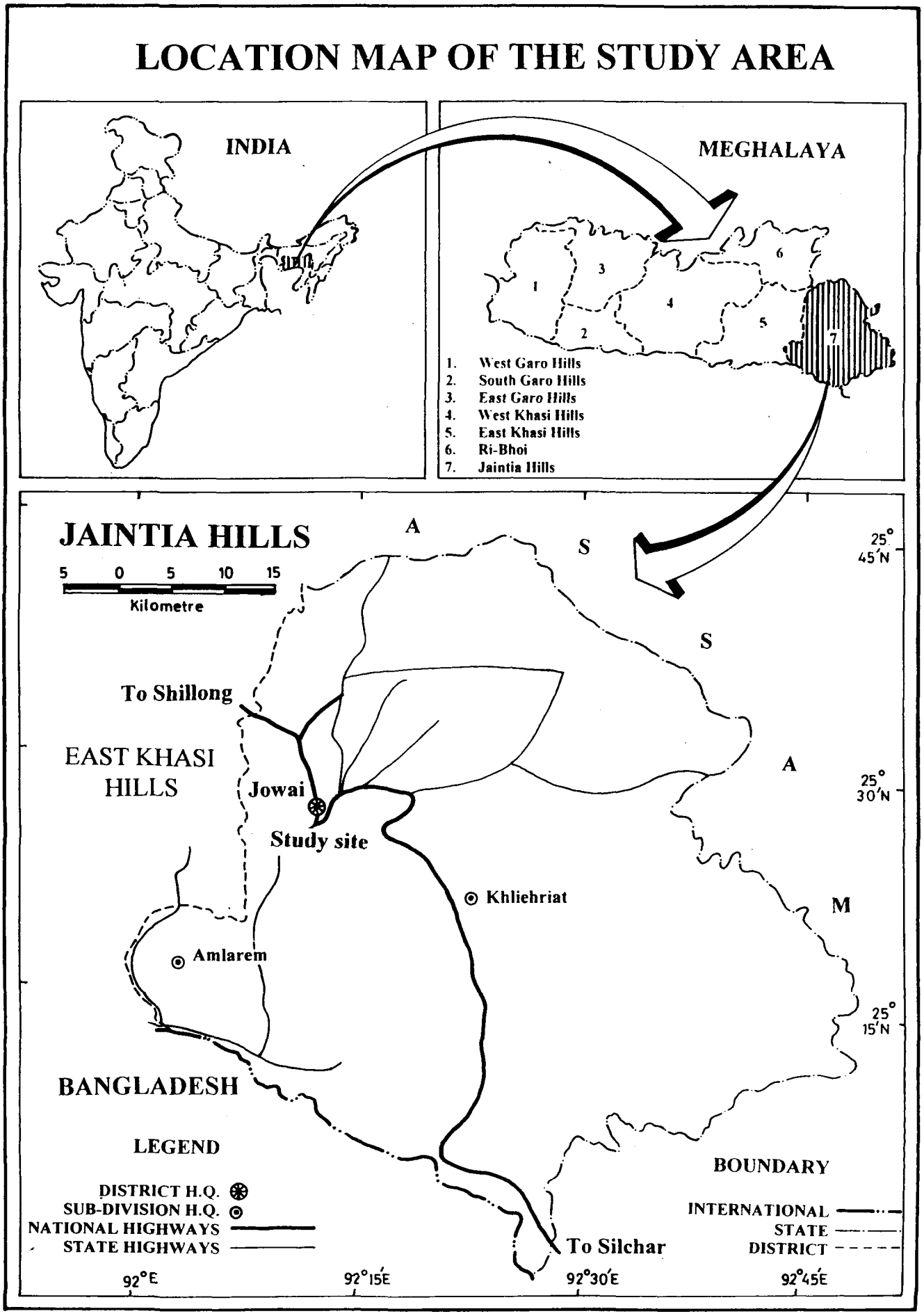

LOCATION MAP OF THE STUDY AREA
INDIA
MEGHALAYA
1. West Garo Hills
2. South Garo Hills
3. East Garo Hills
4. West Khasi Hills
5. East Khasi Hills
6. Ri-Bhoi
7. Jaintia Hills
JAINTIA HILLS
5 0 5 10 15
Kilometre
To Shillong
EAST KHASI HILLS
Jowai
Study site
Khliehriat
Amlarem
BANGLADESH
To Silchar
25° 45'N
25° 30'N
25° 15'N
92°E
92°15'E
92°30'E
92°45'E
LEGEND
DISTRICT H.Q.
SUB-DIVISION H.Q.
NATIONAL HIGHWAYS
STATE HIGHWAYS
BOUNDARY
INTERNATIONAL
STATE
DISTRICT

Fig. 3.1

cross bedding, ripple marks and burrow markings (Sarma et al.1993). A major portion of the Jaintia Hills is characterized by hard sandstone (Ahmad 1993), soft loose sands, hard conglomerates, sandstones, sandy shales and sandy clays.

Climate

The climate of the area is monsoonic with marked seasonal variation in rainfall and temperature. The rainy season starts in early April with interrupted showers, but incessant rain begins in June and continues till September often stretching upto October. Very high rainfall was recorded during the months of August in 1998 (1640 mm) and July 1999 (1557 mm) (Fig.3.2). About 75% of the total annual rainfall was received during May to August in both the years of the study period. The mean minimum and maximum temperatures were 4^0C and 26^0C, respectively (Fig.3.2), and relative humidity varied between 45% and 87%. Thus, monthly variation in rainfall, soil moisture, temperature and relative humidity were quite prominent.

Materials

On the basis of literature survey and field trips conducted during March to June 1997 in the sacred groves, three canopy trees: *Acer laevigatum*, a rare deciduous species in Meghalaya, having high timber value and used for making agricultural implements, *Podocarpus neriifolia* a gymnospermous species of high timber value and also rare in Meghalaya and *Syzygium tetragonum*, a common evergreen species, bearing edible fruits (Plate 3.1, 3.2 & 3.3 respectively) were selected for detailed ecological study. The tree species were identified with the help of Floras (Hooker 1872-97, Kanjilal et al. 1934-40, Balakrishnan 1981-83, Haridasan and Rao 1985-87). The plant specimens were compared with the Herbarium (ASSAM) of Botanical Survey of India, Eastern Circle, Shillong, for correct identification.

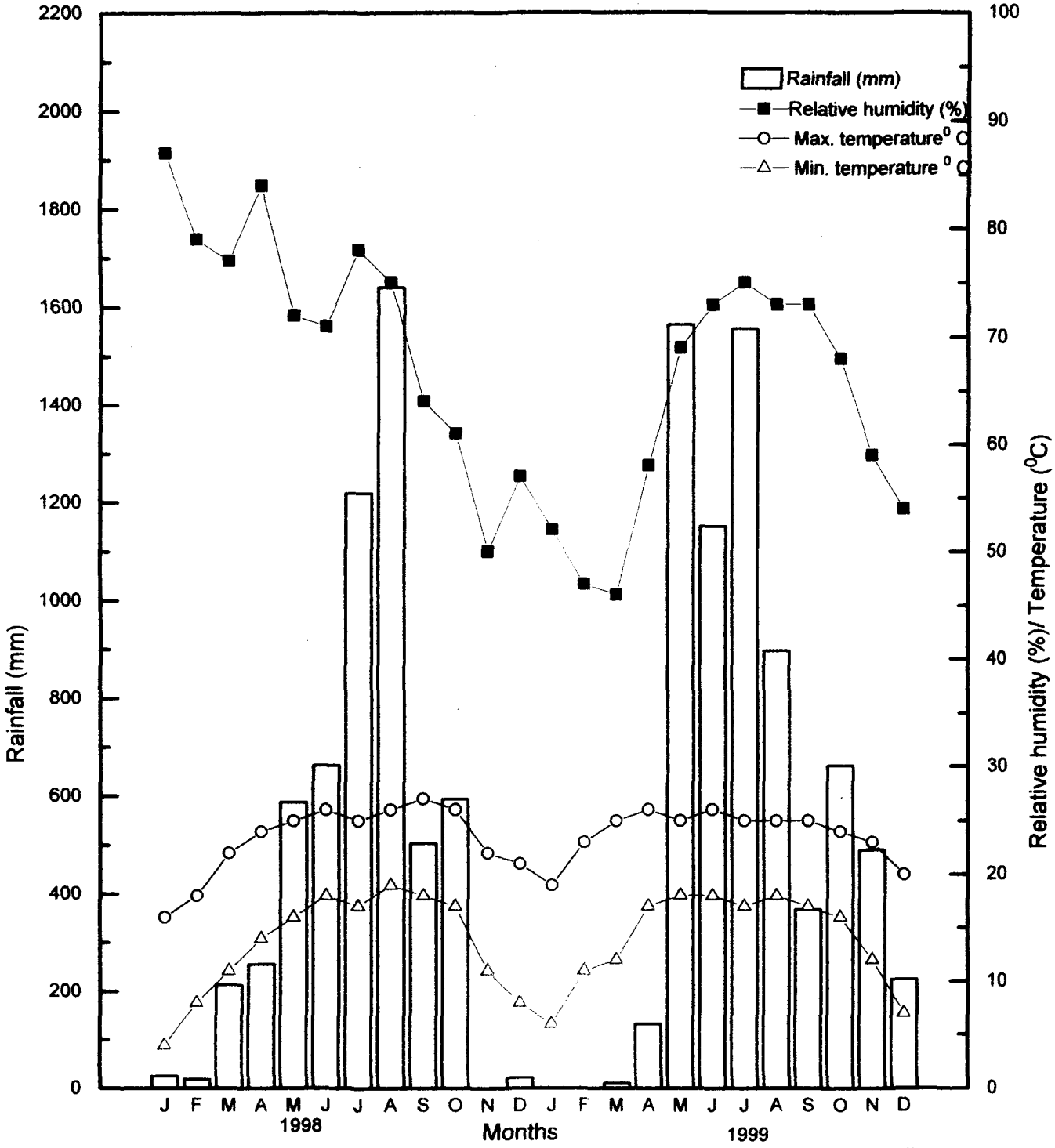


Fig. 3.2. Mean monthly maximum and minimum temperatures, relative humidity and monthly rainfall at the study site.

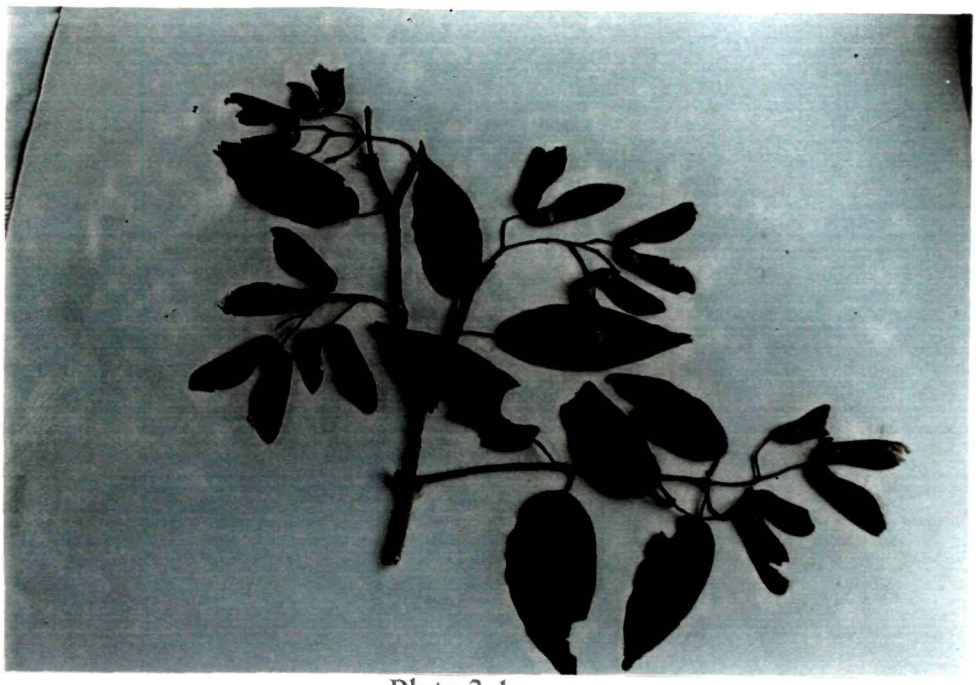


Plate 3.1

Acer laevigatum Wallich, (Aceraceae) Pl. Asiat. Rar. 2: 3-4, t. 104. 182. 1830; Hiern in Hook.f. Fl. Brit. India 1: 693. 1875.

Medium to large deciduous trees, upto 15 m tall with irregularly oval, spreading crown; bark dark greyish-green. Leaves simple, oblong, ovate or elliptic lanceolate, 5-12 X 2.5-5 cm, base rounded or subacute, acuminate at apex, glabrous, entire or minutely serrulate along margins, glabrous, chartaceous; lateral nerves 6-9 pairs, petioles 1.5-1.8 cm long. Racemes subcorymbose or panicled, glabrous, appearing with leaves terminal, 5-10 cm long; flowers white; sepals 5, ovate-lanceolate, *ca* 2 mm long, purplish-green; petals 5, obovate, clawed; ovary pubescent. Samarss glabrous; nuts elliptical, almost terete reticulate; wings 1.5-3 X 0.5-0.8 cm, divergent, reddish when young. Wood white, hard and close-grained.

Vernacular name : Dieng-tyrthiaiong, Dieng-than, Dieng-sohtyrkum (Khasi)

Flowering and fruiting : March to November

Distribution: India- UP, WB, Arunachal Pradesh, Nagaland and Manipur, rare in Meghalaya. Nepal, N. Myanmar, West and Central China.

Uses: Capable of being used as planks and scantlings and for making agricultural implements.

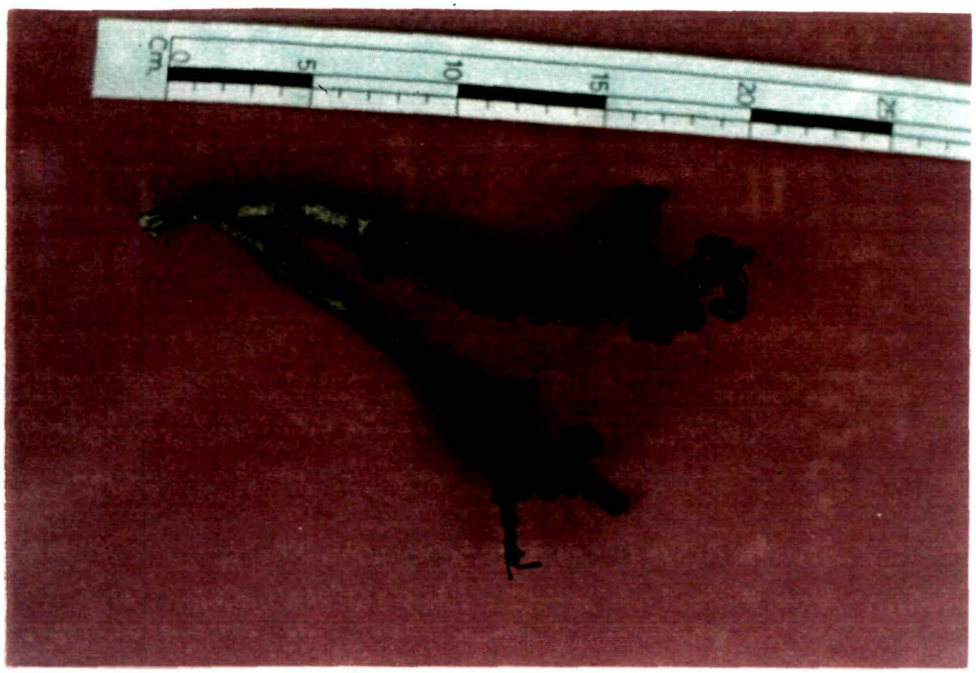


Plate 3.3

Syzygium tetragonum Wallich ex Kurz in J. Asiat. Sco. Bengal 46 (2): 66. 1877; *Eugenia tetragona* Wt. Duthie in Hook.f., Fl. Brit. India 2: 497. 1878.

Trees upto 25 m high, crown ovoid, compact, dense, bark white or greyish, often with black patches, leaves 6-9 X 3-7 cm, oblanceolate, oblong-oblanceolate or oblong elliptic, abruptly shortly acuminate to subacute, base cuneate, attenuate, margin recurved, glaucous beneath; panicles just below the leafy areas, upto 5 cm long, fascicled; flowers 0.5-0.7 cm across, white, fragrant; petals calyptrate, berries 0.5-0.7 cm long, globose, orange yellow or red, crowned by the calyx-limb, edible.

Flowering and fruiting : July to May

Distribution: Bangladesh, Burma, Bhutan and India; very common in Meghalaya.

Vernacular name : Dieng-sohumkynthei, Dieng-sogthiangum (Khasi)

Uses : Wood often used for charcoal.

Plate 3.2

Podocarpus neriifolia D. Don (Podocarpaceae) in Lamb. Desc. Gen. Pinus 2:21, 1824. Hook.f. Fl. Brit. India 5: 649. 1888.

Large evergreen trees 12-18 m high with whorled branches. Bark cinnamon brown, peeling off in long papery flakes, reddish and finely fibrous inside. Leaves scattered, 10-15 X 1-2 cm, linear-elongate, lanceolate, acuminate, entire, thickly leathery, glabrous; midrib very prominent on both surfaces; longitudinal nerves rather obscure; base cuneate; petiole 0.3-1cm long, nearly sessile. Strobilus in clusters or spicate. Peduncle of the female solitary, axillary, single flowered. Receptale of the fruit oblong, fleshy. Seeds solitary, globose, bluish black when ripe. Wood yellowish, even grained. Annual rings rather faint; medullary rays numerous, very fine.

Flowering and fruiting : May to October

Distribution : E. Himalayas upto 900 m in Sikkim, Arunachal Pradesh, Andamans, Malay Peninsula, Bhutan, S.W. China. Rare in Meghalaya.

Uses: Timber of some importance in Surma Valley, highly prized in Burma.

Methods

Vegetation analysis

Phytosociological status of the studied species in the forest was ascertained by randomly laying twenty 10m x 10m quadrats in both the sacred groves. Density of the woody species (≥ 5cm dbh) were recorded and calculated according to Misra (1968).

Total tree density in Urkhla was 1299 plants/ha whereas in Khloo Langdoh it was 1496 plants/ha. *Syzygium tetragonum* was quite common in Urkhla, with a density of 47 individuals/ha. The density of *Acer laevigatum* and *Podocarpus neriifolia* was 32 and 24 individuals/ha respectively in Khloo Langdoh sacred grove.

The canopy of the forest is composed of both evergreen and deciduous broad-leaved trees, not exceeding 30 meters height. In Urkhla the canopy is composed of *Betula alnoides*, *Cinnamomum glanduliferum*, *Castanopsis tribuloides* and *Syzygium tetragonum*, whereas in Khloo Langdoh *Drimycarpus racemosus*, *Acer laevigatum*, *Cinnamomum bejolghota*, *Garcinia anomala* and *Glochidion lanceolarium* are the canopy species. The sub-canopy in Urkhla is composed of *Helicia nilagirica*, *Quercus kamroopii*, *Lithocarpus elegans*, *Croton oblongus*, *Pithecellobium monadelphum*, *Myrsine semiserrata*, whereas in Khloo Langdoh this layer is composed of *Coffea khasiana*, *Microtropis discolor* and *Acronychia pedunculata*. The canopy and subcanopy tree together forms a continuous dense cover. At places the continuity of the canopy cover is broken by the gaps created by tree falls. The forest floor in gaps was covered by dense herbaceous vegetation including tree seedlings. Woody climbers and twiners were common in the forest.

Soil analysis

Soil samples were collected on seasonal basis from the two sacred groves by using a soil corer (diameter 6.3 cm and length 30 cm). On each sampling date, five cores were obtained from three depths (0-10, 10-20 and 20-30 cm). The replicated soil samples from each depth were mixed thoroughly to obtain a homogenous sample. The samples were passed through 2mm sieve to remove large stones and roots.

Soil moisture was determined gravimetrically by drying 10g freshly collected soil at 105^0C to constant weight in a hot air oven (Allen et al. 1974). Soil pH was determined by a digital pH meter taking 1:2.5 suspension of fresh soil and distilled water (Anderson and Ingram 1993).

Air-dried and sieved (0.2 mm) soils were used for organic carbon, total Kjeldahl nitrogen (TKN), available phosphorus and exchangeable potassium. Organic carbon was determined by rapid titration method (Allen et al. 1974). TKN was determined by digesting the soil samples with concentrated sulphuric acid using Kjeltab as catalyst in a block digester. Distillate obtained from micro-distillation set was titrated with N/140 HCl (Allen et al. 1974). Available phosphorus was determined by molybdenum blue method after extracting the soil-P in 0.5M sodium bicarbonate (Anderson and Ingram 1993). Exchangeable potassium was determined by flame photometer after extracting with ammonium acetate (pH. 7) as outlined by Allen et al. (1974).

Physicochemical characters of the sacred grove soil

The soils are sandy loam in both the sacred groves. The soil moisture showed marked seasonal variation with a peak during July when it was almost saturated (86%), and a minimum of 15 % during February (Fig. 3.3). There was no marked seasonal variation in other soil properties in both the groves, except for organic matter

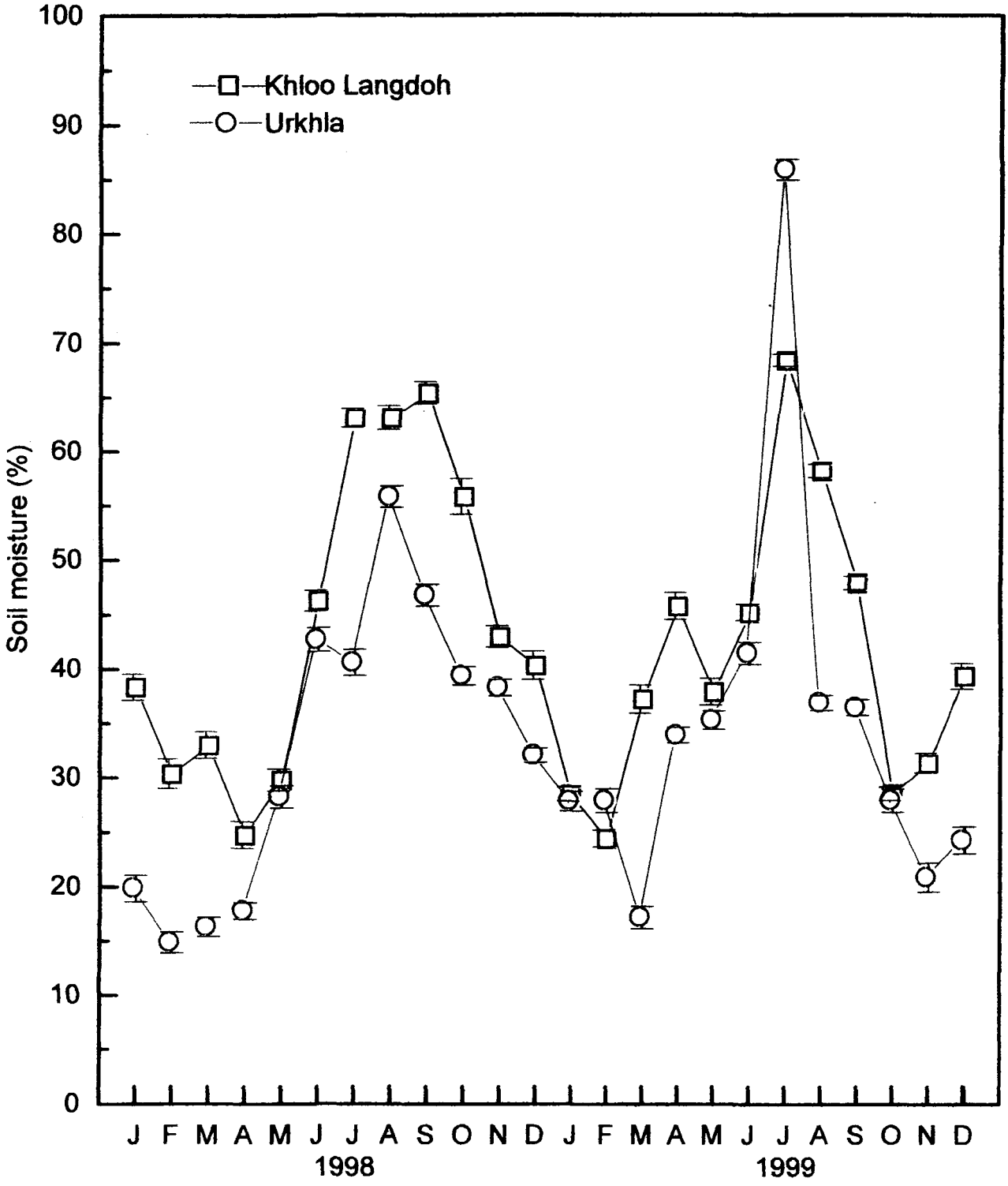


Fig. 3.3. Monthly soil moisture content (%) in the two sacred groves.

content (Table 3.2). The soil was acidic in nature with pH ranging between 4.5 and 4.9 (Table. 3.2).

Table 3.2. Physico-chemical characters of soil of the two sacred groves.

Name of the sacred grove	Texture	pH	TKN	Organic matter (%)	Available Phosphorus (%)	Exchangeable potassium (%)
Urkhla	Sandy loam	4.51 to 4.88	0.41 to 0.45	7.62 to 7.8	0.015 to 0.017	0.24 to 0.26
Khloo Langdoh	Sandy loam	4.54 to 4.86	0.36 to 0.40	5.17 to 5.34	0.016 to 0.017	0.20 to 0.21

Seed germination

Mature seeds of *Podocarpus neriifolia* and *Acer laevigatum* were collected in October 1997, while seeds of *Syzygium tetragonum* were collected in March 1998 in bulk from the two sacred groves. The seeds were brought to the laboratory and cleaned. 20 seeds were randomly picked from the lot and initial weight recorded to determine moisture loss on drying. One lot of seeds were germinated immediately in plastic trays (35 cm x 30 cm wide and 5 cm deep) filled with sand of particle size 0.05 mm to 0.8 mm diameter (ISTA 1985). In this experiment three replicates of 100 seeds each were pressed into the sand after moistening it with distilled water. The seeds germinated immediately after collection was considered as the initial percentage viability. Another lot was air dried at room temperature (20^0C) for one month and stored in plastic bottles in the laboratory for viability tests. Viability tests were conducted at a temperature of 25^0C in dark, as maximum germination percentage was recorded at this temperature. The one month drying period was also considered as storage period.

Germination response to a range of constant temperature regimes was tested by incubating the seeds at 20^0C, 25^0C and 30^0C in a germination chamber (Myers et al. 1989, De Villiers et al. 1994, Teketay 1995, 97). Seeds were inspected every day and were considered germinated when the radicles were about 2mm long. In light treatment seeds were exposed to constant fluorescent light (320 lux). Seeds receiving dark treatment were wrapped in aluminum foil to provide complete darkness and placed randomly in the same germination chamber at the three temperatures.

Seedling study

The experiment was started at the same time for all the three species in the month of May when *Podocarpus* and *Acer* seedlings were six months and that of *Syzygium* two months old.

Pot culture

Soil samples were collected in bulk from 0-20 cm surface layer in replicates from the sacred groves. The homogenised air-dried soil samples weighing 3 kg were filled into plastic buckets (20-cm height and 16-cm diameter). To facilitate proper water drainage holes were made at the base of the buckets. Altogether 135 buckets were prepared for growing the seedlings. Fifteen buckets with two seedlings of a given species per bucket were raised at the three soil moisture level viz. 20%, 30% and 40% each.

Similarly seedlings of three species were grown at three levels of NPK fertilizerviz. half, full and double dose. Nitrogen as urea 60 kg/ha, phosphorus as single superphosphate 30 kg/ha and potassium as muriate of potash 40 kg/ha was considered as full dose (Singh et al.1996). Considering that soil water content for unstressed plants is about 27% (Osonubi et al. 1985), one set of pots was maintained at 30% (3000g dry

soil + 160g bucket +900g water), second set at 20% (3000g dry soil +160g bucket + 600g water) and third set at 40% (3000g dry soil + 160g bucket + 1200 g water) soil moisture level. Soil water contents of the buckets were maintained by weighing the pots at regular time intervals and tap water was added whenever necessary.

Field study

The field experiments were simultaneously carried out with the laboratory experiments. For studying seedling performance, Urkhla sacred grove was selected, since Khloo Langdoh sacred grove is surrounded by human habitation and is disturbed by domestic animals. Fifty seedlings of each species were transplanted in a medium sized (ca. 20 m^2) canopy gap and in the forest understorey to study the effect of light on their growth. The seedlings were tagged with aluminum foil and their fate was monitored at an interval of 4 month for one year.

Light intensity in gap, forest understorey, net-house and full sun were measured at monthly intervals by digital Lux meter during the experiment period. Mean light intensity as percentage of full sun was 82% in net house, 31% in gap and 2% in the forest understorey.

Growth performance of the transplanted seedlings was studied by harvesting five seedlings at 120, 240 and 360 days intervals. Proper care was taken to prevent minimal loss of fine roots. On each harvest, leaf number, leaf area, root and shoot length was measured. Leaf area was measured using Leaf Area Meter (Licor, USA). The leaf, stem and root were oven dried at 80^0C to constant weight and weighed. The different plant parts were powdered in a Cyclotec grinding mill (Tecator) and stored for NPK analysis.

Nutrient analysis in plant parts

For the analysis of total phosphorus and potassium the powdered samples were digested in tri-acid (1ml $HclO_4$ + 5ml HNO_3 + 0.5ml H_2SO_4) mixture on a block digester. Total phosphorus concentration was determined colorimetrically by molybdenum blue method and total potassium was measured by flame photometer method (Allen et al. 1974). Total Kjeldhal nitrogen (TKN) was estimated by digesting the samples with concentrated H_2SO_4 in a block digester using Kjeltab as a catalyst. Distillation was carried out in a semi micro Kjeldhal distillation set and the distillate was collected in boric acid indicator. The distillate was titrated with N/140 Hcl (Allen et al. 1974).

Calculations

I. Percentage germination = No. of germinated seeds/total no. of seeds sown X 100 (Schelin et al. 2003).

II. Germination rate = Σ G/t, where, G = percentage of seeds germinated everyday, t = total germination period (Khan and Ungar 1984).

III. Allocation and accumulation of nutrients in different plant parts were calculated by multiplying the mean dry mass with their elemental concentration

IV. Nutrient use efficiency (NUE) of the seedlings was expressed as dry matter produced per g nutrient uptake (Gholz et al. 1985).

V. Relative growth rate (RGR) was calculated. as $R = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$ (Beadle 1985)

where, $\ln W_2$ = Natural logarithm of final weight
$\ln W_1$ = Natural logarithm of initial weight

t_1 and t_2 = Time between harvest (days)

VI. Moisture content in soil and seeds was calculated as,

% moisture = Loss in weight on drying/dry weight X 100 (Air drying for one month in case of seeds and oven drying at 105^0C for soil)

Statistical analysis

Wherever required, data were statistically analysed through one-way and two-way analysis of variance to determine effect of different treatments and between the species.

CHAPTER – IV
GERMINATION

Natural regeneration of tree species depends upon seed production, viability, dormancy, germination and successful establishment of seedlings (Kumar et al. 2000). Germination is regulated by several intrinsic factors and environmental conditions on the forest floor. The interactions between environmental stresses and endogenous dormancy determine the fate of a particular seed that germinates under a given habitat condition (Bradford et al. 1992). Dormancy is a seed characteristic, the degree of which defines the condition that should be met to make the seed germinate (Vleeshouwers et al. 1995). The wider the range of conditions at which a seed is able to germinate, the smaller its degree of dormancy (Hilhorst 1993). However, most seeds can be stored for short periods without affecting their viability. Seeds gradually lose viability during storage (Rehman et al. 1999). The germination percentage decreases with increase in age of the seeds (Palma et al. 1995). The ageing of the seeds is generally indicated by reduced germination (Kalpana and Rao 1995, 1996), reduced germination rate (Chhetri et al. 1993) and reduced growth (Coin et al. 1996).

Among the several environmental factors, temperature is the single most important factor governing germination percentage and rate of germination (Bewley and Black 1985). The fraction of seeds which germinate and the rate of germination usually remains constant over a wide range of temperatures. Most workers have reported that the optimum temperature for seed germination is 20^0C or more and declines sharply on either side of this temperature (Thompson 1970). The rate of germination, also called embryo developmental rates (Sorensen 1999), usually

increases linearly with temperature at least within a well-defined range (Mwale et al. 1994; Ramin 1997).

In germination experiment under 90%, 52% and 28% full light, Khan and Uma Shankar (2001) reported best germination of *Quercus semiserrata* under 52% light. Raich and Gong (1990) investigated the germination of 43 Malaysian tree species in clearing, gap and forest understorey sites receiving 60%, 40% and 1.2% of full-sun PAR. Only seven species germinated equally well at all sites. In the clearing, 16 species showed low rates of germination, or failed completely; 22 species germinated at higher rates in the understorey than the clearing and 12 species germinated better in one or the other open sites than they did in the understorey. Raich and Gong (1990) argued that a clear dichotomy of species on germination response to light was not easy to discern. Similar picture also emerged from a study of 19 tree species from tropical West Africa (Kyereh et al. 1999). Only three species germinated in significantly lower proportions in complete darkness than under light treatment and only one species responded to variation in F: FR ratio. All the species showed some germination in the forest understorey.

The response of the seeds of three tree species to different temperatures, storage time and light on germination percentage and rate of germination have been presented in this chapter.

Results

a). **Effect of storage time**

After 30 days of air drying, the seeds of *Podocarpus neriifolia* and *Syzygium tetragonum* lost 28% and 50% moisture respectively. *Acer laevigatum* lost only 2% moisture.

The germination percentages of *Acer*, *Podocarpus* and *Syzygium* seeds immediately after collection were 85%, 82% and 92% respectively. The time taken for initiation of germination was 2 days in *Podocarpus neriifolia*, 9 days in *Syzygium tetragonum* and 10 days in *Acer laevigatum*. Germination was completed by 21, 20 and 24 days in *Podocarpus neriifolia*, *Syzygium tetragonum* and *Acer laevigatum* respectively. Germination percentage decreased with increase in storage time. In case of *Acer* it decreased from 74% at 30 days to 9 % at 150 days (Table: 4.1). Seeds of *Syzygium tetragonum* showed a trend to similar that of *Acer laevigatum*. Its germination was 21% at 30 days and the seeds became non-viable after 60 days of storage, therefore there was no germination. The germination percentage of *Podocarpus neriifolia* was very high (82%) immediately after collection, but seeds did not germinate beyond 30 days of storage.

Table: 4.1. Effect of storage period on germination of *Acer laevigatum*, *Podocarpus neriifolia* and *Syzygium tetragonum* seeds at 25^0C (values are mean of three replicates each of 100 seeds)

Storage time (days)	Germination (%)	Time taken for initiation of germination (days)	Mean time taken to achieve 50% germination (days)	Mean time taken for completion of germination (days)
Acer laevigatum				
0 days	85.00	10	17	24
30 days	74.33	10	16	21
60 days	70.66	12	18	25
90 days	31.33	14	18	26
120 days	20.00	18	22	27
150 days	9.33	22	24	29
180 days	0	-	-	-
Podocarpus neriifolia				
0 days	82	2	8	21
30 days	0	-	-	
Syzygium tetragonum				
0 days	92.5	9	14	20
30 days	21.00	10	13	17
60 days	0	-	-	

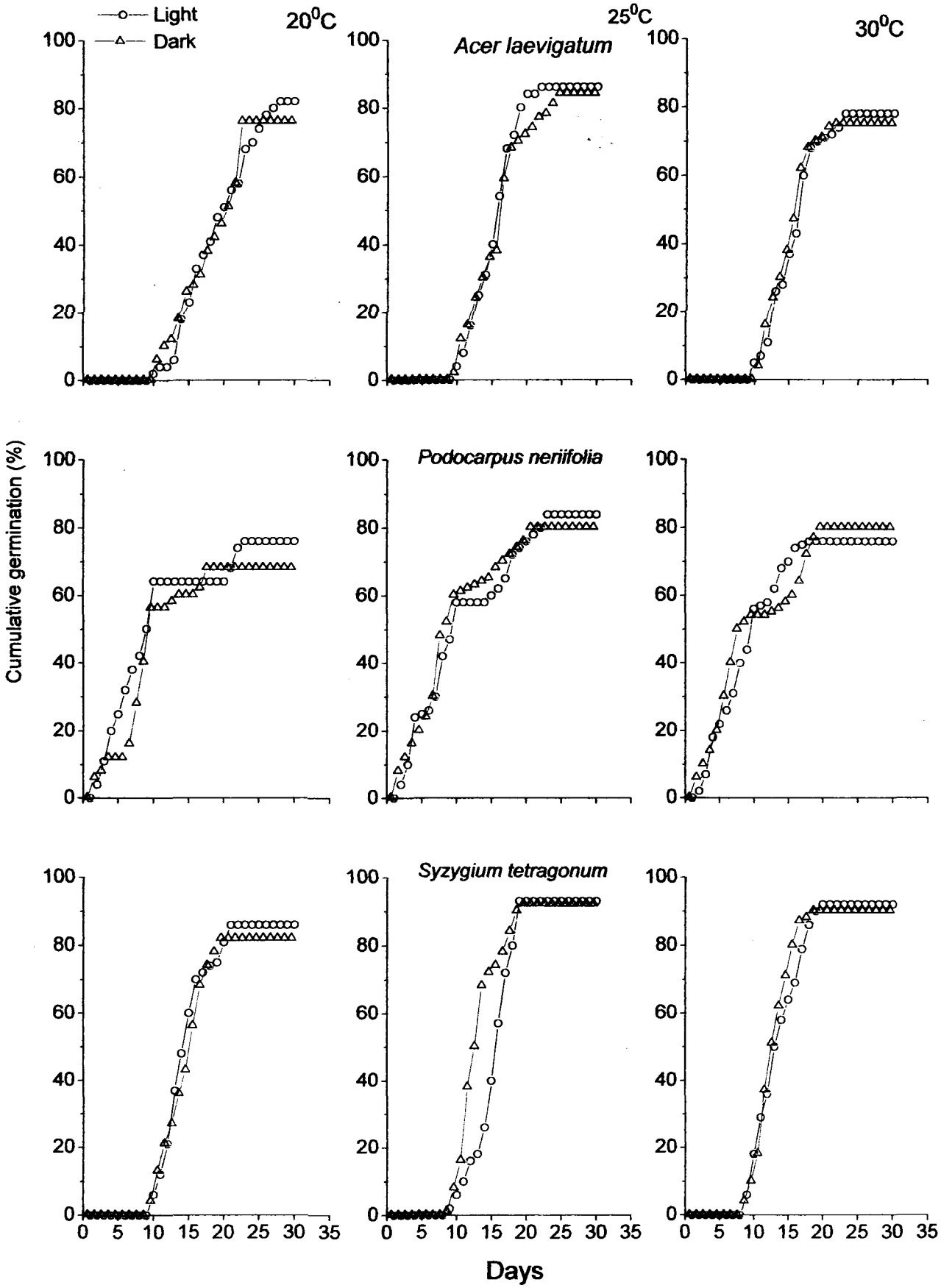


Fig. 4.1. Germination (%) of the three tree species under light and dark condition at different temperatures.

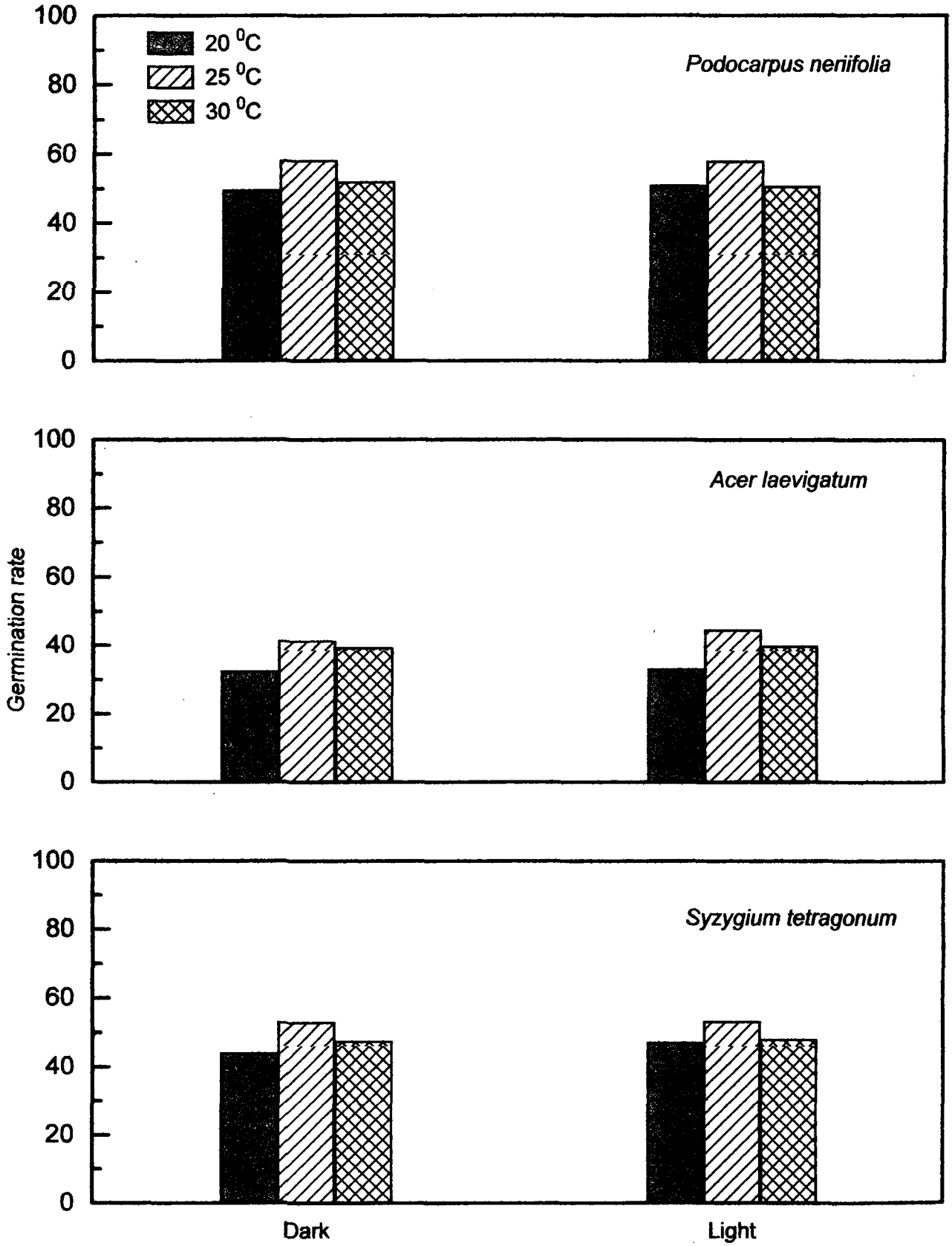


Fig. 4.2. Rate of germination of *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetragonum* at 20^0 25^0 and 30 ^{0}C under dark and light conditions.

b) **Effect of dark and light at different temperatures**

The germination of *Acer laevigatum* seeds in dark at 20^0, 25^0 and 30^0C was 82, 86 and 78% respectively. The corresponding values under light condition were 76, 84 and 75% (Fig. 4.1). Similarly, *Podocarpus* and *Syzygium* seeds showed higher germination at 25^0C both in light and dark. There was no significant difference in germination between light and dark. ANOVA of the results did not show any significant effect of temperature on germination.

