THE ROLE OF LITTER AND FINE ROOTS IN ORGANIC MATTER AND NUTRIENT DYNAMICS DURING THE RECOVERY OF DEGRADED SUBTROPICAL FOREST ECOSYSTEMS

Abstract

By

A. ARUNACHALAM

Thesis Submitted in Fulfilment of the Degree of

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Thesis

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The humid subtropical broadleaved forests of Meghalaya are exposed to various kinds of anthropogenic disturbances of varying magnitude caused by shifting agriculture and massive tree felling for developmental and fuelwood purposes. The disturbed forests are often left for natural recovery of vegetation and soil fertility. The main objective of the present study was to study the relative importance of litter and fine roots in organic matter and N and P dynamics in soil during recovery of degraded humid subtropical forest ecosystem in Meghalaya. Besides emphasising the role of litter and fine roots, changes in soil and vegetation characteristics and microclimatic conditions were also investigated. The study was conducted during 1993-94 in 7-, 13- and 16-year old stands, regrowing after selective tree cutting in a subtropical humid forest ecosystem located near Shillong (latitude 25°34'N, longitude 91°56'E, altitude 1900 m asl), the capital of Meghalaya, India.

VEGETATIONAL CHANGES

The 7-year old regrowth was dominated by early successional species like *Eupatorium adenophorum, Litsea elongata, Pinus kesiya* and sprouting stumps of *Quercus dealbata, Corylopsis himlalayana* and *Schima khasiana.* The 13-year old regrowth having thin ground vegetation was dominated by *Q. dealbata* and *C. kurzii. Rhododendron arboreum* and *Q. dealbata* were dominant in the 16-year old regrowth. In this stand the forest floor had a dense growth of shade-tolerant herbs, pteridophytes and mosses.

The number of species in the community sharply declined from 41 in the 7-year old stand to 25 in the 16-year old regrowth. But the number of tree species as well as its species richness index markedly increased during the same period. The species richness index of shrub and herb species, however gradually declined with the regrowth of the forest.

Density and basal area of trees increased significantly from 180 plants ha^{-1} and 3.1 m^2 ha^{-1} in the 7-year old regrowth to 1140 plants ha^{-1} and 44.2 m^2 ha^{-1}, respectively in the 16-year old regrowth. The shrub density was lowest in the 16-year old regrowth and highest in the 13-year old regrowth. Density and basal area of herbaceous species were maximum in the 7-year old stand and minimum in the 13-year old stand. Dominance in the 16-year old community was more evenly distributed than in the 7- and 13-year old regrowths. In all regrowths, tree density and diameter showed an overall straight-line negative relationship.

Broadleaved tree species regenerated mainly through sprouts, while the needleleaved *P. kesiya* reproduced through seeds. Sprouting stumps constituted 43, 75 and 87% of the total stump density in 7-, 13- and 16-year old regrowths, respectively. As a result, density increased from 220 ha^{-1} in the 7-year old regrowth to 1350 ha^{-1} in the 16-year old regrowth. The sprout growth in terms of number and basal area was relatively faster between 7- and 13-year old regrowth than between 13- and 16-year old stands.

MICROENVIRONMENTAL AND EDAPHIC CHANGES

Light intensity and air temperature near the ground showed a significant decline from 7- to 16-year old stand. Relative humidity, however, showed a reverse trend. Soil moisture content increased with increasing stand age, while soil temperature showed a reverse trend. Generally, the temperature and moisture content in the surface soil layer (0-10 cm) were higher during rainy and autumn seasons, but subsurface layers (10-20 and 20-30 cm) had greater soil moisture content during winter and spring seasons. Both WHC and CEC declined with soil depth, but increased with stand age.

Soil texture varied from sandy loam in the 7-year old regrowth to sandy clay loam in the 13-year old regrowth and clay loam in the 16-year old regrowth. Soil pH fluctuated within a narrow range of 4.9-5.6 without showing significant seasonal and depthwise variations. SOC and SOM were significantly lower during rainy season and higher during autumn in all three forest regrowths. Both of them decreased with the increase in soil depth. Seasonal trends of TKN and available-P were similar to SOC. In general, SOC, SOM, TKN, available-P increased with the progressive development of vegetation.

ROLE OF LITTER

Litter accumulation on the forest floor increased significantly from 1231 kg ha^{-1} in the 7-year old regrowth to 2007 kg ha^{-1} in the 13-year old regrowth, and then it became levelled-off. Leaf litter mass on the forest floor increased with the progression of vegetation recovery. Accumulation of woody litter (<20 mm diameter) was more in the 13-year old regrowth compared to the 7- and 16-year old regrowths. In all stands, litter accumulation was maximum during winter or spring and minimum during autumn.

Litterfall increased significantly from 11902 kg ha^{-1} in the 7-year old regrowth to 17402 kg ha^{-1} in the 16-year old regrowth. The contribution of leaf litter to the total litter production in the three stands ranged between 78 and 88%. Production and accumulation of litter were positively correlated with density and basal area of woody species, and OM, TKN and available-P in soil. In all regrowths, turnover rate of the leaf litter was faster than the woody and miscellaneous litter.

N concentration in the forest-floor litter was maximum either during autumn or winter, and minimum during spring in all three regrowths. While its concentration in the fresh litter was higher during autumn and lower during rainy season. Seasonal variation in P concentration both in forest-

floor litter and fresh litter was not significant. Leaf and miscellaneous litter had higher N and P concentrations than the woody litter.

Mean standing state of N and P in the forest-floor litter was maximum in the 13-year old regrowth and minimum in the 7-year old regrowth. Generally, leaf litter accumulated more N and P than the woody and miscellaneous litter fractions. Seasonal variation was significant only for N. Addition of N and P to the forest floor through litter in the three regrowths exhibited a marked seasonality with highest inputs during February-April and lowest during June-September. Leaf litter contributed to about 80-99% N and 70-80% P annual nutrients input thorugh litter. N input through litter was maximum in 13- and 16-year old regrowths, and minimum in the 7-year old regrowth, while P input increased from young to old stand.

Decay pattern of leaf litter varied significantly between species and stands. Needles of *P. kesiya* decomposed in a three-phased manner, whereas, all broadleaved tree species except, *R. arboreum* showed only two phases. Leaves of *R. arboreum* decomposed at a constant rate throughout the study period. A composite linear decay model ($Y=a+bX_1+cX_2+dX_3$), fitted well for the decay pattern of *P. kesiya*, while a simple linear regression function, $Y=a+bX$ explained the weight loss pattern of *R. arboreum* leaf litter during decomposition. For other species, a multiple regression equation, $Y=a+bX_1+cX_2$ was more appropriate.

Decompositon of leaf litter (weight loss, mg day^{-1}) was significantly correlated with initial lignin and N concentrations and lignin/N ratio of the litter, soil moisture, pH and TKN, and mean daily rainfall and mean monthly air temperature. N and P mineralization patterns during decomposition of leaf litter were similar in all five tree species studied. All of them were characterized by a phase of active N mineralization during rainy season followed by a period of microbial immobilization during winter.

ROLE OF FINE ROOTS

Fine root mass (FRM, <2 mm diameter) increased significantly from 6751 kg ha^{-1} in the 7-year old regrowth to 9088 kg ha^{-1} in the 16-year old regrowth. Coarse root mass (CRM, 2-15 mm diameter) as well as total root mass (TRM=FRM+CRM) increased significantly from the 7-year old regrowth to the 13-year old regrowth, beyond this age the increase was not significant. The proportion of FRM decreased from 87% in the 7-year old regrowth to 77% in the 16-year old regrowth. The contribution of coarse roots followed a reverse trend. As a result, FRM/CRM ratio was significantly higher in the 7-year old regrowth than the 13- and 16-year old regrowths. In all three forest regrowths, the ratio was generally higher during winter and lower during rainy season.

Fine roots were concentrated (upto 65% of the TRM) mainly in the top soil layer (0-10 cm) in all three stands, and their proportion declined upto 19% in the 10-20 cm layer and further down (20-30 cm depth) to 15%. The amount of fine roots in the top soil layer increased with the increase in the age of the stand, but their proportion declined from 63% in the 7-year old regrowth to 57% in the 16-year old regrowth.

Annual fine root production increased upto 13 years of forest regrowth, after this age, the production declined by *ca.* 10% during next 3 years of regrowth. The contribution of fine roots to total root production decreased significantly from 88% in the 7-year old regrowth to 50% in the 16-year old regrowth.

Fine root productivity (kg m^2 day^{-1}) was positively correlated with mean monthly rainfall and maximum and minimum temperatures, SOM, TKN and available-P. Apart from these edapho-climatic factors, density and basal area of the woody species in the community also influenced the production and accumulation of fine roots. Turnover rate of fine roots did not vary significantly between regrowths and soil depths.

Fine roots had greater N and P concentrations than the coarse roots. Similarly live fraction of the fine roots had greater nutrients concentration than the necromass.

In all three regrowths, N accumulation in fine roots was maximum either during autumn or winter, and minimum during rainy season. On the other hand, maximum N stock in coarse roots was obtained during rainy or post-rainy seasons, and minimum during spring. N stock in fine roots was significantly ($P<0.05$) higher in the surface soil layer than the subsurface layers. Seasonal trend of P accumulation in fine and coarse roots was similar to N, but its stock was inversely related to soil depth.

Maximum amount of N (189 kg ha^{-1} yr^{-1}) was returned to the soil through fine roots in the 13-year old regrowth and the input was minimum (158 kg ha^{-1} yr^{-1}) in the 7-year old regrowth. P input through fine roots was also maximum (12 kg ha^{-1} yr^{-1}) in the 13-year old regrowth, but its minimum value (9 kg ha^{-1} yr^{-1}) was recorded in the 16-year old regrowth.

Fine roots decomposed in a three-phased manner. The decay rate was positively correlated with mean daily rainfall, soil moisture and pH, and negatively correlated with initial lignin concentration. The decay constant (k=1.62-1.74) increased with the age of the regrowth.

Release of nutrients from decaying fine roots was also influenced by seasonal cycle of mineralization and immobilization processes. Winter represented the period of N and P immobilization, while rainy season was the period of rapid mineralization when N and P contents in the decomposing fine roots recorded 46-58% decrease from the preceding spring season. The net annual N mineralization showed a marginal decrease from about 51% in the 7-year old regrowth to 46% in the 16-year old regrowth, while P showed a reverse trend by registering an increase from 37 to 51%, thereby contributing to its greater availability in the soil supporting the older regrowth.

CONCLUSION

The three forest regrowths differed markedly in community structure, soil physico-chemical properties and detritus (litter and fine roots) input, accumulation and turnover, despite the fact that all of them are located on a similar toposequence and have developed under similar climatic conditions. Recovery in soil fertility in the disturbed stands was closely related to the regrowth of woody vegetation, since production and accumulation of litter and fine roots were significantly correlated to the density of woody elements in the community. Litter production increased during vegetation regrowth until 16 years, but the fine root production showed a steady increase upto 13 years of forest regrowth, beyond this it levelled-off. Similar trend was observed in case of litter and fine root accumulation also. Accumulation of litter and fine roots were related to each other, but the latter added more organic matter, N and P to the soil thereby playing a more important role than the former in nutrient restoration in soil during the recovery of disturbed subtropical forest ecosystem.

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I certify that the thesis entitled "**The role of litter and fine roots in organic matter and nutrient dynamics during the recovery of degraded subtropical forest ecosystems**" submitted by **Shri A. Arunachalam**, for the degree of **Doctor of Philosophy in Botany** of the North-Eastern Hill University, Shillong, embodies the record of original research carried out by him under my supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of Ph.D. degree. The work has not been submitted for any degree of any other Universities.

H.N. Pandey
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CONTENTS

PREFACE

In the humid tropical region of north-east India, land degradation has reached to an alarming level due to continued influence of age old practice of shifting agriculture, massive tree felling, mining and a variety of other human activities. Recovery of vegetation on degraded forest sites is mainly controlled by soil nutrient status and other factors of edaphic complex provided it is protected from human disturbances. So far, limited efforts have been made to study the mechanism of recovery of soil fertility at the degraded sites during the course of vegetation regrowth. In view of the above, the present study was undertaken to quantify the relative importance of litter and fine roots in influencing the soil nutrient budget in the regrowing forest communities in the humid subtropics in a holistic manner. The data generated on the various aspects highlight the mechanism of nutrient restoration in soil during ecosystem recovery following human disturbance in the form of tree cutting.

The field data collected during 1993-94 from three regrowing stands of a cut-over subtropical humid forest ecosystem in Meghalaya have been presented in CHAPTERS 4 to 8. Chapter 4 is preceded by a introduction (CHAPTER 1), literature review pertaining to various relevant aspects of the study (CHAPTER 2) and description of the location, climate, soil and vegetation of the study sites (CHAPTER 3). Microclimate and Soil Nutrient Dynamics of the study sites have been dealt in CHAPTER 4, and Community Structure and Dynamics in CHAPTER 5. Data on litter and fine roots have been critically discussed in CHAPTERS 6 & 7, respectively. The major findings of the study have been discussed in an integrated manner in CHAPTER 8. A Summary of the work has been given in CHAPTER 9. The literature cited in the text is listed in the end.

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20/4/96.
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CHAPTER 1

INTRODUCTION

Forests form an important component of natural vegetation in the tropical and subtropical world. A dense forest cover reduces soil erosion, regulates streamflow, increases precipitation 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.

Forests all over the world are exposed to different kinds of natural and human disturbances. Natural disturbances and concomitant recovery are integral aspects of normal ecosystem behaviour (White 1979). Human disturbances on the other hand, differ sharply in kind, scale, intensity and frequency and sometimes they may be more severe and extensive than the natural disturbances. Shifting cultivation and timber and fuel wood extraction, the major human disturbances in the humid tropics (Reiners 1980), have destroyed vast tracts of the humid tropical forest ecosystem. The unscientific land-use practices have caused irrepairable loss to the land resources of the earth in general, and forest wealth in particular. The process is continuing at an increasing rate. Like other developing countries of the world, over-exploitation and unscientific management of forests have caused enormous reduction in the forest cover in India. At present only 64.01 million ha or 19.47% of the total geographical area of the country is under forest cover (FSI 1989). Although the National Forest Policy of India (1985) aims at maintaining one third of its land under forest, the actual progress made in this direction is rather disappointing.

As per the assessment carried out during 1989, the annual rate of loss of forest cover in India was 47,500 ha (FSI 1989).

The undisturbed forest ecosystem tends to maintain its structure and function year after year through homeostatic mechanism. Such forests exist in the state of equilibrium with the prevailing environmental conditions and do not show any marked change in species composition, density, biomass, productivity and nutrient inputs and outputs processes. Generally, the undisturbed forests are dominated by long-lived tree species possessing high density wood, low annual growth and high insect resistance. In contrast, recently disturbed forests are dominated by fast growing short-lived tree species having low wood density and poor insect resistance capacity (Ramakrishnan 1992).