Germination rate was high at 25^0C (Fig: 4. 2) both in light and dark in all the three species. One-way ANOVA showed significant effect of temperature on germination rate of *Syzygium* and *Acer* ($P<0.05$) and *Podocarpus* ($p<0.05$).

Discussion

The results of the present study are in conformity with the findings of Bradford et al. (1993), and Thornton and Powell (1995) who found that germination is delayed with ageing of seeds. Pradhan (2000) also reported that the germination vigour of *Alnus nepalensis* seeds decreased exponentially with increasing storage time interval and reached lowest value after 395 days.

The germination percentage decreased with increase in storage time in all the three species but in *Syzygium tetragonum* the value was much lower (21%) as compared to that of *Acer laevigatum* (74%) during the first 30 days of storage. Seeds of *Syzygium tetragonum* became totally non-viable beyond 60 days and those of *Podocarpus* failed to germinate beyond 30 days of storage. Similar trends have been reported by Uma Shankar and Khan (2001) in *Aquilaria malaccensis* where germination declined sharply during storage, and it was negligible after 30 days. Nath et al. (1999) recorded a progressively declining germination percentage of seeds sown

in sand with increasing storage time. The low germination in the present studied species with the increase in the storage time could be due to the loss of moisture content of the seed at room temperature as cold storage of seeds prolong viability retention time. Boojh and Ramakrishnan (1982) reported in *Schima* species that, there was a marked decrease in germination percentage with the passage of time, but the seeds stored at 0^0C maintained better viability and germinability even after 1 year of storage.

The optimum temperature range of 20^0C to 30^0C for germination of seeds as observed in the present study has been reported by many workers (Teketay 1995; Castellani and Aquiar 2001; Finneseth et al. 1998; Meyer et al. 1989). Teketay (1995) reported that germination of *Moringa stenopetala* increased with increase in temperature until 25^0C, but it gradually declined thereafter, germination was inhibited to a larger extend at 15^0C and completely inhibited at 10^0C. *Chrysothamnus nauseosus* seeds germinated to full viability within 4 weeks at 20^0C, 25^0C and 30^0C indicating that any dormancy exhibited at lower temperatures was conditional or temperature dependant (Myers et al. 1989). Castellani and Aguiar (2001) also concluded that for seeds of a pioneer tree species *Trema micrantha*, 20^0C to 30^0C was required for germination.

The germination of *Acer laevigatum*, *Podocarpus* and *Syzygium* seeds was high (above 70%) both in light and dark. The ability of some species to remain dormant in the shade and germinate only in direct sunlight has been recognized as a characteristic feature uniting a group of tropical tree species of similar ecology. Swaine and Whitmore (1988) used this as a key character to define 'pioneer' species, which are fast-growing, shade-intolerant typically found only in gaps or other early successional sites in the forest. The more shade-tolerant species have germination that is generally

not dependent on degree of shading. Swaine and Whitmore (1988) referred to these species as 'non-pioneers'. Raich and Gong (1990) investigated the germination of 43 Malaysian tree species in clearing, gap and forest understorey sites. They argued that a clear dichotomy of species on germination response was not easy to discern as a more complex pattern of seed responses was seen. Similar picture emerged from a study of 19 tree species from tropical West Africa (Kyereh et al. 1999). Only in three species germination was significantly lower in complete darkness than under light treatment, and only one species responded to variation in R: FR ratio. All the species showed some germination in forest understorey conditions. The sample included several species that were strongly light-demanding such as *Ceiba pentandra* and *Ricinodendron heudelotii*. Finneseth et al. (1998) also did not observe significant effect of light on germination of *Asimina triloba*.

The results of the present study show that in the absence of other limiting factors (eg. water, light, and media), the germination of *Acer laevigatum, Podocarpus neriifolia* and *Syzygium tetragonum* seeds are influenced by temperature and storage time. The optimum temperature for germination of the above three species was 25 ± 3^{0}C.

CHAPTER – V
SURVIVAL AND GROWTH OF THE SEEDLINGS

Survival, growth and establishment of tree seedlings under different environment are mainly determined by the availability of light, water and nutrient resources and by the competitive ability or adaptive strategies of the species along these environmental gradients (Law 2002). Adaptability of plants to various environmental conditions is determined by their differences in morphological and physiological traits and attributes. Morphological attributes are predominantly associated with differences in capacity of dehydration avoidance (Kramer 1983), with root and leaf adaptations playing an important role in promoting better plant water balance (Pallardy and Rhoads 1993). Development of vigorous root system is critical to the successful establishment of seedlings because soil water resources must be exploited to make up for the transpirational losses of rapidly growing seedlings (Harper 1977; Meyer and Boyer 1981). The pattern of allocation of dry matter to root and shoot affects water relations; greater drought tolerance has been associated with smaller investments in shoot growth as compared to the root growth in numerous species (Pallardy 1981; Abrams 1990).

Light is a major environmental factor limiting growth and survival of many forest species (Chazdon et al. 1996; Whitmore 1996). Gap formation due to tree fall or dropping of branches in the forest provides suitable micro-sites for recruitment of seedlings of pioneer or shade intolerant tree species. Gap increases environmental heterogeneity of forests in many ways. Light and soil parameters (moisture, nutrients) vary with gap size; the centers of large gaps are different from the centers of small gaps, which are different

from the surrounding understorey (Runkle et al. 1995). The entire process of seedling establishment starting from germination, seedling recruitment and their growth and development is strongly influenced by micro-site heterogeneity and micro-climatic conditions prevailing in the gaps (Vance and Running 1985; Barik et al. 1992; Rao et al. 1997; Coomes et al. 1998).

In forest ecosystems, low light intensity often proves to be a limiting factor for seedling growth and plays a significant role in determining the outcome of the competitive struggle between seedlings and established plants (Rao and Singh 1985). Neighbouring plants may interfere with and reduce each other's supply of light by direct interception (Harper 1977). Light availability decreases during succession from early to late successional stage, as biomass increases (Parrish and Bazzaz 1982). Obviously, the species, which appear in later stage of succession, should have better ability to utilize light than those appearing in the earlier stages (Zangerl and Bazzaz 1983). Seedlings of primary or shade tolerant species perform better in the under canopy or shade (Whitmore 1975). In a study from Borro Colorado Island, Welden et al. (1991) reported that growth of seedlings and saplings of majority of species was more rapid in areas of low canopy gaps where light was more than in the areas of high canopy trees. The emergent and dominant canopy layer species showed high sapling mortality rate than the less common species (Okuda et al. 1997).

Field studies have left no doubt that desiccation is a major source of seedling mortality in the understorey of a wide range of forest types including rain forests. Water and nutrient deficits are caused by water and nutrients not being supplied to plants at the

rate required for their maximum growth. Low nutrient availability and effects of neighbouring vegetation are other factors, which determine seedling growth and establishment (Weih and Karlsson 1999). Competition between roots of different species for uptake of water and nutrients depends on whether they coexist in the same soil zone or whether their demands are segregated spatially or temporally. Differences in the morphological and anatomical features of the root system may also be important in this respect (Nambiar and Sands 1993).

The present chapter deals with the survival and growth of seedlings of *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* under different light, and soil water and nutrient conditions.

Results

Survival of the transplanted seedlings in gap and forest understorey

Survival of transplanted seedlings of all three species was poor in the understorey than in the gap. At the end of 360 days *Acer laevigatum* showed 67% mortality in the understorey and 58% in gap. In *Syzygium tetragonum* 58% mortality was observed in understorey and 50% in gap. *Podocarpus neriifolia* exhibited 37% mortality in the understorey and only 16% in gap (Table 5.1).

Table 5. 1. Average mortality (%) of transplanted seedlings in gap and understorey

Name of the species	Observation period (Days)	Mortality	
		Gap	Understorey
Podocarpus neriifolia	120	0	2
	240	8	25
	360	16	37
Acer laevigatum	120	8	15
	240	40	50

	360	58	67
Syzygium tetragonum	120	2	10
	240	48	53
	360	50	58

Seedling growth in gap and understorey

Root and shoot length

Root and shoot growth of the three species was significantly ($P<0.001$) higher in gap than in the forest understorey (Fig. 5.1; Plate 5.1).

Leaf

Mean leaf area and LMA was significantly ($P<0.01$) higher in gap than in forest understorey in all the species (Table 5. 2). In gap the LMA was 18.4 mg/cm^2 in *Acer laevigatum* followed by *Syzygium tetragonum* (5.4 mg/cm^2) and *Podocarpus neriifolia* (5.1 mg/cm^2). The corresponding values in forest understorey were 14.3, 3.0 and 3.6 mg/cm^2 (Table 5. 3).

Table 5. 2. ANOVA showing effects of gap and understorey on leaf area of *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetràgonum* seedlings

Species	Harvest period (days)	F value	Probability level (P<)
Podocarpus neriifolia	120	7.42	0.05
	240	19.14	0.01
	360	32.31	0.01
Acer laevigatum	120	33.31	0.01
	240	12.10	0.01
	360	14.91	0.01
Syzygium tetragonum	120	52.72	0.01
	240	11.17	0.01
	360	13.09	0.01

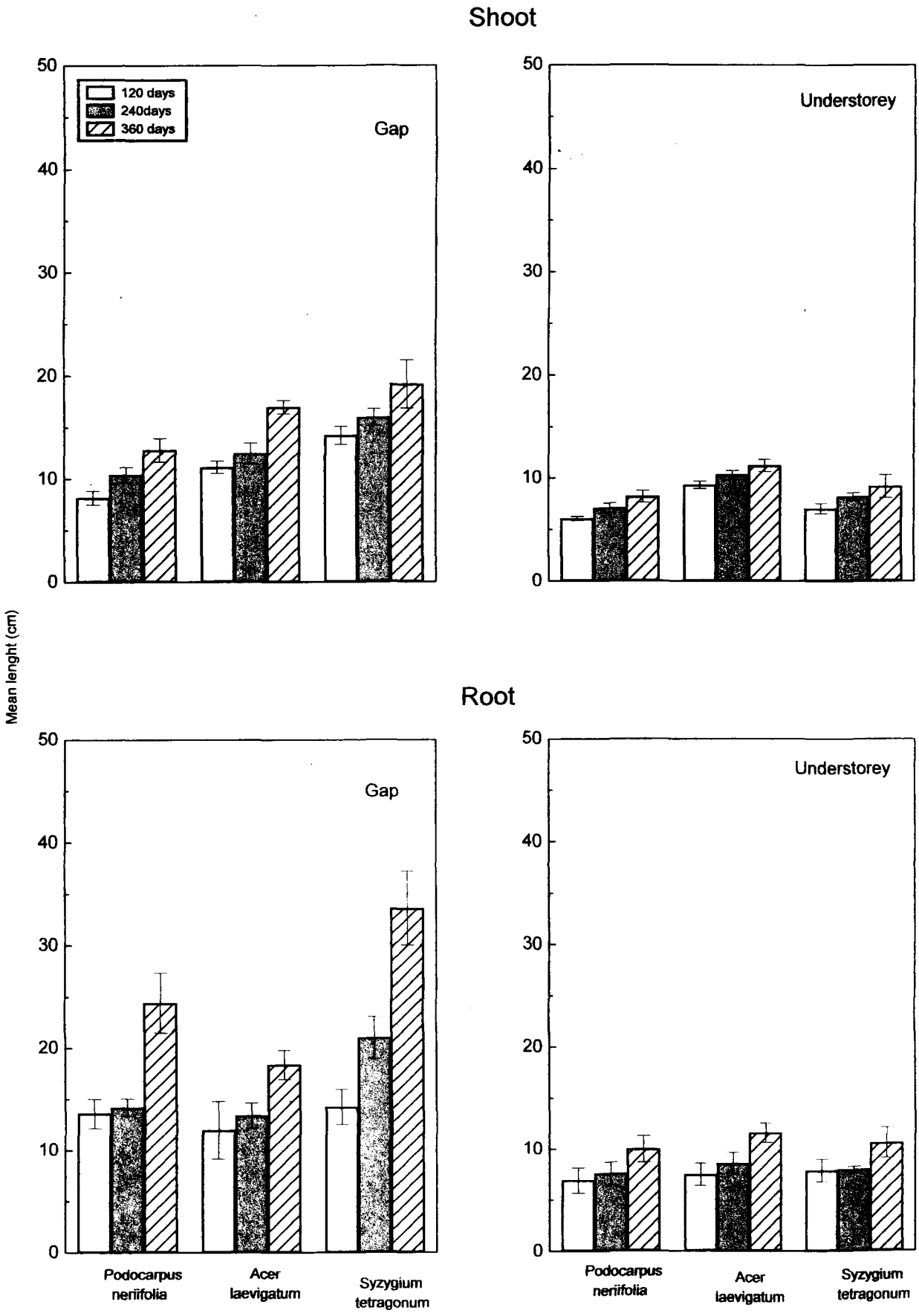
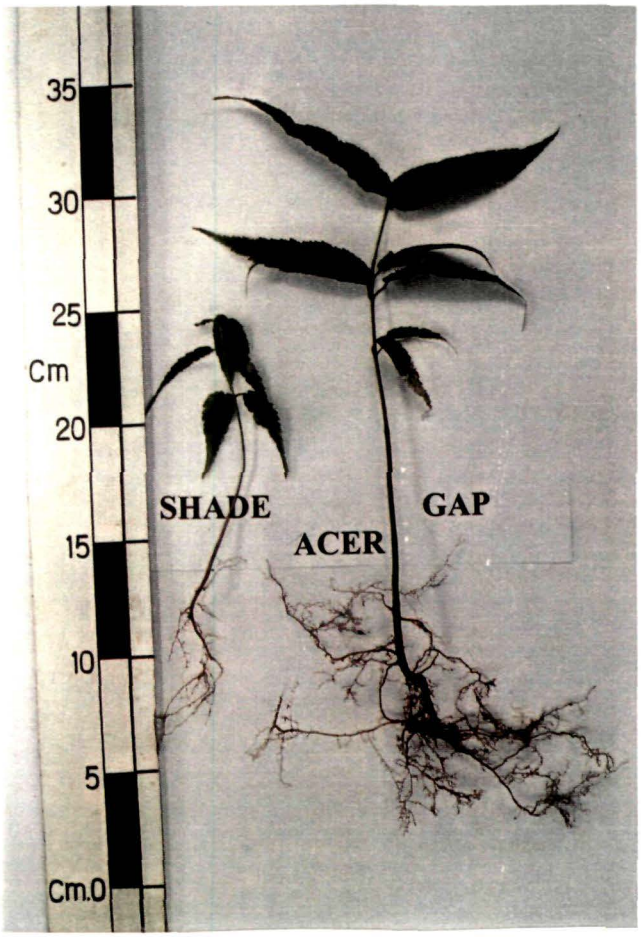


Fig. 5.1. Mean shoot and root length (cm) of the sedlings under gap and understorey.



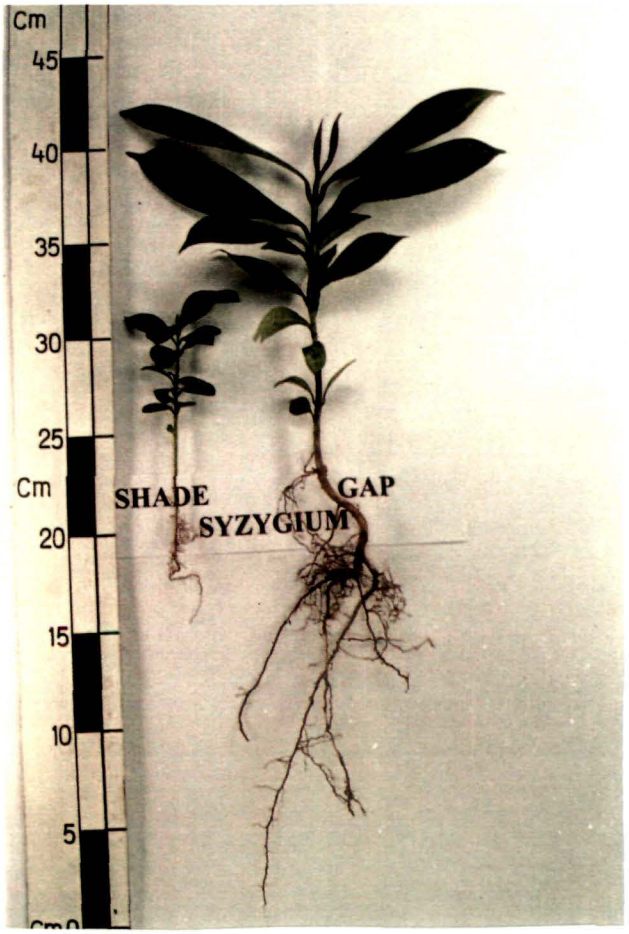


Plate. 5.1. *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetragonum* seedlings after 360 days of growth in gap and understorey (shade)

Table 5. 3. Mean leaf area (cm^2), number of leaves/plant and leaf mass per unit area (LMA) in gap and understorey.

Species	Light conditions	Leaf area	Leaf number	LMA (mg/cm^2)
Podocarpus neriifolia				
	Gap	3.65	22	5.1
	Understorey	1.93	11	3.6
Acer laevigatum				
	Gap	4.37	10	18.4
	Understorey	2.21	6	14.3
Syzygium tetragonum				
	Gap	16.96	17	5.4
	Understorey	3.18	12	3.0

Dry mass

The seedlings in gap had higher dry mass than those in the understorey. The mean dry mass at the end of the experiment was 2838 mg/plant in *Syzygium tetragonum*, 952 mg/plant in *Podocarpus neriifolia* and 516 mg/plant in *Acer laevigatum* in the gap. The corresponding values in the understorey were 97, 160 and 124 mg/plant (Table 5. 4).

Table 5. 4. Mean dry mass (g $plant^{-1}$) accumulation in *Podocarpus neriifolia, Acer laevigatum* and Syzygium *tetragonum* in gap and understorey.

Species		Dry mass		
	Light conditions	120 days	240 days	360 days
Podocarpus neriifolia	Gap	238	316	952
	Understorey	54	90	160
Acer laevigatum	Gap	196	292	516
	Understorey	52	82	124
Syzygium tetragonum	Gap	796	1720	2838
	Understorey	50	72	97

Root: shoot ratio

In all three species root: shoot ratio was higher in gap than in the understorey (Table 5.5).

Table. 5. 5. Mean root: shoot ratio in *Acer laevigatum*, *Podocarpus neriifolia* and *Syzygium tetragonum* in gap and understorey after 360 days of growth.

Species	Light conditions	Root: shoot ratio
Podocarpus neriifolia	Gap	0.516
	Understorey	0.333
Acer laevigatum	Gap	0.70
	Understorey	0.50
Syzygium tetragonum	Gap	0.347
	Understorey	0.266

Relative growth rate (RGR)

The RGR of all three species was higher in gap than in understorey. *Syzygium tetragonum*, *Acer laevigatum* and *Podocarpus neriifolia* seedlings showed 5.5, 4.5 and 2.8 times, respectively, higher RGR in gap than in the forest understorey during the first four month of growth. Thereafter the seedlings did not exhibit significant difference in RGR (Table 5.6).

RGR in gap during the first four month was 77 mg day^{-1} $plant^{-1}$ in *Syzygium*, 46 mg day^{-1} $plant^{-1}$ in *Podocarpus* and 41 mg day^{-1} $plant^{-1}$ in *Acer*. The corresponding values in understorey were 14 mg day^{-1} $plant^{-1}$, 16 mg day^{-1} $plant^{-1}$ and 9 mg day^{-1} $plant^{-1}$.

Table 5.6. RGR (mg day^{-1} $plant^{-1}$) of *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetragonum* in gap and understorey.

Species	Light conditions	Sampling period (days)		
		120	240	360
Podocarpus neriifolia				
	Gap	46	25	14
	Understorey	16	13	12
Acer laevigatum				
	Gap	41	14	11
	Understorey	9	8	8
Syzygium tetragonum				
	Gap	77	19	9
	Understorey	14	7	7

Seedling growth under different soil moisture levels

Root and shoot length

At the end of the experiment *Podocarpus nèriifolia* and *Syzygium tetragonum* showed highest shoot growth at 40% soil moisture level, while the best shoot growth of *Acer laevigatum* was observed at 30% soil moisture level (Fig. 5.2; Plate 5.2, 5.3 and 5.4). The root growth of *Podocarpus neriifolia* and *Acer laevigatum* was better at 20% level (Fig. 5.3). However, a significant progressive growth in shoot and root length with increasing soil moisture was observed only in *Syzygium tetragonum*. With age there was an increase in shoot and root length in all the three species.

Leaf

The mean leaf area of *Syzygium tetragonum* increased significantly (Table 5.7) with the increase in soil moisture while that of *Acer laevigatum* and *Podocarpus neriifolia* did not respond to watering. Variation in leaf area with age was not observed in any of the three species. With the increase in soil moisture LMA decreased in *Acer laevigatum* while it increased in *Syzygium tetragonum* and in *Podocarpus neriifolia* no definite trend was observed (Table 5.8).

Table 5. 7. ANOVA showing effect of moisture level on leaf area of *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings.

Species	Harvest period (days)	F value	Probability level (P<)
Podocarpus neriifolia	120	1.16	NS
	240	1.15	NS
	360	3.63	0.05
Acer laevigatum	120	3.75	0.05
	240	0.65	NS
	360	0.45	NS
	120	13.84	0.01

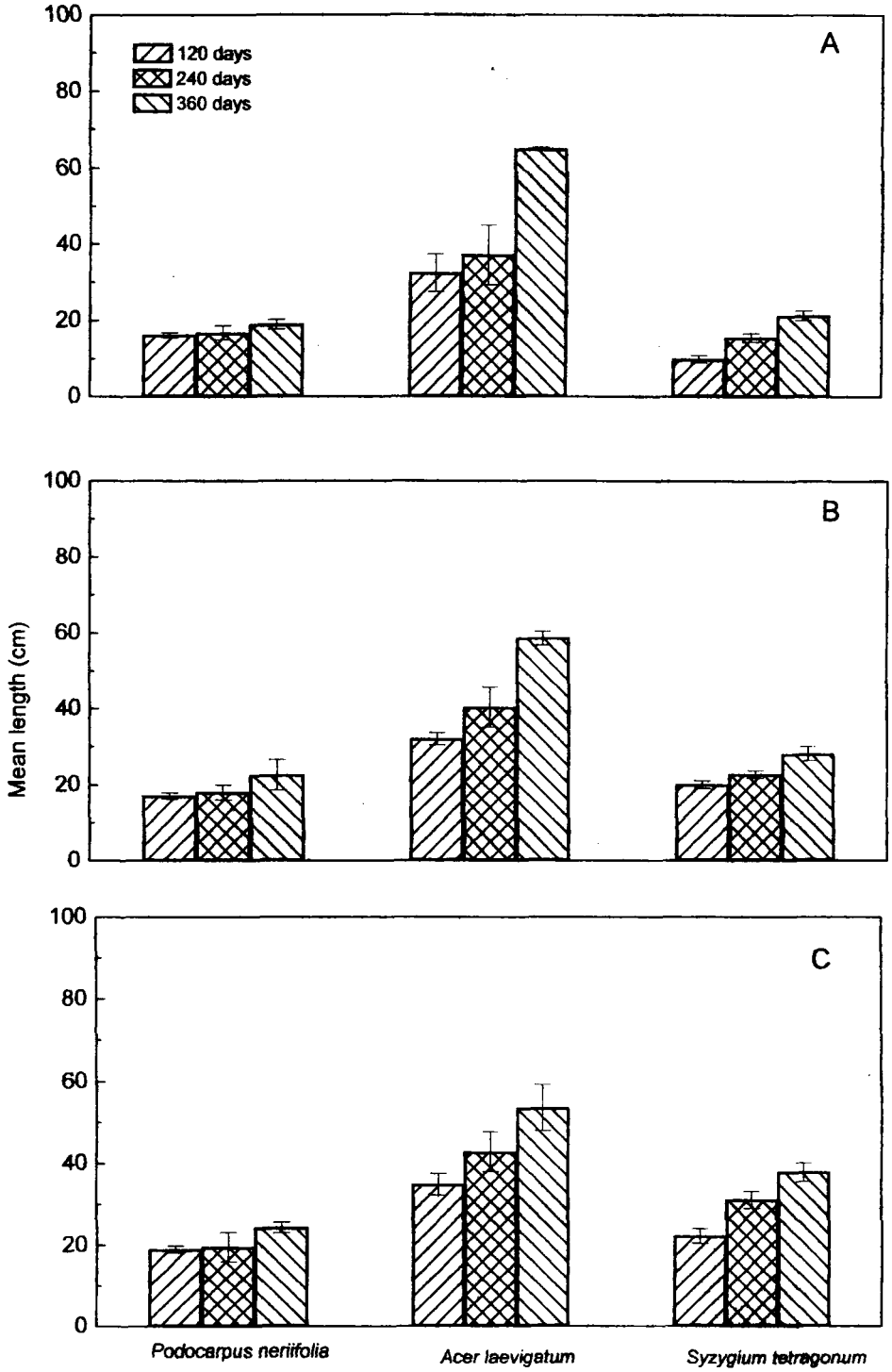


Fig. 5.2. Mean shoot length (cm) of the seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC)

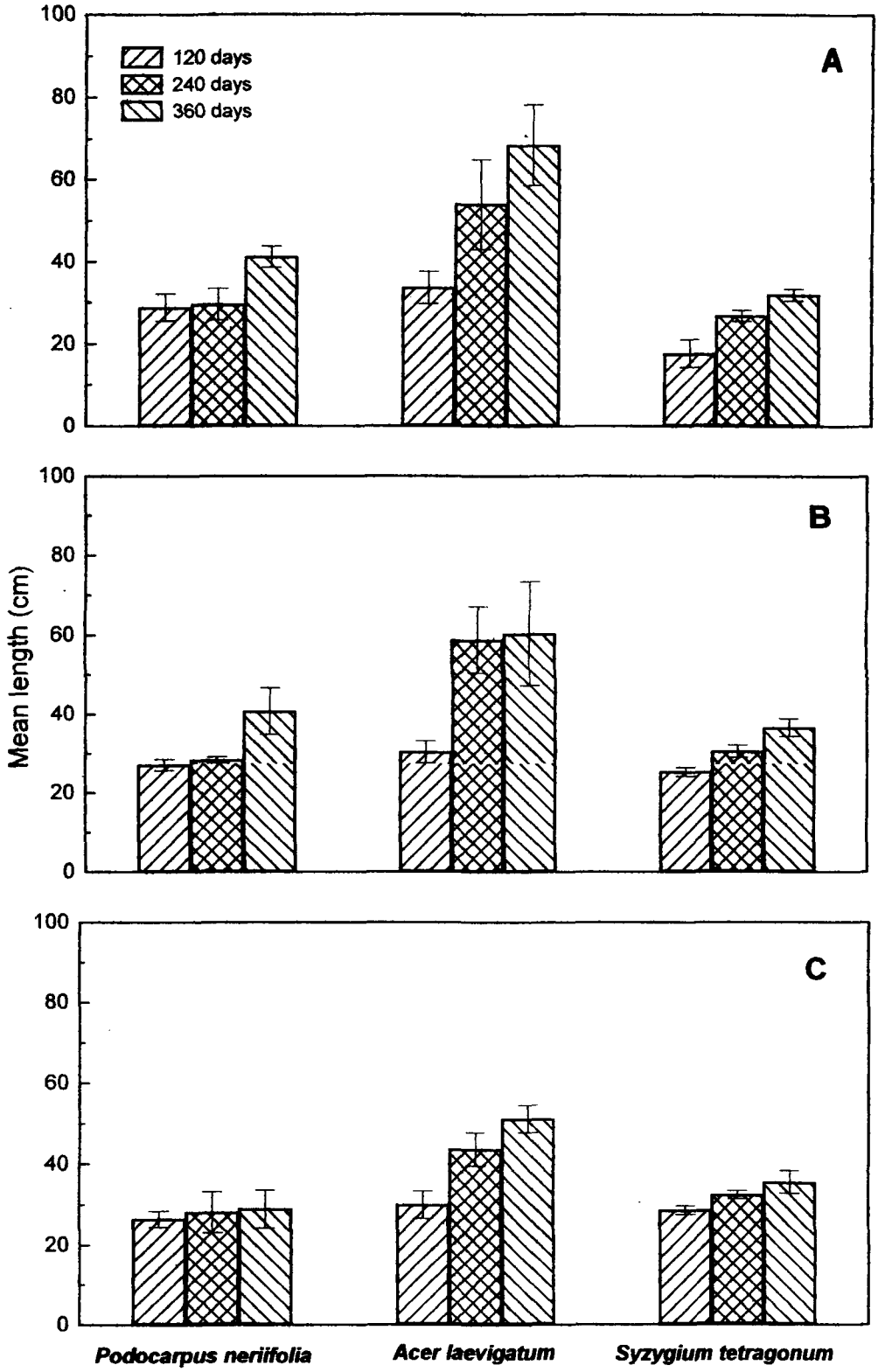
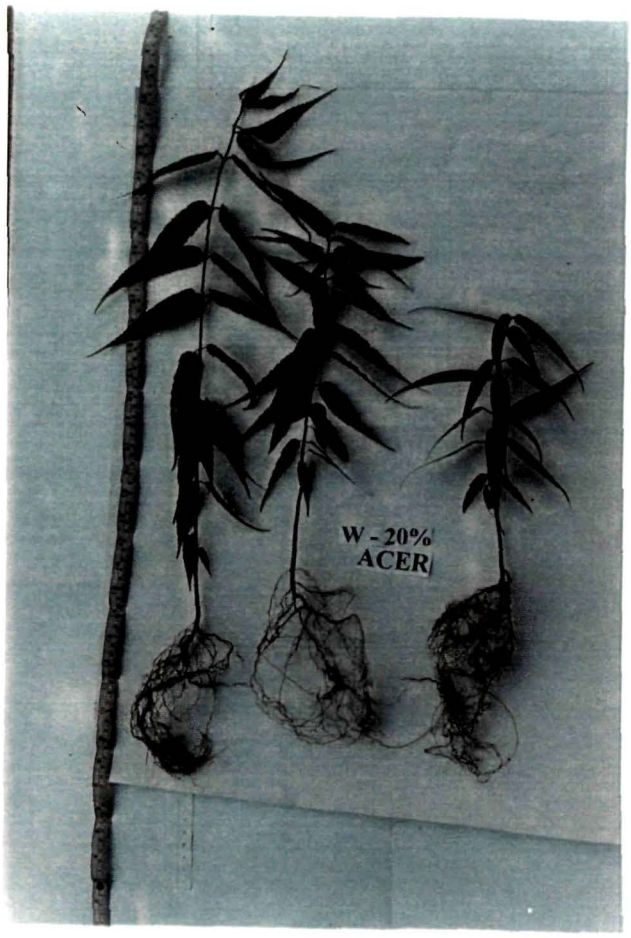


Fig. 5.3. Mean root length (cm) of the seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C-40% SMC)

Plate. 5.2. *Podocarpus neriifolia* seedlings after 360 days of growth under three soil moisture (%) levels.



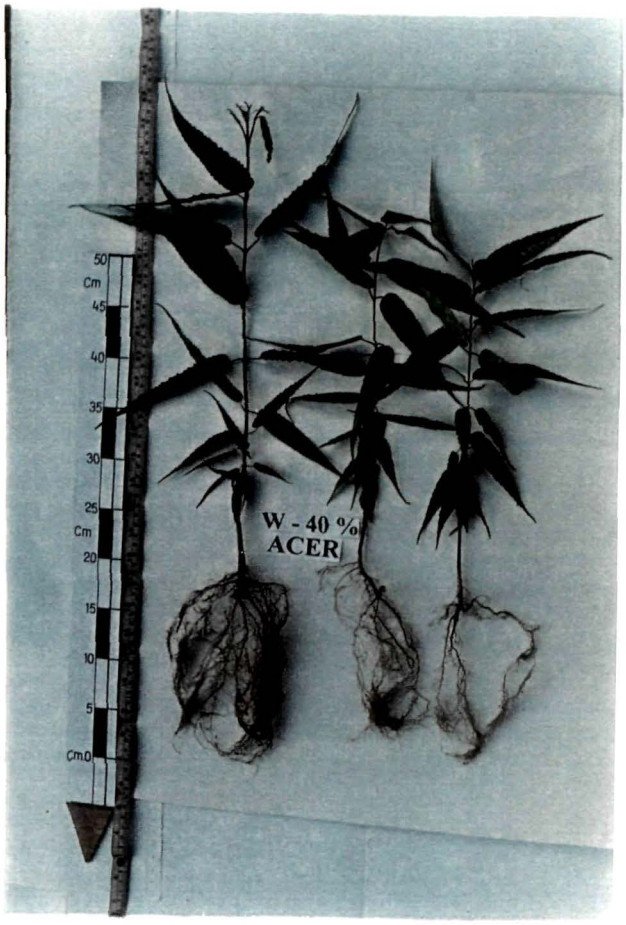
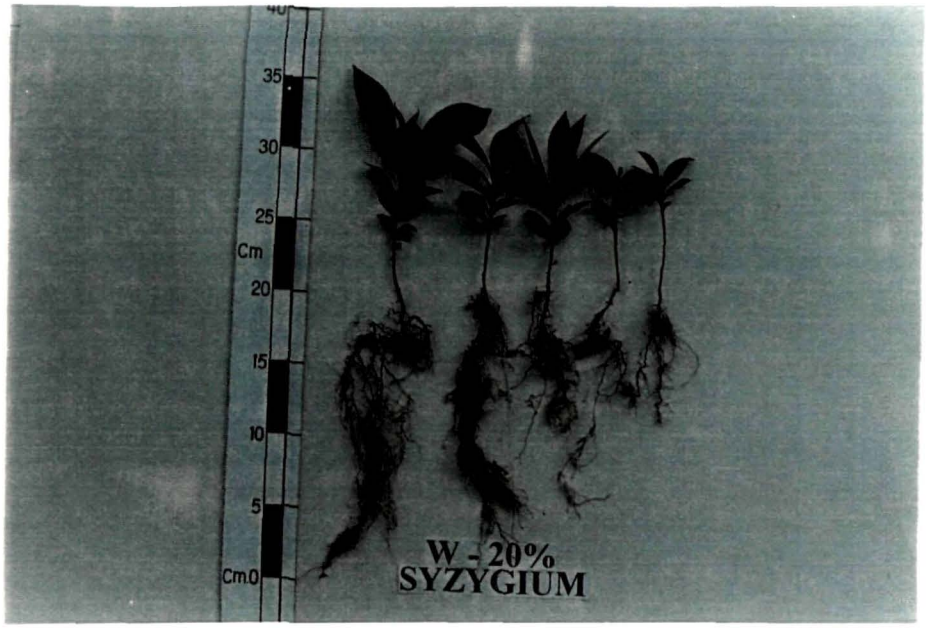


Plate. 5.3. *Acer laevigatum* seedlings after 360 days of growth under three soil moisture (%) levels.



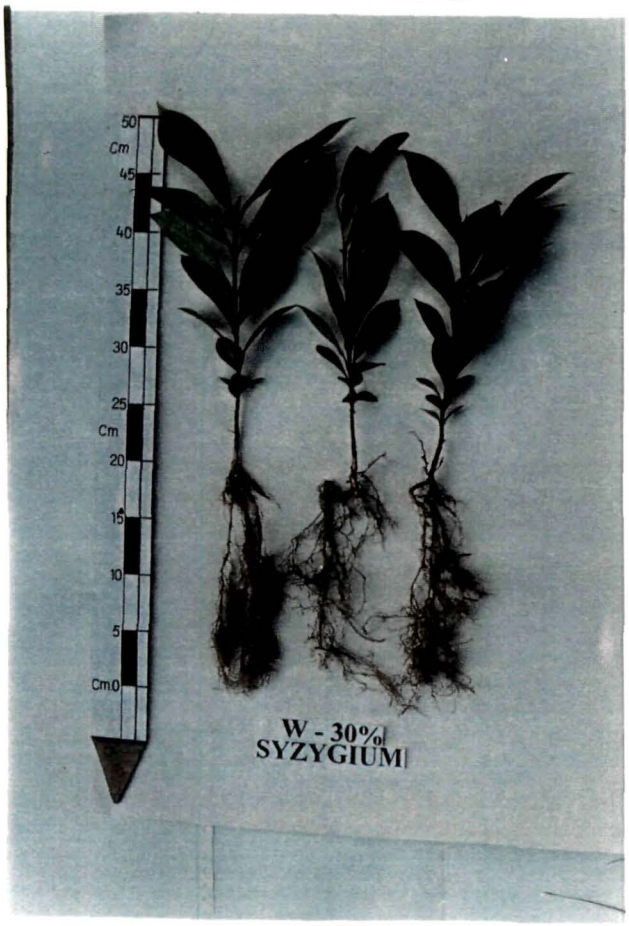


Plate. 5.4. *Syzygium tetragonum* seedlings after 360 days of growth under three soil moisture (%) levels

Syzygium tetragonum	240	5.69	0.05
	360	12.02	0.01

Table 5. 8. Mean leaf area (cm^2), number of leaf/plant and mass per unit leaf area (LMA) under three soil moisture levels.

Species	Soil moisture level (%)	Leaf area	Leaf number	LMA (mg/cm^2)
Podocarpus neriifolia				
	20	5.73	28	8.7
	30	5.47	34	10.3
	40	5.81	37	9.2
Acer laevigatum				
	20	12.57	19	5.3
	30	11.48	39	4.3
	40	12.82	41	3.8
Syzygium tetragonum				
	20	10.99	19	8.6
	30	15.75	17	9.4
	40	23.85	16	9.7

Dry mass

There was a progressive increase in dry mass of *Syzygium tetragonum* seedlings with increase in soil moisture level. The other two species did not respond to soil moisture level. Progressive increase in dry mass accumulation with age was observed in all three species. In all the species shoot dry mass was higher than root under all soil moisture levels (Table. 5.9).

Table.5. 9. Mean dry mass (g $plant^{-1}$) accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* under three moisture levels.

		Dry mass		
Species	Soil moisture levels (%)	120 days	240 days	360 days
Podocarpus neriifolia	20	1.22	2.06	3.16
	30	1.32	1.79	4.16
	40	1.93	2.64	3.91
Acer	20	2.09	6.12	10.32
	30	2.09	7.94	11.26

laevigatum	40	2.35	4.76	11.36
	20	0.87	2.48	5.36
Syzygium	30	2.51	6.56	9.71
tetragonum	40	3.60	9.81	10.61

Root: shoot ratio

The effect of soil moisture levels on root: shoot ratio was prominent only at the end of the experiment (360 days). It gradually decreased with increasing moisture level in all the species (Table 5.10).

Table 5. 10. Mean root: shoot ratio in *Acer laevigatum*, *Podocarpus neriifolia* and *Syzygium tetragonum* under three soil moisture levels after 360 days

Species	Soil moisture level (%)	Root: shoot ratio
Podocarpus neriifolia	20	0.59
	30	0.52
	40	0.39
Acer laevigatum	20	0.98
	30	0.70
	40	0.63
Syzygium tetragonum	20	0.88
	30	0.58
	40	0.46

Relative growth rate (RGR)

In all species maximum value of RGR was recorded at 120 days, thereafter it gradually declined. *Syzygium tetragonum* exhibited a marked increase in RGR with the increase in soil moisture level during the first four months of growth attaining the highest value of 115 mg day^{-1} $plant^{-1}$. As compared to this, the peak values of *Acer laevigatum* (106 mg day^{-1} $plant^{-1}$) and *Podocarpus neriifolia* (98 mg day^{-1} $plant^{-1}$) were low (Table 5.11).

Table 5. 11. RGR (mg day^{-1} $plant^{-1}$) of *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* under three soil moisture level.

Species	Soil moisture level (%)	Sampling period (days)		
		120	240	360
Podocarpus neriifolia				
	20	86	12	12
	30	88	30	21
	40	98	9	11
Acer laevigatum				
	20	104	25	8
	30	103	31	6
	40	106	16	19
Syzygium tetragonum				
	20	80	24	18
	30	106	24	9
	40	115	25	6

Seedling growth under three NPK levels

Root and shoot length

Soil NPK levels did not have any significant effect on the growth of all three species (Fig. 5.4 & 5.5; Plate 5.5, 5.6 and 5.7).

Leaf

Acer laevigatum, Podocarpus neriifolia and *Syzygium tetragonum* seedlings did not exhibit any significant variation (Table 5.12) in mean leaf area (cm^2) and LMA (mg/cm^2) under different levels of NPK (Table 5.13).

Table 5. 12. ANOVA showing effect of three NPK levels on leaf area of *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings

Species	Harvest period (days)	F value	Probability level (P<)
Podocarpus neriifolia	120	2.22	NS
	240	1.97	NS
	360	1.49	NS

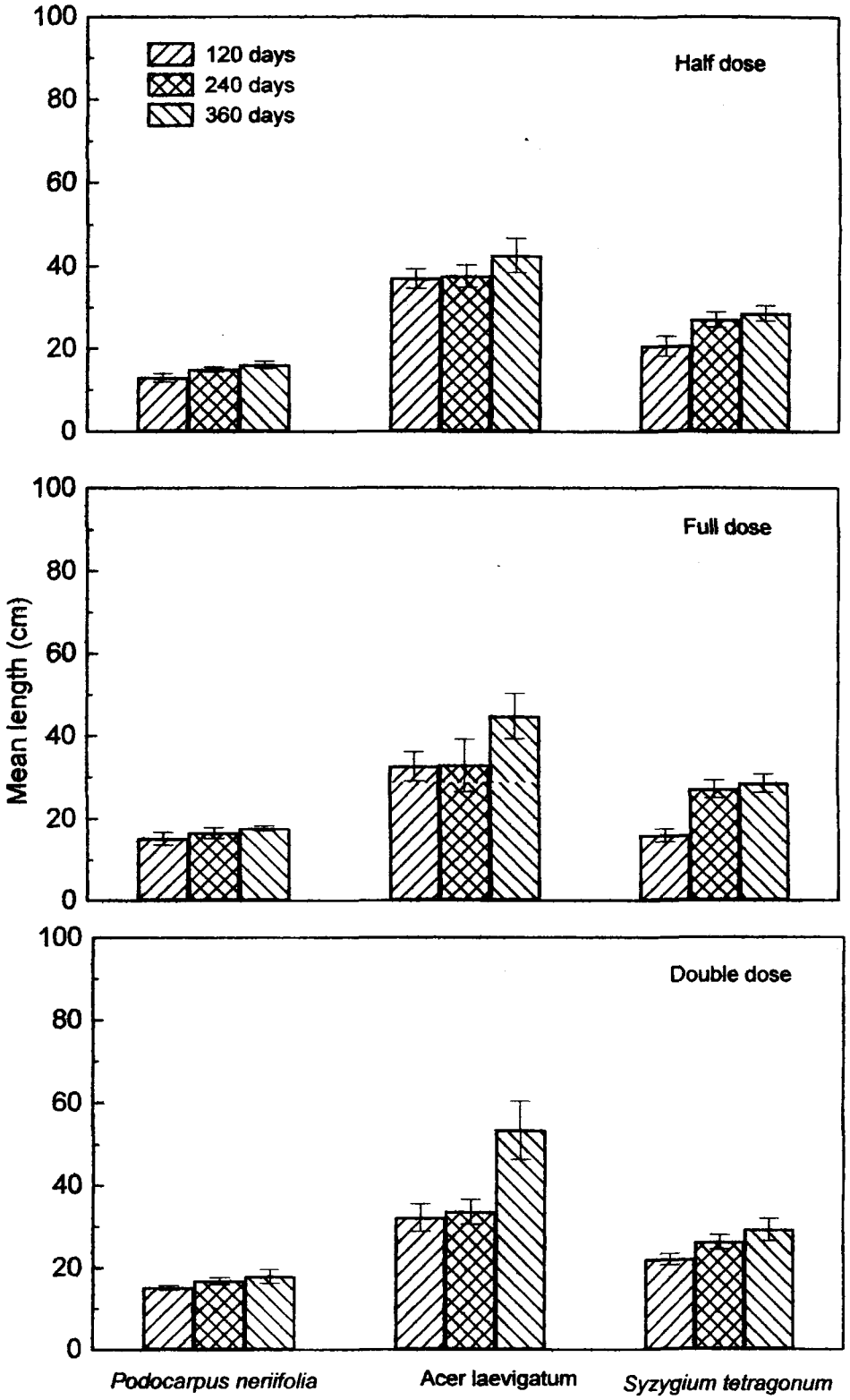


Fig.5.4 . Mean shoot length (cm) of the seedlings under three NPK levels.

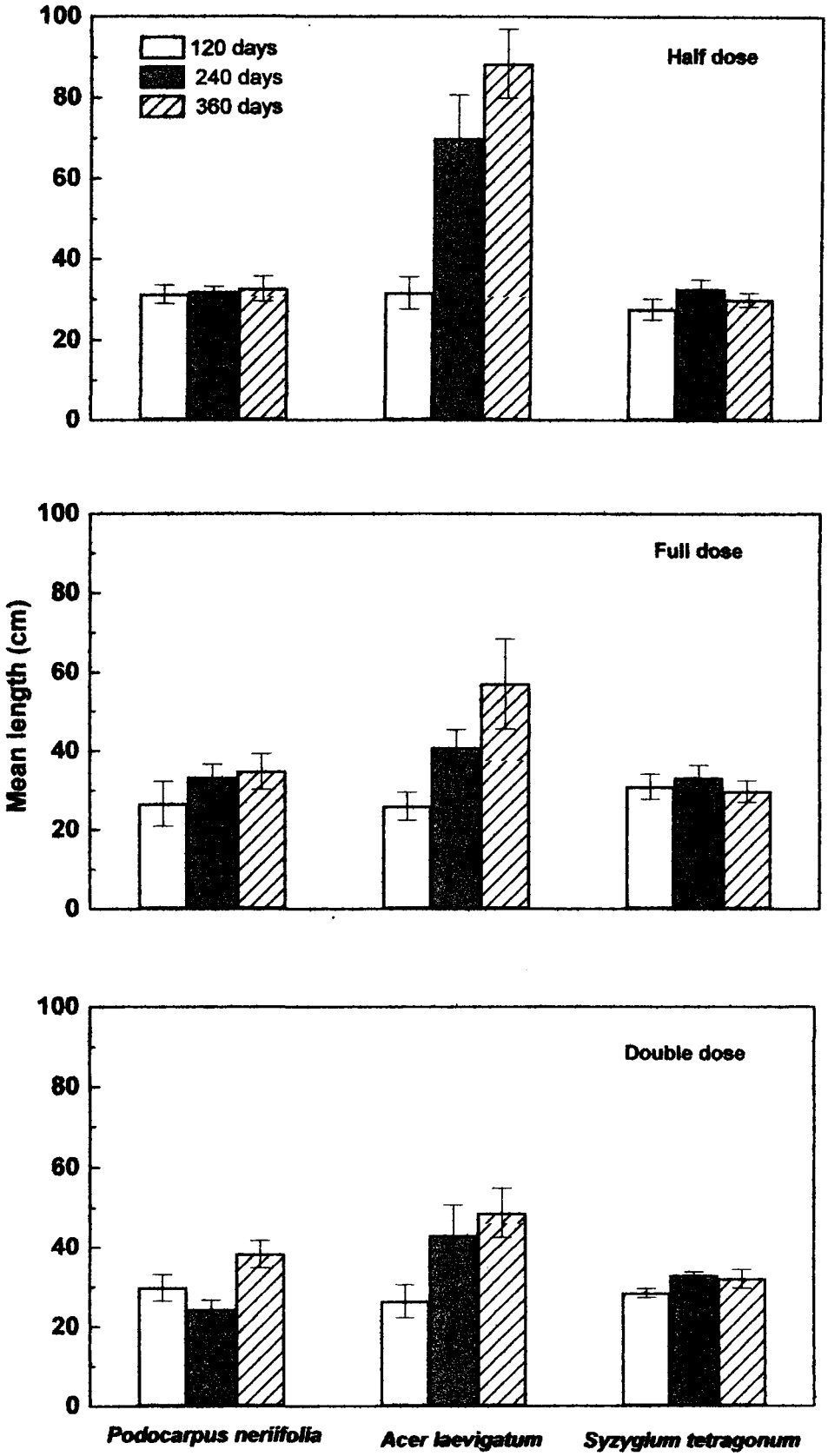
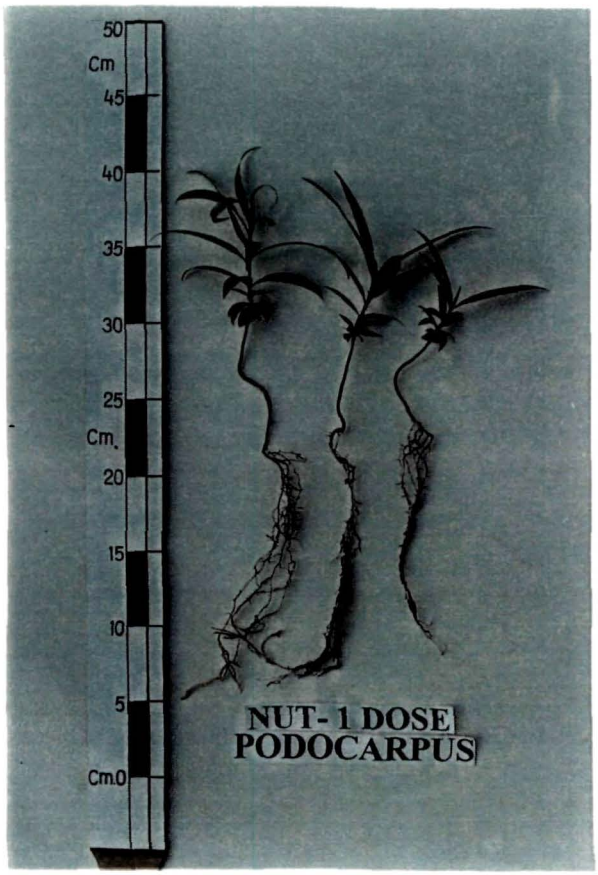


Fig. 5.5. Mean root length (cm) of the seedlings under three NPK levels.



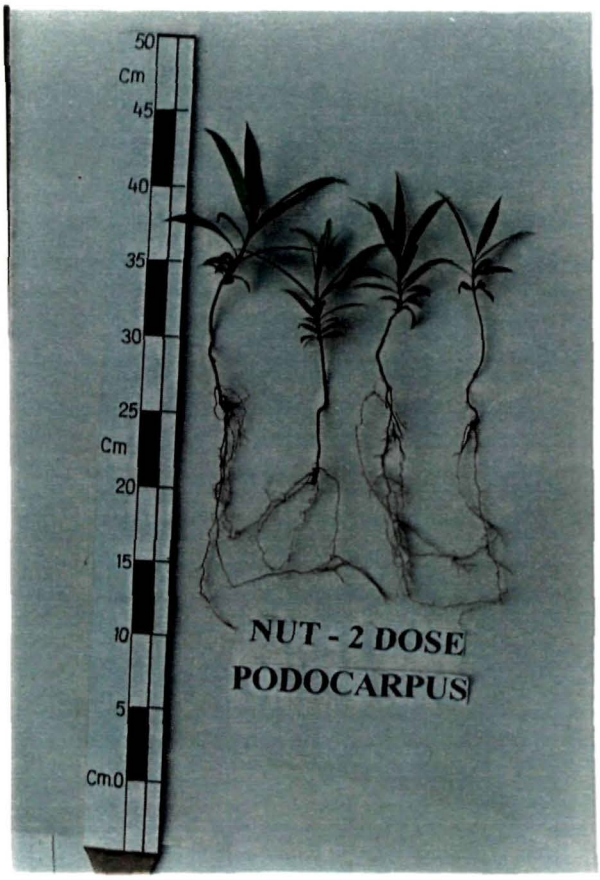
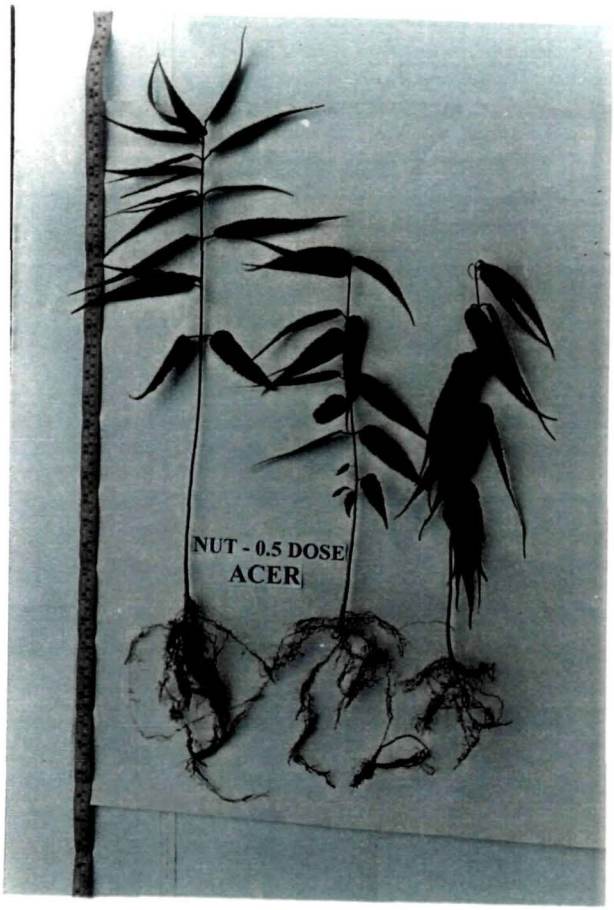


Plate. 5.5. *Podocarpus neriifolia* seedlings after 360 days of growth under three NPK levels (Nut-0.05 dose = half dose, Nut-1dose = full dose, Nut-2 dose = double dose)



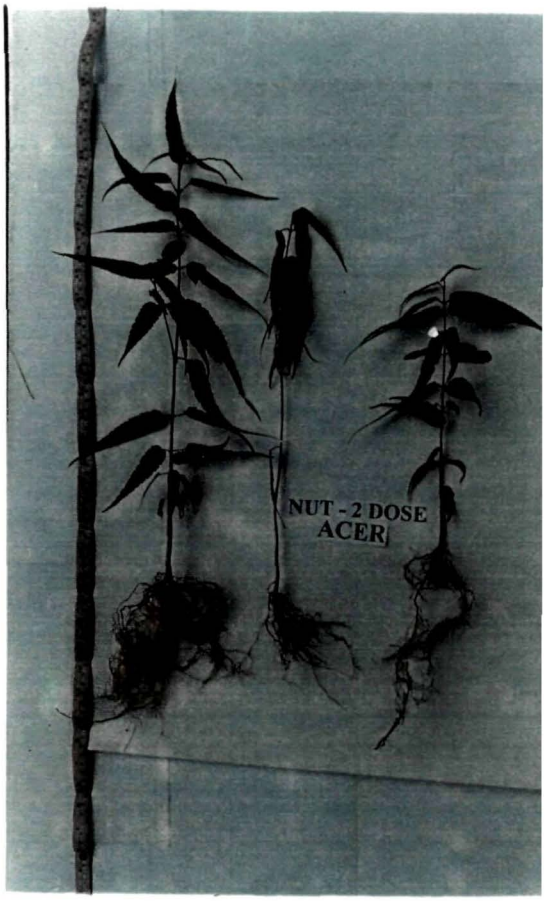


Plate. 5.6. *Acer laevigatum* seedlings after 360 days of growth under three NPK levels (Nut-0.05 dose = half dose, Nut-1dose = full dose, Nut-2 dose = double dose)

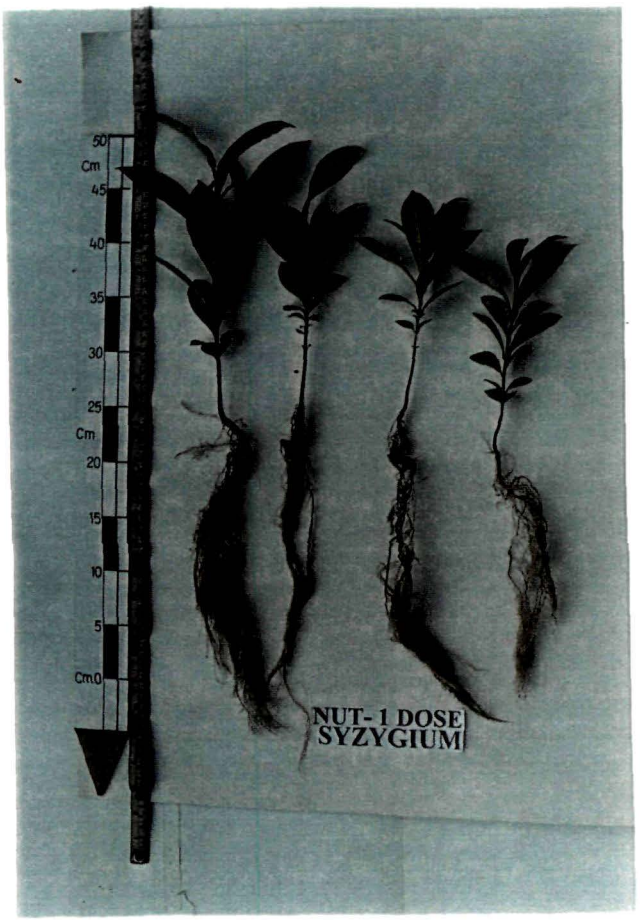


Plate. 5.7. *Syzygium tetragonum* seedlings after 360 days of growth under three NPK levels (Nut-0.05 dose = half dose, Nut-1dose = full dose, Nut-2 dose = double dose)

Acer laevigatum	120	0.33	NS
	240	0.03	NS
	360	1.42	NS
Syzygium tetragonum	120	1.42	NS
	240	0.76	NS
	360	3.27	0.05

Table 5. 13. Mean leaf area (cm^2), number of leaf/plant and leaf mass per unit area (LMA mg/cm^2) under three NPK levels.

	NPK levels	**Leaf area**	**Leaf number**	**LMA (mg/cm^2)**
Podocarpus neriifolia				
	Half dose	3.73	18	10.5
	Full dose	5.15	21	8.5
	Double dose	4.68	21	8.1
Acer laevigatum				
	Half dose	10.24	29	4.4
	Full dose	11.31	22	4.9
	Double dose	13.33	20	5.5
Syzygium tetragonum				
	Half dose	21.86	19	7.3
	Full dose	17.50	21	7.1
	Double dose	17.70	22	7.9

Dry mass

There was no significant effect of NPK doses on dry mass accumulation in all the three species. Only progressive dry mass accumulation with age was observed (Table 5. 14).

Table 5. 14. Mean dry mass (g $plant^{-1}$) accumulation in *Podocarpus neriifolia, Acer laevigatum* and Syzygium *tetragonum* under three NPK levels.

Species	**Dry mass**			
	NPK levels	**120 days**	**240 days**	**360 days**
Podocarpus neriifolia	Half dose	0.95	1.23	1.32
	Full dose	0.92	1.67	1.82
	Double dose	1.10	1.56	1.82
Acer laevigatum	Half dose	2.27	6.41	8.78
	Full dose	1.73	4.64	7.72

	Double dose	1.96	4.70	8.28
Syzygium tetragonum	Half dose	3.42	6.73	8.45
	Full dose	1.92	7.00	7.68
	Double dose	3.35	5.73	7.82

Root: shoot ratio

The effect of NPK levels on root: shoot ratio was distinct only at the end of the experiment. With the increase in NPK doses R:S ratio increased in *Podocarpus neriifolia* and decreased in *Acer laevigatum*, *Syzygium tetragonum* did not show any trend with almost the same value at different NPK levels (Table 5. 15).

Table 5. 15. Mean root: shoot ration of *Acer laevigatum*, *Podocarpus neriifolia* and *Syzygium tetragonum* under three NPK levels after 360 days of growth.

Species	NPK level	Root: shoot ratio
Podocarpus neriifolia	Half dose	0.434
	Full dose	0.467
	Double dose	0.504
Acer laevigatum	Half dose	0.930
	Full dose	0.930
	Double dose	0.776
Syzygium tetragonum	Half dose	0.650
	Full dose	0.687
	Double dose	0.615

Relative growth rate (RGR)

NPK levels had no effect on RGR of all three species. RGR attained peak during the first four month of growth in all cases. The values were 106 mg day^{-1} $plant^{-1}$ in *Syzygium tetragonum*, 101 mg day^{-1} $plant^{-1}$ in *Acer laevigatum* and 81 mg day^{-1} $plant^{-1}$ in *Podocarpus neriifolia* (Table 5. 16).

Table 5.16. RGR (mg day^{-1} $plant^{-1}$) of *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* under three NPK levels.

Species	NPK level	Sampling period (days)		
		120 days	240 days	360 days
Podocarpus neriifolia				
	Half dose	81	4	2
	Full dose	79	14	2
	Double dose	85	7	4
Acer laevigatum				
	Half dose	106	23	6
	Full dose	97	23	6
	Double dose	100	20	12
Syzygium tetragonum				
	Half dose	110	16	4
	Full dose	100	34	5
	Double dose	110	10	6

Discussion

Seedlings of *Acer laevigatum, Syzygium tetragonum* and *Podocarpus neriifolia* showed higher mortality in the forest understorey than in the gap. This indicates that for better growth and establishment the seedlings depend on the availability of light. Similar observation under natural condition has been made by Law (2002), in primary subtropical forests at Raliang and Ialong in Jaintia hills of Meghalaya, where the seedlings of *Acer laevigatum* and *Syzygium tetragonum* showed a stunted growth in the forest understorey.

In the field condition desiccation is a major cause of seedling mortality in the understorey of a wide range of forest types including rain forests. For example, the dry season mortality in first-year seedlings was 73% for *Shorea* spp. in Malaysia (Turner 1990). It has been argued that among the potential causes of seedling mortality under natural condition various abiotic stresses such as shade, drought and flooding (Walters et

al. 1993) and biotic influences such as herbivory, disease, and root competition play an important role (Jones et al. 1994).

Plants common to dry sites tend to allocate proportionally more carbon to roots than do plants from moist sites, even when both plants are grown in similar environmental conditions (Bongarten and Tesky 1987; Matsuda et al. 1989; Miller et al. 1990). Greater allocations of dry mass to shoot in all three species in the present study indicate that the range of soil moisture levels maintained in the experiment was not stressful for the seedling growth. However, better growth response of *Syzygium tetragonum* to increasing soil moisture level suggests that the species requires higher soil moisture level for better growth and is less tolerant to water stress.

Water stress principally affects two main processes in plants; the development of leaf area and the carbon exchange rate per unit leaf area (Zelitch 1982; Lawlor 1987). Plants experiencing drought during vegetative growth tend to develop smaller, often fewer leaves well before photosynthetic rates are markedly affected and the rate of leaf area growth decreases progressively with increasing drought (Muchow 1985; Zelitch 1982). Stress during the vegetative stage reduces the leaf area index (LAI) thereby decreasing light interception (Kramer 1983) leading to a fall in the efficiency of production per unit incident radiation.

Water conservation in low rainfall regions takes place through a reduced LAI, development of specialized leaves with thick cuticles and increased cytoplasmic tolerance to desiccation, or deciduousness during dry spells. Besides conserving water, plants in dry areas commonly develop deep root systems that make use of water stored in the subsoil

between rainfall events, and roots that run far outside the crown and capture water from the intercrown areas. Greater allocation to root development comes at the cost of reduced allocation to leaves and/ or stems (Coomes and Grubb 2000).

In general plants are likely to compete for photosynthetically active radiation (PAR), water and essential nutrients (Lewis and Tanner 2000). Pot experiments have shown that in many plant species growth rate increases with nutrient addition, but species differ as to the lowest PAR level at which they will respond to added nutrients (Latham 1992; Grubb et al. 1996). Experiments on tropical rain forest tree seedlings have shown that some species can respond to nutrient additions down to 0.5 – 3.0 % photosynthetic photon flux density (Burslem 1996).

Nutrient addition in soil did not show any significant increase in dry mass in the present study. The finding is similar to that observed in case of *Azadirachta indica*, *Albizia amora*, *Acacia planifrons*, *Acacia lenticularis*, *Hardwickia binata* and *Tamarindus indicus*, where there was a decrease in dry mass due to nutrient application (Joshi 1980). This indicates that these species may grow on marginal to poor fertility level.

The results of the present study, however, do not agree to the findings of Weetman et al. (1993) on *Tsuga heterophylla*, *Abies amabilis* and *Thuja plicata*, where species responded to sewage sludge and N & P treatments during the first growing season with a doubling or tripling of growth rates and improved nutrition. Wang et al. (1991) found up to 10 times differences in five tropical tree species in respect of the amount of nutrients they required to produce unit biomass. Nitrogenous fertilization significantly increased average

plant height, collar diameter, number of leaves, leaf area, and fresh weight and total biomass of *Acer oblongum* seedlings (Masoodi et al. 1996).

Allocation of biomass and nutrient resources in various parts or organs of plant species is the result of ecological factor and evolutionary process, which are related to natural selection and play important role in determining the niche width of different species within the natural ecosystem (Ramakrishnan 1978). In general, tree seedlings show an increased allocation to shoot and reduced allocation to roots in deeper shade (Ashton 1995; Veenendal et al. 1996; Lee et al. 1997). Shading reduced root biomass allocation, root N uptake rate, plant N concentration and productivity of *Betula pubescens* seedlings (Weih and Karlsson 1999).

The seedling of all three species had lower allocation of dry mass to root. The decrease in R/S ratio with increase in soil moisture level indicates that allocation to roots increase as soil moisture level decreased, as it had to compete for acquisition of water. In gap also allocation to shoot was relatively more than in the understorey in all the three species. Their better growth in gap is also evident from significantly higher leaf area and LMA in the forest understorey. Seedling leaves in forest understorey tend to be thinner (Ashton and Berlyn 1992; Strauss-Debenedetti and Berlyn 1994; Poorter 1999) and have a lower LMA (Fetcher et al. 1983; Veenendal et al. 1996; Davies 1998) than under higher irradiance. This is also true in the present case where all species had higher LMA in gap than the forest understorey.

Mass per unit leaf area (LMA) is the product of leaf thickness and density. In respect of LMA, the leaves of juvenile plants are quite comparable to the adults except in

size (Bullock 1984). High leaf dry mass per unit area is associated with greater leaf thickness, which is due to accumulation of photosynthetic compounds. The higher LMA of these species indicate that they are better adapted to gaps where light intensity is greater than the forest understorey (Law 2002).

Increase in RGR of seedlings with increase in light intensity reported by several workers (Osunkoya et al. 1994; Veneklass and Poorter 1998; Kitajima 1994) may not continue over a high irradiance level (Veenendal et al. 1996; Boot 1996). Rather it may decline at high light intensity (Thompson et al. 1992; Osunkoya et al. 1994; Veneklass and Poorter 1998).

Relative growth rate (RGR) serves as a fundamental measure of dry-matter production and can be used to compare the performance of a species or the effects of treatments under strictly defined conditions. In general RGR was highest in *Syzygium tetragonum* followed in decreasing order by *Acer laevigatum* and *Podocarpus neriifolia*. Popma and Bongers (1988) put forward the hypothesis that RGR in understorey conditions was the best measure of shade tolerance, arguing that ultimately growth was what mattered. The seedlings of all three species in the present study showed higher RGR and survival in gap than the forest understorey suggesting the crucial role of light in growth and survival of the seedlings.

CHAPTER VI
NUTRIENT ALLOCATION, ACCUMULATION AND USE EFFICIENCY

Resource allocation to different plant parts determines the fitness of the species. Plants show adaptive response in respect of nutrient uptake, water conservation, temperature tolerance, pollinator's attraction, herbivore avoidance and seed dispersal etc. At some point of time in the life cycle, each of these traits makes a positive contribution towards the fitness of a species (Abrahamson and Caswell 1982).

The success of a plant in an environment can be predicted by relative apportionment of biomass and or nutrients in different parts (MacArthur and Wilson 1967; Gadgil and Solbrig 1972 and Abrahamson 1975). Species differences in morphology, physiology and behaviour arises from their divergent ability to deal with various environmental constraints and from their allocation patterns of nutrient and biomass (Cody 1966; Mooney 1972). Some plant species allocate high proportion of their biomass to the root allowing them to acquire more soil resources than plants with less root biomass, and thus making them superior competitors for soil nutrient resources (Tilman and Wedin 1991). By allocating more biomass to the root, plant species necessarily have less allocation to stem, leaf and reproductive buds and are unavoidably inferior in their ability to utilize light and to disperse seeds. The increased allocation in one trait necessarily causes a decrease in proportional allocation to other traits (Mooney 1972).

The present chapter deals with the allocation of N, P and K to shoot and root, their total accumulation in plant over time and use efficiency by the seedlings of *Podocarpus*

neriifolia, Acer laevigatum and *Syzygium tetragonum* under different light, soil water and nutrient environments.

Results

I. Effect of gap and understorey

Nutrient concentration

Nitrogen concentration in *Podocarpus neriifolia* and *Syzygium tetragonum* seedlings was higher in the forest understorey while that of *Acer laevigatum* seedlings recorded higher N concentration in gap. N concentration was higher in leaf followed by root and stem. It decreased significantly ($p< 0.05$) with the increase in age of the seedlings of all three species (Fig. 6.1, 6.2 and 6.3).

Phosphorus concentration was higher in leaf followed by stem and root in all three species. Seedlings under forest understorey had significantly ($P<0.01$) higher P concentration than those in gap. The concentration decreased with age of the seedlings in both the situations (Fig.6.4, 6.5 and 6.6).

The leaf had higher K concentration followed by stem and root in all three species both in gap and forest understorey. The concentration decreased with the age in *Syzygium* both in gap and forest understorey. In *Podocarpus* and *Acer* there was no significant difference due to seedling age and forest habitats (Fig. 6.7, 6.8 and 6.9).

Nutrient accumulation and its allocation pattern in root, stem and leaf

N accumulation (mg plant^{-1}) in all plant parts was significantly ($p<0.01$) higher in gap than the forest understorey in all species. Leaf accumulated maximum N followed by root and stem at both the places, and it increased with age of the seedlings (Fig. 6.10).

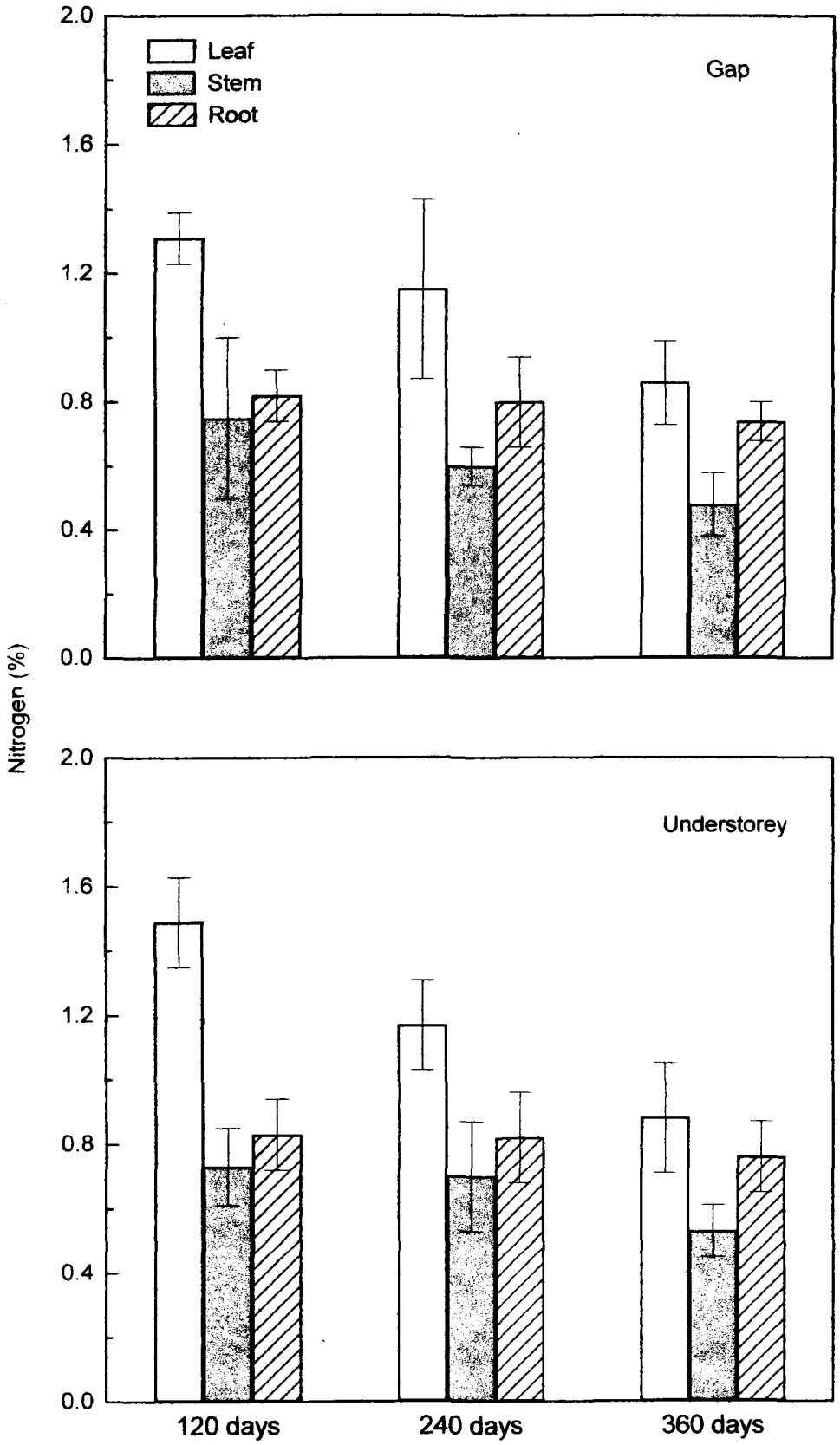


Fig. 6.1. Nitrogen concentration in different parts of *Podocarpus neriifolia* seedlings in gap and understorey.

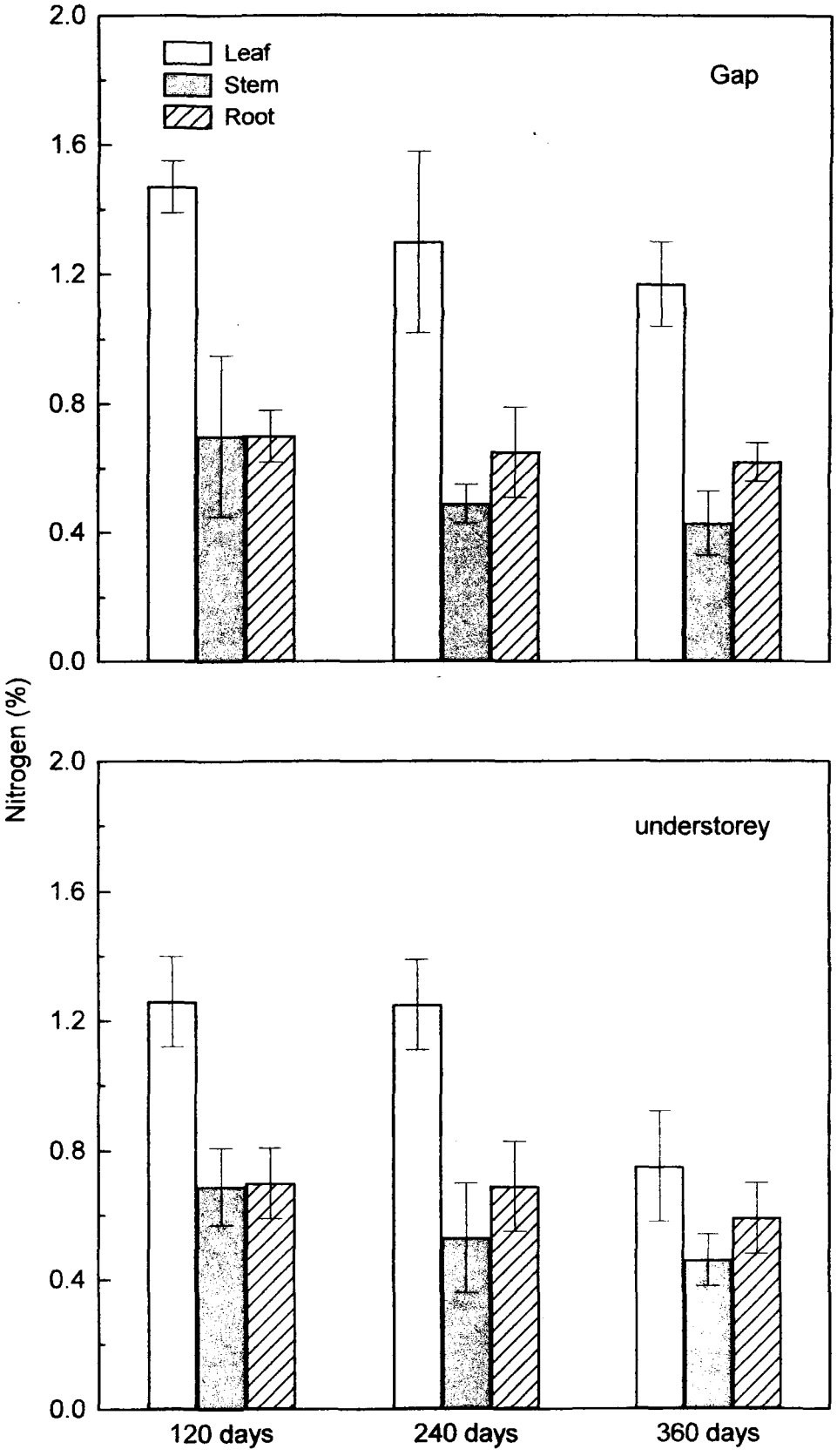


Fig.6.2. Nitrogen concentration in different parts of *Acer laevigatum* in gap and understorey.

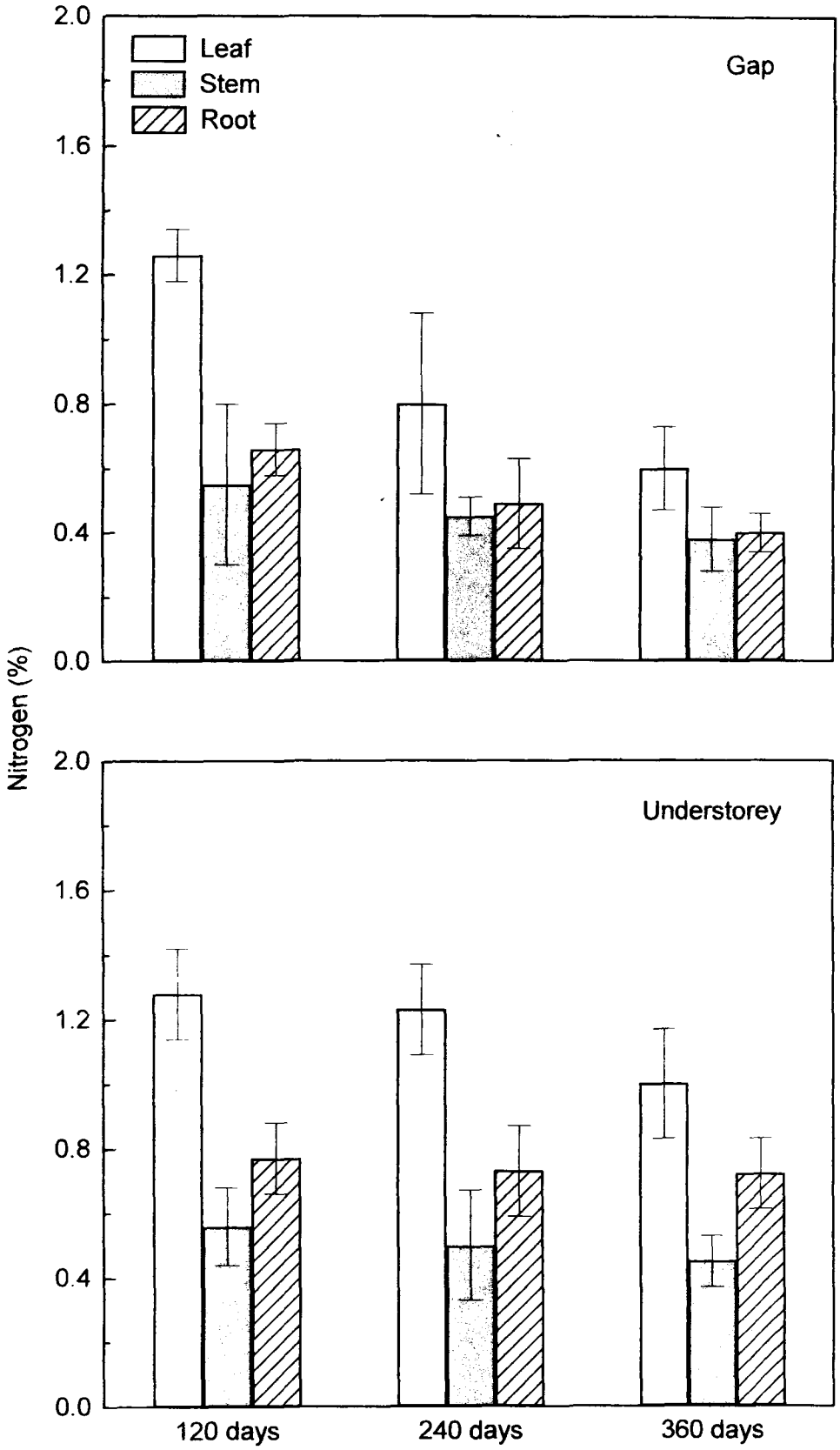


Fig.6.3. Nitrogen concentration in different parts of *Syzygium tetragonum* in gap and understorey.

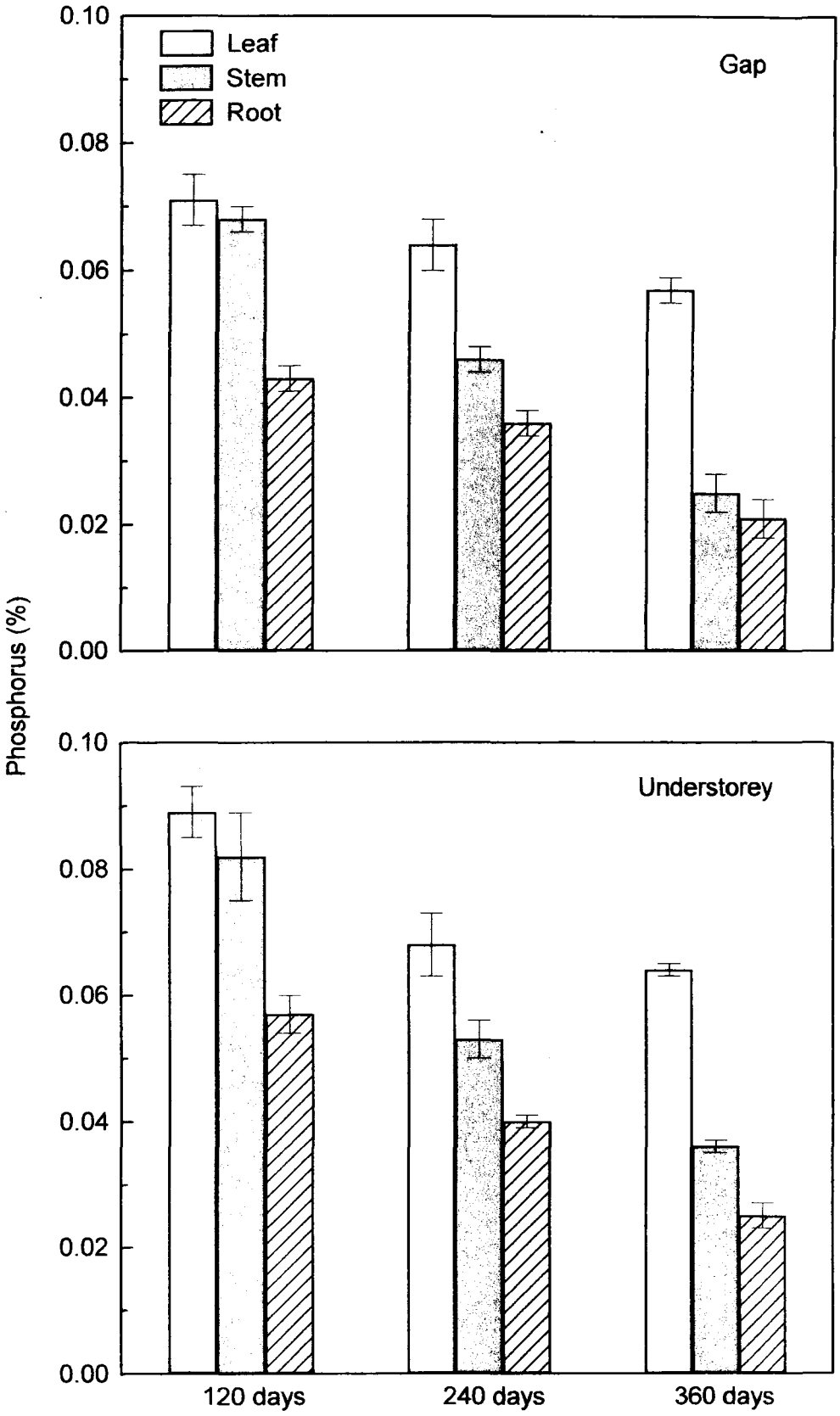


Fig.6.4. Phosphorus concentration in different parts of *Podocarpus neriifolia* seedlings in gap and understorey.