The species composition and structure of plant community and its development subsequent to disturbance is strongly influenced by the nature and intensity of the stress (White 1979, Pandey and Singh 1984/1985). The time period required by the community to again reach to the pre-disturbance level depends on a number of factors such as the degree of damage caused initially, availability of propagules to initiate regrowth of the vegetation, and the environmental constraints that limit the growth of plant species. Very often the original species composition, abundance and interaction of species in the community is not attained during the development phase in the disturbance free time interval, rather a new state of equilibrium is achieved where the resultant community looks similar to the original vegetation.

Effects of human intervention on basic ecosystem processes such as energy flow and nutrient and hydrologic cycles have been studied both in temperate and tropical climatic zones of the world (Lamottee 1981). Available quantitative data permit us to predict the temporal variation in nutrient flux and water balance in the forest system during its

recovery following disturbance (Mooney 1977, Buschbacher *et al.* 1987). But, still our understanding of the structure and function of human impacted natural ecosystem is far from complete.

Removal of tree canopy either through selective felling or clear cutting of forests and subsequent abandonment of land for few years without further disturbance, provide suitable site for the commencement of secondary succession. The communities developing on such sites differ from one another in species composition, diversity, dominance and population behaviour of the constituent species depending on the extent of damage caused to the original vegetation and site conditions. Such a variability in the regrowing plant community influences the overall energy and nutrient budgets of the ecosystem. The functional attributes of plant communities such as organic productivity, litter production and decomposition and mineral cycling during forest succession have been examined by Golley *et al.* (1974), Likens *et al.* (1978) and Gorham *et al.* (1979). In most cases, immediately after clear felling net ecosystem production becomes negative and nutrient output rates exceed input rates (Gorham *et al.* 1979). However, during the reorganization phase of the recovery process the regrowing vegetation tends to compensate organic matter loss and reduces nutrient output. This is followed by an aggradation phase. This phase is characterized by rapid accumulation of plant biomass and soil organic matter and redistribution of nutrients in the ecosystem components. The pace of the aggradation phase depends largely on the reconstruction of photosynthetic cycles. Development of litter layer, fine-root mat and associated decomposition subsystem are the major steps in the reestablishment of the forest nutrient cycles. During stabilization phase forest functions with strong biotic control (Singh and Tripathi 1992).

Regrowth of vegetation in disturbed ecosystems is closely linked with the restoration of biogeochemical cycle and *vice-versa*. Recovery of

nutrient cycle during succession is linked to the increasing capacity of the ecosystem to entrap and hold nutrients (Odum 1969). Vegetation regrowth enhances input of organic matter and nutrients to soil through litter and detrital root mass and helps in conservation of nutrients by reducing losses and increasing their availability by favourably altering the hydrology and physico-chemical properties of the soil. Aboveground litter is the major pathway joining the living biological component to the non-living soil component of the ecosystem through organic matter decomposition cycle (Meentemeyer *et al.* 1982). It acts as an input-output system on the soil surface and determines several other functions of the ecosystem. Therefore, much emphasis has been placed on determining the nutrient flux accompanying the litterfall and decomposition in forest ecosystems.

Several studies, however, showed that aboveground litterfall may not be the dominant pathway of organic matter and nutrient circulation in some forest ecosystems (Vogt *et al.* 1986). This hypothesis is gaining ground as more and more studies are being conducted on the dynamics of fine roots in different ecosystems. These roots generally comprise only a small proportion of total root mass in the ecosystem and were earlier regarded unimportant in the nutrient dynamics. The fine roots seem to play a key role not only in water and nutrient absorption, but also add a large amount of organic matter to soil through extremely rapid turnover rate (Harris *et al.* 1977, Kummerow *et al.* 1990). According to the existing model of nutrient cycling, belowground inputs from fine-root turnover may contribute more to the organic matter decomposition cycle than the aboveground litterfall (Shugart *et al.* 1977, Aber *et al.* 1983). Therefore a study of both litter and fine root dynamics becomes an essential prerequiste for better understanding of nutrient restoration mechanism in soil and its circulation in the ecosystem.

The north-eastern India is characterized by luxuriant growth of deciduous, humid evergreen and mixed coniferous types of forest vegetation. The subtropical semi-evergreen forest is the dominant vegetation in the region between 1500-2000 m asl (Champion and Seth 1968). In Meghalaya small patches of dense subtropical forest occur in the form of sacred groves. These groves have been preserved by tribals of the area due to their religious beliefs. However, continuing age-old practice of shifting cultivation, massive tree felling and other developmental activities have destroyed a major portion of natural forest vegetation in the state. According to FSI report (1989) 4.97% of the forest cover in Meghalaya has been lost during the period between 1983 and 1987. The rate of deforestation is much higher than the rate of replenishment of forest cover either through natural or artificial regeneration. Effects of human disturbances on community composition, tree population structure and natural regeneration of forest trees in disturbed and undisturbed subtropical humid forest of Meghalaya have been studied by Khan *et al.* (1987), Rao *et al.* (1990) and Barik *et al.* (1992).

Litter dynamics on 'jhum' fallows of different ages (Toky and Ramakrishnan 1983, Mishra and Ramakrishnan 1983), in pine (*Pinus kesiya* Royle Ex. Gordon) forests of different ages (Das and Ramakrishnan 1985, Singh 1990) and in mature broadleaved forests (Singh and Ramakrishnan 1982, Boojh and Ramakrishnan 1983, Khiewtam and Ramakrishnan 1993) of this region have been studied in detail. So far as fine roots are concerned, data are available for mature climax semi-evergreen forest (Khiewtam and Ramakrishnan 1993) at Cherrapunji (1300 m asl) and for a 50-year old 'jhum' fallow (Ramakrishnan and Singh 1983) at Lailad (290 m asl).

OBJECTIVES

The objective of the present research was to study the dynamics of litter and fine roots in human impacted subtropical humid forest ecosystems undergoing recovery after disturbance in Meghalaya, India. The study aims to understand the relative importance of litter and fine roots in the restoration of soil fertility level during forest regrowth. The specific objectives of the study were as follows:

1. To study the changes in the species composition, diversity and dominance pattern of plant species in the community during forest regrowth.

2. To study the changes in forest microclimate and soil properties and nutrient build-up during forest regrowth.

3. To study the role of litter in organic matter and N and P dynamics on the forest floor during regrowth of disturbed forest.

4. To evaluate the relative importance of fine roots in organic matter and N and P dynamics in regrowing forest stands.

CHAPTER 2

REVIEW OF LITERATURE

* STATUS OF TROPICAL FOREST
* ECOLOGICAL CONSEQUENCES OF DISTURBANCE IN FOREST ECOSYSTEM
  - Microenvironment and soil fertility
  - Carbon, nitrogen and phosphorus cycling
* RECOVERY OF DEGRADED FOREST ECOSYSTEMS
* LITTER DYNAMICS
  - Litterfall
  - Litter decomposition
  - Litter dynamics in successional communities
* FINE ROOT DYNAMICS
  - Root categories
  - Fine and coarse root biomass
  - Fine root production
  - Fine root chemistry and nutrient flux
  - Fine root decomposition

STATUS OF TROPICAL FOREST

Tropical forests cover about 7% of the land surface and constitute one of the most important natural resources on the Earth. With a high biological diversity and endemism, these forests harbour about two-third (*ca.* 30 million) of total living species (Mitra and Pal 1994). Besides, sustaining local environment through soil and water conservation, they also influence regional and global climate. The influence of tropical forests on local environment is well documented, but, their role in regulating global climate is less clearly understood.

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 their destruction. Mounting pressure on forested areas due to rapid population growth for agriculture,

livestock grazing, fuelwood and other domestic needs of humans often end in over-exploitation of tropical moist forests. They are being cleared at an estimated rate of over 11 million hectares per year. It is predicted that at this rate, at least 225 million hectares of tropical forests will be cleared by the year 2000 (Ramakrishnan 1992).

Utilization of forests for economic growth has infact 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 resource base and life-support system of the forest dwellers. The important global effects of deforestation are related to the role of forests in recycling carbon and water vapours. Forests play a significant role in regulating the concentration of CO_2 in the atmosphere and about 15% of the CO_2 concentration in the atmosphere is due to both burning of fossil fuels and deforestation (Ramakrishnan 1992a).

Another major effect of deforestation of tropical forests is loss of biological diversity. With tropical forests disappearing at the rate of 76 to 90 thousand km^{-2} yr^{-1}, the implications for biological diversity are enormous. According to Ramakrisnnan (1992) if the present trend of deforestation continues in Latin America and in the Asian and African tropics outside the Zaire basin, at least 15% loss in biota would occur by 2000 AD. If Amazonian deforestation is added to this, species extinction could be over 70%.

Desertification, a term used to explain the process of decline in the biological productivity of an ecosystem is often linked to the arid, semiarid and subhumid ecosystems. However, in the humid tropics, the human-impacted terrestrial ecosystems show accelerated erosion and salinization and decline in site quality. The ultimate consequence of site desertification is soil degradation and decline in available water and its

quality, leading to decline in food, fodder and fuelwood yields essential for the economic well-being of rural communities.

During the last two decades, a large number of studies have been carried out to assess the ecological consequences of human disturbances on the structure, function and dynamics of forest ecosystems both in temperate and tropical zones. A brief review of literature relavant to the proposed research is presented in the ensuing pages.

ECOLOGICAL CONSEQUENCES OF DISTURBANCE IN FOREST ECOSYSTEM

MICROENVIRONMENT AND SOIL FERTILITY

The climate within the tropical forest communities has not been extensively studied because of many logistic and technical problems. One of the most comprehensive studies on the effect of disturbance on forest ecosystem dynamics has been carried out by Bormann and Likens (1979). According to them, canopy thinning, creation of distinct canopy openings and destruction of much of the top strata of the forests are visible effects of disturbances. Canopy disturbances directly affect the hydrology within the forest ecosystem by reducing canopy evoporation and increasing water input on the forest floor. Most of the water reaching the forest floor is lost by runoff, and the litter layer rapidly dries up. Increased insolation at the forest floor due to canopy opening may elevate air and soil temperatures (Fetcher 1985), and enhance dryness in the soil, which in turn may affect soil microbiological processes. Thin canopy increases wind velocity in the forest environment leading to better dispersal of wind dispersed light seeds of pioneer species thereby causing alteration in regeneration pattern in disturbed forests (Likens *et al.*1978). Lee (1978) and Denslow (1980) have argued that variation in microclimatic condition in the forest depends on the disturbance size. Barik *et al.* (1992) reported

a marked change in the forest microenvironment due to partial canopy harvesting in a humid subtropical forest ecosystem and emphasised its role in natural regeneration of tree species in the forest.

Clearfelling followed by natural regeneration or artificial replanting, and conversion of forest land to agriculture, pastures and other non-forest uses are important landuse practices in forested area. The effect of forest land conversions for agricultural purposes are generally more severe than that of clear cutting (Vitousek 1984). Soils of disturbed ecosystems provide a very rigorous condition for both plant and microbial growth because of low organic matter contents, unfavourable pH, low nutrient supply, and unfavourable moisture conditions either due to coarse texture (low water retention capacity) or due to compact structure (poor drainage) (Meyer 1973, Doubleday and Jones 1977). Power and Bennett (1977) reported that deficiency of N and P, and toxicity of Al, Mg, B, Mo, soil compaction and steep slopes adversely affects the reestablishment of species on the degraded sites.

The direct effects of tree cutting on soil includes changes in chemical and physical conditions, nutrient supply, root dynamics, soil biota and decomposition rate of litter (Baath *et al.* 1980, Seastedt and Crossley 1981, Vitousek and Matson 1985). The maintenance of soil fertility in hot-humid and high rainfall areas is a serious problem particularly when the frequency of cutting or destruction is high.

Nye and Greenland (1960) and Om Prakash (1980) have reported heavy losses of C, N and S after forest cutting. In the tropical semi-deciduous forest of Ghana, Cunningham (1963) found that clear felling of the vegetation decreased the total N by about 30% within a period of three years. On the other end, in the temperate climate N level in the soil remained more or less at the same level over hundred years in a temperate climate at Rothamsted, England (Daubenmire and Prusso 1963, Madge 1965).

Nevoboshi (1980) reported 10-25% reduction in soil N pools as a result of moderate to heavy thinning in teak plantations of Nigeria. The leaching losses of nitrate from the natural ecosystem is often increased following disturbance (Vitousek and Matson 1985).

A large number of studies have assessed the impact of whole tree harvesting (WTH) on soil nutrient reserves in forest ecosystem (Boyle and Ek 1972, Hornbeck and Kropelin 1982, Johnson *et al.* 1982, Hornbeck *et al.* 1983, Snyder and Harter 1985, Freedom *et al.* 1986, Huntington and Ryan 1990). The quantities of nutrient elements removed from the site with WTH are significantly higher than with stem harvesting only (Hornbeck 1977, Freedom *et al.* 1986). Studies of Boyle and Ek (1972) and Johnson *et al.* (1982) revealed that net N removal with WTH was small (less than 10%) compared to total N reserve in soil. Raghubanshi (1990) showed that harvesting of bamboo plantations deplete soil organic C and total N by about 13 and 20%, respectively.

Redistribution of N and C reserves in soil within the rooting zone is also influenced by tree cutting (Edwards and Ross-Todd 1983, Meentemeyer and Berg 1986). Sollins and McCorison (1981), Gholz and Fisher (1982) and Mattson and Swank (1989) reported increased translocation of N and C vertically downwards in the soil profile following cutting. Nitrate that percolates down in the profile is absorbed rapidly by the roots of developing vegetation. Pare and Cleve (1993) suggested that the decreased nutrient availability following tree cutting could be responsible for low aboveground biomass production on post-harvested white-spruce sites in interior Alaska. Chauvel *et al.* (1991) reported that deforestation of the forest in Central Amazon led to a dramatic modification in the chemical composition of the clay latosols influencing relative distribution of the pore size in soil, which was crucial for determining the water availability to the plants.

CARBON, NITROGEN AND PHOSPHORUS CYCLING

Deforestation causes increased loss of carbon, nitrogen, phosphorus and sulphur (Eyre 1968). As much as one-half of the organic carbon stored in the aboveground and belowground compartments of the forest ecosystems may be lost in gaseous and particulate forms following deforestation (Vitousek 1984). Alteration in the major ecosystem processes which brings about organic carbon loss from the system are (a) harvesting and burning of dry matter leading to CO_2 release, (b) decrease in production of wood and roots causing reduction in organic carbon addition to the soil, (c) accelerated decomposition and mineralization after canopy removal, and (d) increased particulate transport due to enhanced erosion especially from the sites having steeper slopes.