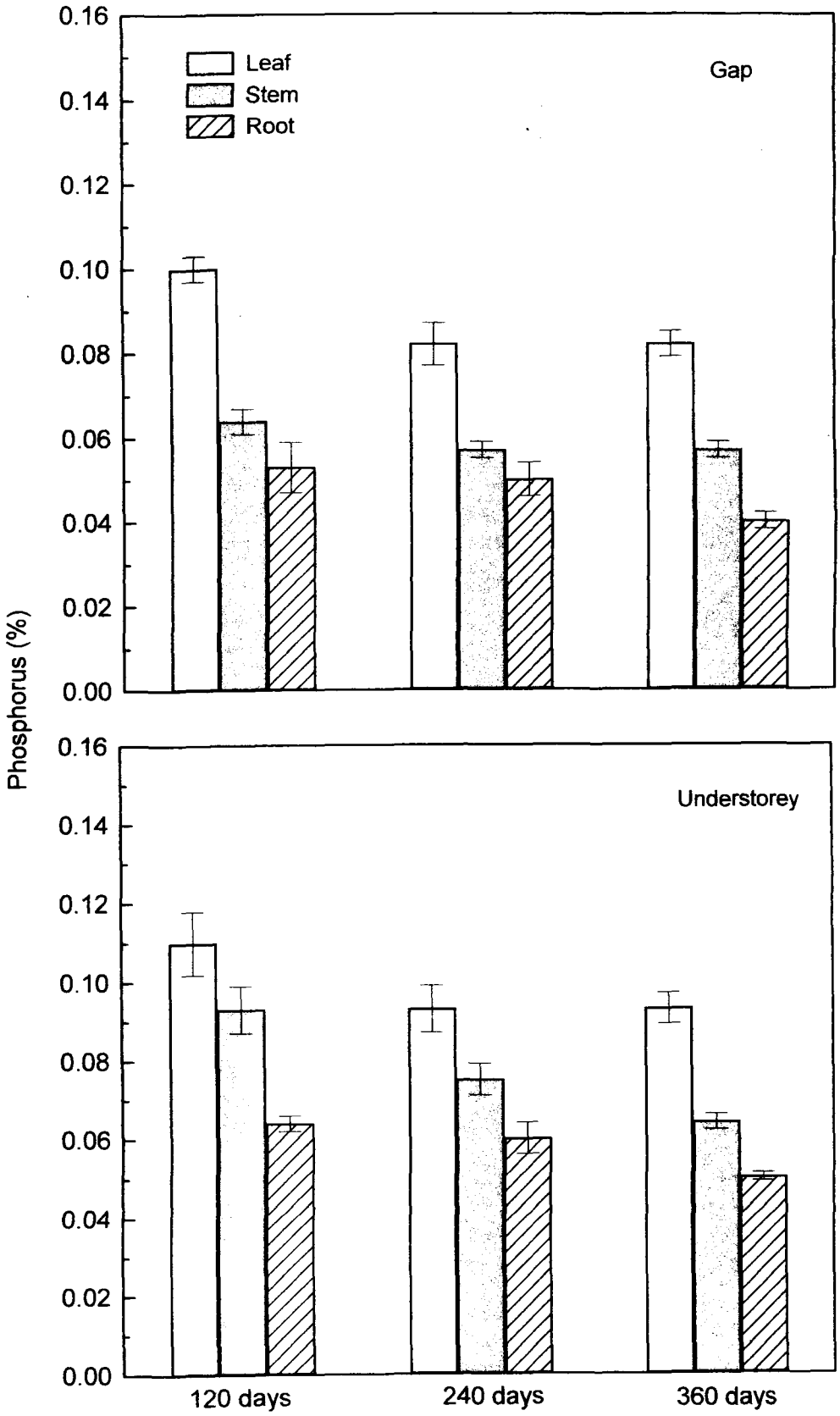


Fig.6.5. Phosphorus concentration in different parts of *Acer laevigatum* seedlings in gap and understorey.

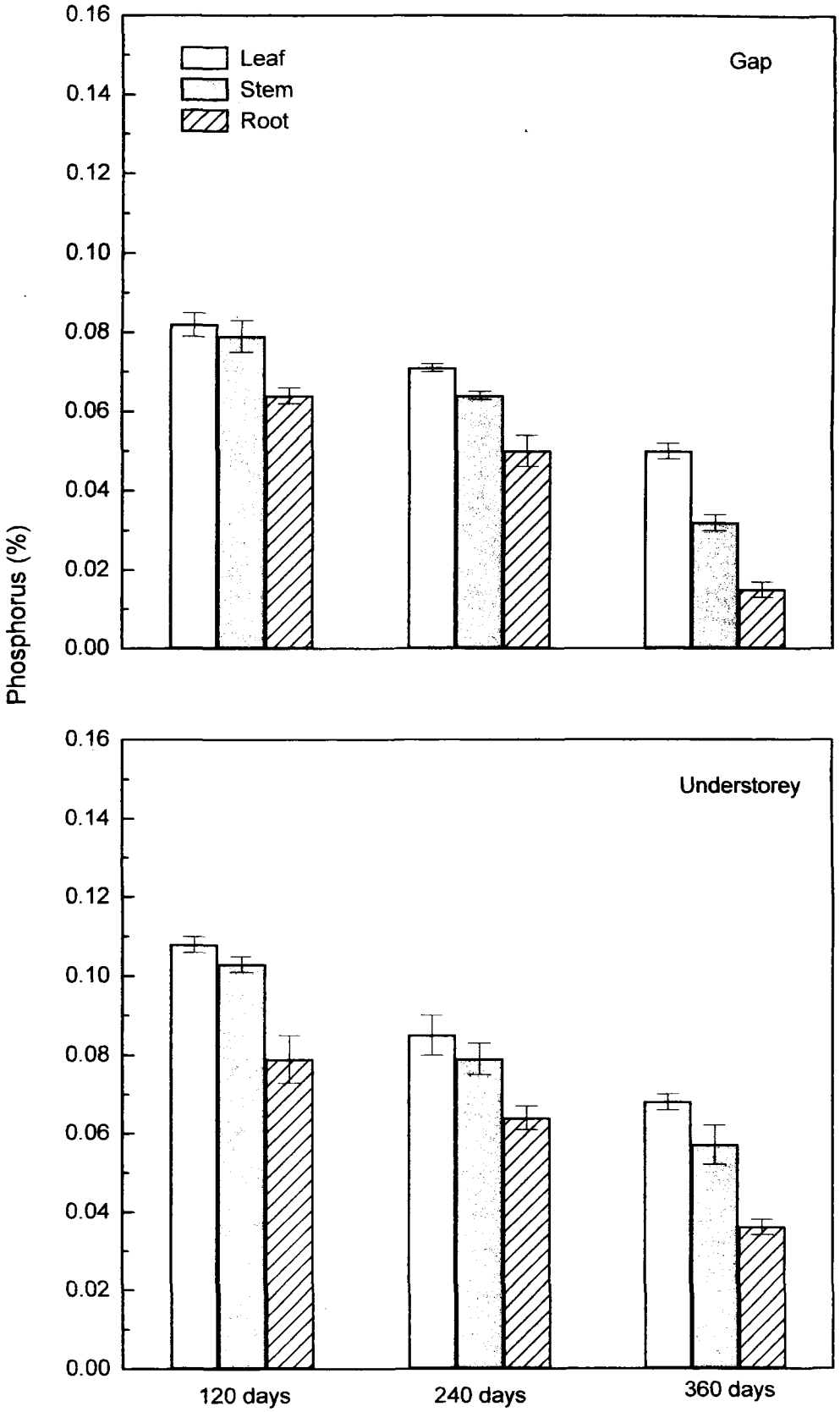


Fig.6.6. Phosphorus concentration in different parts of *Szygium tetragonum* seedlings in gap and understorey.

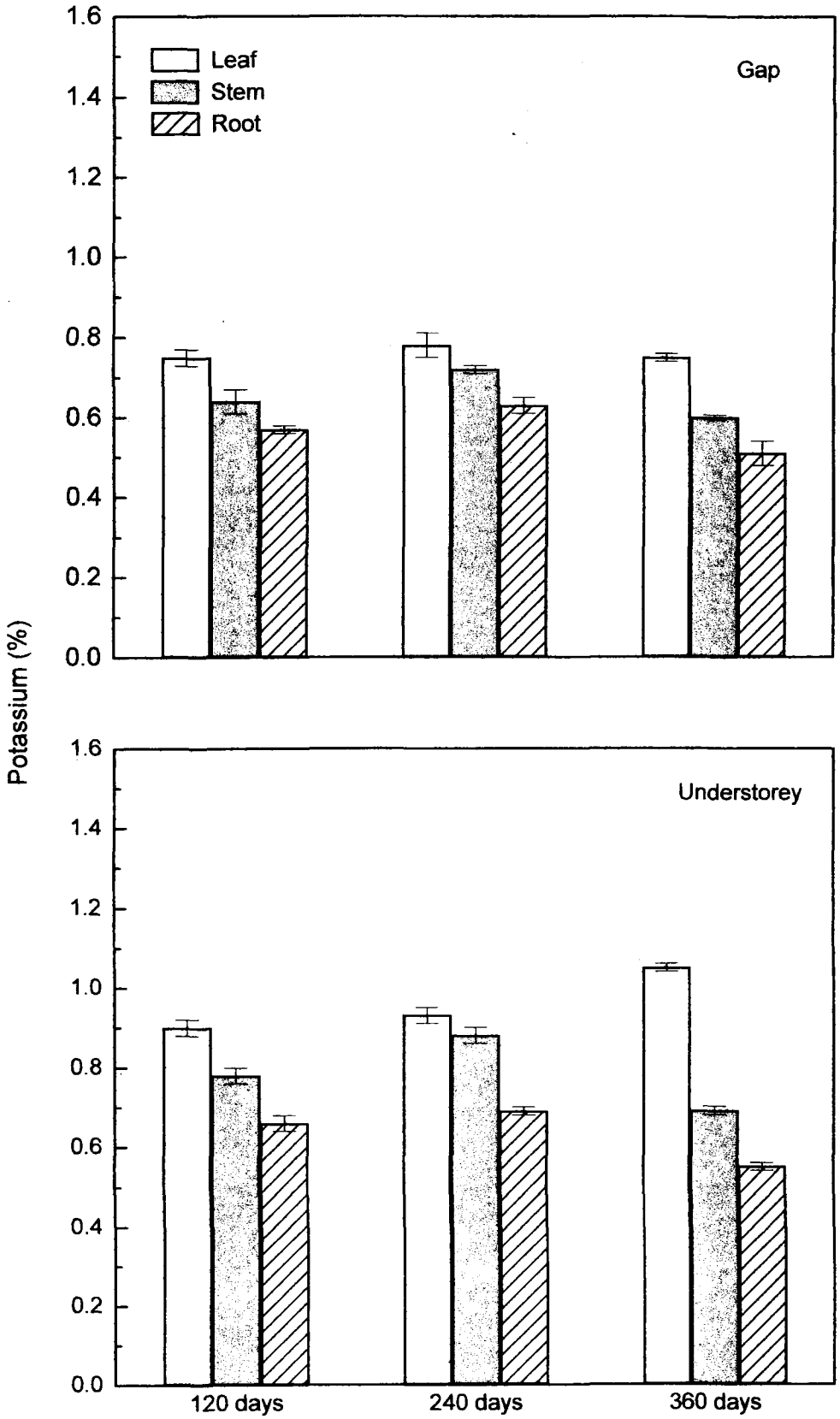


Fig. 6.7. Potassium concentration in different parts of *Podocarpus neriifolia* seedlings in gap and understorey.

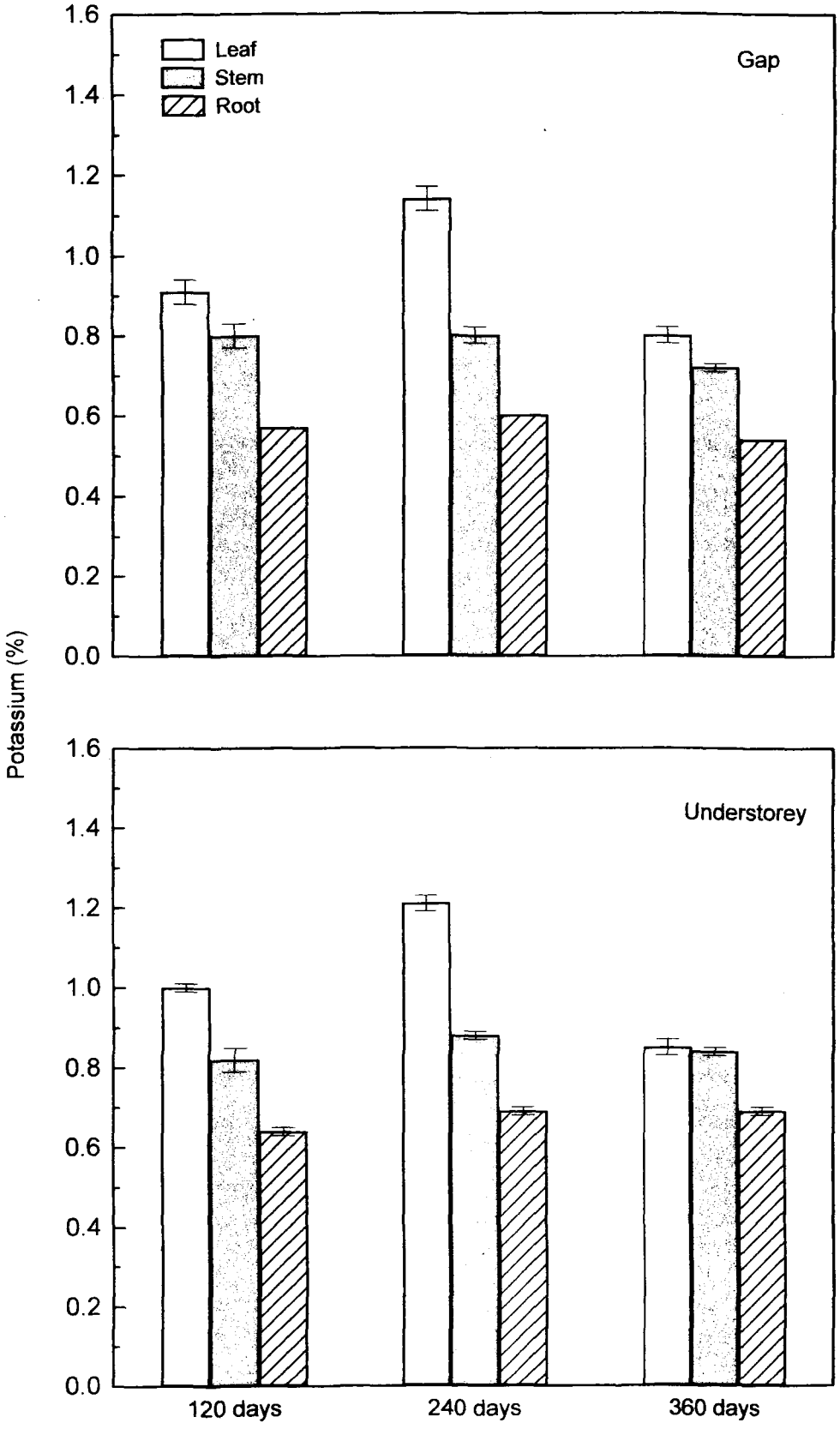


Fig. 6.8. Potassium concentration in different parts of *Acer laevigatum* seedlings in gap and understorey.

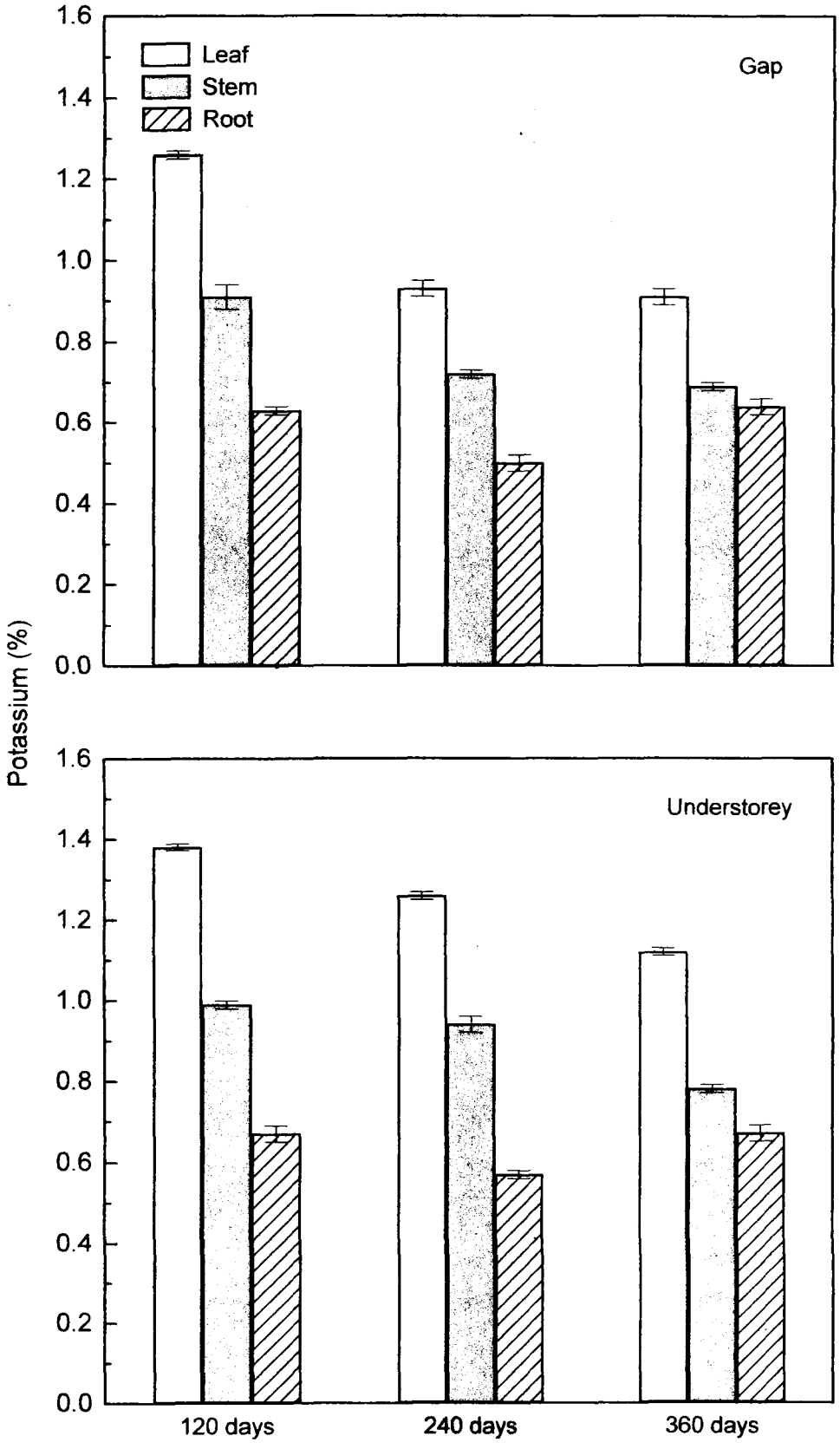


Fig.6.9. Potassium concentration in different parts of *Syzygium tetragonum* seedlings in gap and understorey.

P accumulation was also higher in gap than the forest understorey in all species. P accumulation was more in leaf. Stem and root did not show any significant difference in P accumulation (Fig. 6.11).

K accumulation was significantly higher in gap ($P<0.05$) as compared to the forest understorey. Variation in K accumulation in different plant parts was noticed only in *Syzygium* where leaf had higher accumulation followed in decreasing order by root and stem (Fig. 6.12).

Nutrient use efficiency

The seedlings of all the three species in gap were more efficient in terms of NPK use (Table 6.1).

Table. 6.1. Nitrogen, phosphorus and potassium use efficiency (mg dry weight produced /mg nutrient uptake) of *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetragonum* in gap and understorey.

Nutrient use efficiency	Light conditions	*Podocarpus neriifolia*	*Acer laevigatum*	*Syzygium tetragonum*
Nitrogen use efficiency	Gap	171	170	155
	Understorey	133	104	136
Phosphorus use efficiency	Gap	2729	1655	1293
	Understorey	1487	1332	1033
Potassium use efficiency	Gap	155	143	119
	Understorey	122	124	86

II. Effect of soil moisture

Nutrient concentration in different plant parts

In all species, N concentration was more in leaf followed by root and stem. The different soil moisture levels had no significant effect on it. In *Podocarpus neriifolia* it ranged from 1.25-1.79% in leaf, 0.40-0.75% in stem and 0.68-1.18% in root. In *Acer*

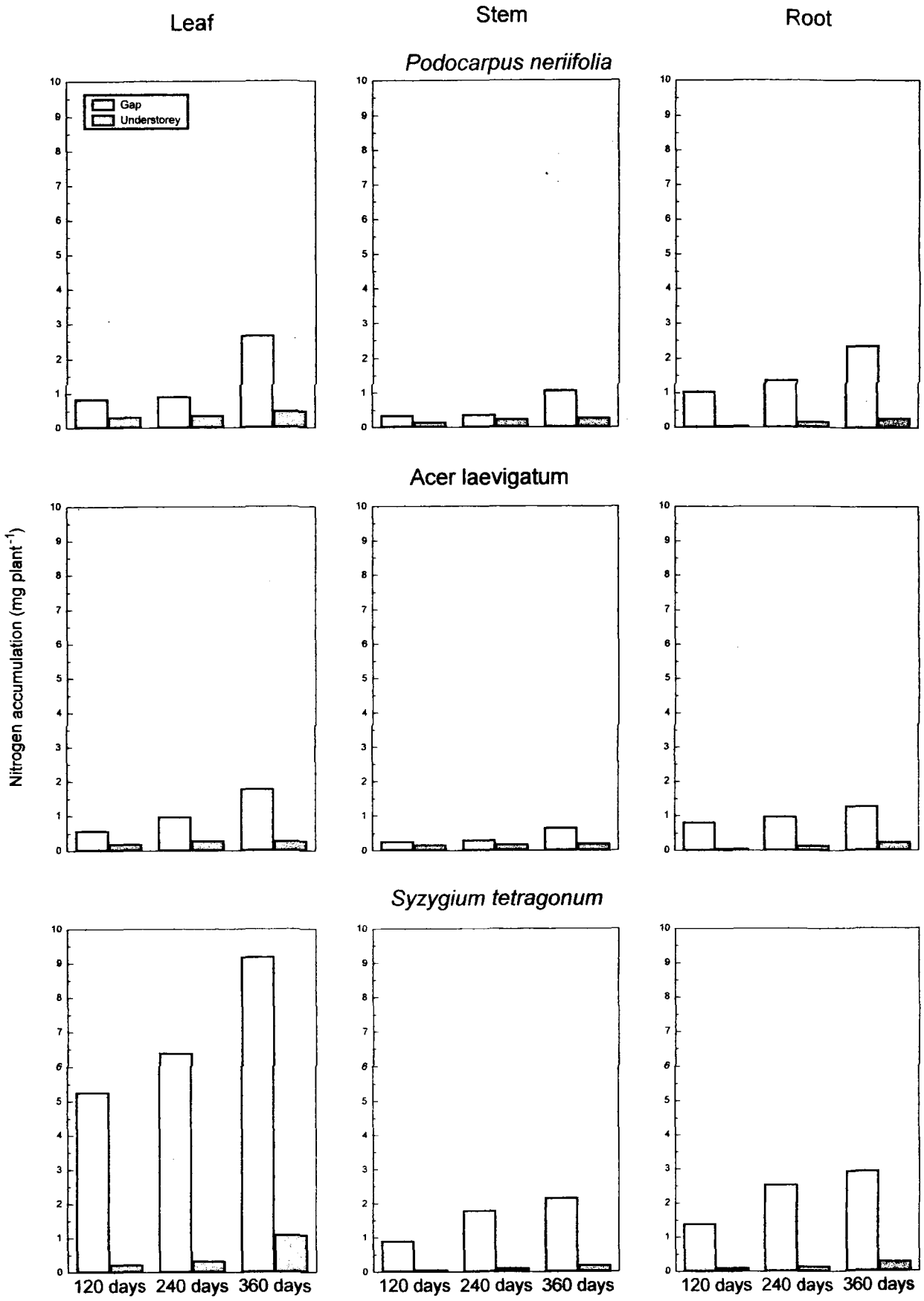


Fig. 6.10. Nitrogen accumulation in *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetragonum* seedlings in gap and understorey.

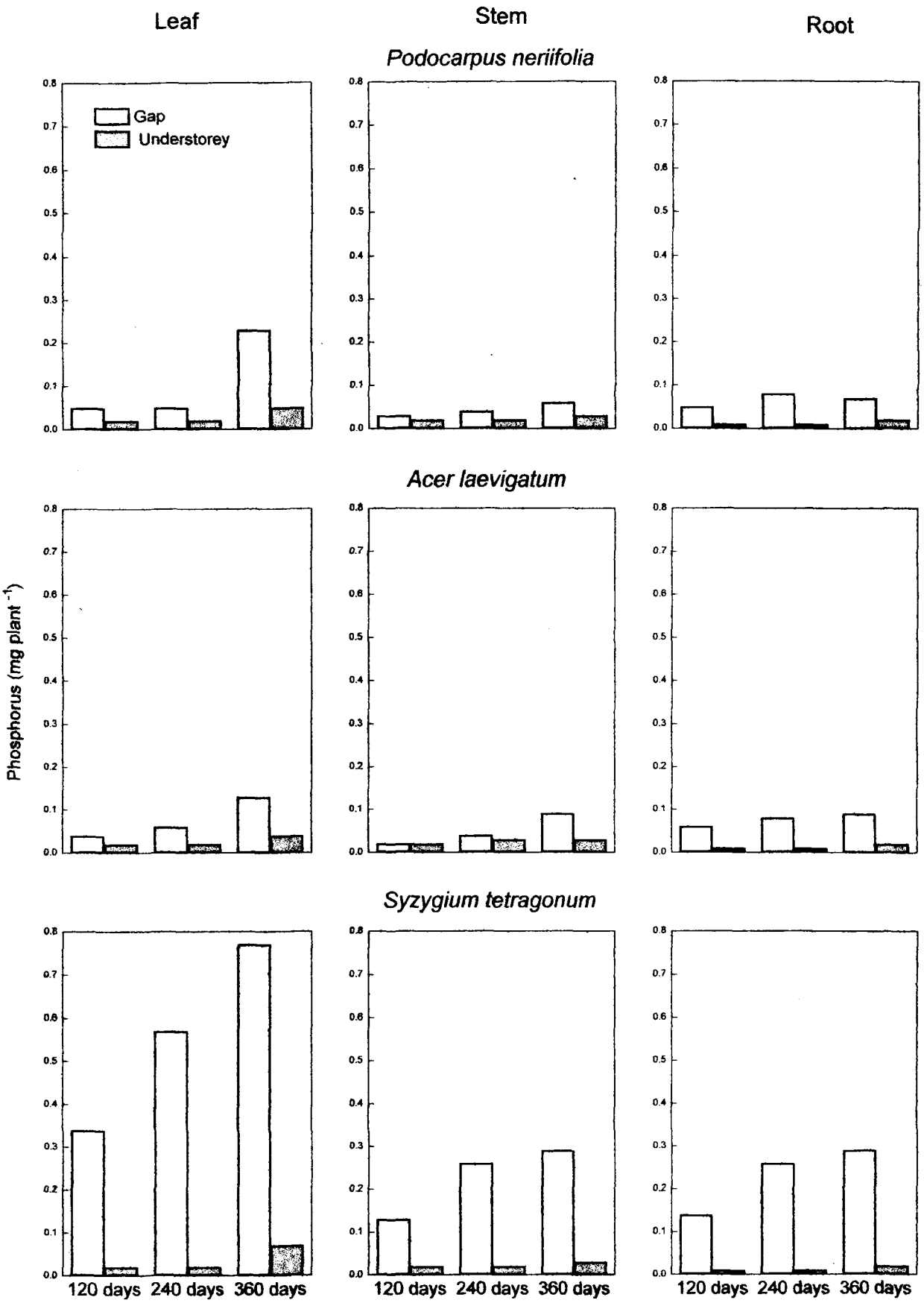


Fig.6.11. Phosphorus accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings in gap and understorey

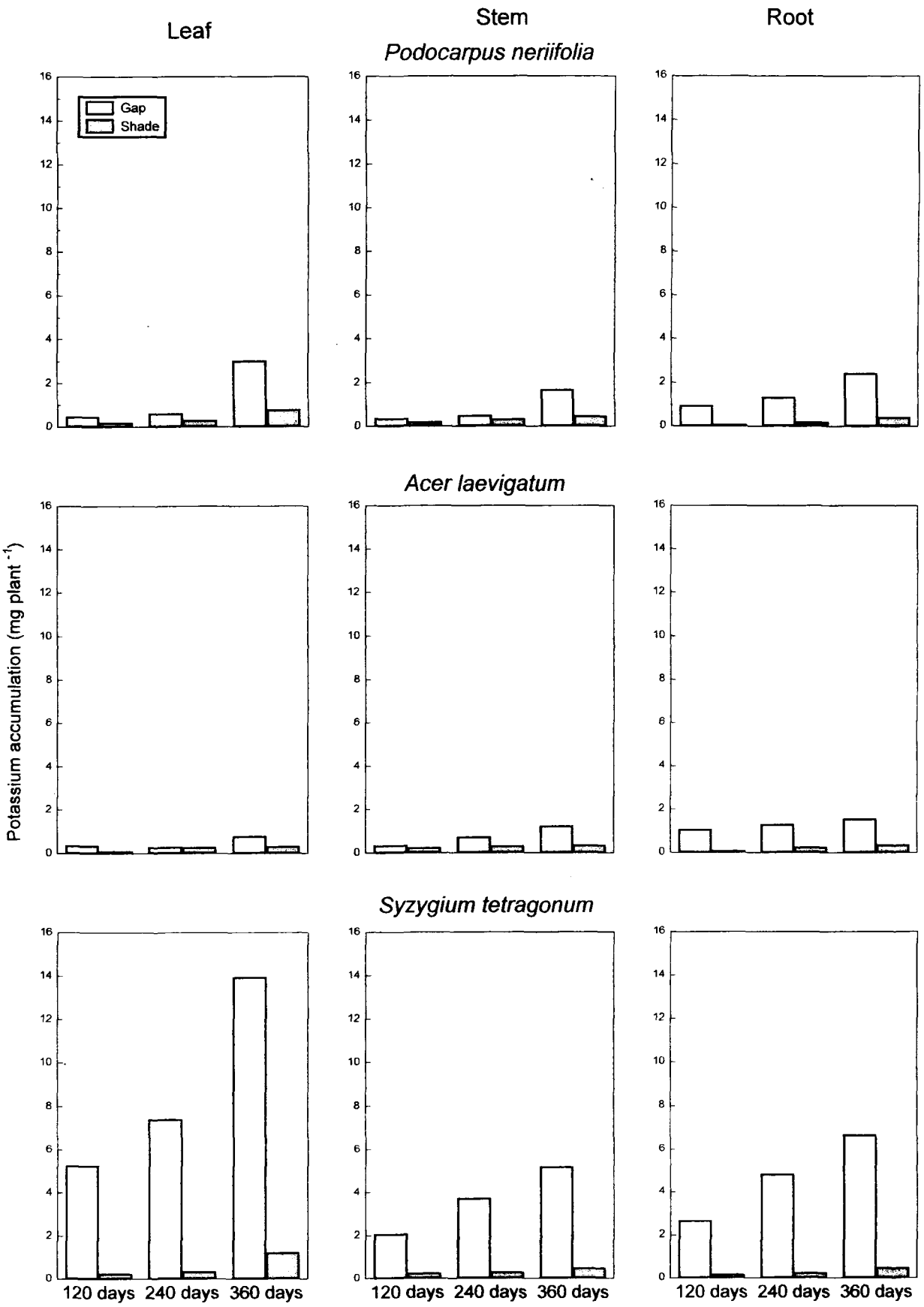


Fig.6.12. Potassium accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings in gap and understorey.

laevigatum the respective values were 0.78-2.10, 0.30-0.99% and 0.47-1.21%. In *Syzygium tetragonum* concentration in leaf, stem and root were 0.49-1.45, 0.15-0.76% and 0.20-0.88% respectively. The concentration in different parts decreased significantly ($p< 0.05$) from 120 days to 360 days old seedlings (Fig. 6.13, 6.14 and 6.15).

Phosphorus concentration pattern was similar to that of N, with higher value in leaf followed by stem and root in *Acer laevigatum* and *Syzygium tetragonum*. *Podocarpus neriifolia* seedlings had high concentration in leaf followed by root and stem. Soil moisture levels did not have significant effect on P concentration in different plant parts of all species. It decreased significantly ($p< 0.05$) after 120 days of seedling growth (Fig. 6.16, 6.17 and 6.18).

Soil moisture levels did not have a significant effect on K concentration in different plant parts of the seedlings (Fig. 6.19, 6.20 and 6.21).

Nutrient accumulation and allocation pattern in root, stem and leaf

N accumulation was more in leaf followed by root and stem at all soil moisture levels in all the species (Fig. 6.22). With the increase in age, there was an increase in N accumulation except in *Acer laevigatum* in which accumulation in the leaf decreased at 360 days at 30% soil moisture level. There was no definite trend of N accumulation in *Podocarpus neriifolia* and *Acer laevigatum* with the increase in moisture level. However, in *Syzygium tetragonum* N accumulation in all parts increased significantly ($p< 0.01$) with increase in soil moisture level (Fig. 6.22).

P accumulation in *Podocarpus neriifolia* and *Acer laevigatum* did not show significant variation at different soil moisture levels, but it increased with increasing soil

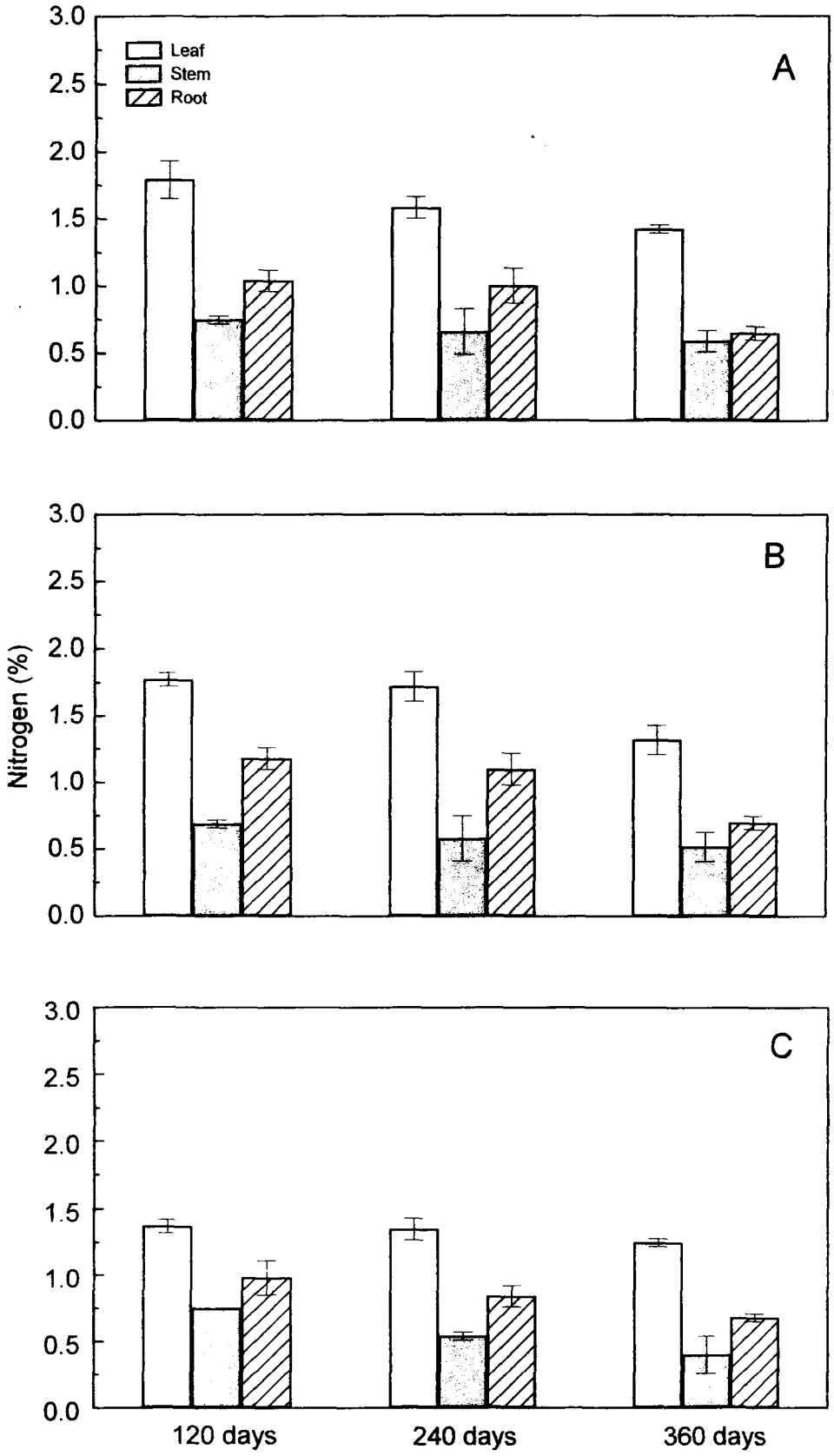


Fig.6.13. Nitrogen concentration in different parts of *Podocarpus neriifolia* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC).

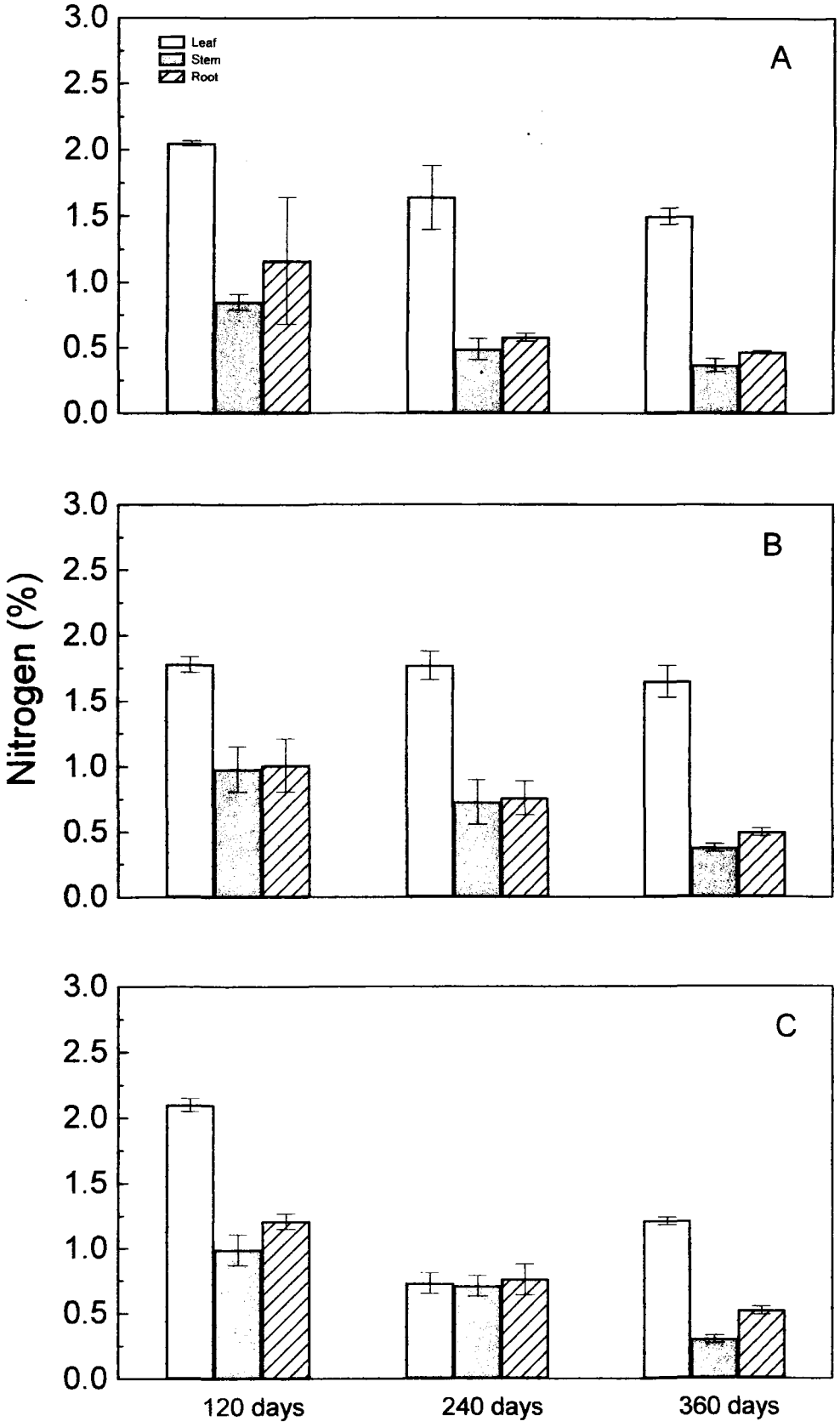


Fig.6.14. Nitrogen concentration in different parts of *Acer laevigatum* seedlings under three soil moisture levels
(A- 20% SMC; B- 30% SMC; C- 40% SMC)

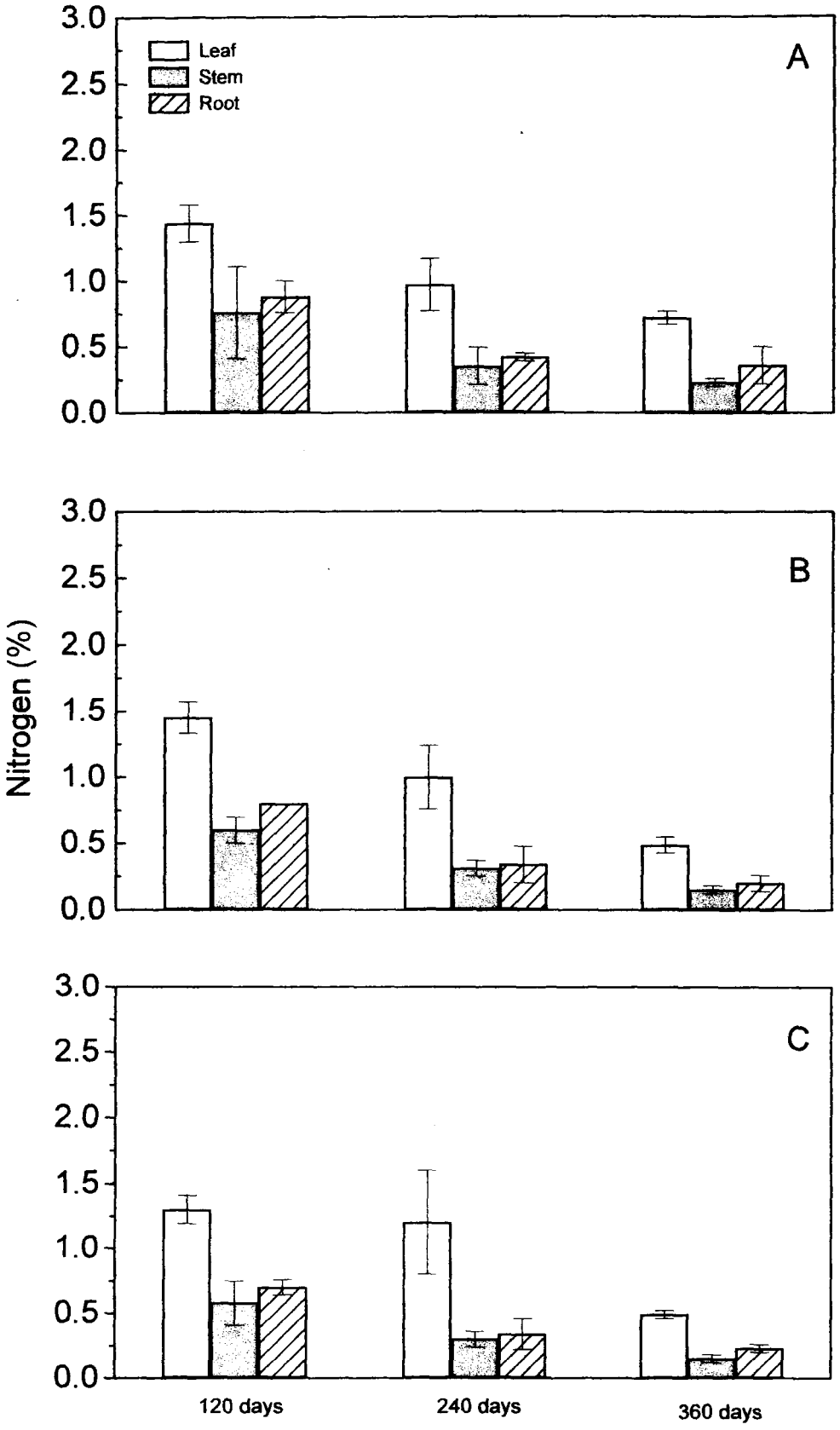


Fig.6.15. NItrogen concentration in different parts of *Syzygium tetragonum* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC).