Cycling of nitrogen, which is probably the most competed for nutrient, is relatively closed in undisturbed forests (Eyre 1968). The internal soil-plant-microbe cycle in most forests involve 10-30 times more nitrogen than annual nitrogen inputs or outputs (Rosswall 1976). In aggrading forests, however, annual inputs generally exceed annual outputs (Likens *et al.* 1977). Deforestation disrupts soil-plant-microbe cycle and forces many deviations in nitrogen dynamics by influencing the rate of mineralization and fate of the end products. The mineralized nitrogen may be (a) held for varying durations at the site due to microbial immobilization, (b) lost to atmosphere through ammonia volatilization and N_2 and N_2O production during denitrification, and (c) lost as dissolved organic nitrogen or nitrate through deep seepage and runoff. Deforestation induces changes in transformations and storages of nitrogen in the forest ecosystems, contribute significantly to poor plant growth, and produce deleterious effects in downhill streams, and human health in adjoining areas due to leaching of nitrate from the forest ecosystem (Magee 1977).

Effect of deforestation on cycling of phosphorus differs considerably from that of carbon and nitrogen cycling. Phosphorus does not have any significant gaseous phase and its supply in available forms comes from solubilization of immobilized forms and rock weathering (Lal 1987). Thus, phosphorus losses following deforestation occurs mainly through the removal of forest products and particulate transport to streams and lakes.

Interactions of carbon, nitrogen and phosphorus cycles in forest ecosystem (Vitousek 1984) is also influenced by deforestation. For instance, availability of nitrogen and/or phosphorus may control the rate of carbon fixation and organic matter accumulation. Phosphorus availability may affect nitrogen fixation rate and carbon:nitrogen ratio in the litter may influence its decomposition rate and net nitrogen mineralization (Roy and Singh 1995).

RECOVERY OF DEGRADED FOREST ECOSYSTEMS

Regrowth of vegetation on disturbed forest sites is regulated by a number of factors. Buschbacher *et al.* (1987) have given a comprehensive list of factors which influence this process. The notable among them are, competition, seed dispersal, seed predation, seedling herbivory, mycorrhizal association, soil compaction, and water stress and nutrient availability.

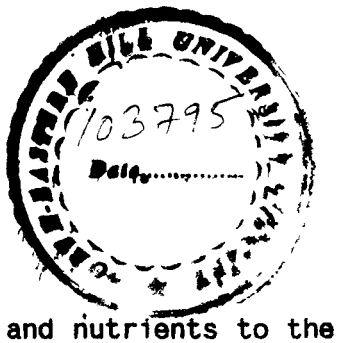
In most cases of forest secondary succession after clear felling, net ecosystem production (NEP) is negative immediately after the disturbance, and nutrient output rates generally exceed the input rates (Gorham *et al.* 1979). Negative NEP results from higher organic matter losses due to decomposition and export compared to the assimilation by the regenerating vegetation. Later during reorganization phase, the regrowing forest tends to compensate organic matter loss and reduces nutrient output. This is

followed by the aggradation phase of the forest recovery which is characterised by rapid accumulation of plant biomass and soil organic matter, and redistribution of nutrients in the ecosystem components (Odum 1969, Borman and Likens 1979). The pace of the aggradation phase depends mainly on the reconstruction of photosynthetic structure of the forest and restitution of the nutrient cycles. Likens *et al.* (1978) studied recovery pattern of different nutrients in northern hardwood forest and reported that the net loss of calcium and potassium continued even after seven years of recovery, but aggradation of nitrogen began only after four years of disturbance. They emphasised that development of the litter layer, associated decomposition subsystem and microbial biomass are important steps in the reestablishment of the forest nutrient cycles.

Analysis of successional sequence of higher plants during post-disturbance period helps in understanding the recovery mechanism (McIntosh 1980). Since it is rarely possible to follow succession in disturbed forests from its initiation to the climax stage at the same site, the convenient alternative is to investigate separate sites in the same region where different lengths of time have elapsed since the specific disturbance (Drury and Nisbet 1973, Austin 1981). The time interval between dates of disturbance and the investigation represents the duration for which secondary succession has occurred. Following this assumption, Pandey and Singh (1984/1985) and Singh and Tripathi (1992) studied the vegetation recovery mechanism in disturbed moist temperate oak forest ecosystem in Kumaun Himalayas. In north-east India, Toky and Ramkrishnan (1983) studied the community composition and biomass, productivity and nutrient cycling in successional communities on jhum fallows of different ages.

Aweto (1981) argued that soil plays a key role in vegetation development on disturbed site by providing favourable microenvironmental conditions for growth and establishment of plants. Plants in turn add

organic matter and nutrients to soil through aboveground and belowground litter production and decomposition. Apart from litter, microbial biomass in soil also acts as an important reservoir of nutrients (Jenkinson 1978, Singh *et al.* 1989, Henrot and Robertson 1994).



LITTER DYNAMICS

LITTERFALL

Litter is the major pathway for supplying energy and nutrients to the decomposer sub-system in the forest ecosystem. The role of litter in forest ecosystem function has long been recognised and a large number of studies have been carried out in different forest ecosystems all over the world. Since the classic work of Ebermayer (1876) huge amount of data on litterfall has been generated from all major types of terrestrial ecosystem of the world. These results have been reviewed from time to time by many workers like Bray and Gorham (1964), Jordan (1971), etc. While most of the studies on litterfall have been done in the temperate forests (Jenny *et al.* 1949, Laudelot and Meyer 1954, Klinge and Rodriques 1973, Malaisse *et al.* 1975), tropical and subtropical forest ecosystems have also been studied from this point of view (Singh 1968, Edwards 1977, Saxena *et al.* 1978, Tanner 1980, Pandey *et al.* 1980, Boojh and Ramakrishnan 1982, Singh and Singh 1987, Singh 1990, Khiewtam and Ramakrishnan 1993, Chandrasekhara and Ramakrishnan 1994, Couteaux *et al.* 1995).

The litterfall pattern varies greatly in different climatic zones of the world (Vogt *et al.* 1986). In the deciduous forest of northern hemisphere, leaf-fall is concentrated during short autumn season with a pronounced peak in October-November (Anderson 1973). In Eucalyptus forests of Australia, maximum litterfall occur in summer (O'connel and Menage 1982). In humid tropical forests, litterfall is more or less continuous all

around the year with a tendency for extensive falls during or after relatively short dry period (Laudelot and Meyer 1954, Nye 1961, Madge 1965, Hopkins 1966, Rodin and Brazilevich 1967). A distinct seasonal pattern with peak litterfall during dry period has also been reported from the tropical dry deciduous forests of north India (Singh 1968, Pandey *et al.* 1980, Prasad Ram and Mishra 1985 and Singh and Singh 1987), tropical dry evergreen forests of south India (Visalakshi 1992 & 1993) and in the subtropical humid forests of north-east India (Singh and Ramakrishnan 1981, Toky and Ramakrishnan 1983, Das and Ramakrishnan 1985, Singh 1990, Khiewtam and Ramakrishnan 1993).

Seasonality in litterfall largely depends on the factors which control leaf senescence and abcission in the tree species. This aspect has been discussed in detail by Addicott (1968), Whitmore (1975) and Jackson (1978). Among the climatic variables, rainfall (Brassel *et al.* 1980), wind velocity (Hopkins 1966, Toky and Ramakrishnan 1983, Das and Ramakrishnan 1985), and maximum temperature (Turnbull 1983) play more important role in litterfall in forest ecoystems. However it is not correlated with any single environmental factor (Hopkins 1966, Singh and Gupta 1977, Klinge 1977, Facelli and Pickett 1991).

The predominant role of climate on litter production has been revealed by Bray and Gorham (1964). According to them, mean annual litterfall in forest ecosystems gradually increases from artic-alpine zone to equatorial regions. It has also been shown that the rate of litterfall decreases with the decrease in light intensity during the growing season along a worldwide gradient (Jordan 1971). Apart from climate, a number of other factors such as topography, vegetation type, species composition etc. which influence litter production have been dealt-with in length by Bray and Gorham (1964), Vogt *et al.* (1986) and Facelli and Pickett (1991).

Leaf litter constitutes the major portion of the total litterfall all over the world. Its contribution ranges between 60 and 70% of the total litter production (Bray and Gorham 1964, Meentemeyer *et al.* 1982, Rout and Gupta 1990a,b). In the tropical forests, leaf litter production ranges from 4.4 to 6.9 t ha^{-1} (Klinge 1977, Rodrigues 1968, Cornforth 1970, Edwards 1977, Tanner 1980, Toky and Ramakrishnan 1983a).

Accumulation and turnover of woody litter on the forest floor have been poorly understood except in a very limited number of forest types (Satchell 1974). The woody litterfall in forest ecosystem is generally characterised by a large year-to-year variation. This is mainly due to the non-periodic occurrence of high wind force during when dead wood materials are dislodged. However, other factors also act in a complex way creating a non-seasonal pattern in woody litterfall. In temperate forests, Gosz *et al.* (1972) have reported a bimodal pattern of wood fall. They also pointed out that branch fall is apparently a good indicator of storm intensity. In a moist-semi-deciduous forest of tropical west Africa (John 1973), the peak wood fall corresponded to the dry periods when trees are expected to be under greater water stress. He further emphasised that a complex combination of intrinsic and extrinsic factors influence time and triggering off of the litterfall. Addicott (1968) noted that almost all discrete parts of higher plant species are abscissed. However, abscission of organs other than leaves and to a lesser extend flower and fruits have received only sporadic attention (Klinge 1977, Boojh and Ramakrishnan 1982, Singh 1990, Khiewtam and Ramakrishnan 1993). Bray and Gorham (1964) estimated that on an average, woody litter amounts to about 30% of the total annual litterfall. In temperate forests, 19-39% of the total annual litterfall is formed by the woody fraction. This means that a considerable amount of litterfall accumulates as dead wood on the forest floor, constituting a significant nutrient and energy reservoir. The non-leaf

litter accounts for 33% of the total litterfall in most forests, sometimes as much as 50% in climax forests (Kira and Schidei 1967, Vogt *et al.* 1986).

Much attention has been paid in developing suitable and reliable techniques for studying the decomposition of litter and the rate of decomposition of different types of plant litter in different climatic zones (Anderson* 1973, Wood 1974, Das and Ramakrishnan 1985, Singh 1990, van Wesemael 1993). Many of these studies have analysed the organic and inorganic constituents of litter and have measured the micro-climatic variables affecting litter decay at the study site. The importance of C:N ratio and lignin content in controlling decomposition rate has been studied by Laishram and Yadava (1988) and Bloomfield *et al.* (1993). Meentemeyer (1978) examined the role of climatic factors and lignin content of litter on its decomposition. Anderson (1973), Laishram and Yadava (1988), Elliott *et al.* (1993), Arianoutsou (1993) and Bloomfield *et al.* (1993) have clearly established the importance of chemical composition in decomposition of leaf litter. Reports indicated that the live roots may accelerate the decomposition rate and nutrient mineralization of aboveground litter (Cuevas and Medina 1988). These results are contrary to those reported by Gadgil and Gadgil (1975) who found that litter decomposition rates were suppressed by live mycorrhizal roots. Vogt *et al.* (1991) have reported that in temperate climate, mycorrhizae do not appear to reduce decomposition rates of litter, rather they contribute a sizeable quantity of easily decomposable material to the detritus cycle. Role of soil fauna in litter decomposition has been studied by Madge (1965). Termites digest large quantities of woody litter in tropical ecosystems (Lee and Wood 1971), while fungi are the main decomposers of leaf litter in the tropical rain forests (Fittkau and Klinge 1973, Swift *et al.* 1979). Nutrient cycling through decomposition of leaf and woody litter in the tropical and temperate forests has been studied by Nye (1961), Olson (1963), Bray and

Gorham (1964), Ovington (1957), Bernhard (1970), Anderson (1973), Singh and Ramakrishnan (1983), Vogt *et al.* (1986) and Vogt and Bloomfield (1990).

The most striking feature of a woodland community from the nutrient circulation point of view is the annual return of nutrients to the soil through litterfall. In this context, the amount and quality of nutrients in litter is of vital importance for the exchange of organic and inorganic materials between living organisms and soil. Therefore, nutrient content of the litter both in the tropical and temperate forests has been analysed by Laudelout and Meyer (1954), Nye (1961), Singh and Singh (1987), Singh and Ramakrishnan (1983), and Visalakshi (1993). Vogt *et al.* (1986) in their comprehensive review paper on detrital nutrient dynamics, calculated that about 80-90% of the total annual return of nutrients occur through annual leaf-fall.

LITTER DECOMPOSITION

The release of nutrients from decomposing litter is one of the most important processes contributing to nutrient cycling in forest ecosystem. For this reason, a large number of studies have been carried out on litter decomposition in forest ecosystems all over the world. Findings of most of the studies have been reviewed by Singh and Gupta (1977), Vogt *et al.* (1986) and Couteaux *et al.* (1995).

Studies on litter decomposition are confined mainly to leaf litter, although woody litter also forms a significant proportion of the detritus on the forest floor (Vogt *et al.* 1986). Woody litter decompose very slowly than leaves. The decomposition of woody litter has been studied by determining loss in weight and CO_2 evoloution as measures of decomposition rate (Facelli and Pickett 1991). Anderson and Swift (1983) studied the decomposition process and nutrient loss from leaf litter in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak and concluded that decay and nutrient cycling processes are more complex and

variable than is generally reported in the ecological literature of the humid tropics. Upadhyay (1993) studied the decomposition dynamics of thirteen tree leaf litter in Himalayan forest ecosystem. He reported that the decay rate mostly depends on the seasonal cycle prevailing in the region, and on the initial chemistry of the plant material.

LITTER DYNAMICS IN SUCCESSIONAL COMMUNITIES

The role of litter in organic matter and nutrient dynamics in secondary successional forest communities has been studied by Odum (1960), Gaur and Pandey (1978), Vogt *et al.* (1983), Das and Ramakrishnan (1985), Singh and Ramakrishnan (1983) and Chandrashekara and Ramakrishnan (1994). These studies have been carried out in the old-field communities, slash/burn agricultural lands, jhum fallows and landslided hills. Recently, Mattson and Smith (1993) studied the dynamics of litter and its contribution to total soil metabolism in regenerating forest stands following tree cutting in the temperate climate. In the tropical forests Golley *et al.* (1974) emphasized the importance of leaf-fall during early stages of succession. Gomez Pompa (1974) and Ewel (1976) studied the rate of litterfall and nutrient input in several seral communities in the humid tropics and affirmed the importance of litter turnover in community development during succession.

FINE ROOT DYNAMICS

Roots, especially the fine roots (<2 mm diameter) contribute significantly to the soil organic pool. Input of root tissue into the soil can occur from root respiration, losses of mucilage, exudation of carbon compounds (Smith 1976, Rovira *et al.* 1979), sloughing of root tissues during root senescence, autolysis of cortical tissues during conversion of fine roots to the older ones with secondary thickening, release of

epidermal and cortical tissues, senescence of woody and fine roots, and root tissue loss or damage due to animal grazing or microbial root diseases (Waid 1974). Of all these processes, root mortality is generally assumed to contribute more to the soil organic matter. Therefore, any ecosystem level study of carbon and nutrient cycles without considering the role of roots is incomplete (Vogt *et al.* 1991).

ROOT CATEGORIES

Based on the size and morphology, roots have been divided into 3 categories *viz.* coarse structural supportive roots having lower turnover rates, smaller diameter roots which act as the "conduits" having intermediate turnover rates, and fine or mycorrhizal roots (<2 mm diameter) having higher turnover rates (Vogt *et al.* 1989).

The structural parts of the root system accumulate about 30% of the biomass of trees in forest ecosystems (Ovington 1957). The turnover of structural support roots is very infrequent and usually occurs when the entire plant dies. The input of organic matter and nutrients by such roots to the soil is dependent on the site disturbance cycles (*i.e.* hurricances, high winds, etc.) that cause tree fall, competitive exclusion of non-dominant trees during canopy closure (Vogt *et al.* 1986), and mortality due to root rot or other pathological agents (Wargo 1977, Chavez *et al.* 1980, Shaw 1980). Since the decay rates of structural roots are slow, their contribution to soil organic matter pool continues for a long period of time (Harmon *et al.* 1986). Turnover of conduit roots is faster than the structural roots. But, since this conduit-root fraction is not usually included in root studies or obtained using sequential coring techniques (Vogt and Persson 1988), little information exists that quantify their contribution to soil organic matter and decomposition processes.

In contrast to conduit and structural roots, the turnover of fine roots is rapid, in some ecosystems within few weeks only (Vogt and

Bloomfield 1990). But at microsite levels, fine roots have been observed to live from 2 years (Lyr and Hoffman 1967) to 12 years (Kolesnikov 1971). The quantity and activity of smaller diameter roots are of primary importance in water and nutrient supply to plants (Lyr and Hoffman 1967). The contribution of fine roots to total root mass is low (9-11%, Vogt *et al.* 1991), but lengthwise, fine roots are the major contributor to tree root system. Lyr and Hoffman (1967) showed that fine roots (<1 mm diameter) may constitute about 86-99% of the total root length in trees.

FINE AND COARSE ROOT BIOMASS

Root biomass estimates are available from forest fallows in Congo (Bartholomew *et al.* 1953), old secondary forest in Nigeria (Greenland and Kowal 1960), oil palms in Nigerian plantations (Rees and Tinker 1963), Ivory Coasts (Huttel 1969) and miombo forests in Zaire (Malaissee *et al.* 1972). Few studies have been carried out in south-east Asian forests (Ogawa *et al.* 1961 & 1965, Kira and Shidei 1967). The root mass values from Central Amazonia, Brazil are reported by Klinge (1973), Fittkau and Klinge (1973) and Klinge *et al.* (1975). Ramakrishnan and Singh (1983), Khiewtam and Ramakrishnan (1993) have estimated the root biomass in mature subtropical humid forests of north-east India. Singh and Singh (1981) and Srivastava *et al.* (1986) have studied the fine-root growth dynamics in teak plantations of north India. Similar studies have also been done in tropical dry evergreen forests of south India (Parthasarathy 1987, Visalakshi 1994).

Lyr and Hoffman (1967), Kostler *et al.* (1968), Sutton (1969), Herman (1977), Santantonio *et al.* (1977), and Vogt *et al.* (1986, 1991) have reviewed the literature relating to the growth of tree roots. In spite of all these research, our knowledge about root growth is limited either to seedlings or young trees planted in isolation. Characteristics of roots of seedlings or young trees grown in isolation differ fundamentally from large trees in a forest, and it is difficult to extrapolate from one to another.

There are relatively fewer studies in the forest ecosystem mainly because of methodological difficulties involved in quantitative assessment of roots. Most studies on roots are confined to temperate zones and very few are available in the tropics (Stark 1978, Singh and Singh 1981, Khiewtam and Ramakrishnan 1993).

FINE ROOT PRODUCTION

Fine roots of the temperate forests undergo large seasonal variation in growth activity (Santantonio *et al.* 1977). Different authors have observed peak root growth in different seasons. One, two or more peaks during an annual cycle have been reported by many workers (Ford and Deans 1977, Harris *et al.* 1977, Persson 1978). Lyr and Hoffman (1967) and Vogt *et al.* (1981, 1991) reported that root growth can occur during winter in evergreen species and during rainy season in deciduous species.

Many workers have concluded that root growth occurs independently of shoot growth (Sutton 1969) and the periodicity of root activity is largely influenced by the conditions of soil and climate. Low moisture and low soil temperature during winter are widely considered to have an adverse effect on root growth (Lyr and Hoffman 1967, Herman 1977). Fine roots are killed periodically by drought and frost, but they keep on regrowing continuously (Persson 1978).

Deans (1981) showed a positive relation between soil temperature and root growth in *Picea sitchensis* forests, but this relation was overridden and halted by low soil moisture later in the season. In addition to the soil temperature and moisture, some other factors such as growth regulating substances, carbohydrates availability, respiration rate, symbiotic and competitive relationships (Lyr and Hoffman 1967, Sutton 1969, Persson 1983) also determine root productivity. Kolesnikow (1971) suggested from his studies on apple trees, that death and renewal of fine roots in trees is a cyclic process and bears resemblance to leaf shedding in evergreen plants.

He concluded that the absorptive roots constantly invade new and fresh soil layers throughout the growth period, and their life span and activity is short, usually few days only.

Studies dealing with production and turnover of fine roots in forest ecosystem have started relatively recently, as a part of large scale ecosystem level studies under the International Biological Programme (Harris *et al.* 1980). Results of all such studies reveal that fine roots serve as an important carbon pathway in temperate forest ecosystem (Harris *et al.* 1980, Persson 1983, Fogel 1983). Findings of several studies suggest that the fine roots contribute significant amount of detritus to the decomposition system (Harris *et al.* 1977, Persson 1978, Grier *et al.* 1981, Keyes and Grier 1981, McClaugherty *et al.* 1982, Vogt *et al.* 1982, Bloomfield *et al.* 1993). At the individual plant level, a multiple of abiotic factors (e.g. nutrient availability, site temperature and moisture conditions) and biotic factors (e.g. phenology, species and age) influence total carbon fixation and partitioning to roots (Vogt and Bloomfield 1990). Ecosystems that have low availability of water, light or nutrients or low soil temperature allocate greater amount of organic matter to fine roots than the foliage (Lyr and Hoffman 1967, Rosberg *et al.* 1981, Coutts 1982, Ingestad 1979, Vogt *et al.* 1986). A strong negative correlation between actual estimates of root production and rates of nitrogen cycling, measured as N returned in litterfall in temperate needleleaved and broadleaved forests has been reported by many workers (Nambiar 1983, Silver and Vogt 1993)). Furthermore, increasing soil nitrogen availability with fertilizer application generally decreases root biomass and production in cold temperate forests (Axelsson 1981, Alexander and Fairley 1983, Blaise and Garbaye 1983, Vogt *et al.* 1983, Aber *et al.* 1985). In general, poorer the nutrient availability of a site, greater will be the proportion of belowground input to total detrital production (Vogt *et al.* 1986 & 1991).

Data on the above and belowground contribution to detrital mass suggest that deciduous species contribute more to the aboveground than belowground detrital pool, while evergreen species add twice as much root material to the detrital mass compared to the deciduous species growing at similar latitudes (Vogt *et al.* 1986). Vogt *et al.* (1991) reported that in a sub-alpine *Abies amabilis* stand in Washington the patterns of nutrient accumulation, circulation and resorption were very different between foliage and root tissues, mostly due to selective elemental accumulation in the roots.

Estimates of the proportion of total carbon annually added to the soil by way of root mortality and decay are highly variable. The values reported by different workers are 25-36% (McClaugherty *et al.* 1984), 42.2% (Edwards 1977), 59-67% (Vogt *et al.* 1982), 54-81% (Gholz *et al.* 1986) and 78-84% (Fogel and Hunt 1983). The variability in the contribution of roots to soil organic matter creates difficulty in generalizing their importance in a given ecosystem. The role of fine roots in organic matter and nutrient dynamics in successional communities is not fully understood, although a few notable works have been done by Berish (1982), Vogt *et al.* (1983) and Persson (1983). In India, such studies are confined to teak plantations of different ages (Srivastava *et al.* 1986) in north India, mature tropical evergreen forest in south India (Visalakshi 1994) and mature sacred grove (Khiewtam and Ramakrishnan 1993) in north-east India.

FINE ROOT CHEMISTRY AND NUTRIENT FLUX

The most significant difference between the chemistry of fine root and foliage tissues lies with lignin (Vogt *et al.* 1991). The fine roots have a lignin content of the order of 50% which is twice the proportion of lignin present in the leaves of *Pinus sylvestris* (Berg and Staff 1981, Persson 1982, Berg 1984), *Pseudotsuga menziesii* (Vogt *et al.* 1991) and *Abies amabilis* (Vogt *et al.* 1983). Concentration of lignin in roots decrease

dramatically with the increase in diameter in *Pinus sylvestris* (Berg 1984). However, this is not true for *Abies amabilis* (Vogt *et al.* 1983). Lignin does not appear to vary between live and sencesced tissues (Vogt *et al.* 1991, Silver and Vogt 1993). The significance of higher lignin concentration in the fine roots is not immediately clear.

It has been shown that the nutrient status of a site can modify plant chemical composition (Horner *et al.* 1987). For instance, if carbon is plentiful relative to nitrogen, the surplus carbon provides the reductant needed to synthesize larger amounts of carbon-based compounds such as lignin, tannins, phenols and terpenoids (Loomis 1953, McClure 1979, Waring *et al.* 1985).

Differences in resorption of nutrients from roots and foliage influence their initial chemical quality. Generally, nitrogen retranslocation from senescent fine roots is small (McClaugherty *et al.* 1982, Nadelhoffer *et al.* 1985). In the subalpine stand studied by Vogt *et al.* (1991), Al accumulation in plant roots appeared to modify the Mg, Mn and Ca contents of roots. Ca, Mn and Zn were, however, resorbed from root tissues but not from the foliage prior to the senescence. This resulted in very different elemental levels of the detritus depending on whether it was composed of foliage or roots. Studies reveal that high levels of nutrient resorption occur even in the presence of well developed mycorrhizal roots (Silver & Vogt 1993). In *Abies amabilis* stands, almost all roots were associated with mycorrhizal fungi, yet 60-70% of the macronutrients were resorbed prior to senescence (Meier *et al.* 1985, Vogt *et al.* 1989). In addition to the changes in nutrient content, mycorrhizae also affect the chemical composition of roots. Krupa and Fries (1971) reported that terpenes and sesquiterpenes are higher in mycorrhizal roots. The influence of mycorrhizae on lignin content is probably indirect and related to the mycorrhizal modification of plant nutrient status (Meier *et al.* 1985).

Fine roots often have higher concentration of nutrients than the foliage (Meier *et al.* 1985). Nambiar (1987) reported minor monthly variation in nutrient concentration in fine roots without any seasonal pattern. In *Pinus radiata*, N and P concentrations were strongly related to the root diameter but the difference between live and dead root fractions was insignificant (Nambiar 1987). Silver and Vogt (1993) reported similiar findings from a subtropical wet forest ecosystem. In temperate forests, the mean allocation of N to fine roots, leaf litter and perennial tissues were 48, 24 and 16%, respectively, while the corresponding allocation of net primary production was 28, 26 and 47% (Nadelhoffer *et al.* 1985). Meier *et al.* (1985) estimated that in *Abies amabilis* stands the allocation of currently absorbed N and P to the belowground parts was about 2-3 times higher than the aboveground parts.

The nutrient stock in fine roots is of considerable importance in nutrient cycling of forest ecosystem, especially in the humid tropics where they may determine the relative fragility of the ecosystem. Root turnover contributed 29 to 255 kg N ha^{-1} yr^{-1} to the forest floor and soil horizon (Vogt *et al.* 1986). Available literature on nutrient dynamics of fine roots have been compiled by Vogt *et al.* (1986 & 1991). They indicated that except for cold temperate broadleaved deciduous forests, more N was contributed to the ecosystem through fine root turnover than aboveground litterfall. In the tropical broadleaved evergreen, warm temperate broadleaved deciduous and cold temperate needleleaved evergreen forests, 53, 18 and 58%, respectively, more N was circulated through fine roots than aboveground litterfall. Similar inputs of P occurred through litterfall and fine root turnover in warm temperate deciduous forests, while 90% more P was added with the turnover of fine roots than litterfall in cold temperate needleleaved evergreen forests.

FINE ROOT DECOMPOSITION

Fogel and Cromack (1977), Fogel and Hunt (1979), Berg and Staff (1981), Persson (1982), Vogt *et al.* (1983), Berg (1984), McClaugherty *et al.* (1984), Gholz *et al.* (1985, 1986) and Bloomfield *et al.* (1993) have studied root decomposition. A variety of field techniques like litter bags (Berg 1981, McClaugherty *et al.* 1982), modified trench-plot design (McClaugherty *et al.* 1984), budget approach which includes changes in live and dead root categories (Santantonio *et al.* 1977), laboratory incubation studies (Herman *et al.* 1977) and changes in specific gravity for coarse roots (Yavitt and Fahey 1982), have been employed to estimate root decay. Fine roots decomposition calculated from litterbag studies tends to be much slower (usually less than 30% per year) than those calculated by other techniques. The trench plot studies generally gave decay rates twice as fast as the litterbag technique (Vogt *et al.* 1993). Using budget method, Santantonio and Hermann (1985) estimated decomposition rate of over 100% during a one year period for Douglas-fir fine roots. Roots of larger diameters decomposed at slower rates than smaller diameter roots in Swedish forests (Berg and Staff 1981, Persson 1982). McClaugherty *et al.* (1982) have reported slower rate of decomposition of very fine roots than the next larger size in the litterbags, but Gholz *et al.* (1986) who used the trench plot technique, reported faster decomposition of very fine roots.

From the literature review presented above, it is clearly evident that studies on the relative importance of litter and fine roots in enrichment of soil during recovery of disturbed forest ecosystem are limited. Further, their role in organic matter and nutrient input, their accumulation and turnover in soil have not been investigated in detail during regrowth of disturbed humid subtropical forest ecosystem.