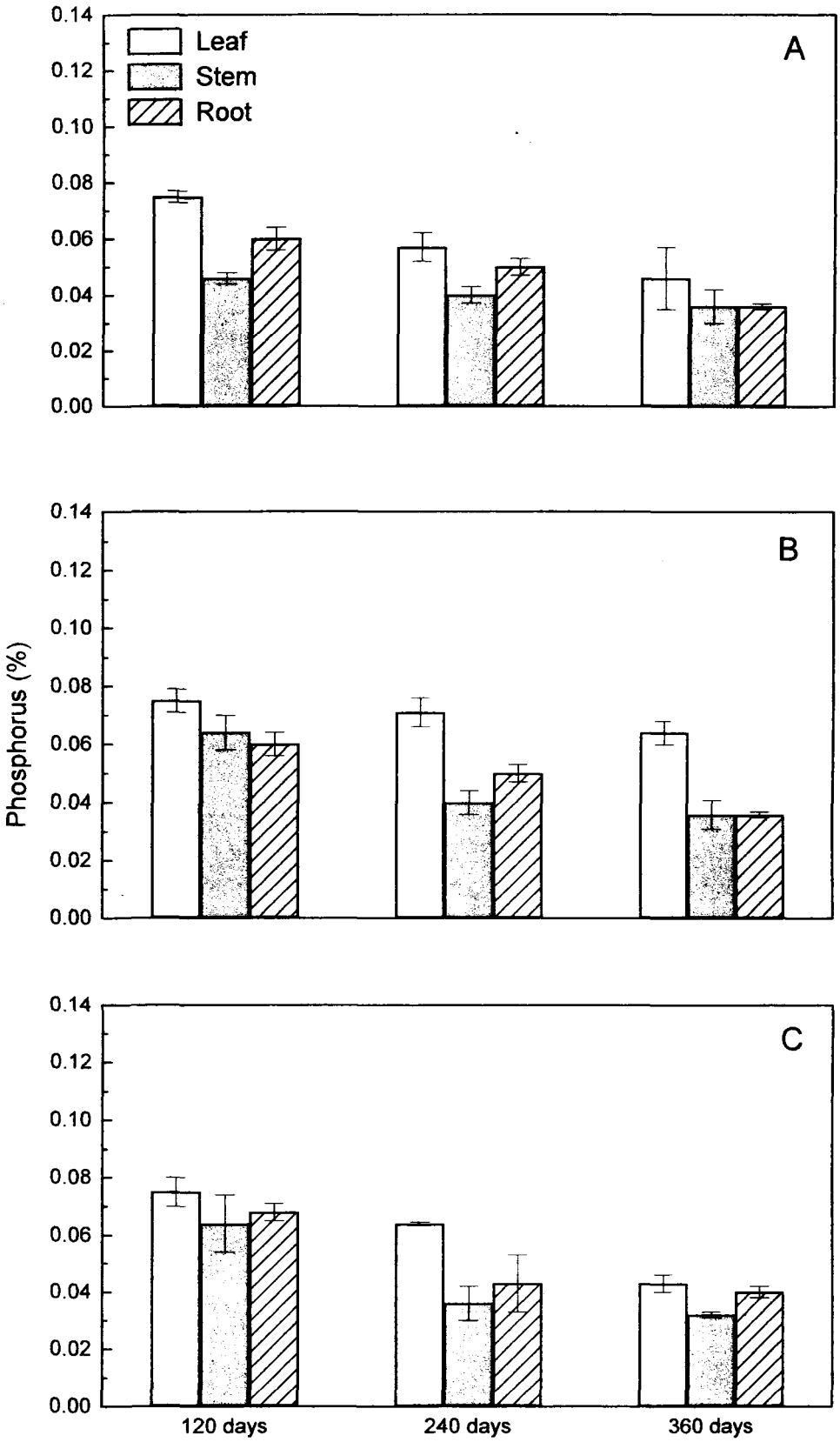


Fig.6.16. Phosphorus concentration in different parts of *Podocarpus neriifolia* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC).

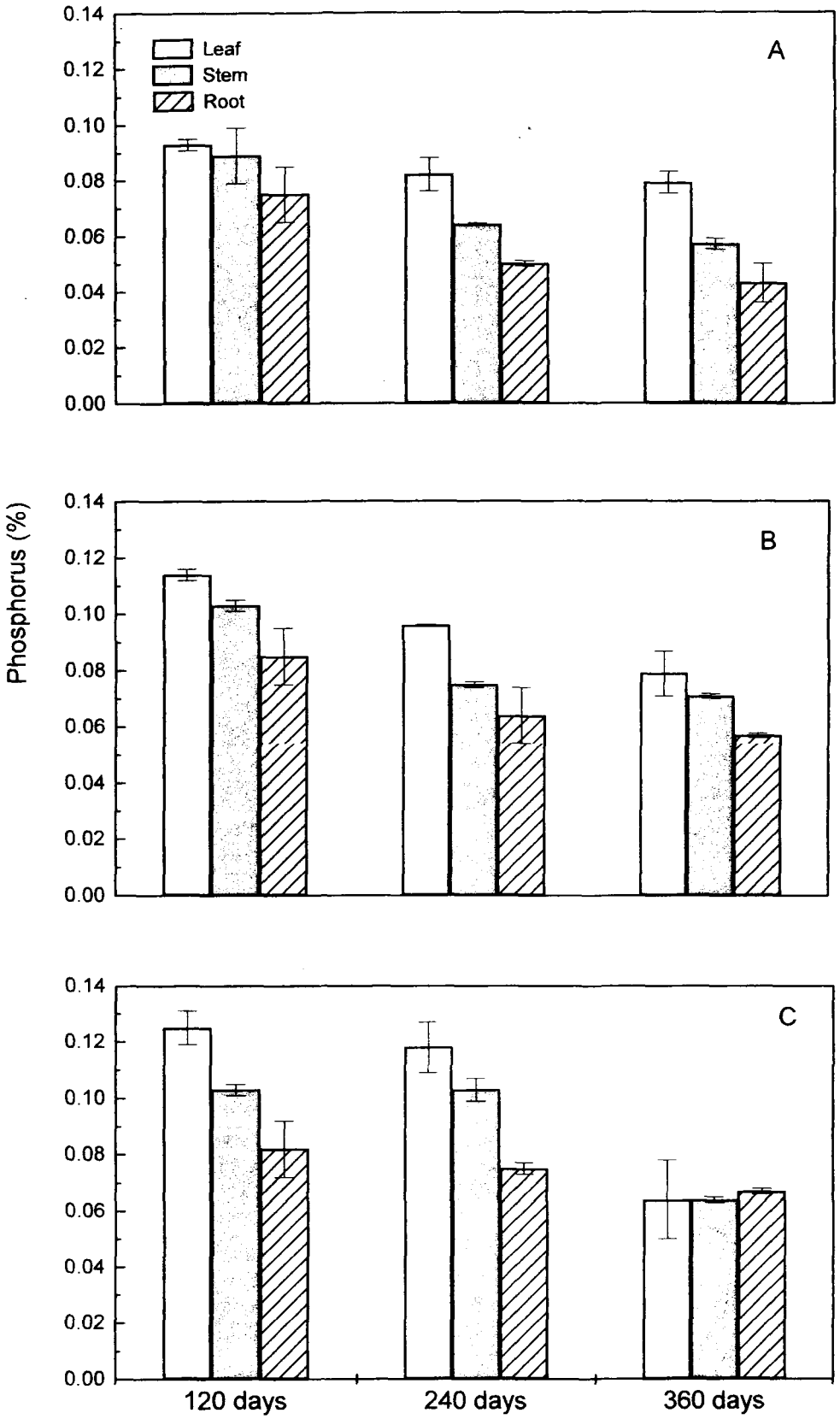


Fig. 6.17. Phosphorus concentration in different parts of *Acer laevigatum* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC).

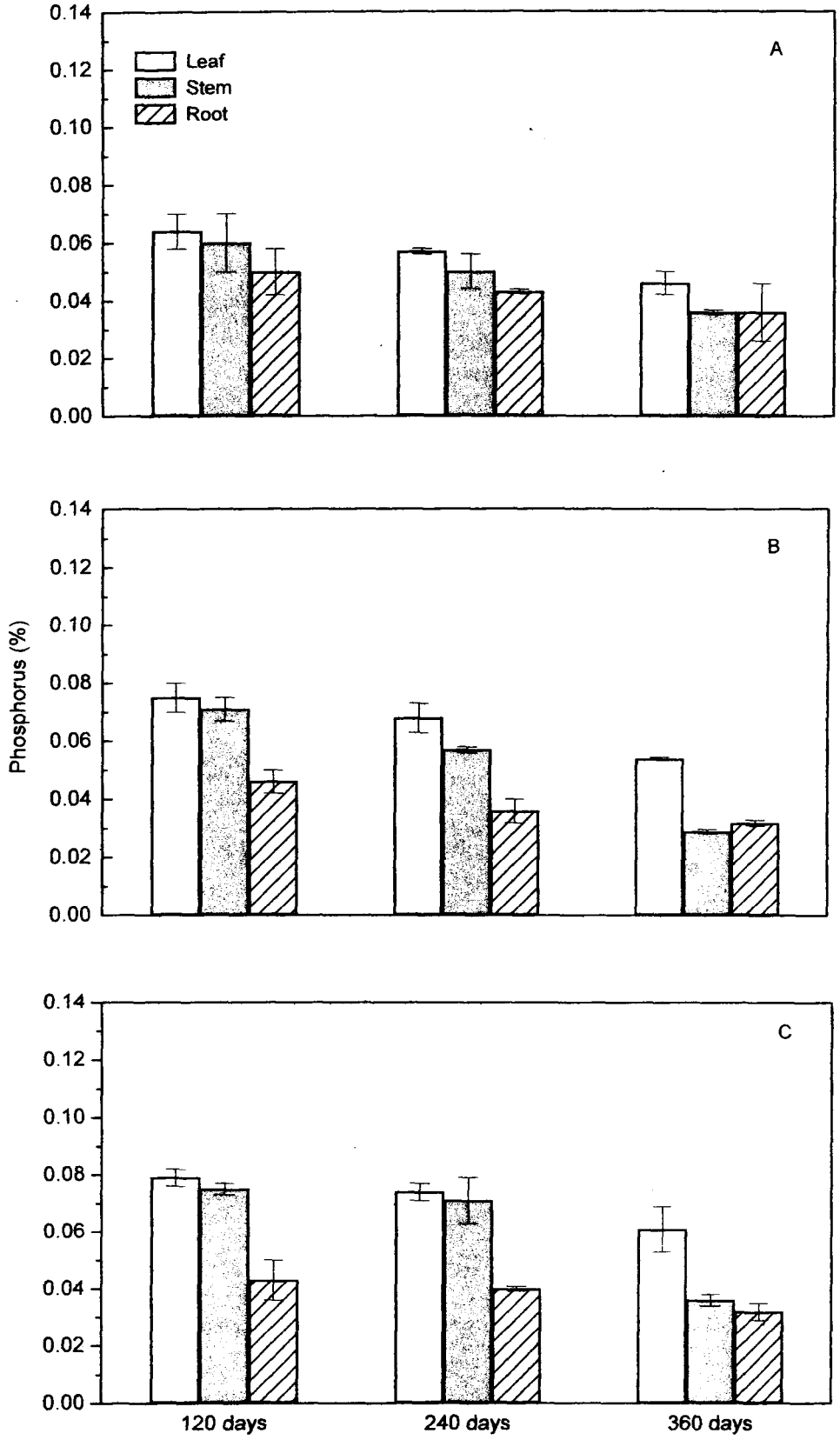


Fig. 6.18. Phosphorus concentration in different parts of *Syzygium tetragonum* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC).

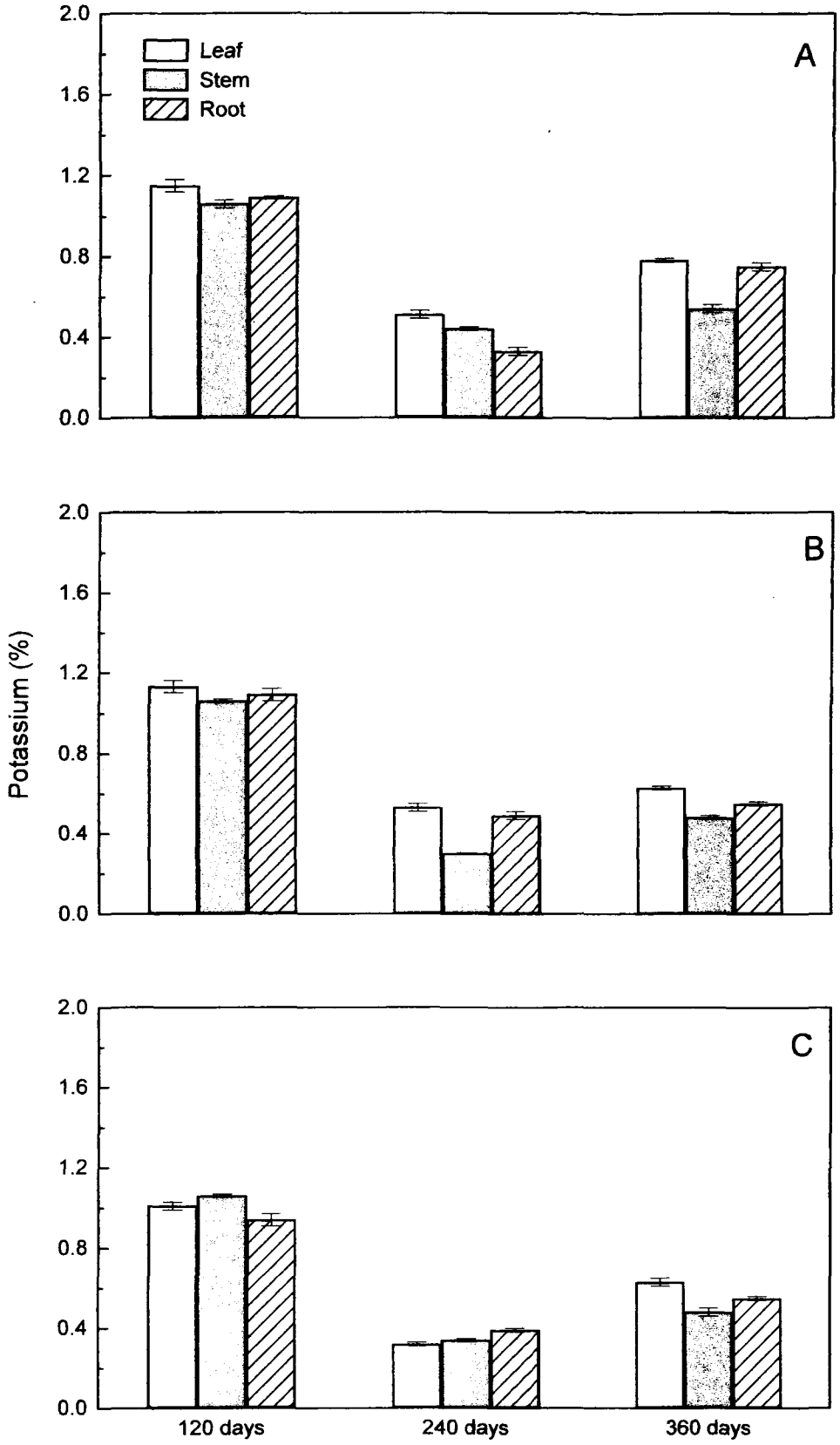


Fig. 6.19. Potassium concentration in different parts of *Podocarpus neriifolia* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC).

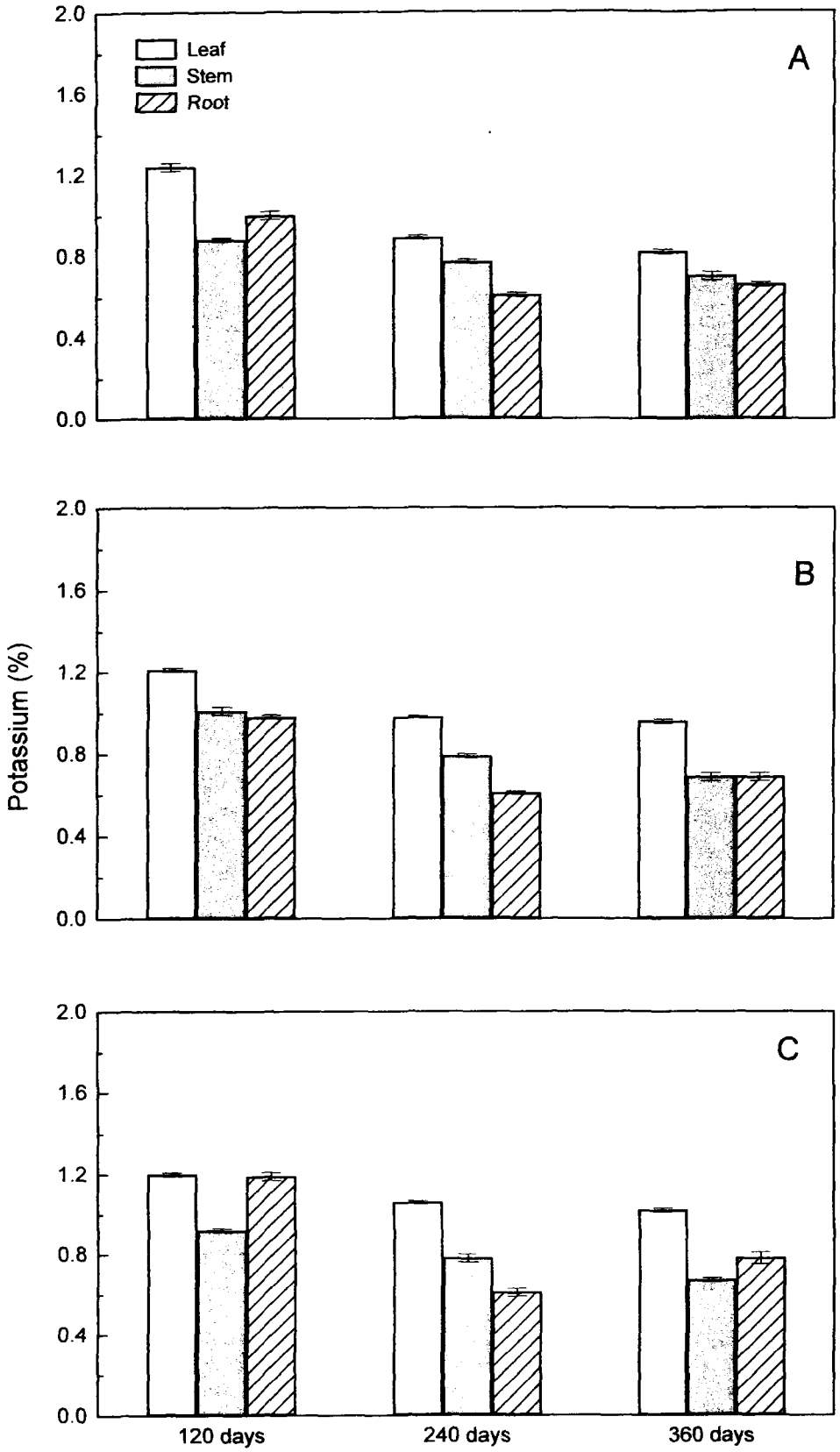


Fig. 6.20. Potassium concentration in different parts of *Acer laevigatum* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC)..

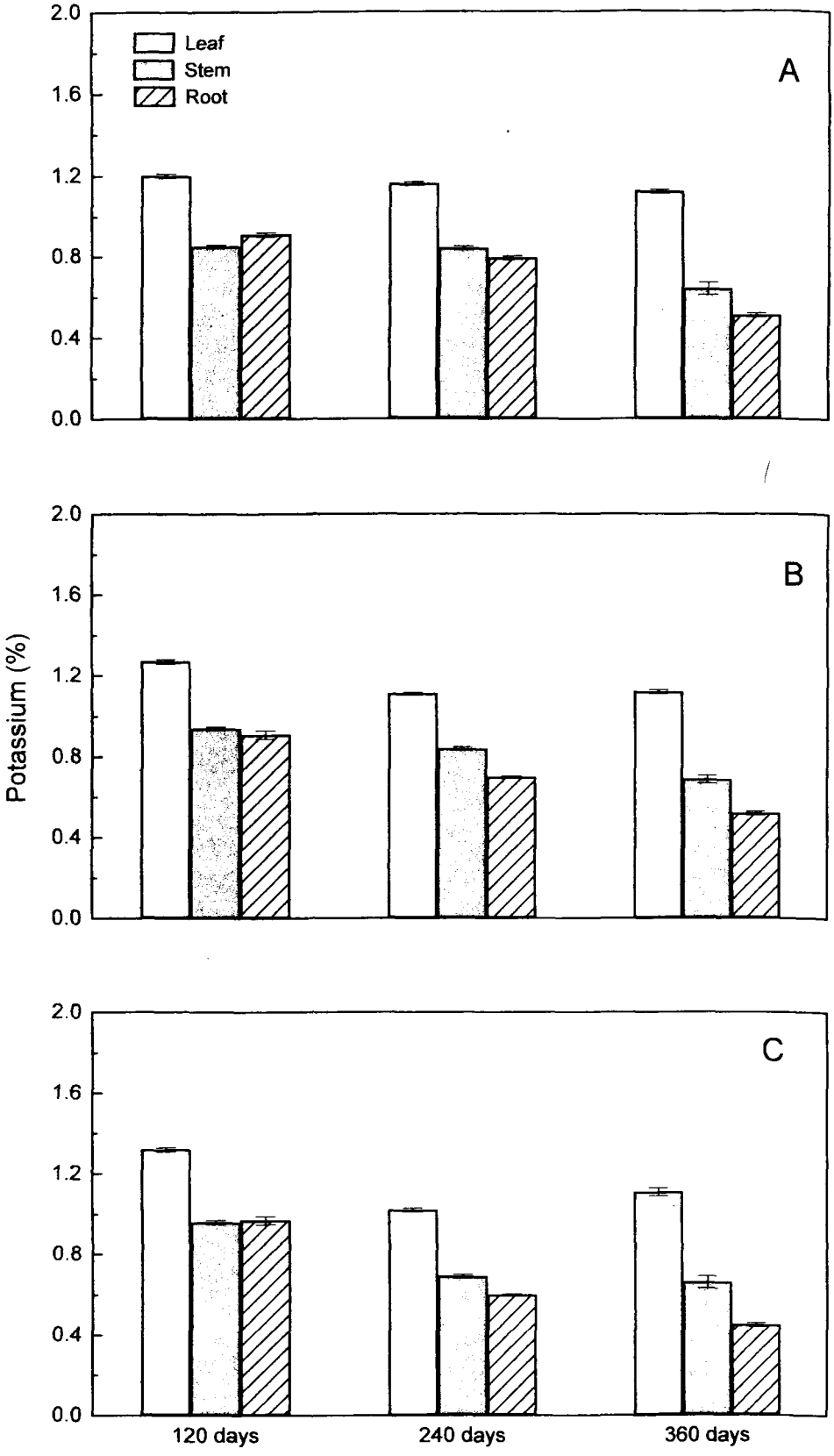


Fig. 6.21. Potassium concentration in different parts of *Syzygium tetragonum* seedlings under three soil moisture levels (A- 20% SMC; B- 30% SMC; C- 40% SMC).

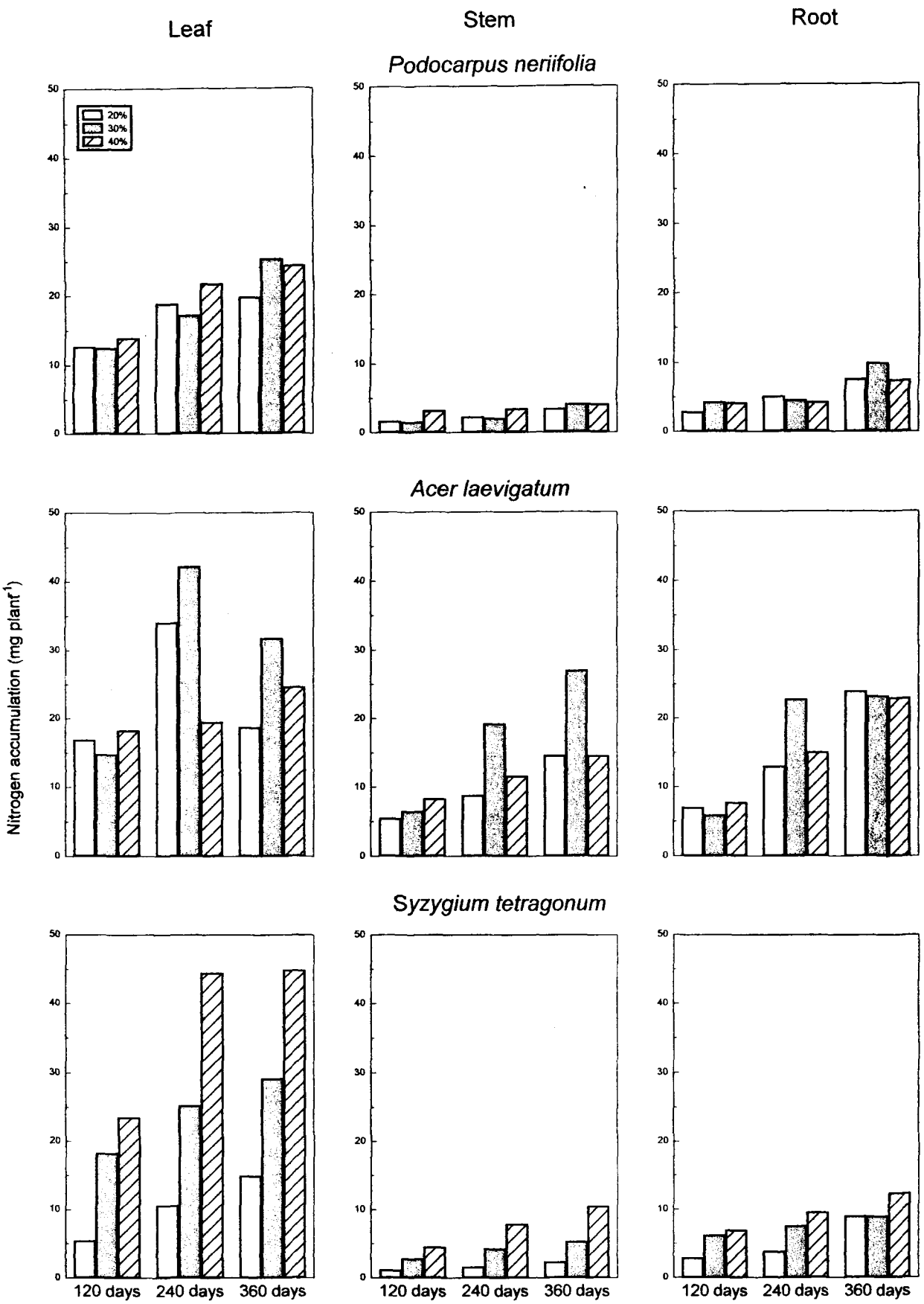


Fig. 6.22. Nitrogen accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings at three soil moisture levels.

moisture in *Syzygium tetragonum*. P accumulation increased in all plant parts with age, except in *Acer laevigatum* which showed a decrease in the leaf at 360 days (Fig. 6.23).

K accumulation did not vary between different plant parts in all three species. It increased with age in all plant parts, except in *Acer laevigatum* which showed a decrease in the leaf at 360 days. *Syzygium tetragonum* showed marked increase in K accumulation with increasing soil moisture level, whereas in *Podocarpus neriifolia* and *Acer laevigatum* this trend was not observed (Fig. 6.24).

Nutrient use efficiency

Nitrogen use efficiency (NUE) increased with increasing soil moisture level in *Podocarpus neriifolia and Syzygium tetragonum. Acer laevigatum* showed a reverse trend (Table. 6.2).

Phosphorus use efficiency (PUE) decreased with increasing moisture level in *Acer laevigatum* and *Syzygium tetragonum* but in *Podocarpus neriifolia* this trend was not observed (Table. 6.2).

The Potassium use efficiency (KUE) of the seedlings showed a trend similar to that of NUE (Table. 6.2).

Table. 6.2. Nitrogen, phosphorus and potassium use efficiency (mg dry weight produced /mg nutrient uptake) of *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* under three soil moisture levels.

Nutrient use efficiency	Soil moisture levels (%)	*Podocarpus neriifolia*	*Acer laevigatum*	*Syzygium tetragonum*
Nitrogen use efficiency	20	93	132	156
	30	98	123	193
	40	124	120	206
Phosphorus use efficiency	20	2178	1492	2163
	30	1932	1204	2047

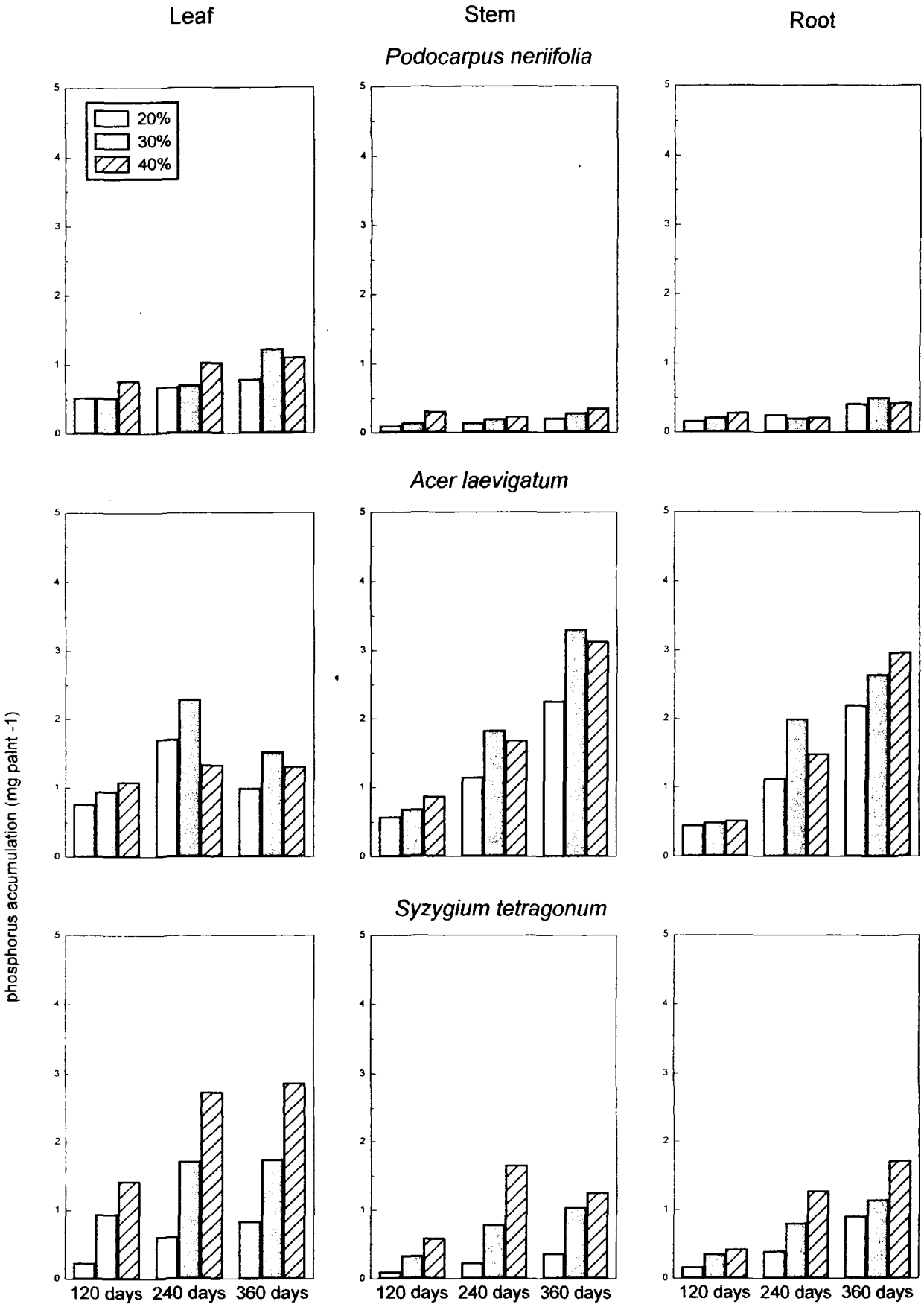


Fig. 6.23. Phosphorus accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings at three soil moisture levels.

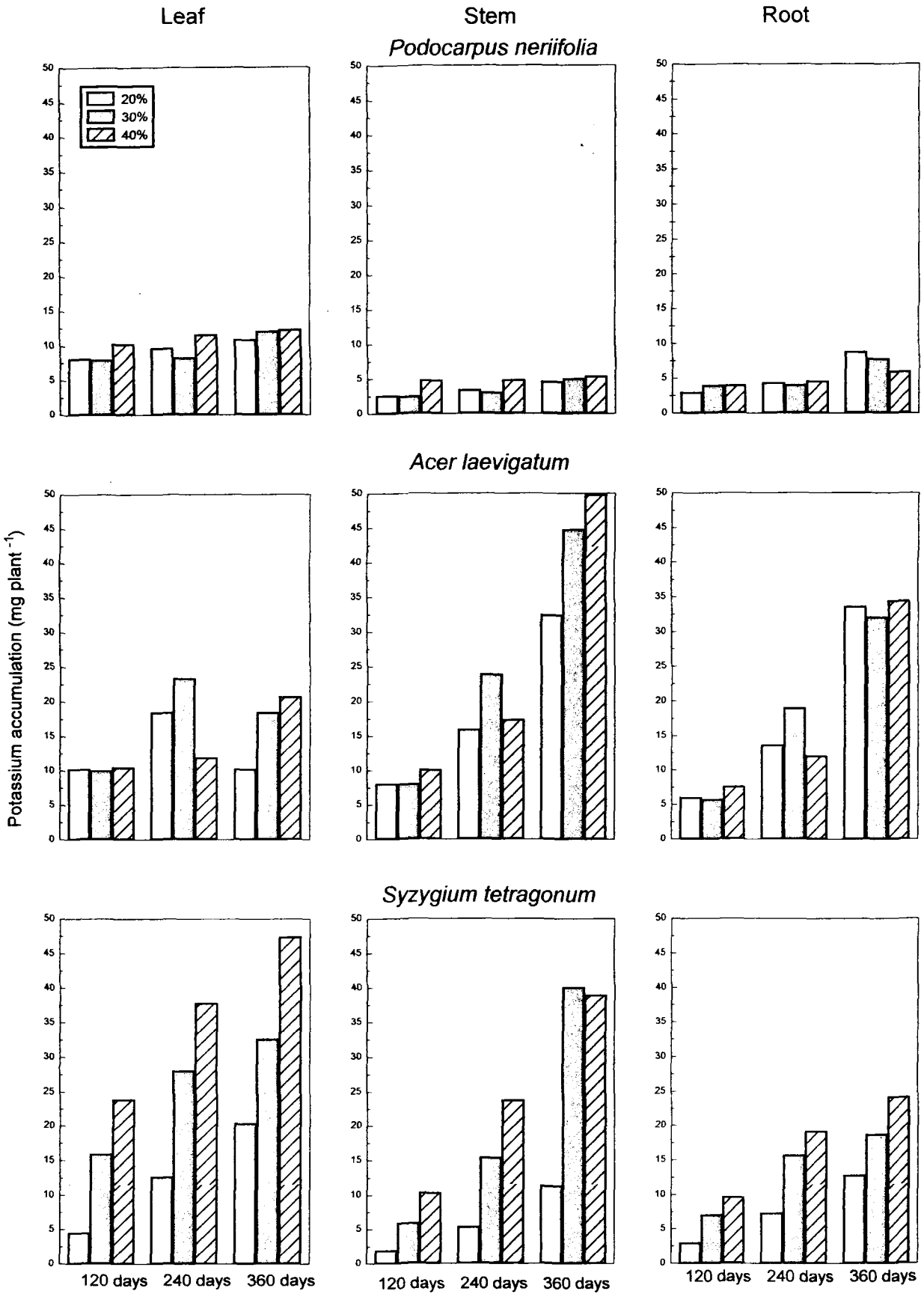


Fig. 6.24. Potassium accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings at three soil moisture levels

	40	2156	1131	1843
Potassium use efficiency	20	151	124	112
	30	161	119	112
	40	191	116	118

III. Effect of NPK level in soil

Nutrient concentration in different plant parts

N concentration (%) in different species and plant parts did not vary significantly at different soil NPK levels. However, it decreased with age in all cases. Leaf had higher N concentration in all species at all three NPK levels. In *Podocarpus neriifolia* N concentration in root was less than stem during the initial 120 days of growth, but later on concentration in root increased (Fig. 6. 25). *Acer laevigatum* did not show any trend (Fig. 6.26). In *Syzygium tetragonum* N concentration in root was more than stem at 120 days, beyond this age no trend was observed (Fig. 6.27).

With increase in the age P concentration (%) in different parts of seedling decreased in all the three species. Leaf had higher concentration in all species at all three NPK levels. *Podocarpus neriifolia* root had higher P concentration than the stem. *Acer laevigatum* and *Syzygium tetragonum* stems had higher concentration (Fig. 6.28, 6.29 and 6.30).

Soil NPK levels has no effect on K concentration in all the species. K concentration was generally higher in the leaf of all species (Fig. 6.31, 6.32 and 6.33).

Nutrient accumulation and allocation pattern in root, stem and leaf

Nitrogen accumulation was more in leaf of all the species at all soil NPK levels. All the species accumulated more N in root than stem. With the increase in age of the seedlings there was an increase in N accumulation except in *Acer laevigatum* leaf where it

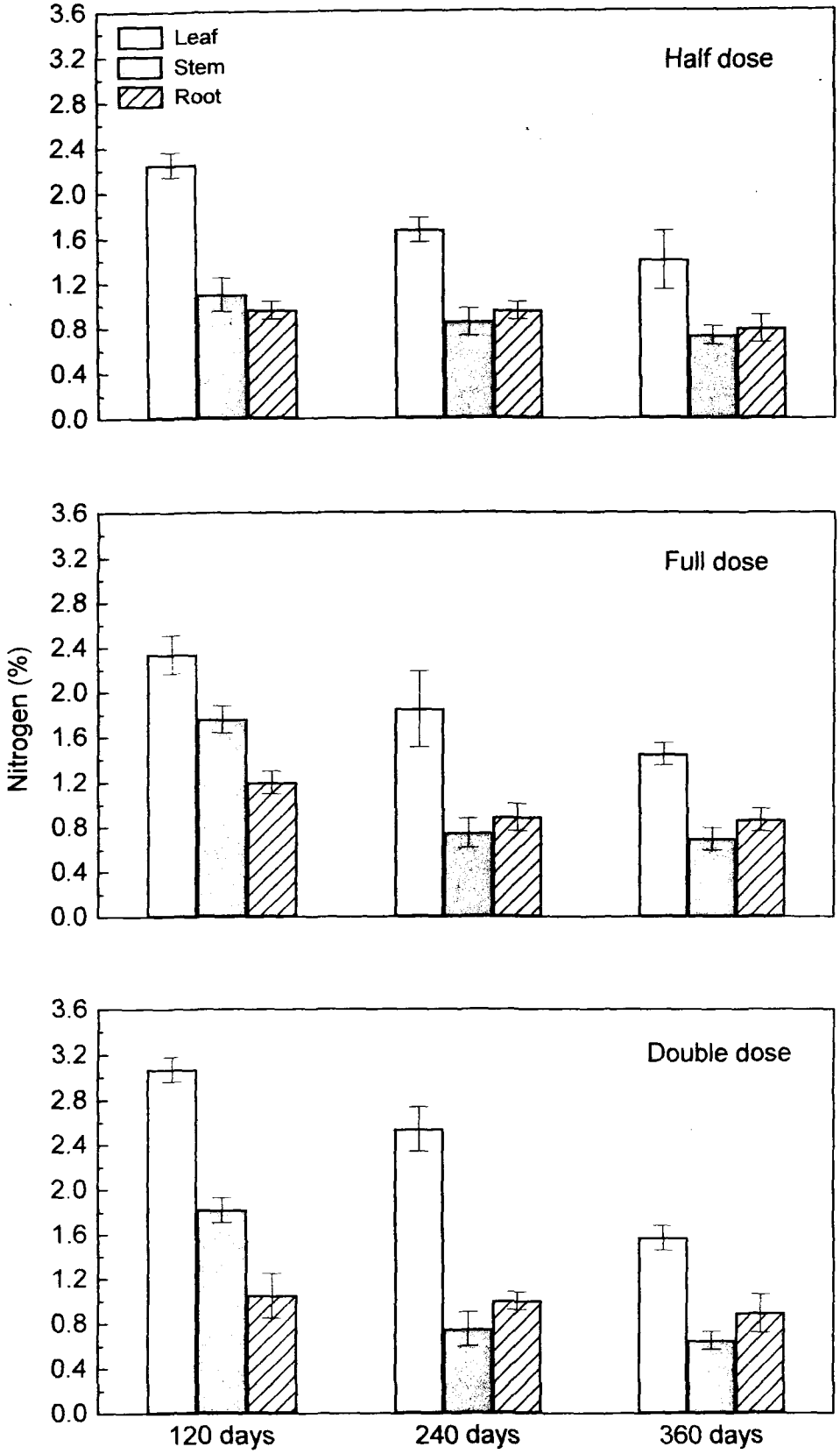


Fig. 6.25. Nitrogen concentration in different parts of *Podocarpus neriifolia* seedlings under three NPK levels.