CHAPTER 3

STUDY SITE

* LOCATION
* CLIMATE
* GEOLOGY
* SOIL
* VEGETATION

LOCATION

The study was conducted in three adjacent forest stands located at Upper Shillong (latitude 25°34'N, longitude 91°56'E, altitude 1900 m asl), 12 km south of Shillong, the capital of Meghalaya, India (Figure 3.1). All three stands are parts of a subtropical humid forest which once covered approximately 100 sq.km area and had the status of a sacred grove ('Shillong Peak Sacred Grove'). The grove is said to be the abode of benevolent spirit, Lei Shillong, the greatest of the Khasi spirits (Mitra and Pal 1994). According to local tradition and beliefs, the grove was preserved from time immemorial. Unfortunately during last two decades the beautiful dense broadleaved forests has been disturbed due to gradual erosion in religious beliefs of the tribal people. As a result, the sacred grove was disturbed from time to time by selective cutting of trees.

The present study was carried out in three disturbed stands where the canopy was harvested about 7, 13 and 16 years ago. These were designated as stands I, II and III, respectively. The stands covered an area of 25-40 ha each and were located on gentle south to south-east facing slopes (6-13°).

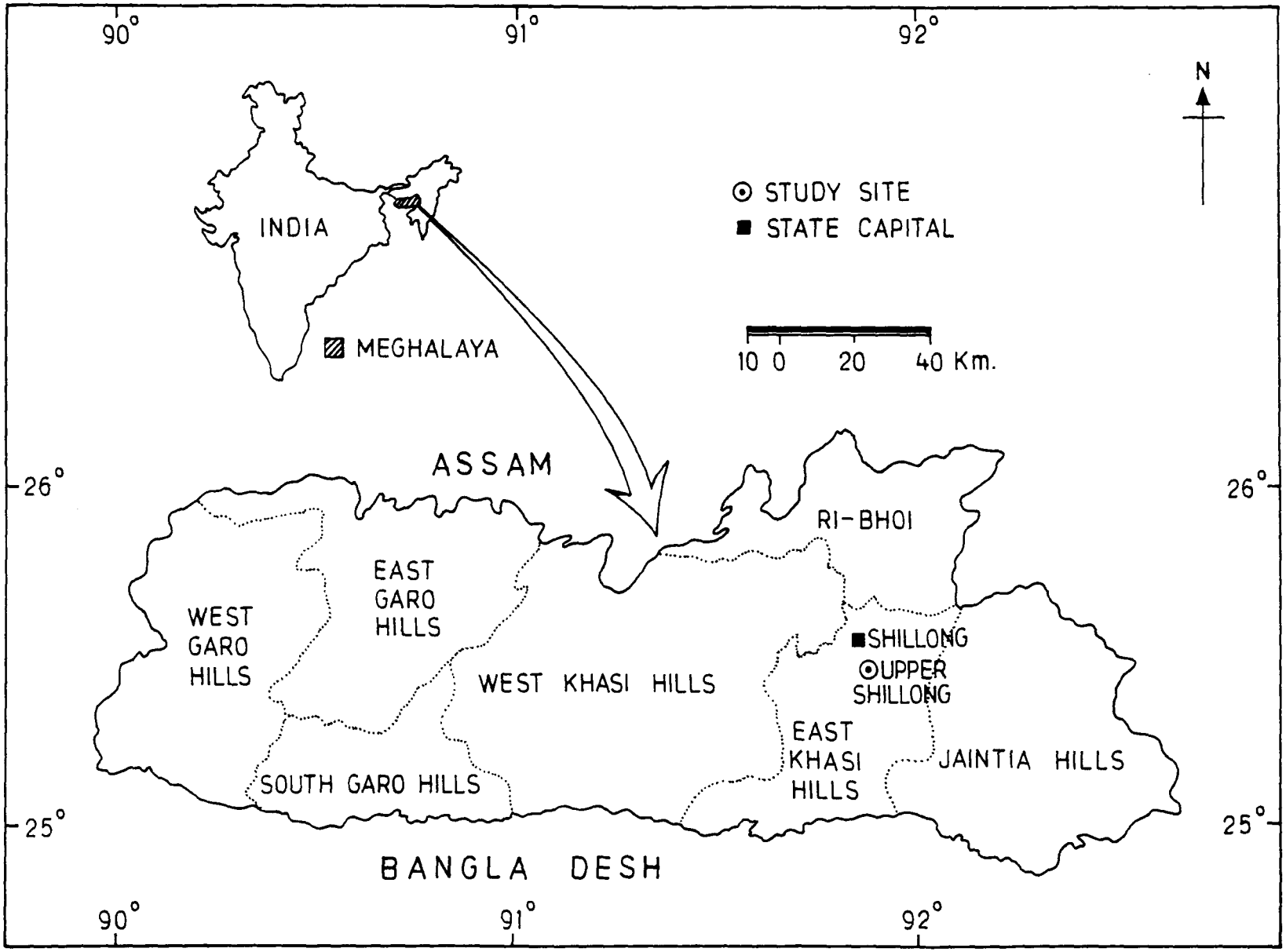


Figure 3.1. Map showing geographical location of the study site.

CLIMATE

The climate of Meghalaya is monsoonic with an average annual rainfall of 2500 mm, distributed over seven months of the year. About 85% of the total annual rainfall occurs during mid-May to September (rainy season). October, and mid-November with occassional rainfall represents autumn, followed by winter during mid-November to February. The period from March to mid-May with small amount of rainfall represents the spring season.

The mean minimum and maximum temperatures during winter are 5 and 17°C respectively, while the corresponding annual means are 13 and 21°C. Monthly rainfall pattern and maximum and minimum temperatures during the study period is shown in Figure 3.2. The annual rainfall was 2094 mm and 1565 mm during 1993 and 1994, respectively. Relative humidity varied between 50 and 80% during the spring and more than 90% during the rainy season (Figure 3.3).

GEOLOGY

The height of Shillong plateau is over 1500 m above the alluvial plain of the Brahmaputra valley. Its southern slope are abrupt scarps following fault zones rejuvenated in the late Tertiary (Gansser 1964). In the north, the plateau slopes towards the Brahmaputra river with a cover of alluvium. The Archaean rocks of the Shillong plateau can be subdivided into Shillong group and older gneisses and granites. The Shillong group outcrops along southern and eastern sides of the uplift and consists of an unknown thickness of mica, chlorite and hornblende schists, as well as amphibolites representing partly altered basic rocks. With a steep but comfortable contact they adjoin micaceous quartzites with intercalated conglomeratic layers, reported to be somewhat younger in age (Anonymous 1937-38).

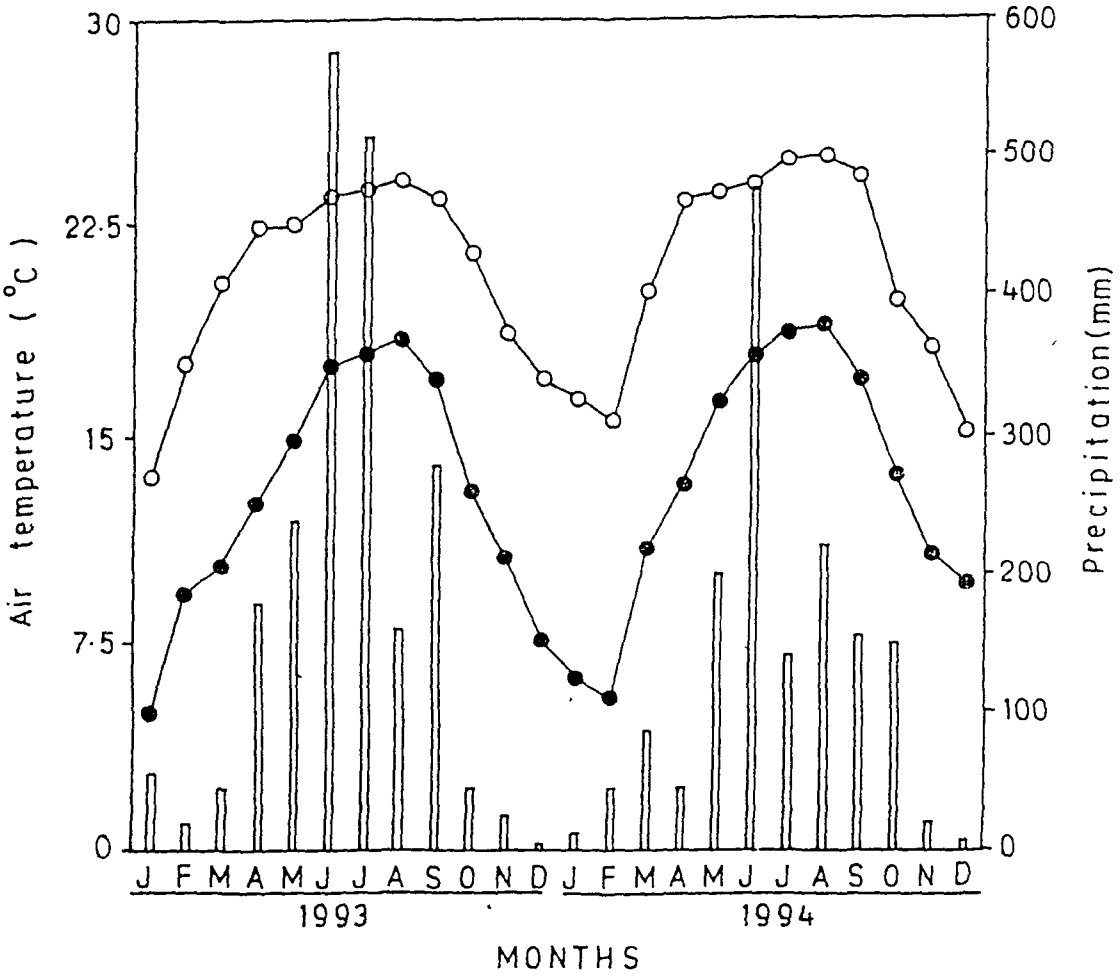


Figure 3.2. Climatograph of the study area during 1993-94.
(□) total monthly rainfall,
(o) mean monthly maximum and (●) minimum temperatures.

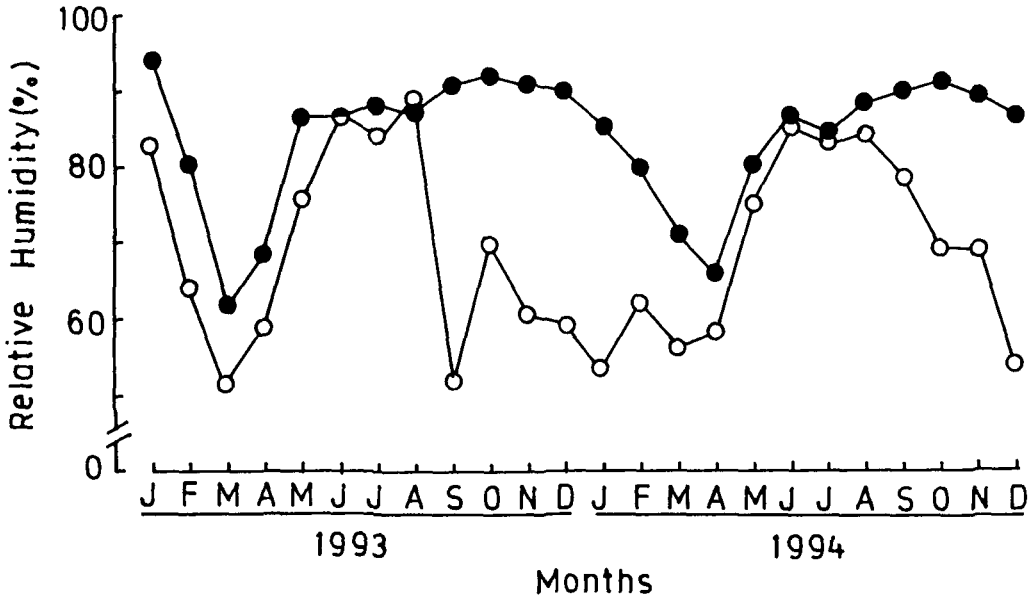


Figure 3.3. Mean monthly variation in the atmospheric relative humidity of the study area.
(o) during day and (●) night hours.

A major portion of the Shillong area is formed by the Archaean gneisses and granites. The gneisses are finely banded, grey to pink in colour and contain microcline, biotite, subordinate quartz and plagioclase. The intrusive granites are mostly porphyritic with large flesh-coloured microclines, some acid plagioclase, orthoclase and biotite. The granites also intrude the Shillong schists, but are less frequent in the Shillong quartzites (Pascoe 1950).

SOIL

The soils of the Shillong plateau are derived from the underlying gneissus, shcists and granites. They have been grouped under latosol (oxisol) type (Pascoe 1950). Soils are red to deep brownish in colour, sandy to clay loam in texture and acidic to neutral in reaction. The range of variation in soil pH, organic matter and nutrients as reported by several workers for different parts of Meghalaya are, soil organic matter: 2.5-9.9% , Nitrogen: 0.1-0.7%, Available-P: 0.5-10 $\mu g\ g^{-1}$ and pH: 4.9-7.4

The soil at the study site varied from sandy loam in the 7-year old stand to clay loam in the 16-year old stand. The water holding capacity, organic matter content, and total nitrogen and available-P concentrations were within the range reported above and they showed an increasing trend from the 7- to 16-year old stands. Soil pH ranged from 4.4 to 5.9.

VEGETATION

The forest at Upper Shillong had the status of a sacred grove (namely the 'Shillong peak sacred grove') until 1982 (Boojh and Ramakrishnan 1982). The evergreen oak forest has been grouped by Champion and Seth (1968) under subtropical wet hill forest type ($8B_2$). *Quercus* spp., *Rhododendron* spp.,

Plate 3.1. The 7-year old regrowth
(a) Over-view,
(b) A young regenerating *Quercus dealbata*
(c) Ground vegetation

Plate 3.2. The 13-year old regrowth
(a) Over-view,
(b) & (c) Sprouting *Quercus dealbata*

Plate 3.3. The 16-year old regrowth
(a) Over-view
(b) Coppicing of *Quercus dealbata*
(c) Sprout growth in *Schima khasiana*

Schima spp., *Bucklandia* spp., *Ficus* spp. etc., are dominant trees of the original forest. At present the original vegetation is confined to a small area and the rest of the forested area is covered by mosaic of successional plant communities developed after logging at different times in the past.