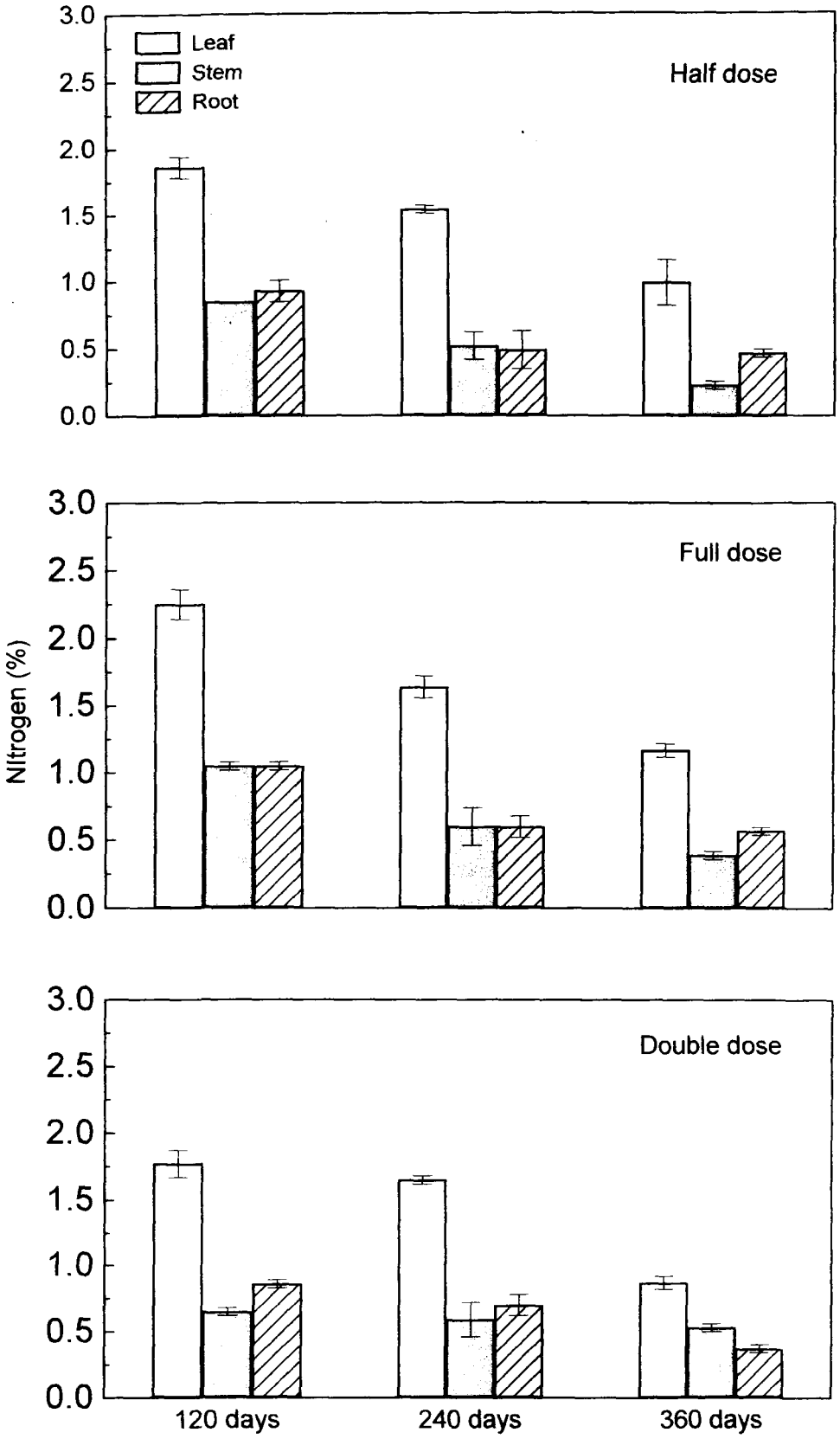


Fig. 6.26. Nitrogen concentration in different parts of *Acer laevigatum* seedlings under three NPK levels.

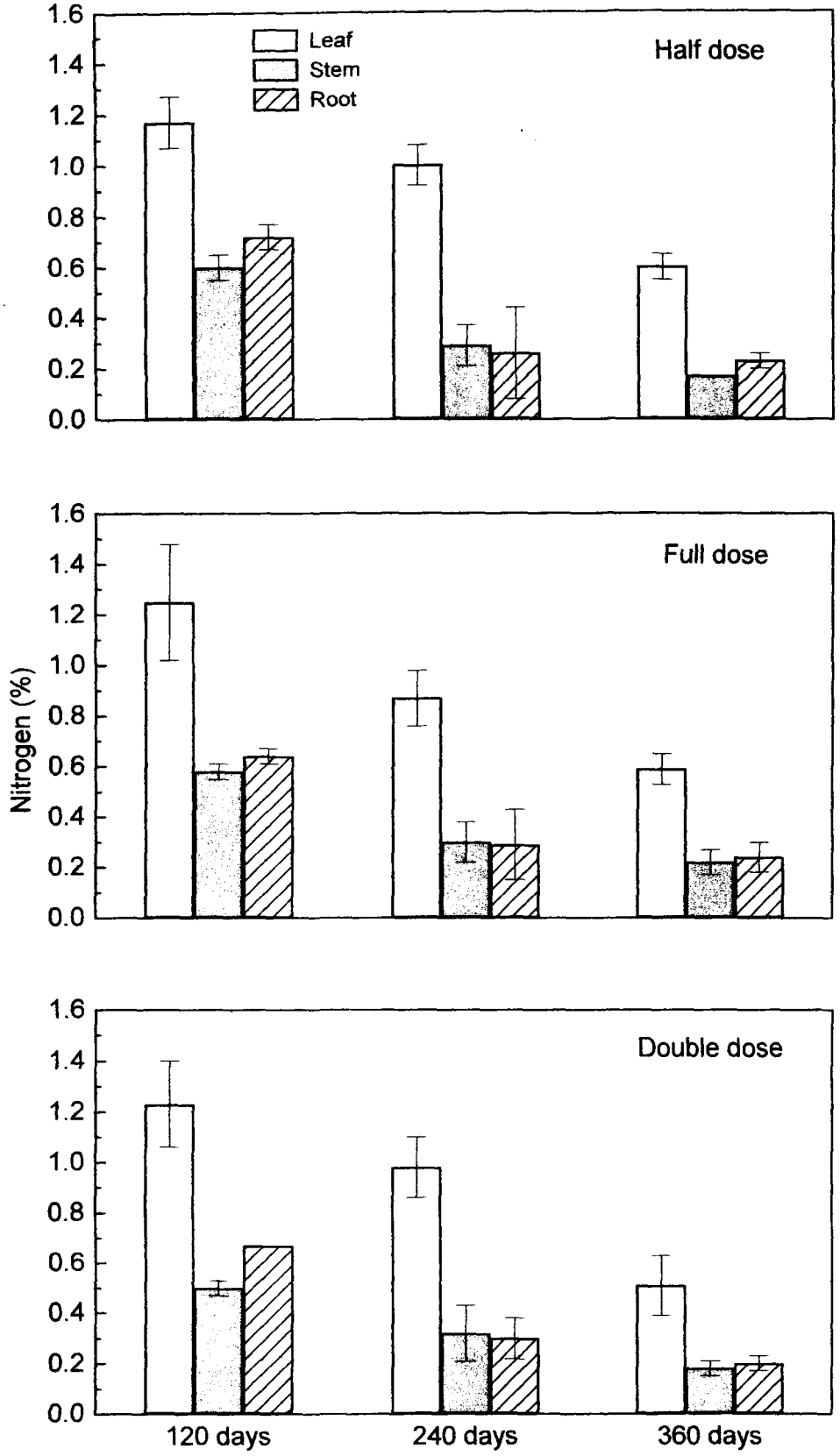


Fig.6.27. Nitrogen concentration in different parts of *Syzygium tetragonum* seedlings under three NPK levels.

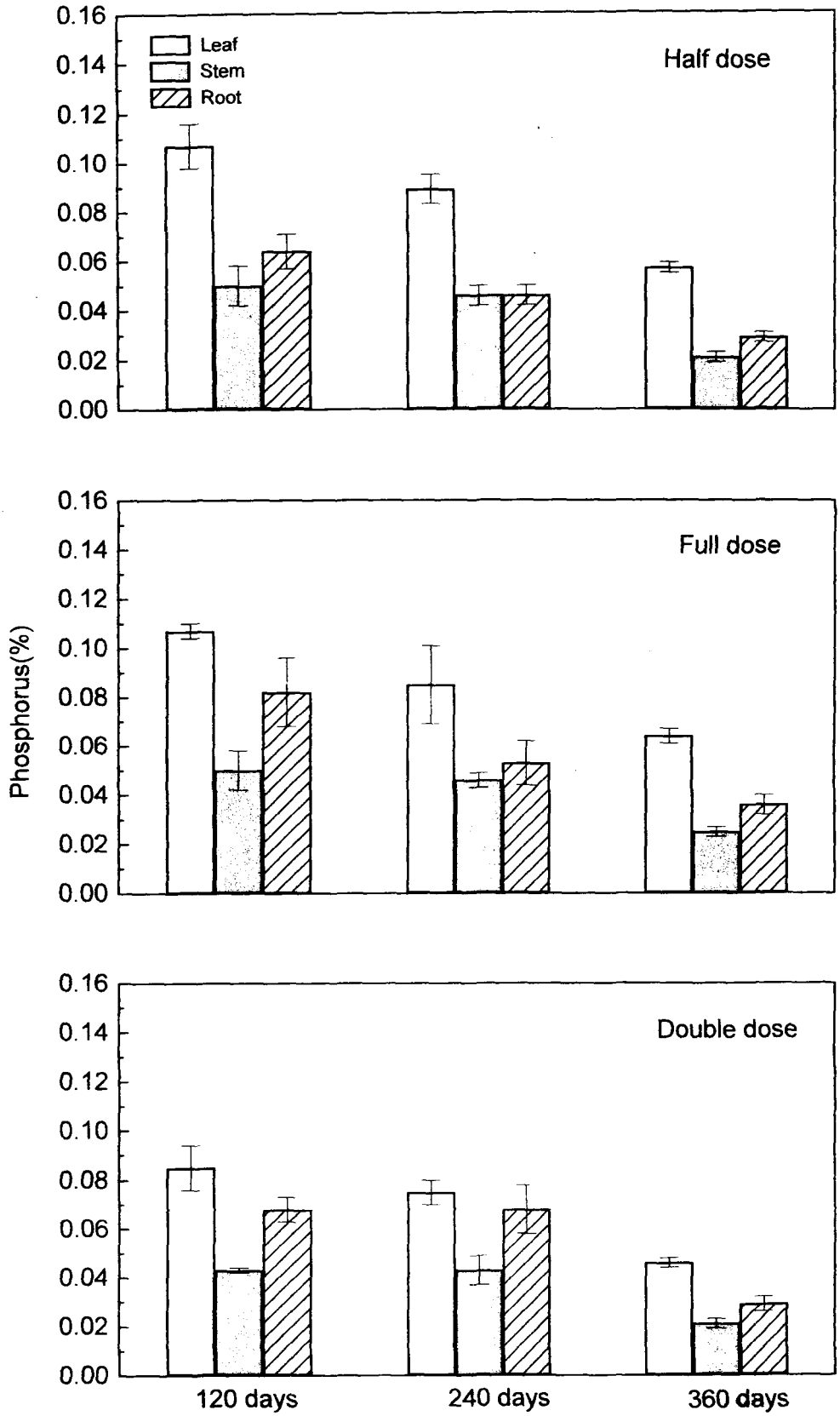


Fig. 6.28. Phosphorus concentration in different parts of *Podoarpus neriifolia* seedlings under three NPK levels.

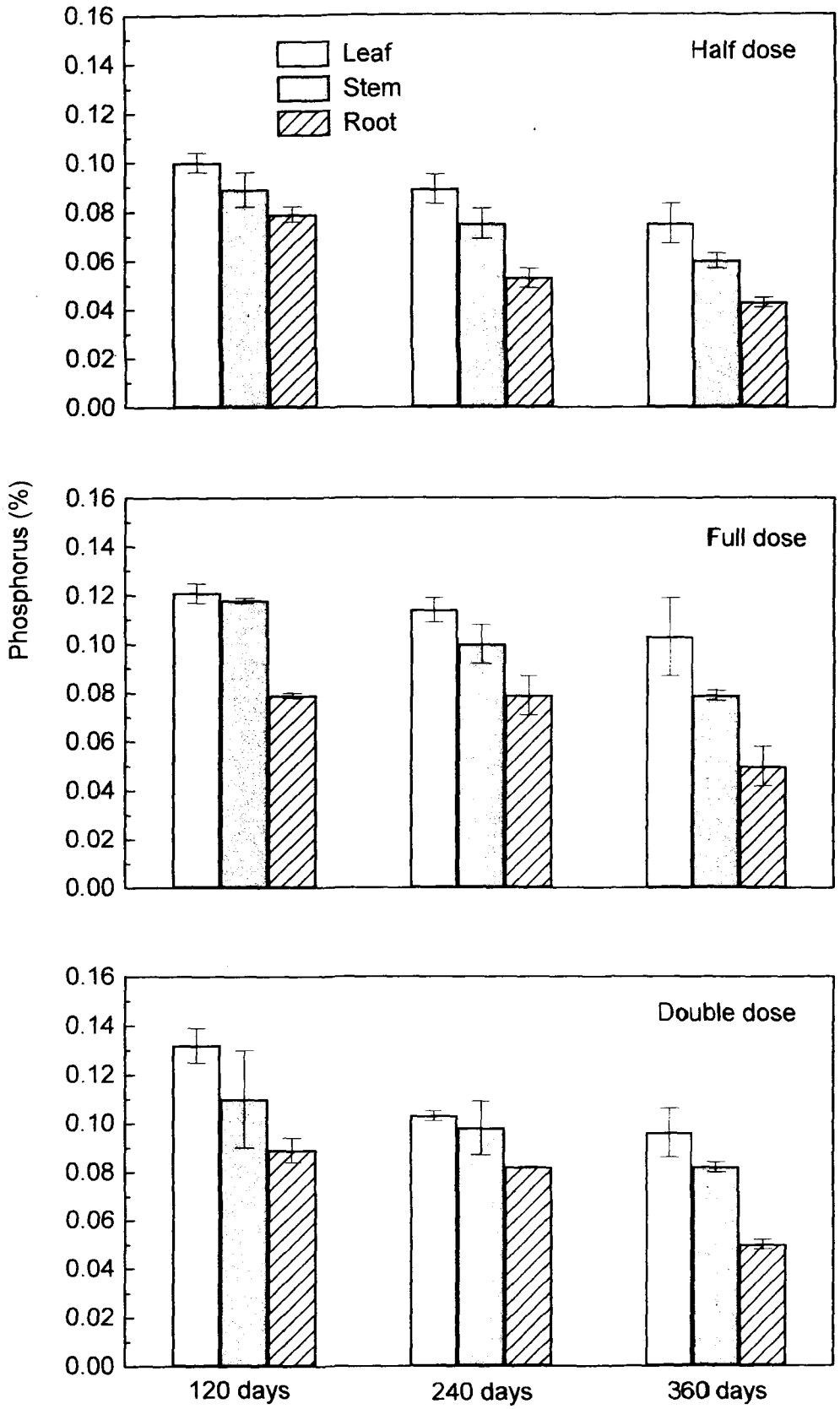


Fig. 6.29. Phosphorus concentration in different parts of *Acer laevigatum* seedlings under three NPK levels.

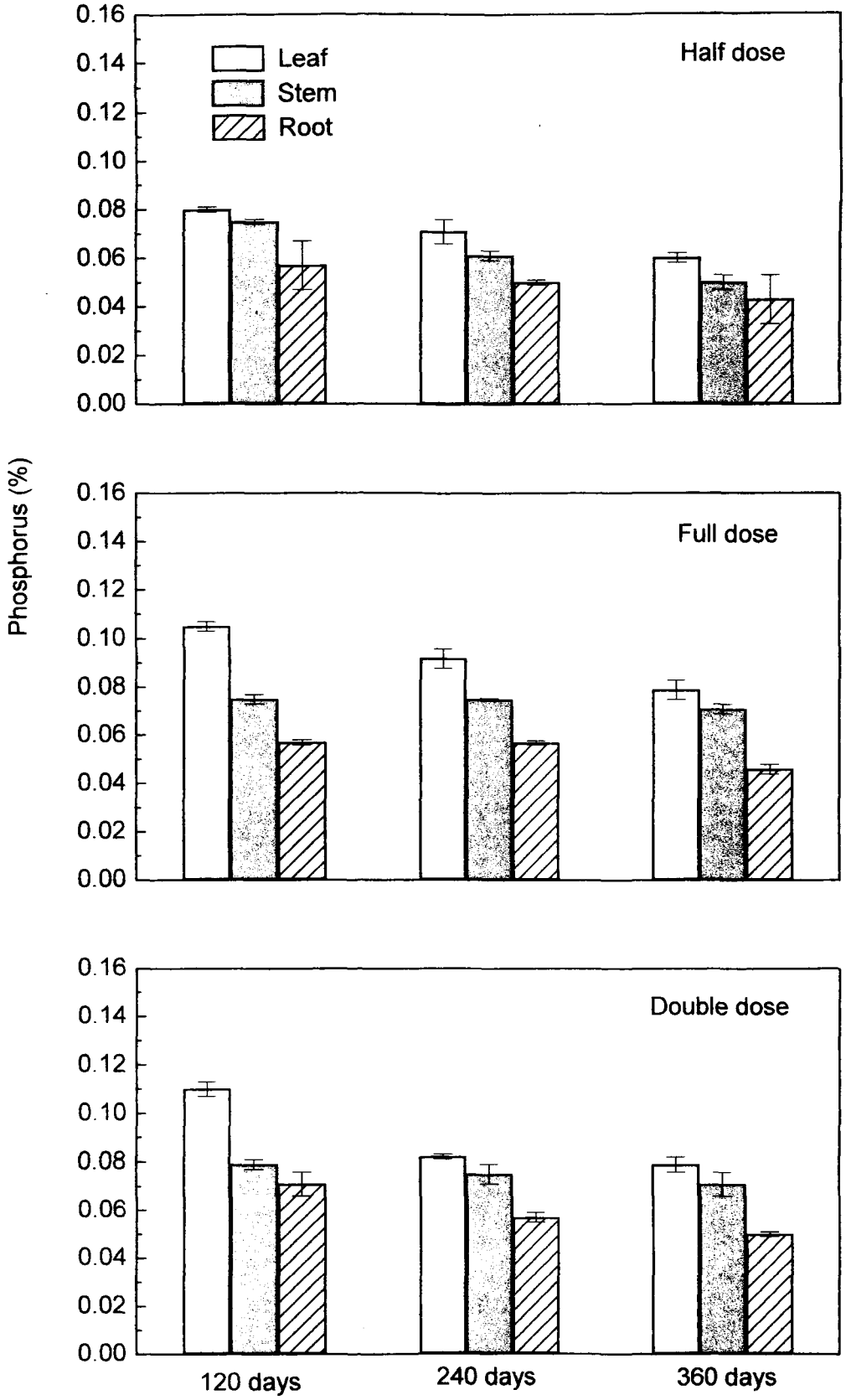


Fig. 6.30. Phosphorus concentration in different parts of *Syzygium tetragonum* seedlings under three NPK levels.

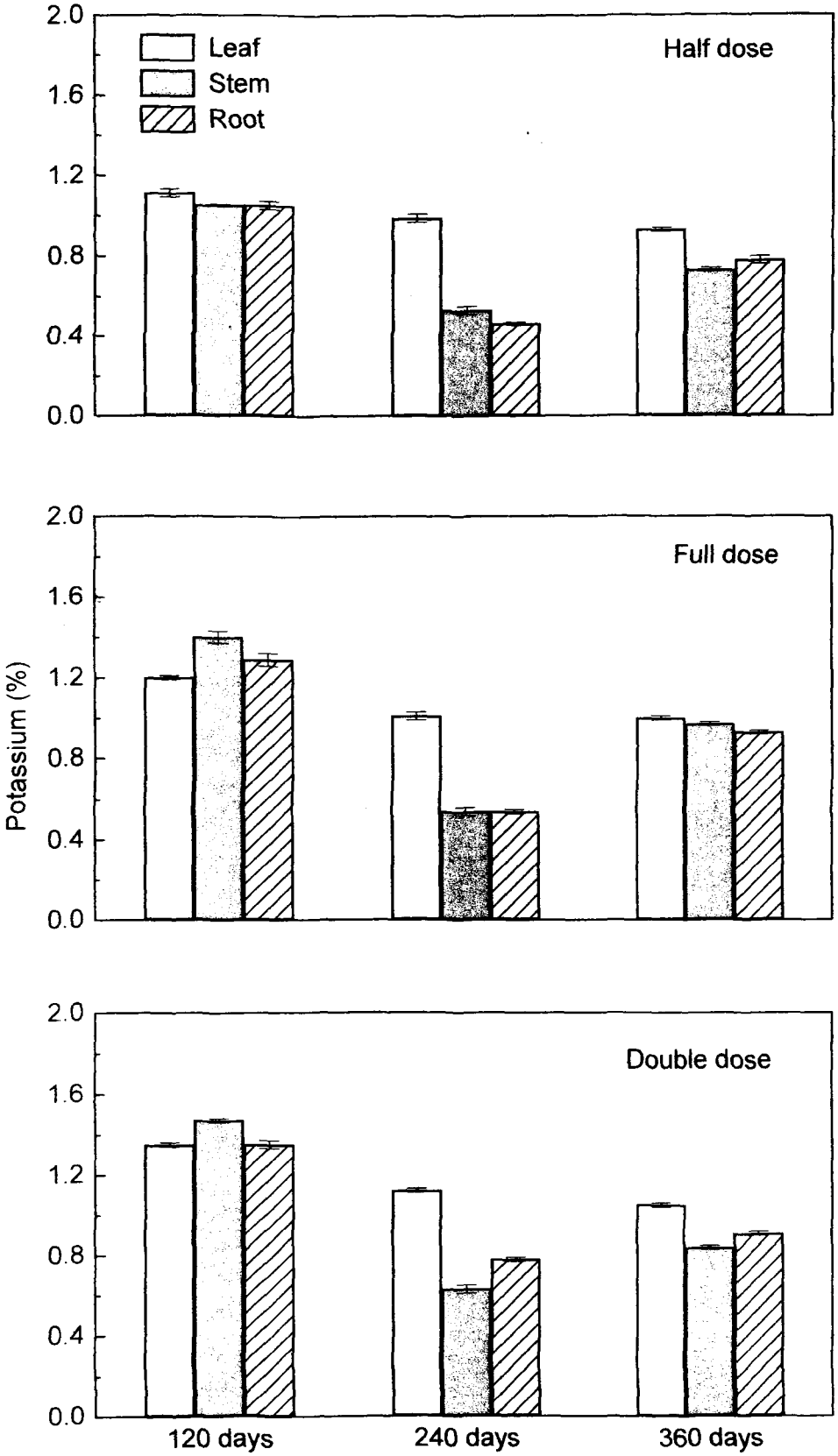


Fig. 6.31. Potassium concentration in different parts of *Podocarpus neriifolia* seedlings under three NPK levels.

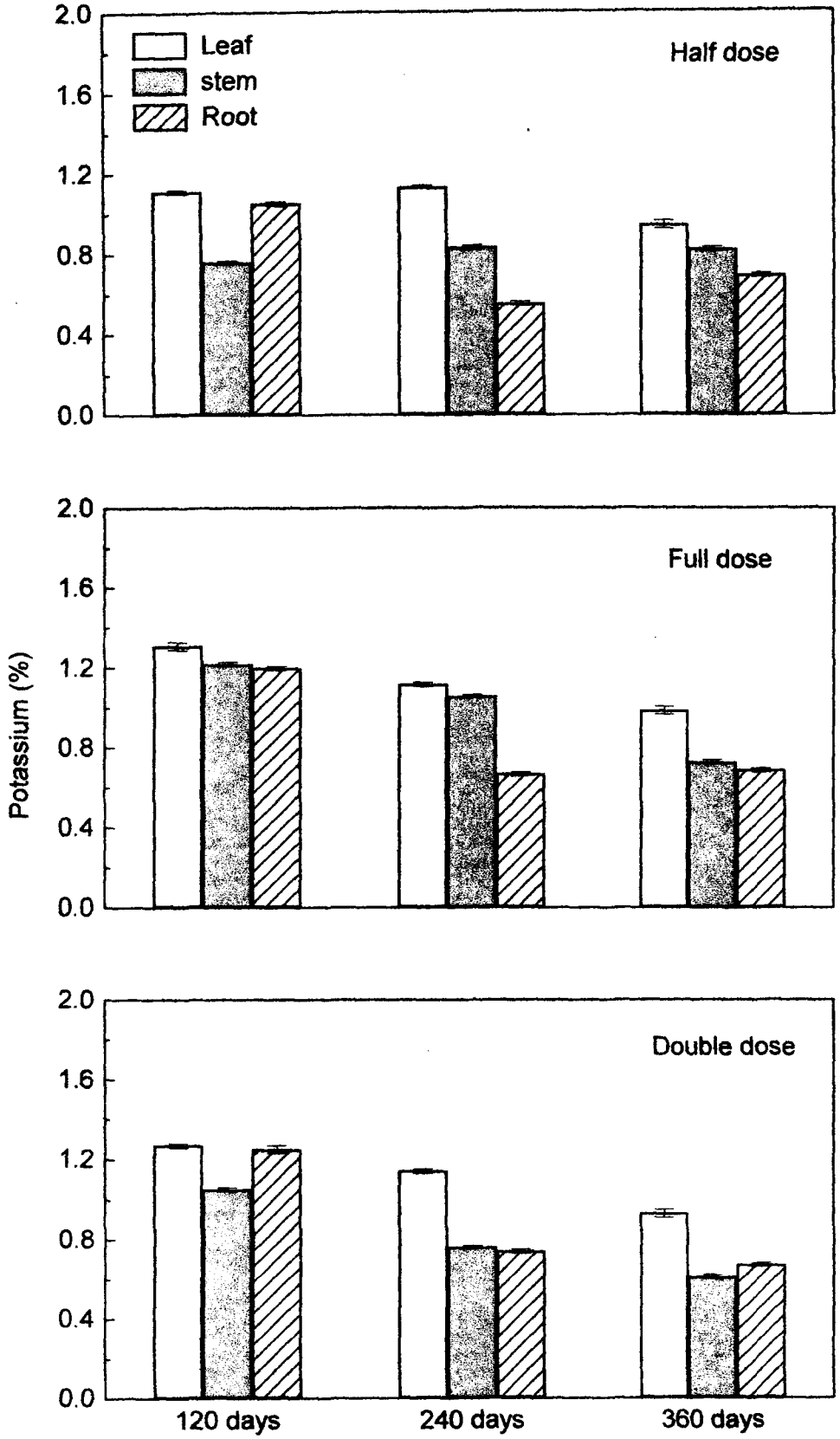


Fig. 6.32. Potassium concentration in differnt parts of *Acer laevigatum* seedlings under three NPK levels.

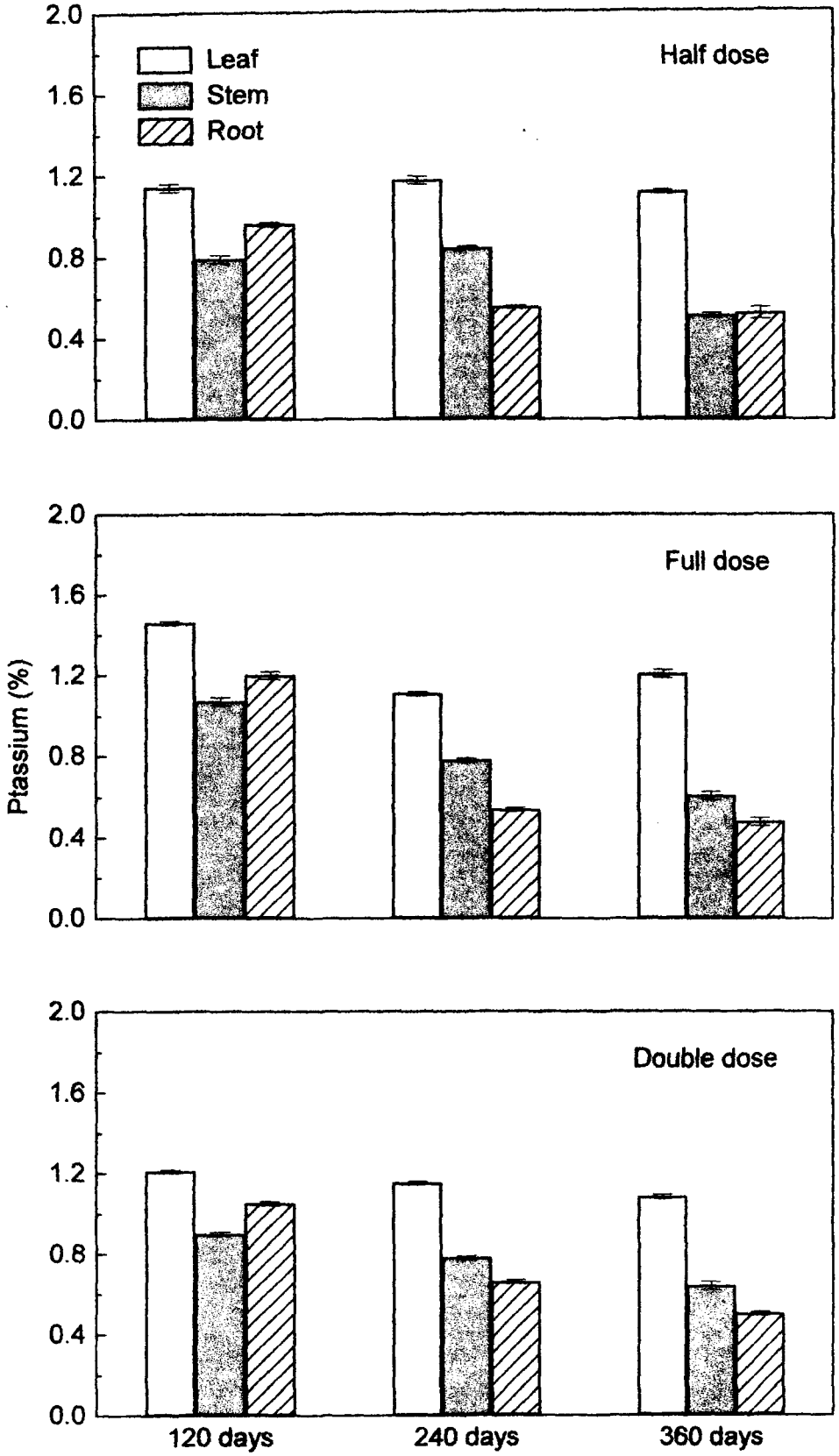


Fig. 6.33. Potassium concentration in different parts of *Syzygium tetragonum* seedlings under three NPK levels.

decreased at 360 days old seedlings at all soil NPK levels. *Podocarpus neriifolia* registered an increase in N accumulation in leaf and stem with increase in soil NPK levels (Fig. 6.34).

P accumulation in *Syzygium tetragonum* and *Podocarpus neriifolia* was higher in leaf followed by root and stem at all soil NPK levels. There was no significantly difference in P accumulation with the increase in soil NPK levels in different plant parts of all three species. There was a progressive increase in P accumulation in different plant parts with age of the seedlings except in the leaf of *Acer laevigatum* which showed a decrease at 360 days at all soil NPK levels (Fig. 6.35).

K accumulation in *Podocarpus neriifolia* was more in leaf followed by root and stem at all soil NPK levels. In *Acer laevigatum* and *Syzygium tetragonum* no definite trend was observed. There was an increase in K accumulation with age in all parts except in *Acer laevigatum*, which showed a decrease in the leaf at 360 days at all soil NPK levels (Fig. 6.36).

Nutrient use efficiency

Nitrogen use efficiency (NUE) increased with increasing soil NPK level in *Podocarpus neriifolia and Syzygium tetragonum*. In *Acer laevigatum* the trend was not clear (Table. 6.3).

In *Syzygium tetragonum* Phosphorus use efficiency (PUE) decreased with increasing soil NPK levels, but it did not happen in *Acer laevigatum* and *Podocarpus neriifolia* (Table. 6.3).

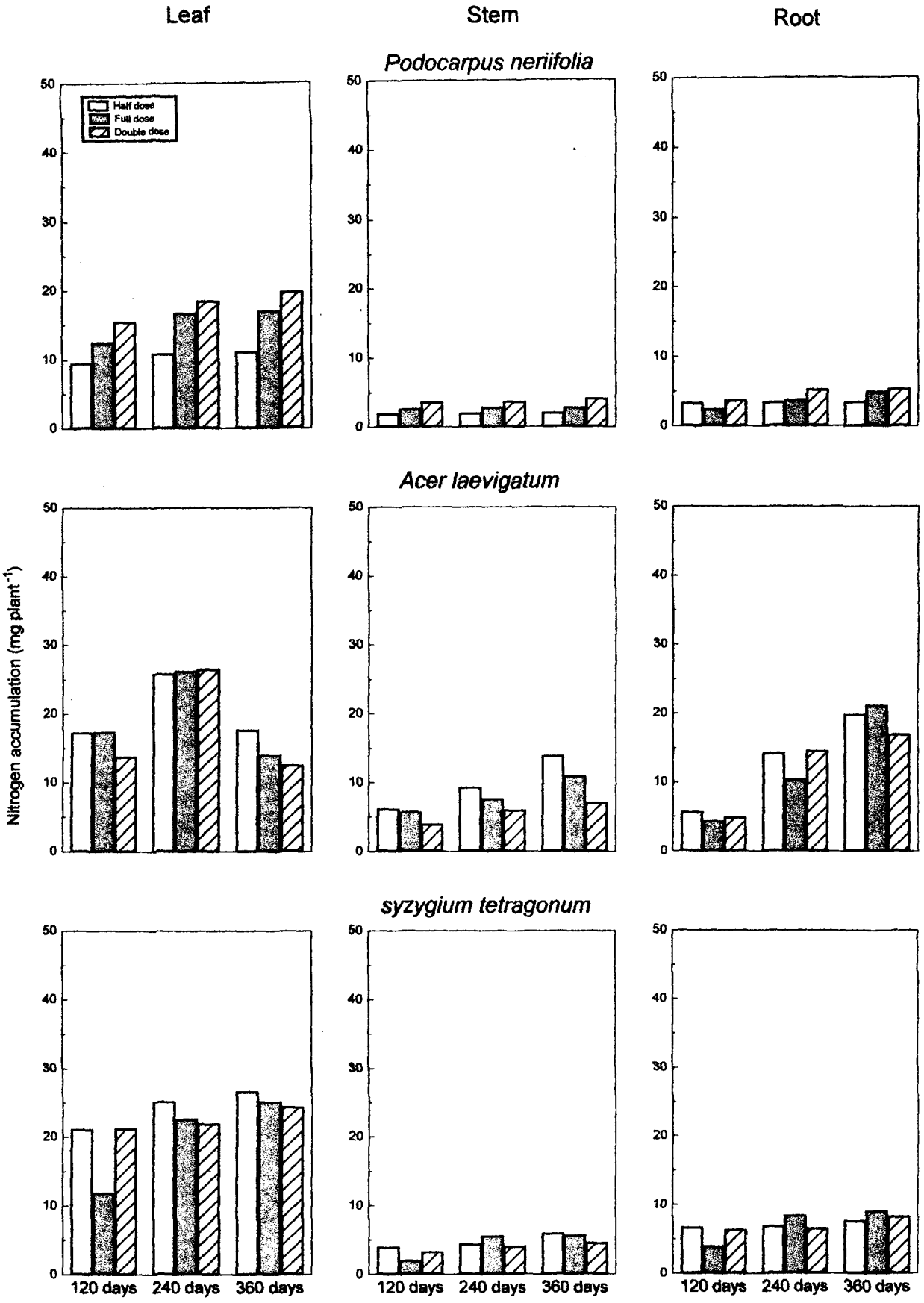


Fig. 6.34 . Nitrogen accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings at three NPK levels.

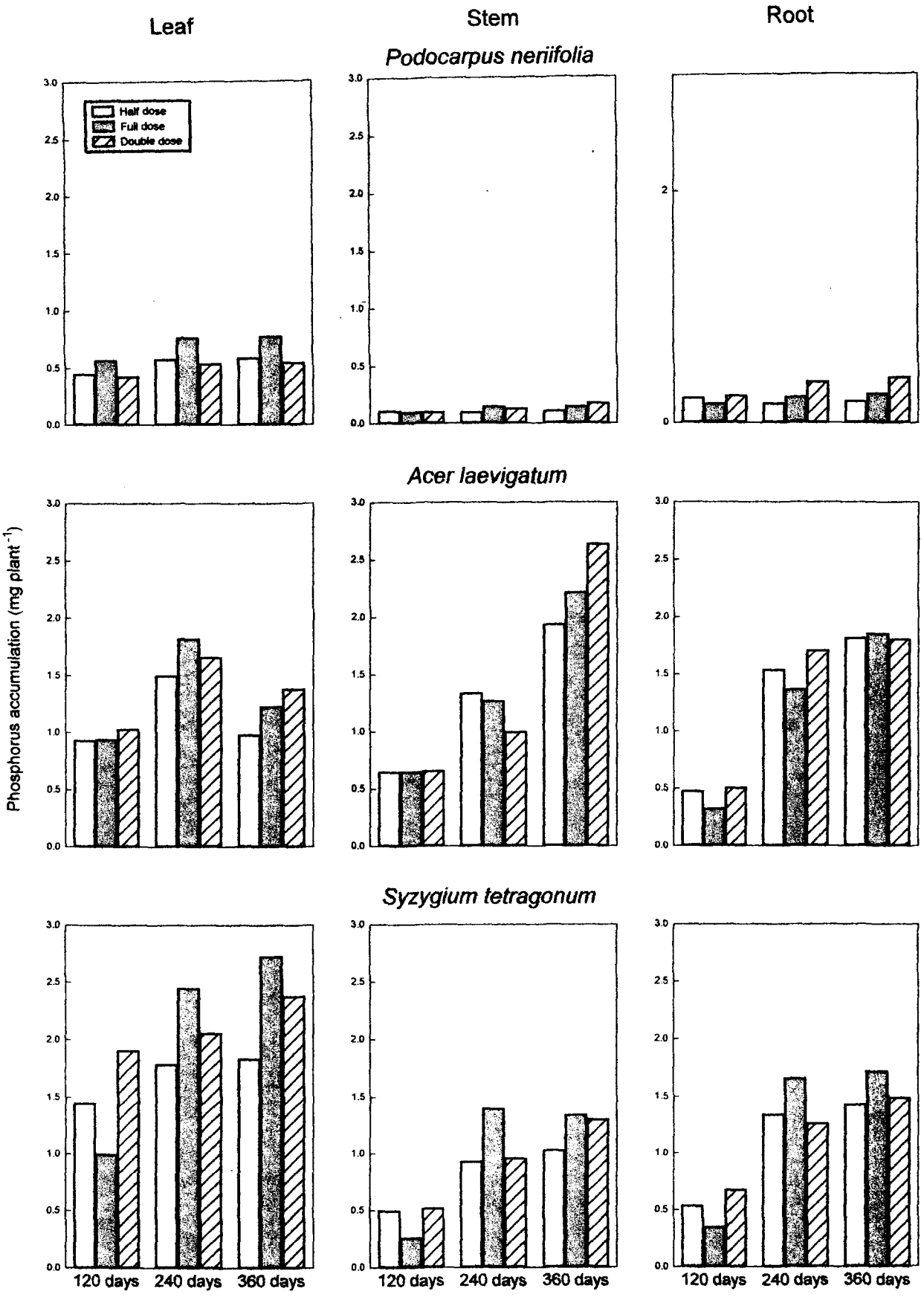


Fig. 6.35. Phosphorus accumulation in *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetragonum* seedlings at three NPK levels.

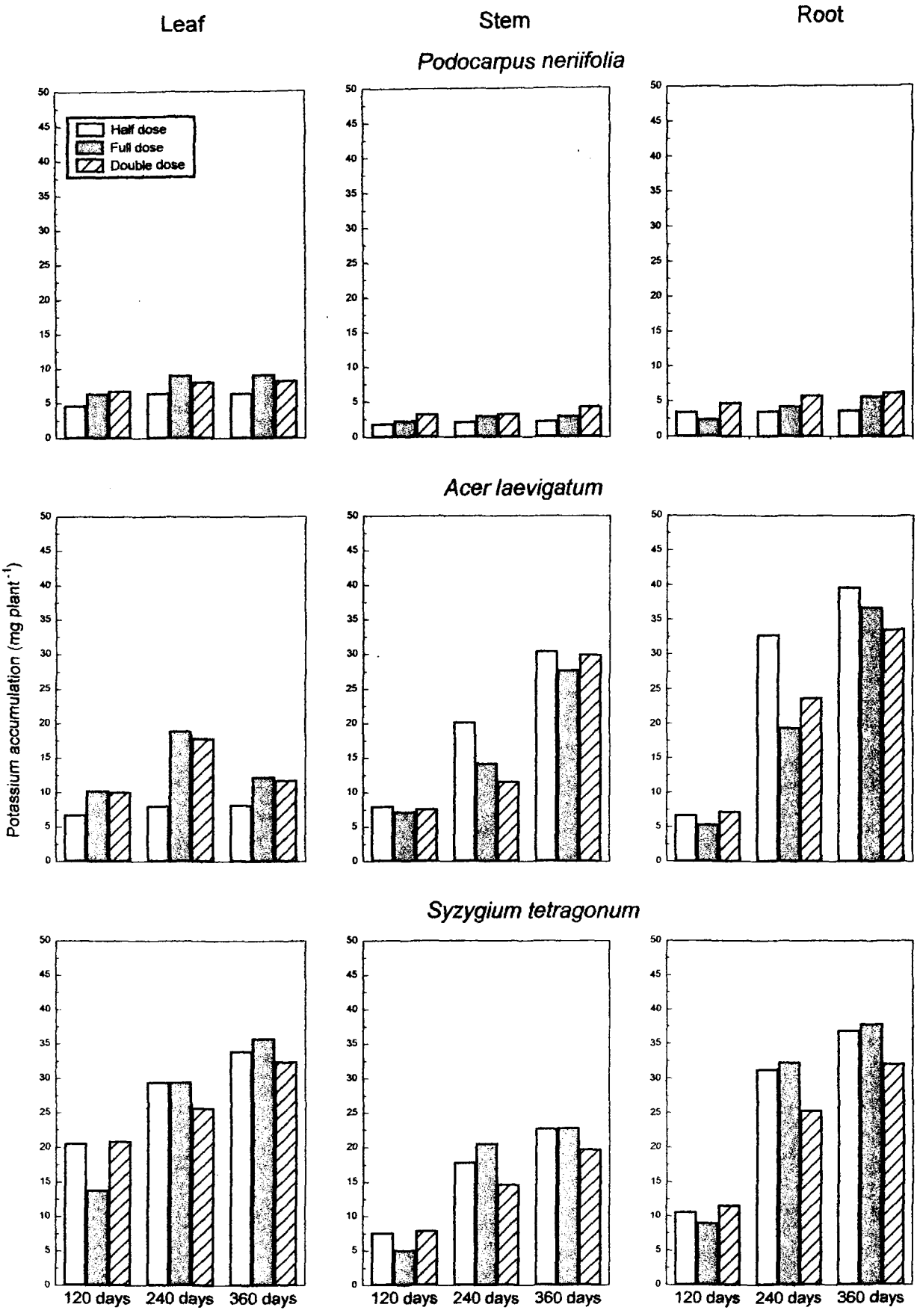


Fig. 6.36. Potassium accumulation in *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* seedlings at three NPK levels

With increase in soil NPK levels Potassium use efficiency (KUE) of *Podocarpus neriifolia* decreased, while *Syzygium tetragonum* and *Acer laevigatum* did not show any definite trend (Table. 6.3).

Table. 6.3. Nitrogen, Phosphorus and Potassium use efficiency (mg dry weight produced /mg nutrient uptake) of *Podocarpus neriifolia*, *Acer laevigatum* and *Syzygium tetragonum* at three soil NPK levels.