The 7-year old stand (Plate 3.1a) was dominated by young trees of *Pinus kesiya*, *Schima khasiana*, *Schima wallichi* and *Corylopsis himalayana*. A few sprouting stumps (*i.e.* coppice regeneration) of *Q.dealbata*, *Schima* spp. and *C. himalayana* having about 25cm DBH were interspersed in the stand (Plate 3.1b). The mean sprout diameter in the stand was 3.7 cm. Shrubs were represented by *Osbeckia stellata*, *Litsea elongata*, *Rhus semi-alata* and *Rubus ellipticus*. The ground vegetation was dominated by *Imperata cylindrica*, *Arundinella benghalensis* and *Eupatorium adenophorum* (Plate 3.1c).

The 13-year old stand (Plate 3.2a) was dominated by *Quercus dealbata*, *Castonopsis kurzii*, *P. kesiya*, *Myrica esculenta* and *L. khasiana* and shrub species like *L. elongata*, *O. stellata*, *Gaultheria fragrantissima*, etc. The average diameter of the sprouting stumps and the sprouts in this stand was 25 and 4.6 cm, respectively. The sprouts had grown to a height of *ca* 4 m (Plate 3.2b,c). The growth of ground vegetation was poor.

Q. dealbata, *Rhododendron arboreum*, *Quercus griffithii*, *S. khasiana* and *P. kesiya* were the dominant tree species in the 16-year old stand (Plate 3.3a). The average diameters of the sprouting stumps and the sprouts were 26 cm and 4.6 cm, respectively. Profuse growth of sprouts (mean height 4.6 cm) of the aforesaid species gave a dense canopied look to this stand (Plate 3.3b,c). The understorey was dominated by *L. elongata*, *Viburnum foetidum* and *R. semi-alata*. The ground layer was dominated by *Commelina benghalensis*, *Oxalis corniculatus*, *Gleichenia longissima* and *Ranunculus diffusus*. There was a heavy growth of epiphytic mosses and ferns in the stand.

CHAPTER 4

MICROCLIMATE AND SOIL NUTRIENT DYNAMICS

INTRODUCTION

Tree regeneration following disturbance in a forest community is influenced by temporal and spatial variations in a wide variety of microenvironmental factors (Thorhaug 1980). Due to inherant difficulties involved in ascertaining the importance of each microenvironmental factor in forest community dynamics, studies dealing with the changes in the microenvironmental conditions following a major or minor disturbance in the forest community are limited. Studies conducted on this aspect by Whitemore (1974), Brokaw (1985) and Barik *et al.* (1992) suggest that the prevailing microenvironmental conditions, especially air temperature and soil moisture regime strongly influence tree seedling regeneration in the forest after disturbance. Factors of soil complex such as pH, organic

matter and nutrient contents also influence plant growth and succession on degraded or disturbed lands (Aweto 1981, Pandey and Singh 1984/1985).

Loss of soil carbon content after forest cutting has been reported by Edwards and Ross-Todd (1983), Miller and Sirois (1986) and Nakane *et al.* (1986). Nutrient regeneration in soil during revegetation of forest fallows of different ages have been studied by Aweto (1981) and Pandey and Singh (1984/1985) in the tropical region and by Ramakrishnan and Toky (1981) and Mishra and Ramakrishnan (1983) in the humid subtropics of north-east India.

Selective cutting of the forest trees for meeting timber and fuel wood requirements of the local tribal communities is the common form of disturbance in the broadleaved forests of north-east India. Such harvests result in canopy opening, which allows increased light penetration and large input of green leaf and woody litter on the forest floor. Besides exposing the top soil layer to direct solar insolation, tree cutting operation often physically disturbs the forest floor. A recent review article by Congdon and Herbohn (1993) on the ecological sensitivity of Australian rain forests to selective logging indicates that relatively few studies have been carried on habitat recovery in the tropical forests.

The present chapter deals with the microclimatic conditions and soil characteristics of forest stands under consideration of the present study.

METHODS

MEASUREMENT OF MICROCLIMATIC VARIABLES

The microclimate in the three stands was studied by measuring light intensity, relative humidity and air temperature in four different months *viz.* January, April, July and October, representing winter, spring, rainy and autumn seasons, respectively during 1993 and 1994. All three parameters were measured randomly at ten places, close to the ground surface in each

stand at 12.00 hr. Light intensity was measured using a lux-meter (LUBRON, LX-101), while relative humidity and air temperature were measured using a hygrometer and a thermometer, respectively.

STUDY OF SOIL CHARACTERISTICS

Soil samples were also collected in January, April, July and October during 1993 and 1994. In each stand, ten replicate samples were collected using a steel corer (6.5 cm diameter) from three soil depths (0-10, 10-20 and 20-30 cm). The replicated samples of a given depth were thoroughly mixed to obtain one composite sample for further analysis. The samples were air-dried, sieved through a 2 mm mesh-sieve to remove stone particles and then passed through 0.5 mm mesh-screen. The screened samples were stored in polythene bags for analysis.

Soil temperature at all three soil depths was measured by a soil thermometer (ELITE) without disturbing the soil. Soil texture and bulk density (BD) were determined by Bouyoucos hydrometer and gravimetric method, respectively (Allen *et al.* 1974). Water holding capacity (WHC) was determined by Keen's box method by using copper cups of 5.6 cm internal diameter and 1.6 cm height (Piper 1942). Soil moisture content (SMC) was determined gravimetrically by taking 10 g of fresh seived soil, and pH was determined electrometrically by a digital pH meter (SYSTRONICS-335) in 1:2.5 suspension of soil in deionized water (Anderson and Ingram 1993). Cation exchange capacity (CEC) was determined after extracting the exchangeable bases from the soil with 1 M ammonium acetate (pH 7.0) followed by the replacement of ammonium-N with potassium chloride and distillation with magnesium oxide (Allen *et al.* 1974).

Organic carbon was determined by rapid titration method (Walkley and Black 1934). Soil organic matter content was obtained by multiplying the organic carbon concentration by 1.724 assuming that the soil organic matter contains 58% of carbon (Allen *et al.* 1974). Total Kjeldahl nitrogen (TKN)

was determined by digesting air-dried soil samples with concentrated sulphuric acid using Kjeltabs (TECATOR) as catalyst on a block digester. Distillation and titration were done simultaneously in a TECATOR KJELTEC AUTO 1030 ANALYSER. Total phosphorus was determined by digesting the air-dried soil samples with tri-acid mixture (nitric acid, perchloric acid and sulphuric acid, in the ratio of 1:10:2, respectively) on a block digester. The digested mixture was filtered through Whatman No. 44 and made to 50 ml volume using double distilled water. The aliquot was analysed for phosphorus following molybdenum blue method (Allen *et al.* 1974). Available-P was determined after extracting soil P in 0.03 N ammonium fluoride in 0.025 N hydrochloric acid (Bray's reagent) according to Jackson (1958). Each analysis was performed in triplicate and the final results are expressed on oven-dry weight basis. Nutrient content (Kg ha^{-1}) in soil was calculated using mean concentration and bulk density data of each depth.

STATISTICAL ANALYSIS

The data were statistically analysed using ANOVA (fixed effects model) to study the effect of the age of the forest regrowth, season, year and soil depth on microclimatic and edaphic variables. Linear regressions were worked out according to Zar (1974), wherever necessary.

RESULTS

MICROCLIMATE

Out of the three microclimatic varibles studied, light intensity and air temperature were significantly higher ($P<0.01$) in 7-year old stand than 13- and 16-year old stands. Relative humidity was, however, significantly higher ($P<0.01$) in the 16-year old stand than the other two stands. In all the three stands, air temperature and light intensity were minimum during winter season, and maximum either during spring or autumn (Figure 4.1a,c).

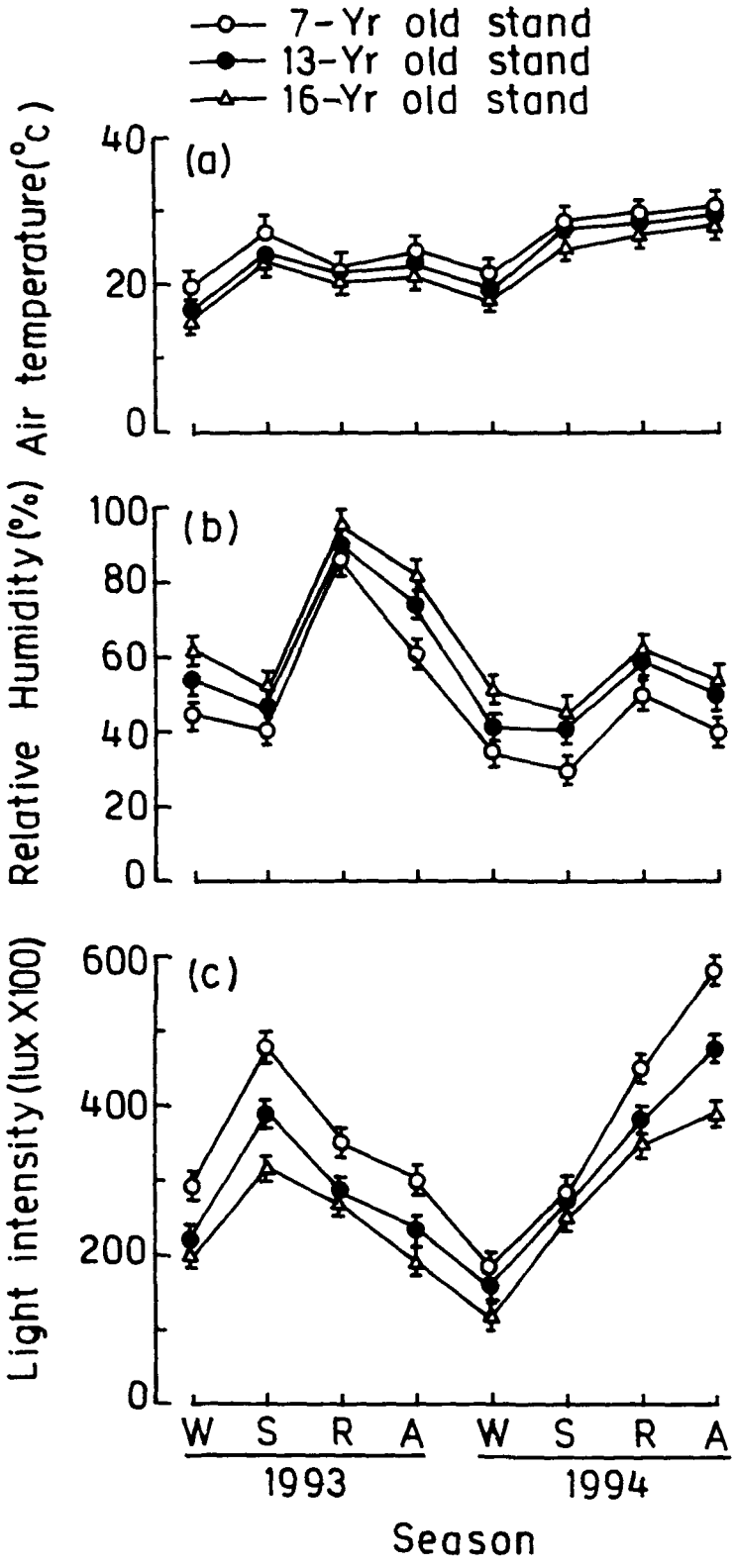


Figure 4.1. Seasonal variation in forest microclimate in the three regrowing communities.
Vertical bars represent standard error (n=10).
W-winter, S-spring, R-rainy, A-autumn

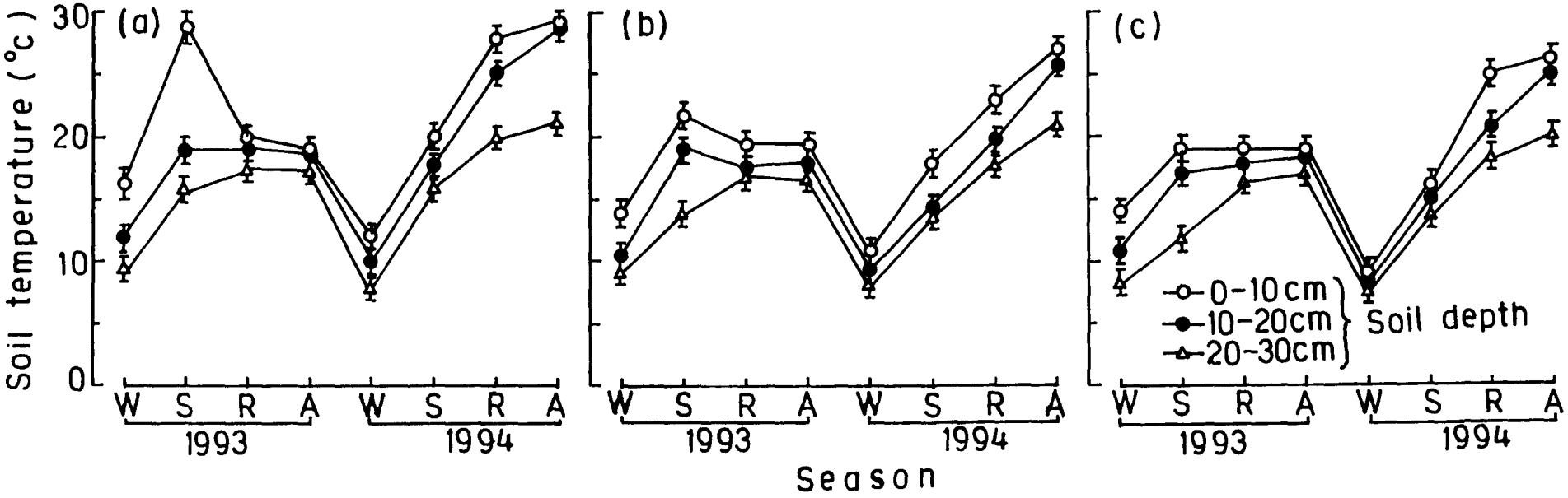


Figure 4.2. Seasonal and depthwise variation in soil temperature in (a) 7, (b) 13 and (c) 16 year old regrowths. Vertical bars represent standard error (n=10). W-winter, S-spring, R-rainy, A-autumn.

Table 4.1. Texure and bulk density of soil in three forest regrowths.

Age of the forest stand	Soil Depth (cm)	Soil texure				Bulk density ($g\ cm^3$)
		Sand (%)	Silt (%)	Clay (%)	Class	
7-yr	0-10	75.25 ±0.25	14.74 ±0.47	10.11 ±0.14	SL	1.32 ±0.03
	10-20	68.04 ±0.05	16.18 ±0.13	15.87 ±0.07	SL	1.39 ±0.02
	20-30	59.70 ±0.39	15.63 ±0.39	25.45 ±0.23	SCL	1.51 ±0.08
	Mean	**67.66**	**15.52**	**17.14**	**SL**	**1.41**
13-yr	0-10	53.51 ±0.46	23.32 ±0.39	23.26 ±0.23	SCL	1.41 ±0.01
	10-20	42.33 ±0.44	29.06 ±0.90	27.32 ±0.17	CL	1.43 ±0.01
	20-30	34.94 ±0.79	30.95 ±0.37	34.11 ±0.09	CL	1.48 ±0.03
	Mean	**43.59**	**27.98**	**28.23**	**SCL**	**1.44**
16-yr	0-10	35.64 ±0.91	33.64 ±0.05	30.89 ±0.13	CL	1.42 ±0.02
	10-20	31.09 ±0.18	33.20 ±0.09	34.63 ±0.62	CL	1.46 ±0.01
	20-30	22.50 ±0.44	33.84 ±0.16	44.29 ±0.12	C	1.51 ±0.02
	Mean	**29.74**	**33.56**	**36.61**	**CL**	**1.46**

SL-Sandy loam, SCL-Sandy clay loam, CL-Clay loam, C-Clay.

± SEM (n=3)

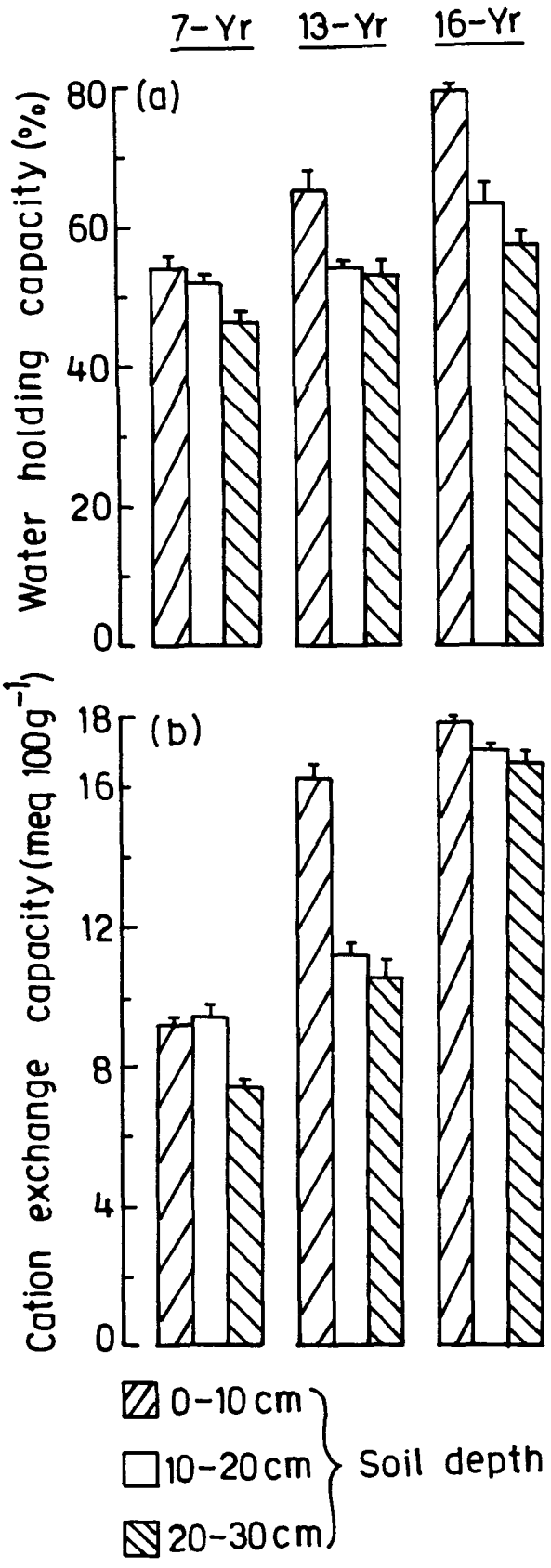


Figure 4.3. Water holding capacity and cation exchange capacity of soils in forest regrowths of three different ages. Vertical bars represent standard error (n=6), Values plotted are the mean of two years.

Relative humidity in all the stands was minimum during the spring season and maximum during the rainy season (Figure 4.1b).

PHYSICAL PROPERTIES OF SOIL

Soil temperature: Soil temperature followed a similar seasonal trend in all the three forest stands by showing higher values during rainy and autumn seasons and lower values during winter (Figure 4.2). In the 16-year old stand, soil temperature was significantly lower ($P<0.05$) than the other two younger stands (Figure 4.2 c). The temperature of upper soil layer (0-10 cm) was generally 1-2°C higher than the sub soil layers.

Soil texture and bulk density: The proportion of clay particles increased significantly ($P<0.01$) from 7-year old to 16-year old stand, while, the percentage of sand particles showed a reverse trend. As a consequence, the texture of the soil gradually changed from sandy loam in the 7-year old stand to sandy clay in 13-year old stand and ultimately to clay loam in 16-year old stand. The proporiton of sand declined significantly ($P<0.01$) with the soil depth (Table 4.1).

Bulk density of the soil though did not vary much between the stands, it showed an increasing trend with the increase in soil depth (Table 4.1).

Water holding capacity and moisture content: Water holding capacity (WHC) of the soil increased significantly ($P<0.01$) from 7-year old (46.4-53.6%) to 16-year old stand (56.6-78.6%) (Figure 4.3 a). WHC being maximum in the surface soil layer (0-10 cm), declined significantly ($P<0.01$) with the increase in soil depth in all the three stands.

Soil moisture content showed a marked seasonality in all the three stands. In all of them, surface soil had higher moisture content during rainy season (Figure 4.4). However during winter and spring seasons, subsurface soil layers (10-20 and 20-30 cm) had higher moisture content than the surface layer. The mean soil moisture content increased from 31% in the 7-year old stand to 48% in the 16-year old stand.

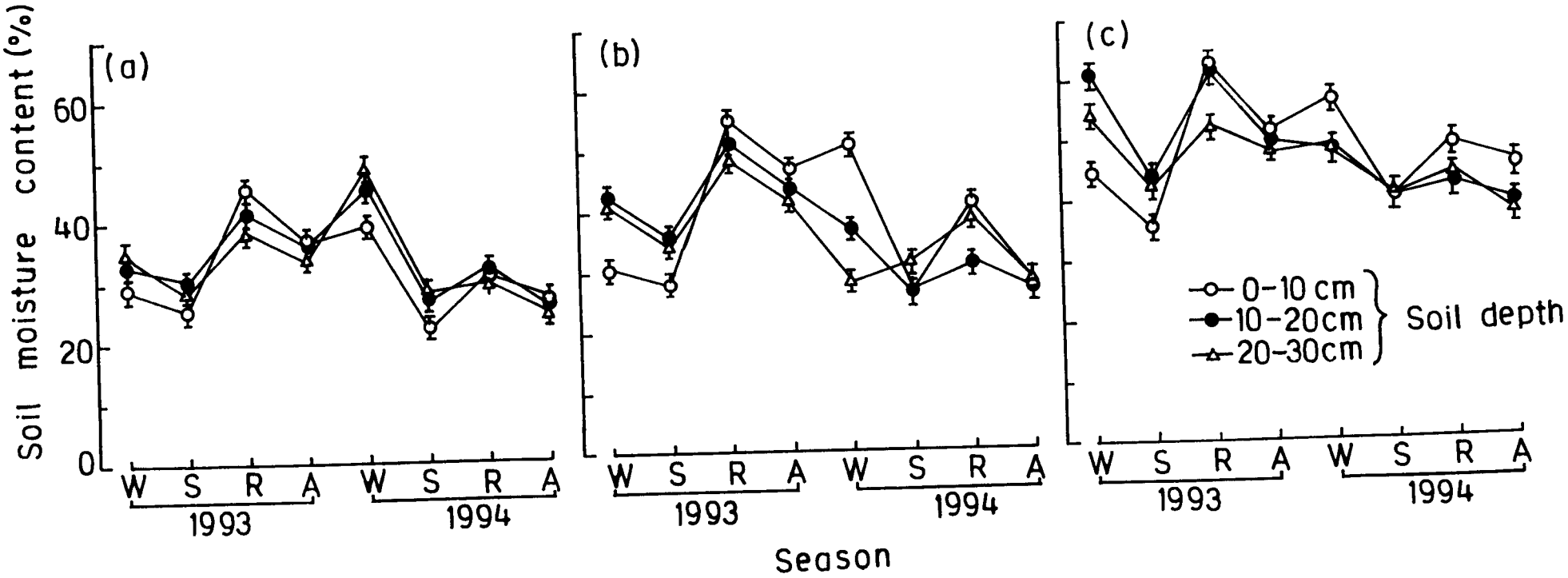


Figure 4.4. Seasonal variation in soil moisture content in three soil depths in (a) 7, (b) 13 and (c) 16 year old stands. Vertical bars represent standard error (n=3). W-winter, S-spring, R-rainy, A-autumn.

Table 4.2. Seasonal variation in soil pH in different forest regrowths.

Age of the forest stand	Soil depth (cm)	1993					1994				
		W	S	R	A	Mean	W	S	R	A	Mean
7-yr	0-10	5.41 ±0.01	5.15 ±0.05	5.25 ±0.01	5.35 ±0.04	5.29	5.45 ±0.01	5.17 ±0.03	5.33 ±0.02	5.47 ±0.15	5.36
	10-20	5.52 ±0.01	5.39 ±0.02	5.63 ±0.13	5.11 ±0.05	5.41	5.85 ±0.20	5.28 ±0.21	5.57 ±0.01	5.73 ±0.02	5.61
	20-30	5.76 ±0.01	5.66 ±0.01	6.08 ±0.05	4.92 ±0.09	5.61	5.80 ±0.12	5.35 ±0.10	5.65 ±0.05	5.74 ±0.05	5.64
	Mean	**5.50**	**5.40**	**5.60**	**5.10**	**5.44**	**5.70**	**5.27**	**5.52**	**5.65**	**5.54**
13-yr	0-10	5.05 ±0.05	4.72 ±0.02	4.41 ±0.05	5.24 ±0.12	4.86	5.21 ±0.01	5.20 ±0.05	5.18 ±0.21	5.42 ±0.01	5.25
	10-20	5.20 ±0.01	5.06 ±0.01	4.81 ±0.06	5.00 ±0.03	5.02	5.27 ±0.02	5.24 ±0.05	5.31 ±0.02	5.45 ±0.01	5.32
	20-30	5.30 ±0.01	5.29 ±0.02	5.33 ±0.12	4.99 ±0.06	5.23	5.51 ±0.01	5.50 ±0.12	5.30 ±0.02	5.47 ±0.05	5.45
	Mean	**5.19**	**5.03**	**4.74**	**5.08**	**5.04**	**5.33**	**5.31**	**5.26**	**5.45**	**5.34**
16-yr	0-10	5.17 ±0.01	4.44 ±0.03	4.50 ±0.05	5.68 ±0.06	4.95	4.80 ±0.01	5.18 ±0.05	5.14 ±0.01	5.06 ±0.01	5.05
	10-20	5.10 ±0.01	5.05 ±0.02	4.50 ±0.05	5.49 ±0.09	5.04	5.00 ±0.01	5.38 ±0.09	5.24 ±0.15	5.31 ±0.05	5.23
	20-30	5.25 ±0.01	5.21 ±0.04	4.79 ±0.06	5.33 ±0.04	5.15	5.00 ±0.02	5.53 ±0.01	4.98 ±0.02	5.31 ±0.01	5.21
	Mean	**5.17**	**4.90**	**4.59**	**5.50**	**5.05**	**4.93**	**5.36**	**5.12**	**5.23**	**5.16**

W-winter, S-spring,R-rainy, A-autumn

± SEM (n=3)

Table 4.3. Seasonal variation in soil organic carbon (%) in different forest regrowths.

Age of the forest stand	Soil depth (cm)	1993					1994				
		W	S	R	A	Mean	W	S	R	A	Mean
7-yr	0-10	3.07 ±0.03	3.81 ±0.01	3.57 ±0.04	3.95 ±0.12	3.60	3.65 ±0.01	3.85 ±0.01	3.65 ±0.01	3.61 ±0.00	3.69
	10-20	2.59 ±0.26	2.73 ±0.02	2.70 ±0.01	2.94 ±0.03	2.74	2.95 ±0.00	2.94 ±0.02	2.61 ±0.00	2.91 ±0.04	2.85
	20-30	2.18 ±0.03	2.39 ±0.01	2.09 ±0.09	2.64 ±0.03	2.33	2.32 ±0.01	2.47 ±0.04	2.12 ±0.04	2.25 ±0.01	2.47
	Mean	**2.62**	**2.97**	**2.79**	**3.18**	**2.89**	**2.97**	**3.09**	**2.79**	**3.16**	**3.00**
13-yr	0-10	5.08 ±0.12	5.05 ±0.02	4.78 ±0.16	6.92 ±0.18	5.46	5.32 ±0.17	5.40 ±0.04	5.10 ±0.04	5.65 ±0.01	5.37
	10-20	3.04 ±0.33	3.60 ±0.04	3.34 ±0.01	3.75 ±0.61	3.43	3.72 ±0.01	3.89 ±0.03	3.80 ±0.17	3.92 ±0.01	3.83
	20-30	2.87 ±0.03	2.84 ±0.05	2.29 ±0.01	2.92 ±0.01	2.73	2.75 ±0.03	2.94 ±0.50	2.60 ±0.12	2.71 ±0.05	2.75
	Mean	**3.66**	**3.83**	**3.71**	**4.19**	**3.87**	**3.93**	**4.08**	**3.83**	**4.09**	**3.98**
16-yr	0-10	6.26 ±0.01	6.31 ±0.01	5.56 ±0.03	7.29 ±0.00	6.36	6.16 ±0.01	6.29 ±0.09	5.91 ±0.08	6.09 ±0.03	6.11
	10-20	5.96 ±0.04	6.25 ±0.02	5.53 ±0.01	6.54 ±0.07	6.07	6.10 ±0.01	6.19 ±0.08	5.91 ±0.01	6.03 ±0.03	6.06
	20-30	4.49 ±0.22	5.05 ±0.05	4.41 ±0.01	5.33 ±0.14	4.82	5.06 ±0.05	5.12 ±0.02	4.90 ±0.05	5.04 ±0.07	5.03
	Mean	**5.57**	**5.87**	**4.44**	**6.39**	**5.75**	**5.77**	**5.87**	**5.57**	**5.72**	**5.73**

W-winter, S-spring,R-rainy, A-autumn

± SEM (n=3)