Nutrient use efficiency	Soil NPK levels (%)	*Podocarpus neriifolia*	*Acer laevigatum*	*Syzygium tetragonum*
Nitrogen use efficiency	Half dose	78	139	194
	Full dose	71	111	197
	Double dose	63	132	202
Phosphorus use efficiency	Half dose	1957	1420	1727
	Full dose	1869	1066	1442
	Double dose	2616	1115	1403
Potassium use efficiency	Half dose	114	120	118
	Full dose	103	107	110
	Double dose	96	114	112

Discussion

In the present study NPK concentration decreased with increase in age of the seedlings of all species. The foliage N concentration in *Acer laevigatum* (0.66 to 3.07), *Podocarpus neriifolia* (0.75 to 2.25) and *Syzygium tetragonum* (0.60 to 1.45) falls within the range (1.49-3.03%) to those reported (2.39-2.65%) by Lodhiyal and Lodhiyal (1997) in *Populus deltoides* and for Poplar plantations (1.49-3.03) raised in different parts of the world (Van Veen et al. 1981; Carlisle and Methven 1997). Hawkins et al. (1999) found that one year seedlings of *Pseudotsuga menziesii* and *Abies amabilis* had higher concentration of nutrients than second year seedlings, indicating that new growth was a stronger sink for nutrients. High N content in leaves as compared to roots and stem confirms the results reported for *Populus ciliata* (Deol and Khosla 1983) and *Acer*

oblongum (Masoodi et al. 1996). Higher allocation of nutrient to different plant parts play significant role in the growth and development of plant species. For example, higher allocation of nutrients to root and stem enables the species to survive in low soil nutrient condition, and a higher allocation of nutrient to leaf has important ecological implications especially in nutrient recycling since leaves constituted the highest proportion of the litter fall in terrestrial communities.

Higher concentration of nitrogen in the leaf during the initial leaf growth has also been reported by Santa Regina et al. (1997), who argued that during spring season, cellular growth is accompanied by high mitotic activity leading to strong demand for nutrients particularly nitrogen. During autumn demand for nutrients decreases due to low cell activity (Ryan and Bormann 1982). The older leaves are known to accumulate much less phosphate than younger leaves, and to export nitrogen, phosphorus and potassium as they age (Leopold and Kriedemann 1980).

Deciduous species have higher concentration of nitrogen, phosphorus and potassium in the leaves than evergreen species (Chapin et al. 1980). In the present study too, concentration of nitrogen, phosphorus and potassium in the deciduous *Acer laevigatum* was higher than evergreen *Podocarpus* and *Syzygium* even at their seedling stage.

Biomass allocation does not reflect qualitative trends in nutrient allocation (Abrahamson and Caswell 1982). However, it is a reasonable currency to measure the nutrient allocation pattern. Studies on nutrient allocation, which could be related directly to

nutrient limitation, is particularly valuable in the assessment of the successful adaptation of a species in the natural ecosystem (Shaver and Chapin 1980).

The nutrient use efficiency (mg dry weight produced/mg nutrient uptake) in the present case is similar to *Populus deltoides* seedlings that ranged between 159 and 175 for Nitrogen, 1405 and 1569 for Phosphorus and 295 and 332 for Potassium (Lodhiyal et al. 1995).

In the present study, there was no trend in nutrient use efficiency with the increase in NPK levels. It appears that the concentration of NPK level in soil was not high enough to cause marked variation in its availability or nutrient requirement of these species was low. Hiremath and Ewel (2002) have reported that nutrient use efficiency of the species is low at high soil fertility. High nutrient use efficiency of the plant species is an adaptive strategy to survive on sites of low soil fertility (Srivastava and Behl 2002). Elliot and White (1994) have suggested that red pine seedlings can adjust their nutrient use efficiency, particularly for N, when light and nutrient availability were limited.

Nutrient use efficiency is also influenced by irradiance. The higher NPK use efficiency in gap in all three studied species suggests that the availability of irradiance rather than major soil nutrients seems to be the limiting factor for the growth of seedlings in this environment. Thus greater nutrient use efficiency in gap appears to be the cause of higher total accumulation in plant body. Increased NUE and PUE in *Euterpa edulies* seedlings with increased irradiance have been reported by Illenseer et al. (2002). High nutrient use efficiency of the plant species could be an adaptive strategy to survive on sites of low soil fertility.

CHAPTER VII
GENERAL DISCUSSION

Seed germination

The seeds of tropical rain-forest trees show a large interspecific variation in time which they take to germinate. Out of 330 species of the Malaysian forests, 65% germinated within 20 weeks of sowing of fresh seeds in a lightly shaded nursery (Ng 1980). The 35% of the species that took longer than 20 weeks to germinate often had hard, thick seed coats or endocarps around the seed. A number of factors can cause delayed germination in tropical rain-forest tree seed (Vazquez-Yanes and Orozco-Segovia 1993). These include low water content of seed at maturity, presence of hard seeds coat, small size and early stage of development of the embryo and presence of chemical germination inhibitors.

Rapid germinators tend to have high seed water content at maturity and soft seed coats. Many such species are difficult to store. They lose viability if dried and germinate if stored at high water content (Turner 2001). This led seed physiologists to develop a classification system based on the potential of seeds to be stored. Orthodox seeds are those that can be stored in a dormant state for a relatively long period (many months), usually at relatively low seed water content. Recalcitrant seeds are the rapid germinators that cannot withstand drying. Many tropical tree species produce large, soft-coated seeds of high water content that are recalcitrant (Roberts 1973) as observed in *Podocarpus neriifolia* and *Syzygium tetragonum*.

The high germination percentage of *Acer*, *Podocarpus* and *Syzygium* seeds immediately after collection and their quick germination starting within 2 days in *Podocarpus neriifolia*, 9 days in *Syzygium tetragonum* to 10 days in *Acer laevigatum* indicate their recalcitrant nature. A rapid loss in viability of these seeds with the exception of *Acer* during storage further show that they do not have the character of orthodox seeds. Highly recalcitrant seeds found in tropical forests and wetlands tolerate very little desiccation, germinate rapidly even when additional water is not available and are usually sensitive to low temperatures (Farrant et al. 1988). *Acer laevigatum* with its dry indehiscent fruit (samara) and 5 months storability under room condition may be considered orthodox, since they generally undergo a period of desiccation prior to shedding from the tree. The recalcitrant-seeded species do not have this final maturation drying stage in their evolutionary strategy and are thus vulnerable to moisture loss (Connor and Bonner 2001).

The five months storability of *Acer laevigatum* seeds is attributed to its dry indehiscent fruit, which undergo a period of desiccation prior to shedding from the tree. The seeds lose only 2% moisture even after air drying in room temperature for one month. *Syzygium tetragonum* and *Podocarpus neriifolia* lose their viability beyond 30 days of seed fall, if temperature is not conducive for their germination during that period. The seed fall in *Syzygium tetragonum* occur during April when day temperature is around 24^0C and moisture is not limiting due to pre-monsoon showers. In case of *Podocarpus neriifolia* and *Acer laevigatum* seed dispersal

takes place during October, when temperature during day is about 26^{0}C and soil is fairly moist.

The field observation was substantiated by laboratory experiment where all the three tree species germination was high between 20^{0}C and 30^{0}C, but rate of germination was significantly high at 25^{0}C in all cases both in dark and light. This implies that 25^{0}C is the optimum temperature for germination of the seeds of these species.

Several workers (Teketay 1995; Castellani and Aquiar 2001; Finneseth et al. 1998; Meyer et al. 1989) have reported a temperature range of 20^{0}C to 30^{0}C for peak germination of seeds. Teketay (1995) reported that in *Moringa stenopetala* germination increased with increase in temperature until 25^{0}C, but gradually started declining thereafter. Germination also declined at 15^{0}C and was completely inhibited at 10^{0}C. *Chrysothamnus nauseosus* seeds germinated to full viability within 4 weeks at 20^{0}C, 25^{0}C and 30^{0}C indicating that the dormancy exhibited at lower temperatures was conditional or temperature dependant (Meyer et al. 1999). Castellani and Aguiar (2001) also concluded that germination requirement of a pioneer tree species *Trema micrantha*, was 20^{0}C to 30^{0}C.

Survivorship

Tree seedling survival in tropical moist forests have been found to be influenced by several microenvironmental factors such as soil moisture (Barik et al. 1992; Hart 1995; Rao et al. 1997), temperature (Pollock 1993; Everham 1996) and relative humidity. The survival of tree seedlings in the tropical rainforest is

generally low in the new germinants (Li et al. 1996). Survivorship appears to improve as seedlings get larger (De Stevan 1994).

The transplanted seedlings of *Acer laevigatum*, *Syzygium tetragonum* and *Podocarpus neriifolia* both in gap and forest understorey experienced higher mortality than the naturally recruited seedlings. The reason for higher mortality in the transplanted seedlings may be due to physical injury to the root system during transplanting and sudden change in environment from net house to the natural forest. Seasonal stress in soil moisture seemed to be the main cause of mortality in the natural forest. In nature desiccation has been reported as a major cause of seedling mortality in the understorey of a wide range of forest types including rain forests (Turner 1990). Besides, it has been argued that the potential causes of mortality under natural condition are various other abiotic stresses such as shade and flooding (Walters et al. 1993) and biotic influences such as herbivory, disease or root competition (Jones et al. 1994).

Higher Seedling mortality of *Acer laevigatum*, *Syzygium tetragonum* and *Podocarpus neriifolia* under forest understorey than in gap indicates that availability of light was responsible for better growth and establishment of the seedlings in the gap. Similar observation has been made by Law (2002) who has reported that under natural condition seedlings of *Acer laevigatum* and *Syzygium tetragonum* show stunted growth in shaded places of the sacred grove at Raliang and Ialong forests in Jaintia hills of Meghalaya.

Seedling growth and survival is nearly always promoted by increased light (King 1994; Coomes and Grubb 1988; van der Meer et al. 1998), except at very high levels (Zagt and Werger 1998). For example, Turner (1990) observed that

seedlings less than 1 m tall grew little under canopy shade conditions in Malaysian dipterocarp forest. Clark et al. (1993) found similar results for saplings (0.5 – 5 m tall) of nine species at La Selva, Costa Rica and Dalling et al. (1998) for eight pioneer species growing in gaps on Barro Colorado Island. The seedlings of shade-tolerant understorey species that survive well in low light conditions may show little difference in survival between gap and understorey sites. For instance, Fraver et al. (1998) found no significant difference in survival over a four-year period of seedlings of *Protium panamense* and *Desmopsis panamensis* growing in gaps and under continuous forest canopy in Panamanian rain forest.

Growth

Importance of canopy gaps in the maintenance of plant diversity and in enhancing growth and development of species have been emphasized by several workers (Ashton 1978; Whitmore 1984; Brokaw 1985; Popma and Bongers 1988 and Bazzaz 1990). Bazzaz and Pickett (1980) assigned tropical trees into two main categories such as primary species and early secondary species based on their adaptability in different gaps size. Primary species germinate under a closed canopy and remain oppressed till gaps are created for their further growth, while the early secondary species are found only in the gaps and grow better in the larger gaps (Whitmore 1984; Popma and Bongers 1988). Primary species have been observed to show higher relative growth rate under the closed canopy than the gaps (Tripathi and Khan 1990; Chandrashekaran and Ramakrishnan 1993), while saplings of pioneer species grow better on the sites having low canopy and their

survival is poor under the dense canopy (Welden et al. 1991). Studies of Khan et al. (1986) and Barik et al. (1992) revealed that the seedlings of *Quercus* sp. were recruited mainly in the small gaps and forest understorey while those of *Schima khasiana* were abundant in larger gaps and disturbed stands.

All the species in the present study showed better growth in gap with higher mean leaf area, LMA, RGR, root and shoot length and greater dry mass accumulation than those growing in the understorey. The higher relative growth rate in gap than the forest understorey in all the present studied species is similar to those reported by Osunkoya et al. (1994), Veneklass and Poorter (1998) and Kitajima (1994). Boot (1996) grew seedlings of Guyanan tree species in understorey and gap-edge and gap-centre and concluded that most species did not show much improvement in growth rate between the gap-edge and gap-centre sites. The allocation component of RGR, leaf area ratio (LAR) declines with increasing light (Thompson et al. 1992; Osunkoya et al. 1994; Veneklass and Poorter 1998), but net assimilation rate (NAR) increases more rapidly with light to achieve increase in RGR.

The seedlings of all species had low root and high shoot dry weight. The higher biomass allocation to the shoot implies that these species are better competitors along light gradient and their growth increase as light condition improves under the canopy in the forest (Law 2002). A comparison of growth between forest understorey, gap and the net house, where light intensities were 2%, 31% and 82% respectively revealed that the growth of the seedlings in the net

house was much better than that of the forest understorey and gap where they have to face other abiotic and biotic stresses of their environment.

Plants experiencing drought during vegetative growth tend to develop smaller, often fewer leaves well before photosynthetic rates are markedly affected and the rate of leaf area growth decreases progressively with increasing drought (Muchow 1985; Zelitch 1982). Stress during the vegetative stage reduces leaf area index (LAI) thereby decreasing light interception (Kramer 1983) so that there is a fall in the efficiency of production per unit incident radiation. The seedlings of all three species in the present experiment had lower allocation of dry mass to root. The decrease in R/S ratio with increase in soil moisture level indicates that allocation to the root increases as soil moisture decreases. However greater accumulation of dry mass to the shoot in the present study indicates that the range of soil moisture levels maintained was not stressful for the seedlings. Besides conserving water, plants in dry areas commonly develop deep root systems that make use of water stored in the subsoil between rainfall events. Greater allocation to root development comes at the cost of reduced allocation to leaves and/ or stems (Coomes & Grubb 2000).

The seedlings did not respond to nutrient application. This indicates that even the highest NPK levels (Nitrogen as urea 120 kg/ha, phosphorus as single superphosphate 60 kg/ha and potassium as muriate of potash 80 kg/ha) was not high enough for the seedlings to show significant response. Similar observation has been reported by Koul et al. (1995) where height and collar diameter of

Bauhinia variegata seedlings did not increase at 90 kg N ha^{-1} and 80 kg P_2O_5 ha^{-1}. Joshi (1980) recorded biomass decrease in *Azadirachta indica*, *Albizia amora*, *Acacia planifrons*, *Acacia lenticularis*, *Hardwickia binata* and *Tamarindus indicus* due to nutrient application suggesting that these species can grow on marginal to poor fertility levels under dry conditions.

Relative growth rate (RGR) serves as a fundamental measure of dry-matter production and can be used to compare the performance of a species or the effects of treatments under strictly defined conditions. However, RGR tells us little about the causal factors, which determine that performance (Beadle 1985). *Syzygium* registered higher RGR with increase in soil moisture but in *Acer* and *Podocarpus* there was no specific pattern. The RGR was almost uniform in all the species under different nutrient concentrations. The higher RGR with increase in soil moisture level in *Syzygium tetragonum* suggest that the species requires higher soil moisture for better growth. The higher RGR in *Syzygium, Podocarpus and Acer* in the gap suggests the important role that light plays in growth of these seedlings. Popma and Bongers (1988) proposed that RGR in the understorey is the best measure of shade tolerance of species.

LMA was also high in gap in all three species. LMA is consistently high in the light demanding canopy tree species as compared to that of the shade-tolerant and canopy tree species. The average LMA in different forest types varies considerably between sites. A more direct study of leaf form on mountain Gunung Silam in Borneo has shown a trend of increasing LMA with altitude (Bruijnzeel et

al. 1993). The LMA observed in the seedlings treated with different NPK levels contradicts the finding of Medina et al. (1990) who reported increases along a soil fertility gradient

The role of microenvironmental variables in determining growth and development of plant species is well documented. Formation of canopy gaps is of particular importance in natural undisturbed forest for the maintenance of diversity of species, which requires high light intensity at least at early stage of their life cycle. Thus the species such as *Acer laevigatum*, *Podocarpus neriifolia* and *Syzygium tetragonum* could be treated as important gap colonizers.

Nutrient allocation, accumulation and use efficiency

The allocation pattern of energy, materials and nutrients to different organs determine fitness and success of plant in diverse environmental conditions (Harper and Ogden 1970; Abrahamson and Gadgil 1973).

High concentration of nutrients in the younger seedlings (120 days old) in all species than the older seedlings (360-months old) could be attributed to the decrease in nutrient concentration and proportional increase in biomass. The concentration of NPK was higher in the leaf of all the species and it decreased with age in all of them. NPK concentration was more in *Acer laevigatum* as compared to that of *Syzygium tetragonum and Podocarpus neriifolia*. This may be attributed to its deciduous nature. Chapin et al. (1980) have reported that concentration of nitrogen, phosphorus and potassium in the leaves of deciduous species is higher than evergreen species.

Increased nitrogen content in plant tissues following addition of nitrogen to nitrogen-poor sites has been documented by a number of studies (Haag 1974; Nygaard and Odegaard 1993; Bowman 1994). However, Shaver and Chapin (1986) found that only a minor part of the nitrogen that was added to soil was included in new biomass. In the present study addition of NPK fertilizer did not have any significant effect on seedling growth. Study on the measurement of nitrogen contents in shoots of *Betula nana* (Paal 1997) showed that comparatively low dosed of nitrogen does not increase the concentration in current-year shoots significantly. Karlsson (1987) demonstrated that leaf nitrogen concentration differs between species growing on soils with equal concentrations of total nitrogen, suggesting an individualistic response of species to fertilization. Parsons (1994) found that N, P, K, fertilization influenced the shoot architecture of *Empetrum nigrum* ssp. *Hermaphroditum*, which produced more branches per meristem, longer stems and greater leaf mass.

All species accumulated more NPK with increase in age under all the treatments. This was due to progressive increment in dry mass with age. Lodhiyal et al. (1995) have also reported that the standing state of nutrients in the vegetation increase with plantation age because of an increase in dry mass accumulation.

The nutrient use efficiency (mg dry weight produced/mg nutrient uptake) in the present case is similar to *Populus deltoides* seedlings that ranged between 159-175 for Nitrogen, 1405-1569 for Phosphorus and 295-332 for Potassium (Lodhiyal et al. 1995).

The nutrient use efficiency of the studied species decreased with the increase in fertilizer application. Hiremath and Ewel (2002) reported that at high soil fertility level, nutrient use efficiency was low. The low nutrient use efficiency in species with the increase in fertility indicates that other factors might be influencing the efficiency of the species. High nutrient use efficiency of the plant species has been recognized as an adaptive strategy to survive on sites of low soil fertility (Srivastava and Behl 2002). Elliot and White (1994) have suggested that red pine seedlings can adjust their nutrient use efficiency, particularly for N, when light and nutrient availability were limited. In the present study NPK use efficiency was generally more in gap, but was not affected by addition of fertilizer in soil. These results suggest that N, P and K availability may not be influencing growth of seedlings in the understorey environment.

Shaver and Chapin (1986) concluded that although shoot growth response to fertilization may be useful indicator of nutrient limitation, it is not a good quantitative predictor of the whole-plant response. Results of Paal et al. (1997), on response of *Betula nana* to nitrogen fertilization also indicate that plant response to fertilization is hard to describe, as the responses of additional nitrogen per se may be masked by response to other environmental parameters.

CHAPTER VIII
SUMMARY

The present work was undertaken to study the seed and seedling ecology of three important tree species viz. *Podocarpus neriifolia, Acer laevigatum* and *Syzygium tetragonum* of subtropical semi-evergreen forest of northeast India with particular emphasis on the effect of light and temperature on seed germination, role of light and soil water and nutrient levels on seedling growth and nutrients concentration, accumulation and their use efficiency.

The field study was carried out in two sacred groves (viz. Urkhla and Khloo Langdoh located at Jowai town (latitude 25^0 26' 32" N, longitude 92^0 12'E, altitude 1200-1300 m asl), representing subtropical semi-evergreen broad-leaved forest and in the net-house of the Department of Botany, North Eastern Hill University, Shillong (latitude 25^0 34' N, longitude 91^0 45' E, altitude 1450 m asl). Seeds of *Podocarpus neriifolia* and *Acer laevigatum* were collected from Urkhla sacred grove while that of *Syzygium tetragonum* from Khloo Langdoh. However, field experiments were conducted at Khloo Langdoh because Urkhla is surrounded by human habitation and much disturbed.

I. Seed germination

After 30 days of air drying, the seeds of *Podocarpus neriifolia* and *Syzygium tetragonum* lost 28% and 50% moisture respectively. *Acer laevigatum* lost only 2% moisture.

The germination percentages of *Acer, Podocarpus* and *Syzygium* seeds immediately after collection were 85%, 82% and 92% respectively. The time taken for initiation of germination was 2 days in *Podocarpus neriifolia*, 9 days in *Syzygium tetragonum* and 10 days in *Acer laevigatum*. Germination was completed by 21, 20 and 24 days in *Podocarpus neriifolia, Syzygium tetragonum* and *Acer laevigatum* respectively.

Germination percentage decreased with increase in storage time. In *Acer* it decreased from 74% at 30 days to 9 % at 150 days whereas in *Syzygium* the seeds became non-viable after 60 days of storage and in *Podocarpus neriifolia* seeds did not germinate beyond 30 days of storage.

Germination rate was high at 25^0C both in light and dark in all the three species. The germination of *Acer laevigatum* seeds in dark at 20^0, 25^0 and 30^0C was 82, 86 and 78% respectively. The corresponding values under light condition were 76, 84 and 75%. Similarly, *Podocarpus* and *Syzygium* seeds showed higher germination at 25^0C both in light and dark.

II. Effect of gap and understorey

Seedlings Survival

Survival of transplanted seedlings of all three species was poor in the understorey than in the gap. At the end of 360 days there was 67% mortality in *Acer laevigatum*, 58% in *Syzygium tetragonum* and only 37% in *Podocarpus neriifolia* in the understorey. In gap, *Acer laevigatum* (58%) and *Syzygium tetragonum* (50%) seedlings experienced higher mortality than *Podocarpus neriifolia* (16%) after 360 days.

Seedling growth

Root and shoot growth of the three species was significantly ($P<0.001$) higher in gap than the forest understorey.

Mean leaf area and leaf biomass per unit area (LMA; mg/cm^2) was significantly ($P<0.01$) higher in gap than forest understorey condition in all the species. In gap the LMA was 18.4 mg/cm^2 in *Acer laevigatum* followed by *Syzygium tetragonum* (5.4 mg/cm^2) and *Podocarpus neriifolia* (5.1 mg/cm^2). The corresponding values in forest understorey were 14.3, 3.0 and 3.6 mg/cm^2.

At the end of 360 days seedlings in gap had a dry mass of 2838 mg/plant in *Syzygium tetragonum*, 952 mg/plant in *Podocarpus neriifolia* and 516 mg/plant in *Acer laevigatum* seedlings. The corresponding values in the understorey were 97, 160 and 124 mg/plant.

In all three species root: shoot ratio was higher in gap than the understorey.

Syzygium tetragonum, *Acer laevigatum* and *Podocarpus neriifolia* seedlings showed 5.5, 4.5 and 2.8 times, respectively, higher relative growth rate (RGR; mg day^{-1} plant^{-1}) in gap than in the forest understorey during the first four month of growth. Thereafter the seedlings did not exhibit significant difference in RGR.

Nutrient concentration, accumulation and use efficiency

Nitrogen concentration in *Podocarpus neriifolia* and *Syzygium tetragonum* seedlings was higher in the forest understorey while *Acer laevigatum* recorded higher N concentration in gap. N concentration was higher in leaf followed by root and stem. It

decreased significantly ($p < 0.05$) with the increase in age of the seedlings of all three species.

Phosphorus concentration was higher in leaf followed by stem and root in all three species. Seedlings under forest understorey had significantly ($P<0.01$) higher P concentration than those in the gap. The concentration decreased with age of the seedlings in both gap and understorey.

The leaf had higher K concentration followed by stem and root in all three species both in gap and forest understorey. With age concentration decreased in *Syzygium* both in gap and forest understorey while in *Podocarpus* and *Acer* there was no significant difference due to age and forest habitats.

N accumulation (mg plant^{-1}) in all plant parts was significantly ($p<0.01$) higher in gap than the forest understorey. Leaf accumulated maximum N followed by root and stem at both the places and it increased with age of the seedlings.

P and K accumulation was high in gap than the forest understorey in all species. The seedlings of all the three species under gap were more efficient in NPK use.

III. Effect of soil moisture level

Seedling growth

Significant progressive growth in shoot and root length with increasing soil moisture was observed only in *Syzygium tetragonum*.

The mean leaf area of *Syzygium tetragonum* increased significantly with the increase in soil moisture. However, LMA decreased in *Acer laevigatum* and increased in *Syzygium tetragonum*. *Podocarpus neriifolia* did not show a definite trend.

The dry mass of *Syzygium tetragonum* seedlings increased with increase in soil moisture level. In all species shoot dry mass was higher than root at all soil moisture levels.

The effect of soil moisture levels on root: shoot ratio was prominent only at the end of the experiment (360 days). It gradually decreased with increasing moisture level in all the species.

In all species maximum value of RGR was recorded at 120 days, thereafter it gradually declined. *Syzygium tetragonum* exhibited a marked increase in RGR (115 mg day^{-1} $plant^{-1}$) with the increase in soil moisture levels during the first four months of growth. As compared to this, the peak values of *Acer laevigatum* (106 mg day^{-1} $plant^{-1}$) and *Podocarpus neriifolia* (98 mg day^{-1} $plant^{-1}$) were low.

Nutrient concentration, accumulation and use efficiency

In all species, N concentration was more in leaf followed by root and stem, and different soil moisture levels had no significant effect on it. The concentration in different parts decreased significantly ($p< 0.05$) from 120 days to 360 days old seedlings.

The pattern of Phosphorus concentration was similar to that of N with higher value in leaf followed by stem and root in *Acer laevigatum* and *Syzygium tetragonum*. *Podocarpus neriifolia* seedlings had high concentration in leaf followed by root and stem. Soil moisture levels did not have significant effect on P concentration in different plant parts of all species. It decreased significantly ($p< 0.05$) from 120 to 360 days.

N accumulation was more in leaf followed by root and stem at all soil moisture levels in all the species. With the increase in age, there was an increase in N accumulation

except in the leaf of *Acer laevigatum*, where accumulation decreased in 360 days old seedlings at 30% soil moisture level. However, in *Syzygium tetragonum* N accumulation in all parts increased significantly ($p< 0.01$) with increase in soil moisture level.

P accumulation in *Syzygium tetragonum* increased with increasing soil moisture. It increased in all plant parts with age, except in *Acer laevigatum* that showed a decrease in the leaf at 360 days.

K accumulation did not vary between different plant parts in all three species. It increased with age in all plant parts, except in *Acer laevigatum* which showed a decrease in the leaf at 360 days.

Nitrogen use efficiency (NUE) and Potassium use efficiency (KUE) increased with increasing soil moisture level in *Podocarpus neriifolia and Syzygium tetragonum.*

Phosphorus use efficiency (PUE) decreased with increasing moisture level in *Acer laevigatum* and *Syzygium tetragonum.*

IV. Effect of soil NPK level

Seedling growth

Soil NPK levels did not have any significant effect on the growth of all three species.

Acer laevigatum, *Podocarpus neriifolia* and *Syzygium tetragonum* seedlings did not exhibit any significant variation in mean leaf area and LMA under different levels of NPK. Similarly there was no significant effect of NPK doses on dry mass accumulation of all the three species.

The effect of NPK levels on root: shoot ratio was distinct only at the end of the experiment. With the increase in NPK doses R:S ratio increased in *Podocarpus neriifolia* and decreased in *Acer laevigatum* while *Syzygium tetragonum* did not show any trend with almost the same value at different NPK levels.

RGR attained peak during the first four month of growth in all cases. The values were 106 mg day^{-1} $plant^{-1}$ in *Syzygium tetragonum*, 101 mg day^{-1} $plant^{-1}$ in *Acer laevigatum* and 81 mg day^{-1} $plant^{-1}$ in *Podocarpus neriifolia*.

Nutrient concentration, accumulation and use efficiency

N concentration in different species and plant parts did not vary significantly at different soil NPK levels. However, it decreased with age in all cases. Leaf had higher N and P concentration in all species at all three NPK levels. It had no effect on K concentration.

Nitrogen accumulation was more in leaf followed by root and stem of all the species at all soil NPK levels. With the increase in age, there was an increase in N accumulation except in *Acer laevigatum* leaf where it decreased at 360 days.

There was no significantly difference in P accumulation with the increase in soil NPK levels in different plant parts of all three species.

K accumulation in *Podocarpus neriifolia* was more in leaf followed by root and stem at all soil NPK levels.

Nitrogen use efficiency increased with increasing soil NPK level in *Podocarpus neriifolia and Syzygium tetragonum*.

Phosphorus use efficiency decreased in *Syzygium tetragonum* and potassium use efficiency decreased in *Podocarpus neriifolia* with increasing soil NPK levels.

REFERENCES

Abrahamson, W.G. 1975. Reproductive strategies in dew berries. *Ecology* 56: 721-726.

Abrahamson, W.G. and Caswell, H. 1982. On the comparative allocation of biomass, energy, and nutrients in plants. *Ecology* 63: 982-991.

Abrahamson, W.G. and Gadgil, M. 1973. Growth form and reproductive effort in golden rods (Solidago, Compositae). *American Naturalist* 107:651-661.

Abrahamson, W.G. and Gadgil, M. 1982. On the comparative allocation of biomass, energy and nutrients in plants. *Ecology* 63(4): 982-991.

Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology* 7: 227-238.

Ackerly, D.D. and Bazzaz, F.A. 1995. Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* 101: 289-298.

Adams, M.B. and Allan, H.L. 1985. Nutrient proportion in foliage of semi mature loblolly pine. *Plant Science* 86: 27-34.

Agren, J. 1988. Sexual differences in biomass and nutrient allocation in dioecious *Rubus chamaemorus*. *Ecology* 69(4): 962-973.

Ahmad, A. 1993. Geological mapping, Meghalaya. An overview. In, "Records of geological survey of India," vol. 126 part 4, pp. 19. Govt. of India.

Allen, S.E. Grimshaw, H.M. Parkinson, J.A. and Quarmby, C. 1974. *Analysis of Ecological Materials*. Blackwell Scientific publications Oxford.

Anderson, J.M. and Ingram, J.S.I. 1993. *Tropical Soil Biology and Fertility – A Handbook of Methods*, 2nd edn., C.A.B. International, Wallingford, UK.

Aphalo, P.J. and Lehto, T. 1997. Effects of light quality on growth and N accumulation in birch seedlings. *Tree Physiology* 17: 125-132.

Armstrong, D.P. and Westoby, M. 1993. Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology* 74: 1092-1100.

Ashton, M.S.1995. Seedling growth of co-occurring *Shorea* species in the simulated light environments of rain forest. *Forest Ecology and Management* 72: 1-12

Ashton, P.M.S. 1990. Methods for the evaluation of advanced regeneration in forest types of south and Southeast Asia. *Forest Ecology and Management* 36: 163-176.

Ashton, P.M.S. and Berlyn, G.P. 1992. Leaf adaptations of some *Shorea* to sun and shade. *New Phytologist* 121: 587-596.

Ashton, P.S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of Linnaean Society London* 1: 155–96.

Ashton, P.S. 1969. Speciationamong tropical forest trees: some deduction in the light of recent evidence. *Biological journal of Linnaen Society London* 1: 155-196.

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

Baker, H,G, 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997-1010.

Balakrshnan, N.P. 1981-83. *Flora of Jowai and vicinity, Meghalaya* 2 vols. BSI, Howrah.

Bargali, K. and Singh, S.P. 1995. Competitive abilities of seedlings of early and late successional tree species of Central Himalaya grown along a light gradient. *Tropical Ecology* 36(2): 237-247.

Barik, S.K., Pandey, H.N., Tripathi, R.S. and Rao, P. 1992. Microenvironmental variability and Species diversity in treefall gaps in a sub-tropical broad-leaved forest. *Vegetatio* 103: 31-40.

Barik, S.K., Tripathi, R.S., Pandey, H.N. and Rao, P. 1996. Tree regeneration in subtropical humid forest: effect of cultural disturbance on seed production, dispersal and germination. *Journal of Applied Ecology* 33: 1551-1560.

Barker, M.G., Press, M.C. and Brown, N.D. 1997. Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for niche partitioning? *Oecologia* 112: 453-463.

Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology and Systematics* 21: 167-196.

Bazzaz, F.A. and Pickett, S.T.A. 1980. Physiological ecology of tropical succession: A comparative review. *Annu. Rev. Ecol. Syst.* 11: 287-310.

Beadle, C.L. 1985. Plant growth analysis. In. *Techniques in Bioproductivity and Photosynthesis* p. 21 (Eds. J. Coombs, D.O. Hall, S.P. Long and J.M.O. Scurlock). Pergamon Press, Oxford.

Benitez-Malvido, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* 12: 380-389.

Berjak, P. and Pammenter, N.W. 1997. Progress in the understanding and manipulation of desiccation-sensitive (recalcitrant) seeds. In: *Ellis, R.H., Black, M., Murdoch, A.J., and Hong, T.D. (eds.) Basic and applied aspects of seed biology.* Kluwer Academic, London. pp. 689-703.

Berkowitz, A.R., Canham, C.D. and Kelly, V.R. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. *Ecology* 76(4): 1156-1168.

Bewley, J.D. and Black, M. 1985. *Seeds, Physiology of Development and Germination.* Plenum Press, New York and London.

Bewley, J.D. and Black, M. 1994. *Seeds: Physiology of Development and Germination.* 2nd edn. Plenum Press, New York.

Bjorkman, O. 1981. Responses to different quantum flux densities. *Encyclopedia of Plant Physiology,* Vol. 12A. *Responses to the Physical Environment* (eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler). pp. 57-107. Springler Verlag, Berlin.

Boerner, R.E.J. 1984. Nutrient fluxes in litterfall and decomposition in four forests along a gradient of soil fertility in Southern Ohio. *Canadian Journal of Forest Research* 14: 794-802.

Boerner, R.E.J. 1985. Seasonal nutrient dynamics and relative growth rates of Hamamelis virginiana in three different microhabitats. *Canadian Journal of Botany* 63: 1476-1481.

Bonfil, C. 1998. The effect of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *American Journal of Botany* 85: 79-87.

Bongers, F. and Popma, J. 1990. Leaf dynamics of seedlings of rain forest species in relation to canopy gaps. *Oecologia* 82: 122-127.

Bonner, F.T. 1973. Storing red oak acorns. *Tree Planters' Notes* 24: 21-13.

Bonner, F.T. 1990. Storage of seeds: potential and limitations for germplasm conservation. *Forest Ecology and Management* 35: 35-43.

Bonner, F.T. and Vozzo, J.A. 1987. Seed biology and technology of *Quercus.* USDA For. Serv. Tech. Rep. 50-66.

Boot, R.G.A. 1996. The significance of seedling size and growth rate of tropical rain forest tree seedlings for regeneration in canopy openings. Pp. 267-283 in *The ecology of tropical forest tree seedlings* (ed. M.D. Swaine).UNESCO, Paris.

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

Botkin, D.B. 1993. *Forest Dynamics: an ecological model.* Oxford university Press, Oxford.

Bowman, W.D. 1994. Accumulation and use of nitrogen and phosphorus following fertilization in two alpine tundra communities. *Oikos* 70: 261-270.

Bradford, J.K. Dahal, P. and Ni, B.R. 1992. Quantitative model describing germination responses to temperature, water potential and growth regulators. *Fourth International Workshop on Seeds. Basic and Applied Aspects of Seed Biology* 1: 239-248.

Bradford, K.J., Tarquis, A.M. and Duran, J.M. 1993. A population based threshold model describing the relationship between germination rates and seed deterioration. *Journal of Experimental Botany* 44: 1225-1234.

Brewster, J.L., Bhat, K.K.S. and Nye, P.H. 1975. The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics- II. The growth and uptake of anions in solutions of constant phosphate concentration. *Plant and Soil* 42: 171-195.

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

Bruijnzeel, L.A. 1991. Hydrological impacts of tropical forest conversion. *Nature and Resources* 27(2): 36-46.

Bruijnzeel, L.A., Waterloo, M.J., Proctor, J., Kuiters, A.T., and Kotterink, B. 1993. Hydrological observations in montane rain forests on Gunung Silam, Sabah, Malaysia, with special reference to the Massenerhebung effect. *Journal of Ecology* 81:145-167.

Brunig, C.F. 1983. *Tropical Rain Forest Ecosystems: Structure and Function*, Elsevier Scientific Publishing Company, pp. 49-75.

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

Burslem, D.F.R.P. 1996. Different responses to nutrients, shade and drought among tree seedlings of lowland tropical forest in Singapore. In: *Swaine, M.D. (ed.) The ecology of tropical forest tree seedlings*. UNESCO. Paris, France. pp. 211-244

Burslem, D.F.R.P., Grubb. P.J. and Turner, I.M. 1995. Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *Journal of Ecology* 83: 113-122.

Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V. and Schnurr, J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Canadian Journal of Forest Research* 26: 1521-1530.

Cardoso, V.J.M. 1999. Thermal-dependence of the germination of *Catharantus roseus* seeds. *Revista Brasileira de Fisiologia Vegetal* 11: 41-49.

Carlisle, A., Methven, J.R. 1979. The environmental consequences of intensive forestry and removal of whole tree. *Proceedings of an International Workshop: Biological and sociological basis for a national use of forest resources for energy and organisms*. Michigan State University, USA. 108-120.

Castellani, E.D. and Aguiar, I.B. 2001. Seed maturation and effect of temperature regime on *Trema micrantha* (L.) Blume seed germination. *Seed Science and Technology* 29: 73-82.

Chabolt, B.F. and Hicks, D. 1982. The ecology of leaf life spans. *Annual review of Ecology and Systematics* 13: 229-259.

Champion, H.C. and Seth, S.K. 1968. *A Revised Survey of the Forest Types of India*. Government of India Publications, Delhi.

Chandran, M.D.S. and Gadgil, M. 1998. Sacred groves and sacred trees of Uttara Kannada. *In: Saraswati, B. (ed.) Life Style and Ecology*, Indira Gandhi National Centre for the Arts, New Delhi. pp. 85-138.

Chandrashekara, U.M. and Ramakrishnan, P.S. 1993. Gap-phase regeneration of tree species of differing successional status in humid tropical forest of Kerala, India. *Journal of Biosciences* 18: 279-290.

Chapin III, F.S. 1980. The Mineral Nutrition of wild Plants. *Annual Review of Ecological Systems* 11: 233-260.

Chapin III, F.S. 1991. Integrated responses of plants to stress. *Bioscience* 41: 29-36.

Chazdon, R.L., Pearcey, R.W., Lee, D.W. and Fetcher, N. 1996. Photosynthetic responses of tropical forest plants to contrasting light environment. In: Mulkey SS, Chazdon RL and Smith AP (eds), *Tropical Forest plant Ecophysiology*. Chapman & Hall, New York, USA. Pp. 5-55.

Chhetri, D.R., Rai, A.S., and Bhattacharjee, A. 1993. Chemical manipulation of seeds longevity of 4 crop species in an unfavourable storage environment. *Seed Science and Technology* 21: 31-44.

Christie, E. K. and Moorby, J. 1975. Physiological responses of semi-arid grasses I. The influence of phosphorus supply on growth and phosphorus absorption. *Australian Journal of Agricultural Research* 26: 423-436.

Clark, D.B., Clark, D.A. and Rich, P.M. 1993. Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. *Biotropica* 25: 397-407.

Cody, M.L . 1966. A general theory of clutch size. *Evolution* 20: 174-184.

Coin, L., Vaissiere, M., Noirot, A., Charrier, A. and Hamon, S. 1995. Comparative effects of natural and accelerated ageing on barley seeds (*Hordeum vulgare* L.). *Seed Science and Technology* 23: 673-688.

Conell, J.H. 1989. Some processes affecting the species composition in forest gaps. *Ecology*. 70:548-550.

Conell, J.H., Lowman, M.D. and Noble, I.R. 1997. Subcanopy gaps in temperate and tropical forests. *Australian Journal of Ecology* 22: 163-168.

Connor, K.F. and Bonner, F.T. 2001. The effects of desiccation on seeds of *Acer saccharinum* and *Aesculus pavia*: recalcitrance in temperate tree seeds. *Trees* 15:131-136.

Coomes, D.A and Grubb, P.J. 1998. Responses of juvenile trees to above and below ground competition in nutrient starved Amazonian rain forest. *Ecology* 79(3): 768-782.

Coomes, D.A. and Grubb, P.J. 1998. A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Functional Ecology* 12: 426-435.

Coomes, D.A. and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* 70: 171-119.

Coomes, D.A. and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* 70: 171-207.

Corlett, R.T. 1993. Reproductive phenology of Hongkong shrub land. *Journal of Ecology* 9: 501-510.

Cornilissen, J.H.C,, Castro-Diez, P, and Carnelli, A.L. 1998. Variation in relative growth rate among woody species. In: Lambers H, Poorter H, Van Vuuren MMI (eds.), *Inherent Variation in Plant Growth, Physiological, Mechanisms and Ecological Consequences*. Bakhuys Publishers, Leiden, The Netherlands. Pp 363-392.

Dale, M.P. and Causton, D.R. 1992. The ecophysiology of *Veronica chamaedrys, V. Montana* and *V. officinalis*. IV. Effects of shading on nutrient allocations – a field experiment. *Journal of Ecology* 80: 517-526.

Dalling, J.W., Hubell, S.B. and Silvera, K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* 86: 674-689.

Davidson, R.L. 1969. Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. *Ann. Bot. London* 33: 571-577.

Davies, S.J. 1998. Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to history. *Ecology* 79: 2292-2308.

De Stevens, D. 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72: 1076-1088.

De Stevens, D. 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. *Ecology* 72:1066-1075.

De Villiers, A.J., Van Rooyen, M.W., Theron, G.K. and Van de Vanter, H.A. 1994. Germination of three Namaqualand pioneer species as influences by salinity, temperature and light. *Seed Science and Technology* 22: 427-433.

De Villiers, A.J., Van Rooyen, M.W., Theron, G.K. and Van De Venter, H.A. 1994. Germination of three namaqualand pioneer species, as influenced by salinity, temperature and light. *Seed Science and Technology* 22: 427-433.

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

Denslow, J.S. 1987. Tropical treefall gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18: 432-451.

Deol,G.S. and Khosla, P.K. 1983. Provenance related growth response of *Populua ciliata* Wall. Ex Royle to 'N' fertilization. *Indian Forester* 109(1): 30-40.

Dodd, I.C., Sukle, R. and Davies, W.J. 1996. Chemical regulation of gas exchange and growth of plants in drying soil in the field. *Journal of Experimental Botany* 47: 1475-1490.

Ducrey, M. 1992. Variation in leaf morphology and branching pattern of some tropical rain forest species from Guadeloupe (French West Indies) under semi-controlled light onditions. *Annales des Sciences Forestieres* 49: 553-570.

Dunlap, J.R. and Barnett, J.P. 1982. Influence of seed size on germination and early development of loblolly pine (*Pinus taeda*L.) germinants. *Canadian Journal of Forest Research* 13: 40-44.

El-Ghonemy, A.A., Wallace, A. and Romney, E.M. 1978. Nutrient concentrations in the natural vegetation of the Mojave Desert. *Soil Science* 126: 219-229.

Elliot, K.J. and White, S.A. 1994. Effects of light, nitrogen and phosphorus on Red pine seedling growth and nutrient use efficiency. *Forest Sccience* 40: 47-58.

Everham III, Edwin, M., Randall, W.M. and Eric Van De Genachte. 1996. Effects of light, moisture, temperature and litter on the regeneration of five species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany* 83(8): 1063-1068.

Farrant, J.M., Berjak, P. and Pammenter, N.W. 1985. The effect of drying rate on viability retention of recalcitrant propagules of *Avicennia maria*. *South African Journal of Botany* 51: 432-438.

Farrant, J.M., Pammenter, N.W. and Berjak, P.1988. Recalcitrance- a current assessment. *Seed Science and Technology* 16: 155-166.

Fetcher, N., Strain, B.R., Oberbauer, S.F. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* 58: 314-318.

Finneseth, C.H., Layne, D.R. and Geneve, R.L. 1998. Requirements or seed germination in North American pawpaw (*Asimina triloba* (L.) Dunal. *Seed Science and Technology* 26: 471-480.

Flood, R.G. and Sinclair, A. 1981. Fatty acid analysis of aged permeable and impermeable seeds of *Trifolium subterraneum* (subterranean clover). *Seed Science and Technology* 9: 475-477.

Foster, S.A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* 52: 269-299.

Foster, S.A. and Janson, C.H. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66(3): 773-780.

Frankie, G.W., Baker, H.G. and Opler, P.A. 1974. Comparative phonological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62: 881-919.

Fraver, S., Brokaw, N.V.L. and Smith, A.P. 1998. Delimiting the gap phase in the growth cycle of a Panamanian forest. *Journal of Tropical Ecology* 14: 673-681.

FSI. 1987. The State of Forest Report. Government of India, Forest survey of India, Dehradun.

FSI. 1997. The State of Forest Report. Government of India, Forest survey of India, Dehradun.

FSI. 1999. *State of Forest Report*. Ministry of Forest and Environment, Dehra Dun.

Gadgil, M. and Solbrig, O.T. 1972. The concept of r- and k-selection: evidence from wildflowers and some theoretical considerations. *American Naturalist* 106: 14-31.

Gholz, H.L., Vogel, S.A., Cropper Jr., W.P., McKelvey, K., Ewel, K.C., Teskey, R.O. and Curran, P.J. 1991. Dynamics of canopy structure and light interception in *Pinus elliottii* stands, North Florida. *Ecological Monographs* 61: 33-51.

Gilbert, L.E. 1980. Food web organization and conservation of neotropical diversity. In: Soule, M.E. and Wilcox, B.A. (eds.) *Conservation Biology: an evolutionary-ecological perspective*. Sinauer, Sunderland. Pp. 11-34.

Gill, D.S. and Marks, P.L. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs* 61: 183-205.

Goldschmidt, E., Hildyard, N. and Bunyard, P. 1987. Save the forests: Save the planet - A plan for action. *Ecologist* 17(4/5): 129-204.

Goodland, R.J.A., Juras, A. and Pachauri R. 1993. Can hydro-reservoirs in tropical moist forests be environmentally sustainable? *Environmental Conservastion* 20(2); 122-130.

Grime, K.L., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mawford, M.A.G., Neil, A.M. and Shaw, S. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69: 1017-1059.

Gross, K.L. 1984. Effect of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology* 72: 369-387.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52: 107-145.

Grubb, P.J. 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology. Evolution and Systematics* 1: 1-29.

Grubb, P.J. and Burslem, D.F.R.P. 1998. Mineral nutrient concentrations as a function of seed size within seed crops: implications for competition among seedlings and defence against herbivory. *Journal of Tropical Ecology* 14: 177-185.

Grubb, P.J., Lee, W.G., Kollman, J. and Wilson, J.B. 1996. Interaction of irradiance and soil nutrient supply on growth of seedlings of ten European tall-shrub species and *Fagus sylvatica*. *Journal of Ecology* 84: 827-840.

Grubb, P.J., Lee, W.G., Kollman, J. and Wilson, J.B. 1996. Interaction of irradiance and soil nutrient supply on growth of seedlings of ten European tall-shrub species and *Fagus sylvatica*. *Journal of Ecology* 84: 827-840.

Grubb, P.J., Lee, W.G., Kollmann, J. and Wilson, J.B. 1996. Interaction of irradiance and soil nutrient supply on growth of seedlings of ten European tall-shrub species and *Fagus sylvatica*. *Journal of Ecology* 84: 827-840.

Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Ashton, P.M.S. and Ashton, P.S. 1998. Seedling growth of Shorea (Dipterocarpaceae) across an elevational range in southwest Sri Lanka. *Journal of Tropical Ecology* 14: 231-245.

Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Perea, G.A.D., Burslem, D.F.R.P., Ashton, P.M.S. and Ashton, P.S. 1997. Response to nutrient addition among seedlings of eight closely related species of *Shorea* in Sri Lanka. *Journal of Ecology* 85: 301-311.

Guo Ke and Werger, M.J.A. 1999. Different responses to shade of evergreen and deciduous oak seedling and the effect of acorn size. *Acta Oecologica* 20(6): 579-586.

Haag, R.W. 1974. Nutrient limitations to plant production in two tundra communities. *Canadian journal of Botany* 52: 103-106.

Hanninen, H. 1990. Modeling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica*. 213: 1-47.

Harcombe, P.A., White, B.D. and Glitzenstein, J.S. 1982. Factors influencing distribution and first-year survivorship a cohort of beech (*Fagus grandifolia* Ehrh.). *Castanea* 47: 148-157.

Haridasan, K. and Rao, R.R. 1985-87. *Forest Flora of Meghalaya* 2 vols. Bishen Singh Mahendra Pal Singh, Dehra Dun, India.

Harper, J. 1977. *Population Biology of Plants*. Academic Press, New York and London.

Harper, J.L. and Ogden, J. 1970. The reproductive strategy of higher plants: in the concept of reproductive strategy with special reference to *Senecio vulgaris* L. *Journal of Ecology* 58: 681-698.

Hart, T.B. 1995. Seed, seedling in sub-canopy survival in monodominant and mixed forests of the Itori forest, Africa. *J. Trop. Ecol.* 11: 443-459.

Hartshorn, G.S. 1978. Tree falls and tropical forest dynamics. *Tropical Trees as Living Systems* (eds. P.B. Tomlinson and M.H. Zimmerman). Pp. 617-638. Cambridge University Press, Cambridge.

Hawkins, B.J., Kiiskila, S.B.R. and Henry, G. 1999. Biomass and nutrient allocation in douglas-fir and amabilis fir seedling: influence of growth rate and temperature. *Tree Physiology* 19: 59-63.

Hay, F.R. and Probert, R.J. 1995. Seed maturity and the effects of different drying conditions on desiccation tolerance and seed longevity in foxglove (*Digitalis purpurea* L.). *Annals of Botany* 76: 639-647.

Heinrich, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. *Ecology*. 57: 890-899.

Hilhorst, H.W.M. 1993. New aspects of seed dormancy. In: *Come, D. and Corbineau, F. (eds.). Basic and Applied Aspects of Seed Biology.* Proceedings of the Fourth International Workshop on Seeds. Angers, France, Universite Pierre et Marie Curie, Paris. Vol. 2, pp. 571-579

Hiremath, A.J., Ewel, J.J. and Cole, T.G. 2002. Nutrient use efficiency in three fast-growing trees. Forest Science 48(4): 662-672.

Hirose, T. 1988. Modelling the relative growth rate as a function of plant nitrogen concentration. *Physiologia Plantarum* 72: 185-189.

Hooker, J.D. 1872-97. *The Flora of British India* 7 vols. London.

Howe, H.E. and Richter, W.M. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53: 347-351.

Howe, H.F. and Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.

Hughes, R.F., Kauffman, J.B. and Jaramillo, V.J. 1999. Biomass, carbon and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80(6): 1892-1907.

Illenseer, R., and Paulilo, M.T.S. 2002. Growth and nutrient efficiency in *Euterpe edulis* Mart. Seedlings under two levels of irradiance, nitrogen and phosphorus. *Acta Botanica Brasilica* 16(4).

Ingestad, T. and Agre, G.I. 1988. Nutrient uptake and allocation at steady-state nutrition. *Physiologia Plantarum* 72: 450-459

International Seed Testing Association 1985. International rules for seed testing. Rules 1985. *Seed Science and Technology* 13: 356-513.

Jacobsen, S.E. and Bach, A.P. 1998. The influence of temperatures on seed germination rate in quinoa (*Chenopodium quinoa* Willd.). *Seed Science and Technology* 26: 515-523.

Jamir, S.A. 2000. Studies on plant biodiversity, community structure and population behaviour of dominant tree species of some sacred groves of Jaintia Hills, Meghalaya. Ph.D. Thesis, North-Eastern Hill University, Shillong.

Jaynes, R.A. 1969. Long term storage of chestnut seed and scion wood. *Annual Report on Northern Nut Growers Association* 60: 38-42.

Jeangros, B. and Nosberger, J. 1990. Effects of an established sward of *Lolium perenne* L. on the growth and development of *Rumex obtusifolius* L. seedlings. *Grass and Forage Science* 45: 1-7.

Jones, E.W. 1945. The structure and reproduction of the Virgin forest of the North Temperate Zone. *New Phytologist* 44: 130-148.

Jones, R.H., Sharitz, R.R., Dixon, P.M., Segal, D.S. and Schneider, R.L. 1994. Woody plant regeneration in four floodplain forests. *Ecological Monographs* 64(3): 345-367.

Jordan, C.F. 1983. Structure and Function. In: *Golley, F.B. (ed.) Tropical Rain Forest Ecosystems*, Amsterdam, The Netherlands, Elsevier Scientific Publishing Company, pp. 117-136.

Joshi, H.B. 1980. *Troup's The Silviculture of Indian Trees*. Controller of Publications, Govt. of India, New Delhi.

Jurado, E. and Westoby, M. 1992. Seedling growth in relation to seed size among species of arid Australia. *Journal of Ecology* 80: 407-416.

Kalpana, R. and Rao, M.K.V. 1995. On the ageing mechanism in Pigeonpea (*Cajanus cajan* (L.) Millsp.) seeds. *Seed Science and Technology* 23: 1-9.

Kalpana, R., and Rao, M.K.V. 1995. On the ageing mechanism in pigeon pea (*Cajanus cajan* (L.) Millsp.) seeds. *Seed Science and Technology* 23: 1-9.

Kalpana, R. and Rao, M.K.V. 1996. Lipid changes during accelerated ageing of seeds of pigeon pea (*Cajanus cajan* (L.) Millsp.) cultivars. *Seed Science and Technology* 24: 475-485.

Kanjilal, U.N., Kanjilal, P.C., Das, A., De, R.N. and Bor, N.L. 1934-40. *Flora of Assam* 5 vols. Govt. Press Shillong.

Karlsson, P.S. 1987. Micro-site performance of evergreen and deciduous dwarf shrubs in a subartic heath in relation to nitrogen status. *Holarc. Ecol.* 10: 114-119.

Khan, M.A. and Ungar, I.A. 1984. The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. *American Journal of Botany* 71: 481-489.

Khan, M.L. and Uma Shankar. 2001. Effect of seed weight, light regime and substratum microsite on germination and seedling growth of *Quercus semiserrata* Roxb. *Tropical Ecology* 42(1): 117-125.

Khan, M.L., Bhuyan, P., Uma Shankar and Todaria, N.P. 1999. Seed germination and seedling fitness in *Mesua ferrea* L. in relation to fruit size and seed number per fruit. *Acta Oecologica* 20(6): 599-606.

Khan, M.L., Menon, S. and Bawa, K.S. 1997. Effectiveness of the protected area network in biodiversity conservation: a case study of Meghalaya state. *Biodiversity and Conservation* 6: 853-868.

Khan, M.L., Rai, J.N.P. and Tripathi, R.S. 1986. Regeneration and survival of tree seedling and sprouts in tropical deciduous and subtropical forests of Meghalaya, India. *Forest Ecology and Management* 14: 293-304.

Khoshoo, T.N. 1995. Census of India's biodiversity: Tasks ahead. *Current Science* 69: 14-17.

Kikuzawa, K. 1989. Ecology and evolution of phonological pattern, leaf longevity and leaf habit. *Evolutionary Trends in Plants* 3: 105-110.

Kikuzawa, K. 1998. Ecology and evolution of phonological pattern, leaf longevity and leaf habit. *Evolutionary Trends in Plants* 3: 105-110.

King, D.A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian Forest. *American Journal of Botany* 81: 948-957.

King, D.A. 1998. Influence of leaf size on tree architecture: first branch height and crown dimensions in tropical forest trees. *Trees* 12: 438-445.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98: 419-428.

Kobe, R.K., Pacala, S.W., Silander, J.A. and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5: 517-532.

Kost, J.A. and Boerner, R.E.J. 1985. Foliar nutrient dynamics and nutrient use efficiency of *Hammamelis virginiana* in three forest microsites. *Canadian Journal of Botany* 63: 1476-1481.

Koul, V.K., Bhardwaj, S.D. and Kaushal, A.N. 1995. Effect of N and P application on nutrient uptake and biomass production in *Bauhinia variegate* seedlings. *Indian Forester* 121(1): 14-22.

Kramer, P.J. 1983. *Water Relations of Plants*. Academic Press, New York.

Kramer, S., Miller, P.M. and Eddleman, L.E. 1996. Root system morphology and development of seedling and juvenile *Juniperus occidentalis*. *Forest Ecology and Management* 86: 229-240.

Kumar, V., Singh, C. and Kukreti, M.C. 2000. Studies on seed germination of twenty one tree species from Central Himalaya. *India Journal of Soil Conservation* 28(1): 54-57.

Kyereh, B., Swaine, M.D., and Thompson, J. 1999. Effect of light on the germination of forest trees in Ghana. *Journal of Ecology* 87: 772-783.

Labouriau, L.G. and Osborn, J.H. 1984. Temperature dependence of the germination of tomato seeds. *Journal of Thermal Biology* 9: 285-294.

Langer, R.H.M. 1966. In: *Milthorpe, F.L. and Irvins D.J. (eds.) The Growth of Cereals and Grasses*, pp. 213-226.

Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* 73: 2129-2144.

Law, P. 2002. Studies on population ecology of keystone species and their role in ecosystem functions in the two sacred groves of Meghalaya. Ph.D. Thesis. North-Eastern Hill University, Shillong.

Lawlor, D.W. 1987. *Photosynthesis: metabolism, control and physiology*. Longman Scientific and Technical, Harlow, England pp. 1-266.

Lechowiez, M.J. 1984. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *American Naturalist* 124: 821-842.

Lee, D.W., Oberbauer, S.F., Baskaran, K., Marzalina, M. Haris, M. and Yap, S.K. 1997. Effects of irradiance and spectral quality on seedling development of two Southeast Asian *Hopea* species. *Oecologia* 110: 1-9.

Lehto, T. and Grace, J. 1994. Carbon balance of tropical tree seedlings: a comparison of two species. *New Phytologist* 127: 455-463.

Leith, H. 1970. Phenology in productivity studies. In: D. Reichle (*ed.*). *Analysis of Temperate Forest Ecosystems.* Heidelberg. Spriner- Verlag.

Leith, H. and J.S. Radford. 1971. Phenology, resource management and synagraphis computer mapping. *Biological Sciences* 21: 62-70.

Lewis, S.L. and Tanner, V.J. 2000. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology* 81(9): 2525-2538.

Li, M., Lieberman, M. and Lieberman, D. 1996. Seedling demography in undisturbed tropical wet forest in Costa Rica. Pages 285-314 in M.D. Swaine (ed.) Ecology of tropical forest tree seedlings. UNESCO/Parthenon, Paris, France.

Lichtenthaler, H.K. 1996. Vegetation stress: an introduction to the stress concept in plants. *Journal of Plant Physiology* 148: 4-14.

Lodhiyal, L.S. and Lodhiyal, N. 1997. Nutrient cycling and nutrient use efficiency in short rotation, high density Central Himalayan Tarai Poplar plantations. *Annals of Botany* 79: 517-527.

Lugo, A.E. and Brown, S. 1992. *Forest Ecology and Management* 54: 239-255.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Islands Biogeography.* Princeton University Press, Princeton, NJ. Pp 203.

Marks PL (1975). On the relation between extension growth and successional status of deciduous trees of north-eastern United States. Bull. Torrey Bot. Club 102: 172-177.

Marks, P.L. and Borman, F.H. 1972. Regeneration following forest cutting: mechanisms for return to steady state nutrient cycling. *Science* 176: 915-924.

Marquis, D.A. Ernst, R.L. and Stout, S.L. 1992. Prescribing silvicultural treatments in hardwood stands of the Alleghenies. *USDA Forest Service General Technical Report.* NE 96.

Marshall, D.L. 1986. Effect of seed size on seedling success in three species of *Sesbania* (Fabaceae). *American journal of Botany* 73: 457-464.

Masoodi, T.H., Masoodi, N.A., Qaisar, K.N. and Joshi, N.K. 1996. Effect of nitrogen and spacing on growth and development of *Acer oblongum* Wall. Seedlings. *Indian Forester*, November 1028-1032.

Matsuda, K., McBride, J.R. and Kimura, M. 1989. Seedling growth form of oaks. *Annals of Botany* 64: 439-446.

Mazer, S.J. 1989. Ecological, taxonomic, and life history correlates of seed mass among Indian dune angiosperms. Ecological Monographs 59: 153-157.

McIntyre, G.I. 1977. In: Jennings D.H. (ed.) *Integration of activity in the Higher Plants, Soc. Exp. Biol. Symp.* 31, Cambridge Univ. Press, pp. 251-273.

Medina, E., Garcia, V. and Cuevas, E. 1990. Sclerophylly and oligotrophic environments: relationships between leaf structure, mineral nutrient content and drought resistance in tropical rain forests of the Upper Rio Negro Region. *Biotropica* 22: 51-64.

Meyer, R.F. and Boyer, J.S. 1981. Osmoregulation, solute distribution and growth in soyabean seedlings having low water potentials. *Planta* 151: 482-489.

Meyer, S.E., McArthur, E.D. and Jorgensen, G.L. 1989. Variation in germination response to temperature in Rubber Rabbitbrush (*Chrysothamnus nauseosus*: Asteraceae) and its ecological implications. *American Journal of Botany* 76(7): 981-991.

Meyer, S.E., McArthur, E.D. and Jorgensen, G.L. 1989. Variation in germination response to temperature in Rubber Rabbitbrush (*Chrysothamnus nauseosus*: Asteraceae) and its ecological implications. *American Journal of Botany* 76(7): 981-991.

Milberg, P. and Lamont, B.B. 1997. Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. *New Phytologist* 137: 665-672.

Milberg, P., Perez-Fernandez, M.A. and Lamont, B.B. 1998. Seedling growth response to added nutrients depends on seed size in three woody genera. *Journal of Ecology* 86: 624-632.

Miller, P.M., Eddleman, L.E. and Kramer, S. 1990. Allocation patterns of carbon and minerals in juvenile and small-adult *Juniperus occidentalis*. *Forest Science* 36: 734-747.

Minoletti, M.L. and Boerner, R.E.J. 1994. Drought and site fertility effects on foliar nitrogen and phosphorus dynamics and nutrient resorption by the forest understorey shrub *Viburnum acerifolium* L. *American Midland Naturalist* 131: 109-119.

Misra, R. 1968. *Ecology workbook*. Oxford & IBH Publishing Co., Calcutta.

Moller, A.P. and Swaddle, J.P. 1997. *Asymmetry, developmental stability and evolution*. Oxford University Press, Oxford.

Mooney, H.A. 1972. The carbon balance of plants. *Annual Review of Ecology and Systematics* 3: 15-46.

Moravie, M.A., Pascal, J.P. and Auger, P. 1997. Investigating canopy regeneration process through individual-based spatial models: application to a tropical rain forest. *Ecological Modelling* 104:241-260.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Canadian Journal of Forest Research* 24: 730-741.

Muchow, R.C. 1985. Canopy development in grain legumes grown under different water regimes in semiarid tropical environment. *Field Crop Research* 11: 99-109.

Mulik, N.G. and L.J. Bhosale. 1989. Flowering phenology of the mangroves from the West Coast of Maharashtra. *J. Bom. Nat. Hist. Soc.* 86(3).

Murali, K.S. 1997. Pattern of seed size, germination and seed viability of tropical tree species in southern India. *Biotropica* 29: 271-279.

Mwale, S.S., Azam-Ali, S.N., Clark, J.A., Bradley, R.G. and Chatha, R.C. 1994. Effects of temperature on the germination of sunflower (*Helianthus annus* L.) *Seed Science and Technology* 22: 565-571.

Myer, S.E., Durant McArthur, E. and Jorgensen G.L. 1989. Variation in germination response to temperature in rubber rabbitbrush (*Chrysothamnus nauseosus*: Asteraceae) and its ecological implications.IAmerican journal of Botany 76(7): 981-991.

Myers, N. 1992. *The Primary Source: Tropical Forests and Our Future*. New York: W.W. Norton.

Nair, G.H., Gopikumar, K., Krishnan, P.G. and Kumar, K.K.S. 1997. Sacred groves of India- vanishing greenery. *Current Science* 72(10): 697-698.

Namabiar, E.K.S., and Sands, R. 1993. Competition for water and nutrients in forests. *Canadian Journal of Forest Research* 23: 1955-1968.

Nayal, J.S., Thapliyal, R.C., Rawat, M.M.S. and Phartyal, S.S. 2000. Desiccation tolerance and storage behaviour of neem (*Azadirachta indica* A. Juss.) seeds. *Seed Science and Technology* 28: 761-767.

Ng, F.S.P. 1980. Germination ecology of Malaysian woody plants. *Malaysian Forester* 43: 406-437.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density and thickness in trees and shrubs. *Ecology* 82(2): 453-469.

Nilsson, M.C., Hogberg, P., Zackrisson, O. and Wang, F.Y. 1993. Allelopathic effects by *Impetrum hermaphrodium* on development and nitrogen uptake by roots and mycorrhiza of *Pinus silvestris*. *Canadian Journal of Botany* 71: 620-628.

Nygaard, P.H. and Odegaard, T. 1993. Long term effects of nitrogen fertilization on vegetation and soil in coniferous forests. (In Norwegian, with English summary). Norwegian Forest Research Institute, As Norway Rep. Skogforsk No. 26/93.

Okuda, T., Kachi, N., Yap, S.K. and Manokaran, N. 1997. Tree distribution pattern and fate of juvenile in a lowland tropical rain forest – implication for regeneration and maintenance of species diversity. *Plant Ecology* 131: 155-171.

Oldeman, R.A.A. 1978. Architecture and energy exchange of dicotylenous trees in forest. In: *Tomlinson, P.B. and Zimmerman, M.H. (eds.) Tropical trees as living systems*. Cambridge University Press, Cambridge, England, pp. 535-560.

Oliver, C.D. and Larson, B.C. 1990. *Forest Stand Dynamics*. McGraw Hill, p.3.

Osonubi, O. Fasehum, F.E. and Fasidi, I.O. 1985. The influence of soil drought and partial water logging on water relations of *Gmelina arborea* seedlings. *Oecologia* 66: 126-131.

Osunkoya, O.O. Ash, J.E., Hopkins, M.S. and Graham, A.W. 1994. Influence of seed size and seedling ecology attributes on shade-tolerance of rain-forest tree species in Northern Queensland. *Journal of Ecology* 82: 149-463.

Pacla, S.W., Canham, C.C., Saponara, J., Silander, J.A. Jr. Kobe, R.K. and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66: 1-43.

Pallardy, S.G. 1981. Closely related woody plants. In: *Kozlowski, T.T. (ed.) Water deficits and plant growth*, Academic Press, New York. Vol. 6, pp. 511-548.

Pallardy, S.G. and Rhoads, J.L. 1993. Morphological adaptations to drought in seedlings of deciduous angiosperms. *Canadian Journal of Forest Research* 23: 1766-1774.

Palma, B., Vogt, G. and Neville, P. 1995. Endogenous factors that limit seed germination in *Acacia senegal* Willd. *Phyton International Journal of Environmental Botany* 57: 97-102.

Pammenter, N.W., Berjak, P., Farrant, J.M., Smith, M.T. and Ross, G. 1994. Why do stored hydrated recalcitrant seeds die? *Seed Science Research* 4: 187-191.

Pammenter, N.W., Vertucci, C.W. and Berjak, P. 1991. Homeohydrous (recalcitrant) seeds: dehydration, the state of water and viability characteristics in *Landolphia kirkii*. *Plant Physiology* 96: 1093-1098.

Park, C.C. 1992. *Tropical Rainforests*. New York: Routledge.

Parrish, J.A.D. and Bazzaz, F.A. 1982. Responses of plants from three successional communities on a nutrient gradient. *Journal of Ecology* 70: 233-248.

Parsons, A.N., Welker, J.M., Wookey, P.A., Press, M.C., Callaghan, T.V. and Lee, J.A. 1994. Growth responses of four sub-artic dwarf shrubs to simulated environmental change. *Journal of Ecology* 82: 307-318.

Perez-Garcia,F., Pita, J.M., Gonzalez-Benito, M.I. and Iriondo, J.M. 1995. Effects of light, temperature, and seed priming on germination of celery seeds. Seed Science and Technology 23: 377-383.

Pojar. 1974. Reproductive dynamic of four plant communities of Southwestern British Columbia. *Canadian Journal of Botany* 52: 1819-1834.

Pollock, C.J., Eagles, C.F., Howard, C.J., Schunmann, P.H.D. and Stoddart, J. 1993. Temperature stress. In Leslie Fowden, Terry Mansfield and John Stoddart (eds.), *Plant adaptation to environmental stress*. James and James (Scientific publication).

Poorter, L. 1999. Growth responses of 15 rainforest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* 13: 396-410.

Popma, J. and Bongers, F. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625-632.

Pradhan, M. 2000. Germination vigour of Himalayan alder seeds under controlled conditions. *Tropical Ecology*. 41(1): 103-106.

Prasad, K.G. Kumarvelu, G., Singh, S.B., Periswamy, R., Mohan, S. and Subramaniam, V. 1984. Fertilizer requirements of *Eucalyptus tereticornius* II. Effects on height growth. *Santarona*: 79-84.

Prasad, K.G., Gupta, G.N., Singh, J. and Mohan, S. 1985. Effects of fertilizer application on biomass production from two year old *Eucalyptus grandis*. *Journal of Tropical Forest* 1(4): 303-308.

Prichard, H.W. 1991. Water potential and embryonic axis viability in recalcitrant seeds of *Quercus rubra*. *Annals of Botany* 67: 43-49.

Priestly, D.A. and Leopold, A.C. 1983. Lipid changes during natural ageing of soyabean seeds. *Physiology of Plant* 59: 467-470.

Pritchard, H.W. 1991. Water potential and embryonic axis viability in recalcitrant seeds of *Quercus rubra*. *Annals of Botany* 67: 43-49.

Pritchard, H.W. and Manger, K.R. 1990. Quantal response of fruit and seed germination rate in *Quercus robur* L. and *Castanea sativa* Mill. to constant temperatures and photon dose. *Journal of Experimental Botany* 41:1549-1557.

Raich, J.W. and Gong, W.K. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *Journal of Tropical Ecology* 6: 203-217.

Raimakers, D. and Lambers, H. 1996. Response to phosphorus supply of tropical tree seedlings: a comparison between a pioneer species *Tapirira obtuse* and a climax species *Lecythis corrugate*. *New Phytologist* 132: 97-102.

Ramakrishnan, P.S. 1978. Observations on biological aspects of productivity of forest ecosystem. In: Singh JS and Gopal B (eds.), Glimpses of Ecology. International Scientific Publications, Jaipur, India. Pp 193-199.

Ramin, A.R. 1997. The influence of temperature on germination of taree Irani (Allium ampeloprassum L. ssp. Iranicum W.). *Seed Science and Technology* 25: 419-426.

Ramos, A. and Zanon, A. 1984. Storage of seeds of native forest species. In *Proceedings of Simposio Brasileiro sobre Technologia de Sementes Florestais.* 1.pp. 285-316. Belo Horizonte, Brasil.

Ramos, J. and Grace, J. 1990. The effects of shade on gas exchange of seedlings of four tropical trees from Mexico. *Functional Ecology* 4: 667-677.

Rao, P., Barik, S.K., Pandey, H.N. and Tripathi, R.S. 1997. Tree seed germination and seedling eastablishment in tree fall gaps and understorey in a sub-tropical forest of north east India. *Australian Journal of Ecology* 22: 136-145.

Rao, P.B. and Singh, S.P. 1985. Response breadth on environmental gradients of germination and seedling growth in two dominant forest tree species of Central Himalaya. *Annals of Botany* 56: 783-794.

Rathcke, B. and E.P Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics.* 16: 179-214.

Rathcke, B. and E.P Lacey. 1988a. Interactions for pollination among co-flowering shrubs. *Ecology.* 69: 446-446.

Rathcke, B. and E.P Lacey. 1988b. Flowering phenologies in a shrub community: competition and constraints. *Jl. Ecology.* **76**: 975-975.

Reekie, E.G. and F.A. Bazzaz. 1987. Reproductive effort in plants. I. Carbon allocation to reproduction. *American Journal Botany* 129: 876- 896.

Rehman, S., Harris, P.J.C. and Bourne, W.I. 1999. Effect of artificial ageing on the germination, ion leakage and salinity tolerance of *Acacia torlilis* and *A. coriacea* seeds. *Seed Science and Technology* 27: 141-149.

Reich, P.B., Walters, M.B. and Ellsworth, D.S. 1992. Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs* 62: 365-392.

Rhoades, D.F and Cates, R.G. 1976. Toward a general theory of plant antiherbivore chemistry. In: Wallace JW and Mansell RL (eds). *Biochemical interaction between plants and insects.* Pp 168-213.

Richards, P.W. 1996. *Tropical Rain Forest, an Ecological Study* 2nd ed. Cambridge University Press, Cambridge. U.K.

Roberts, E.H. 1973. Predicting the storage life of seeds. *Seed Science and Technology* 1: 499-514.

Rollet, B. 1990. Leaf morphology. pp. 1-75 in *Statification of tropical forests as seen in leaf structure*, part 2(ed. B. Rollet, C. Hogermann and I. Roth). Kluwer Academic Publishers, Dordrecht.

Rowe, R., Sharma, N. and Browder, J. 1992. Deforestation: Problems, Causes, and Concerns. In: *Sharma, N.P. (ed.) Managing the worlds forests*, Kendall/Hunt Publishing Company, Iowa.

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

Runkle, J.R., Stewart, G.H. and Veblen, T. 1995. Sapling diameter growth in gaps for two Nothofagus species in New Zealand. *Ecology* 76: 2107-2117.

Ryan, D.F. and Bormann, F.H. 1982. Nutrient resorption in northern hard-wood forests. *Biosciences* 32: 29-32.

Santa Regina, I. Rico, M. and Gallego, H.A. 1997. Seasonal variation in nutrient concentration in leaves and branches of *Quercus pyrenaica*. *Journal of Vegetation Science* 8: 651-654.

Sarma, H., Gill, P.S., Katti, S.Y. and Mullaivendhan, T. 1993. Geology of parts of East and West Garo hills, Khasi hills and Jaintia hills district of Meghalaya. In: *Records of geology survey of India*, Govt. of India, Vol. 126, part 4, pp. 20-22.

Schelin, M., Tigaber, M., Eriksson, I., Swadogo, L. and Oden, P.C. 2003. Effects of scarification, giberellic acid and dry heat treatments on the germination of *Balanites aegyptiaca* seeds from Sudanian savanna in Burkina Faso. *Seed Science and Technology* 31: 605-617.

Schlesinger, W.H. and Chabot, B.F. 1977. The use of water and minerals by evergreen and deciduous shrub in Okefenokee Swamp. Botanical Gazette 138: 490-497.

Schulze, E.D., Robichaux, R.H., Grace, J., Rundel, P.W. and Ehleringer, J.R. 1987. Plant water balance. *Bioscience* 37: 30-37.

Schupp, E.W. 1990. Annual variation in seed fall post dispersal predation, and recruitment of a neotropical tree. *Ecology* 71: 504-515.

Seewaldt, V., Priestly, D.A., Leopold, A.C., Feigenson, G.W. and Goodsaid-Zaluondo, F. 1981 Membrane organization of soybean seeds during hydration. *Planta* 152: 19-23.

Sharma, N.P., Rowe, R. Openshaw, K. and Jacobson, M. 1992. Worlds forests in perspective. In: *Sharma, N.P. (ed.) Managing the worlds forests*, Kendall/Hunt Publishing Company, Iowa.

Shaver, G.R. and Chapin, F.S. III. 1986. Effects of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. *Arct. Alp. Res.* 18: 261-268.

Shaver, G.R., and Chapin. F.S. III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: Nutrient accumulation and growth. *Ecology* 61: 662-675.

Shukkla, R.P. and Ramakrishnan, P.S. 1982. Phenology of trees in a subtropical humid forest in North-eastern India. *Vegetatio* 49: 103-109.

Shukla, R.P. and Ramakrishnan, P.S. 1984. Biomass allocation strategies and productivity of tropical trees related to successional status. *Forest Ecology and Management* 9: 315-324.

Singh, A., Jha, A.K. and Singh, J.S. 1996. Influence of NPK fertilization on biomass production of *Pennisetum pedicellatum* seeded on coal mine spoil. *Tropical Ecology* 37(2): 285-287.

Smith, T.M. and Huston, M.A. 1989. A theory of spatial and temporal dynamics of plant communities. *Vegetatio* 83: 49-69.

Snyadon, R.W. and Howe, C.D. 1986. Root and shoot competition between established ryegrass and invading grass seedlings. *Journal of Applied Ecology* 23: 667-674.

Sorensen, F.C. 1999. Effect of dry storage on germination rate of seeds of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) France var. *menziesii*). *Seed Science and Technology* 27:91-99.

Souza, G.M. and Cardoso, V.J.M. 2000. Effects of different environmental stresses on seed germination. *Seed Science and Technology* 28: 621-630.

Souza, G.M. and Manzatto, A.G. 1999. Self-organized hierarchy in biological systems. In: *Auto-organizacao: estudos interdisciplinares, v.z. Campinas Gonzoles, M.E.Q. (ed.)*. CLE/UNICAMP.

Srivastava, N. and Behl, H.M. 2002. Growth and nutrient use efficiency in *Terminalia arjuna* Bedd. Seedlings grown in various potting mixtures. *Indian Forester* (January): 45-53.

Stapanian, M.A., Cassell, D.L. and Cline, S.P. 1997. Regional patterns of local diversity of trees: associations with anthropogenic disturbance. *Forest Ecology and Management* 93: 33-44.

Stock, W.D., Pate, J.S. and Delfs, J. 1990. Influence of seed size and quality on seedling development under low nutrient conditions in five Australian and South African members of Proteacea. *Journal of Ecology* 78: 1005-1020.

Stranghetti, V. and Ranga, T. 1997. Phenological aspects of flowering and fruiting at the ecological station of Paulo de Faria-SP-Brazil. *Tropical Ecology* 38(2): 323-327.

Strauss-Debenedetti, S and Bazzaz, F.A. 1991. Plasticity and acclimation to light in tropical Moraceae of different successional (sic) positions. *Oecologia* 87: 377-387.

Strauss-Debenedetti, S. and Berlyn, G.P. 1994. Leaf anatomical responses to light in five tropical Moraceae of different successional status. *American Journal of Botany* 81: 1582-1591.

Streng, D.R., Glitzenstein, J.S. and Harcombe, P.A. 1989. Woody seedling dynamics in an East Texas flood plain forest. *Ecological Monographs* 59:177-204.

Swaine, M.D. and Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.

Teketay, D. 1995. The effect of temperature on the germination of *Moringa stenopetala*, a multipurpose tree. *Tropical Ecology* 36(1): 49-57.

Teketay, D. 1997. Germination ecology of *Acacia negrii*, an endemic multipurpose tree from Ethiopia. *Tropical Ecology* 38(1): 39-46.

Thompson, P.A. 1970. Characterisation of the germination response to temperature and ecology. *Nature* 225: 827-831.

Thompson, W.A., Kriedemann, P.E. and Craig, I.E. 1992. Photosynthetic responses to light and nutrients in sun-tolerant and shade-tolerantrainforest trees. I. Growth, leaf anatomy and nutrient content. *Australian Journal of Plant Physiology* 19: 1-18.

Thomson, J.D. 1980. Skewed flowering distributions and pollinator attraction. *Ecology.* **61**:572-572.

Thomson, J.D. 1982. Patterns of visitation by animal pollinators. *Oikos.* 39: 241-241.

Thornton, J.M. and Powell, A.A. 1995. Prolonged aerated hydration for improvement of seed quality in *Brassica oleracea* L. *Annals of Applied Botany* 127: 183-189.

Tiwari, B.K., Barik, S.K. and Tripathi, R.S. 1999. *Sacred forest of Meghalaya. Biological and cultural diversity.* Regional center, National Afforestation and Eco-Development Board, NEHU, Shillong.

Tripathi, R.S. 2001. Sacred groves: community biodiversity conservation model in north-east India. In: Tropical ecosystems: *Structure, diversity and human welfare* (supplement). Proceeding of the International Conference on Tropical Ecosystems. Ganeshaiah, Uma Shaanker R and Bawa KS (eds). ATREE, Bangalore. pp 101-107.

Tripathi, R.S. and Khan, M.L. 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.

Turner, I.M. 1990. Tree seedling growth and survival in a Malaysian rain forest. *Biotropica* 22: 146-154.

Turner, I.M. 2001. *The Ecology of Trees in the Tropical Rain Forest.* P. 61. Cambridge University Press, U.K.

Turner, I.M. and Tan, H.T.W. 1991. Habitat-related variation in tree leaf ,form in four tropical forest types on Pulau Ubin, Singapore. *Journal of Vegetation Science* 2: 691-698.

Turner, I.M., Brown, N.D. and Newton, A.C. 1993. The effect of fertilizer application on dipterocarp seedling growth and mycorrhizal infection. *Forest Ecology and Management* 57: 329-337.

Tyler, G., Gullstrand, C., Holmquist, K. and Kjellstrand, A. 1973. Primary production and distribution of organic matter and metal elements in two heath ecosystems. *Journal of Ecology.*61: 251-268.

Uma Shankar, 1991. *Nutrient cycling in degraded ecosystems (grasslands) of Meghalaya.* Ph. D. Thesis, HEHU, Shillong, India.

UNESCO/UNEP/FAO. 1978. Tropical Forest Ecosystem: A state of knowledge report. Paris.

Upadhaya, K. 2002. Studies on plant biodiversity and ecosystem function in sacred groves of Meghalaya. Ph.D. thesis, North Eastern Hill University, Shillong.

Upadhaya, K., Law, P.S., Pandey, H.N. and Tripathi, R.S. 2003. Tree diversity in sacred groves of Meghalaya, north-east India. *Biodiversity and Conservation* 12: 583-597.

van der Meer, P.J., Sterck, F.J. and Bongers, F. 1998. Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. *Journal of Tropical Ecology* 14: 119-137.

van Veen, J.A., Breteler, H., Olie, J.J. and Frin, M.H. 1981. Nitrogen and energy balance of a short rotation Poplar forest system. *Nethreland Journal of Agricultural Science* 29: 163-172.

Vance, N.C. and Running, S.W. 1985. Light reduction and moisture stress: effects on growth and water relationship of Western larch seedlings. *Canadian Journal of Forest Research* 15: 72-77.

Vazquez-Yanes, C. and Orozco-Segovia, A. 1993. Patterns of seed longevity and germination in tropical rainforest. *Annual Review of Ecology and Systematics* 24: 69-87.

Veenendaal, E,M., Swaine, M.D., Lecha, R.T., Walsh, M.F., Abebrese, I.K. and Owusu-Afriyie, K. 1996. Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* 10: 501-511.

Veneklass, E.J., Poorter, L. 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. Pp. 337-361 in *Inherent variation in plant growth. Physiological mechanism and ecological consequences* (eds. H. Lambers, H. Poorter & M.M.I. van Vuuren), Backhuys Publishers, Leiden.

Vleeshowers, L.M., Bouwmeester, H.J. and Harssen, C.M. 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology* 83(6): 1031-1037.

Walters, M. B., Kruger, E.L. and Reich, P.B. 1993. Relative growth rate in relation to physiological and morphological traits for northern hardwood seedlings: species, light environment and ontogenetic considerations. *Oecologia* 96: 219-231.

Walters, M.B. and Reich, P.B. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77: 841-853.

Walters, M.B. and Reich, P.B. 1997. Growth of *Acer saccharum* seedlings in deeply shaded understories of Northern Wisconsin: Effect of Nitrogen and water availability. *Canadian Journal of Forest Research* 27(2): 237-247.

Wang, D., Borman, F.H., Lugo, A.E. and Bowler, R.D. 1991. Comparison of nutrient use efficiency and biomass production of five tropical tree taxa. *Forest Ecology and Management* 46: 1-21

Watson, D.J. 1963. In: Irvins J.D. and Milthorpe F.L. (eds.) *The Growth of the Potato*. London, Butterworths, pp. 233-247.

Watt, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35: 1-22.

Wedin, D. and Jilman, D. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs* 63: 199-229.

Weetam, G.F., McDonald, M.A., Prescott, C.E. and Kimmins, J.P. 1993. Responses of western hemlock, pacific silver fir and western red cedar plantations of northern Vancouver Island to application of sewage sludge and inorganic fertilizer. *Canadian Journal of Forest Research* 23: 1815-1850.

Weih, M. and Karlsson, P.S. 1997. Growth and nitrogen utilization in seedlings of mountain birch (*Betula pubescens* ssp. *tortuosa*) as related to plant nitrogen status and temperature: a two-year study. *Ecoscience* 4: 365-373.

Welden, C.W., Hewett, S.w., Hubbell, S.P., Foster, R.B. 1991: Sapling survival growth and recruitment: Relationship to canopy height in a Neotropical forest. *Ecology* 72(1): 35-50.

Wenny, D.G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs* 70(2): 331-351.

Wesley-Smith, J., Vertucci, C.W., Berjak, P., Pammenter, N.W. and Crane, J. 1992. Cryopreservation of desiccation-sensitive axes of Camellia sinensis in relation to dehydration, freezing rate and the thermal properties of tissue water. *Journal of Plant Physiology* 140:596-604.

Westoby, M., Leishman, M. and Lord, J. 1996. Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London, Series B. Biological Sciences* 351: 1309-1318.

Whitmore, T.C. 1975. *Tropical Rain Forests of the Far East.* Clarendon, Oxford, England.

Whitmore, T.C. 1984. *Tropical Rain Forest of the Far East.* 2nd edition. Oxford University Press, London.

Whitmore, T.C. 1996. A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. In Swaine MD (ed.) *The ecology of tropical forests tree seedlings.* Parthenon Publishing Group, Paris, France.

Will, R.E., Seiler, J.R., Feret, P.P. and Aust, W.M. 1995. Effects of Rhizosphore inundation on the growth and physiology of wet and dry site *Acer rubrum* (Red maple) populations. *American midland Naturalist* 134(9): 127-139.

Wilson, J.B. 1988. Shoot competition and root competition. *Journal of Applied Ecology* 25: 279-296.

Winn, A.A. and Werner, P.A. 1987. Regulation of seed yield within and among populations of *Prunella vulgaris*. *Ecology* 68: 1224-1233.

World Conservation Monitoring Centre. 1992. *Global Biodiversity: Status of the Earth's living resources.* Chapman and Hall, London.

Zagt, R.J. and Werner, M.J.A. 1998. Community structure and the demography of primary forest species in tropical rainforest. Pp. 193-219 in *Dynamics of tropical communities* (ed. D.M. Newbery, H.H.T. Prins and N.D. Brown). Blackwell Science, Oxford.

Zangeral, A.R. and Bazzaz, F.A. 1983. Responses of an early and late successional species of *Polygonum* to variation in resource availability. *Oecologia* 56: 379-404.

Zelitch, I. 1982. The close relationship between net photosynthesis and crop yield. *Biosciences* 32: 796-802.