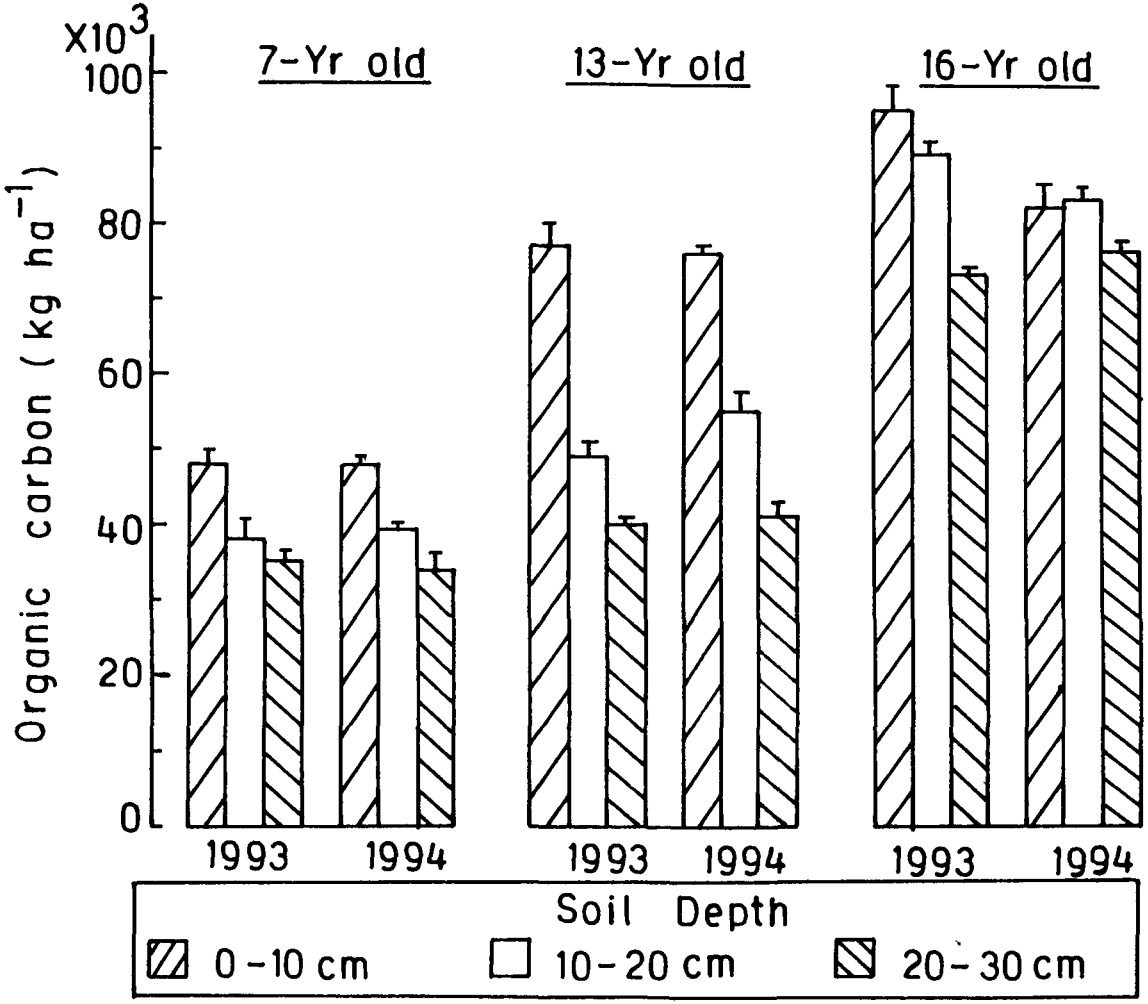


Figure 4.5. Mean stock of organic carbon in three soil depths in forest stands of three different ages.
Vertical bars represent standard error (n=12).

CHEMICAL PROPERTIES OF SOIL

Cation exchange capacity and pH: Cation exchange capacity (CEC) increased significantly from 8.7 meq 100 g^{-1} in the 7-year old stand to 12.7 and 17.2 meq 100 g^{-1} in the 13- and 16-year old stands, respectively (Figure 4.3 b). Generally, the CEC showed a declining trend with the soil depth. Seasonal and depthwise variations in soil pH was insignificant in all the three stands (Table 4.2). However, the pH was relatively high during 1994 (5.05-5.64) than during 1993 (4.95-5.61). The mean value in the 7-year old stand was high (5.5) compared to the 13- (5.2) and 16-year (5.1) old stands.

Soil organic matter: In all three forest regrowths, soil organic carbon (SOC) concentration was significantly lower ($P<0.05$) during the rainy season and higher during autumn season. There was a slight increase in the concentration of SOC during 1994 than during 1993 in the 7- and 13-year old stands, but the values remained almost same in the 16-year old stand (Table 4.3). The concentration of SOC decreased significantly ($P<0.05$) with the increase in soil depth in all stands, but it showed a reverse trend with the age of the stand.

Total SOC content gradually declined from 47.5-87.5 x 10^3 kg ha^{-1} in the 0-10 cm soil layer to 35.2-75.9 x 10^3 kg ha^{-1} in the 20-30 cm layer. Based on mean SOC content (Figure 4.5) the three stands may be placed in the following order: 7-year old stand (40.9x10^3 kg ha^{-1}) < 13-year old stand (56.5x10^3 kg ha^{-1}) < 16-year old stand (83.8x10^3 kg ha^{-1}).

Seasonal variation in the soil organic matter (SOM) content was similar to SOC (Figure 4.6). It decreased significantly ($P<0.01$) with the increase in soil depth in all stands, except between the first two soil depths *i.e.* 0-10 and 10-20 cm in the 16-yr old stand (Figure 4.6 c).

Total Kjeldahl nitrogen: Total Kjeldahl nitrogen (TKN) concentration as well as its total amount in soil varied significantly ($P<0.01$) with depth and stand age. Seasonal and yearly differences were, however,

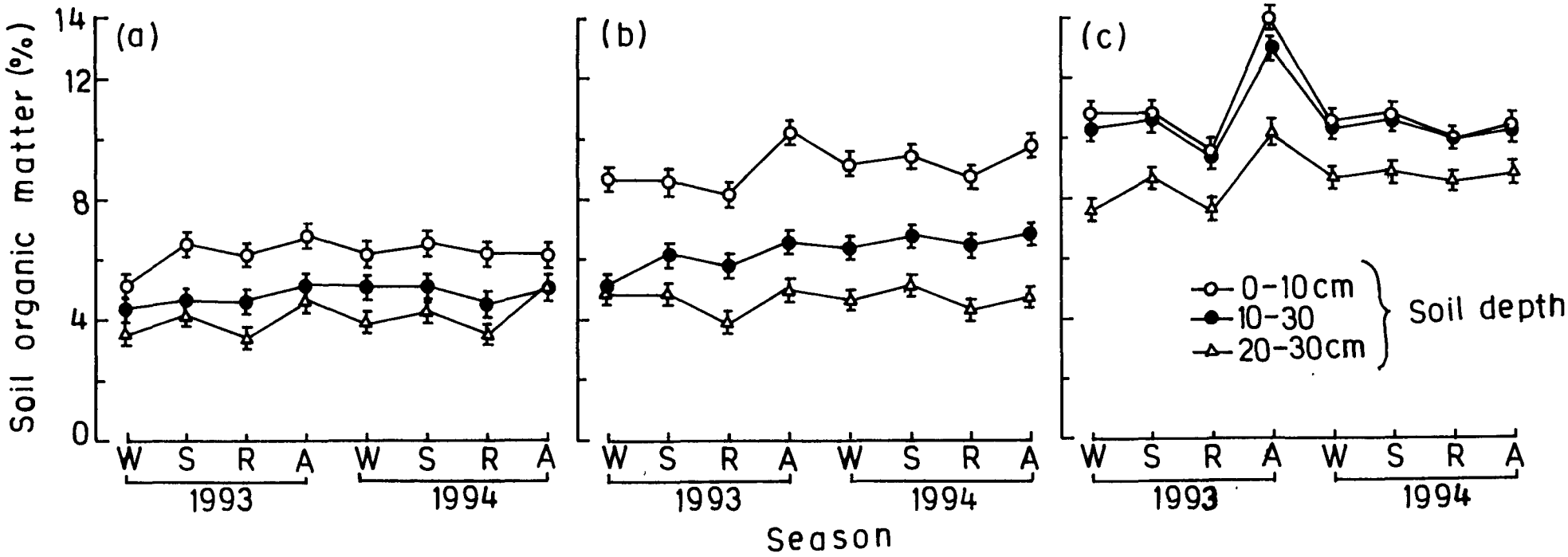


Figure 4.6. Temporal and spatial distribution of soil organic matter in (a) 7, (b) 13 and (c) 16 year old stands. Vertical bars represent standard error (n=3). W-winter, S-spring, R-rainy, A-autumn.

Table 4.4. Seasonal variation in total Kjeldahl nitrogen (%) of soil in different forest regrowths.

Age of the forest stand	Soil depth (cm)	1993					1994				
		W	S	R	A	Mean	W	S	R	A	Mean
7-yr	0-10	0.34 ±0.01	0.35 ±0.01	0.38 ±0.02	0.36 ±0.01	0.36	0.35 ±0.02	0.36 ±0.00	0.37 ±0.00	0.39 ±0.01	0.37
	10-20	0.28 ±0.00	0.28 ±0.00	0.30 ±0.00	0.30 ±0.02	0.29	0.26 ±0.00	0.27 ±0.01	0.24 ±0.02	0.29 ±0.02	0.27
	20-30	0.23 ±0.01	0.24 ±0.00	0.27 ±0.00	0.26 ±0.01	0.25	0.20 ±0.00	0.21 ±0.01	0.22 ±0.01	0.21 ±0.03	0.21
	Mean	**0.28**	**0.29**	**0.31**	**0.30**	**0.30**	**0.27**	**0.28**	**0.28**	**0.30**	**0.28**
13-yr	0-10	0.47 ±0.01	0.49 ±0.00	0.51 ±0.01	0.50 ±0.00	0.49	0.47 ±0.01	0.49 ±0.00	0.50 ±0.01	0.51 ±0.02	0.49
	10-20	0.34 ±0.00	0.37 ±0.00	0.39 ±0.01	0.39 ±0.02	0.37	0.33 ±0.02	0.36 ±0.02	0.36 ±0.01	0.39 ±0.01	0.36
	20-30	0.29 ±0.00	0.30 ±0.01	0.31 ±0.01	0.31 ±0.01	0.30	0.30 ±0.01	0.31 ±0.02	0.31 ±0.01	0.30 ±0.01	0.31
	Mean	**0.37**	**0.38**	**0.40**	**0.39**	**0.39**	**0.37**	**0.39**	**0.39**	**0.40**	**0.39**
16-yr	0-10	0.56 ±0.01	0.61 ±0.01	0.61 ±0.01	0.59 ±0.00	0.59	0.57 ±0.01	0.60 ±0.03	0.60 ±0.02	0.60 ±0.01	0.59
	10-20	0.52 ±0.00	0.53 ±0.03	0.54 ±0.01	0.52 ±0.03	0.53	0.52 ±0.01	0.52 ±0.00	0.51 ±0.00	0.51 ±0.01	0.52
	20-30	0.39 ±0.01	0.42 ±0.01	0.43 ±0.00	0.42 ±0.01	0.42	0.40 ±0.01	0.42 ±0.02	0.41 ±0.01	0.40 ±0.02	0.41
	Mean	**0.49**	**0.52**	**0.52**	**0.52**	**0.51**	**0.50**	**0.50**	**0.51**	**0.50**	**0.51**

W-winter, S-spring,R-rainy, A-autumn

± SEM (n=3)

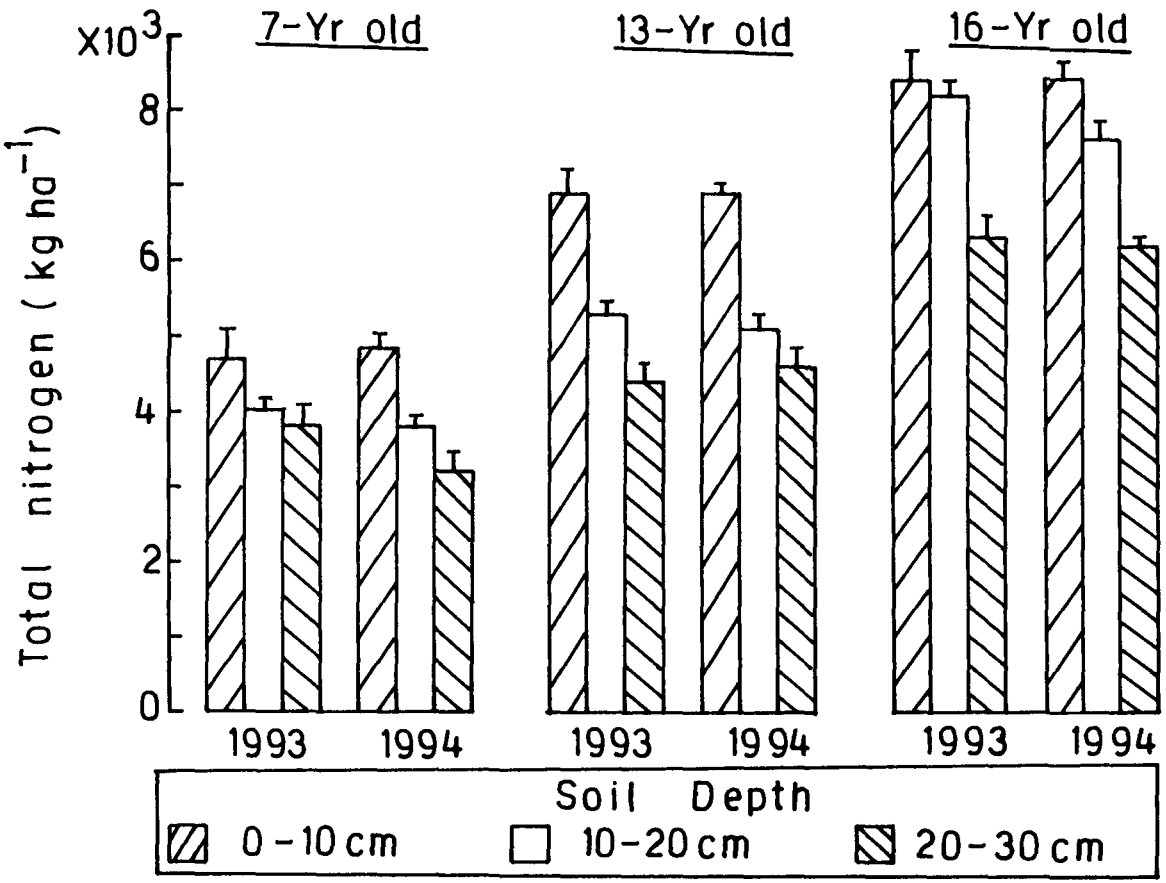


Figure 4.7. Mean total nitrogen content in the soils of the three forest regrowths during 1993 and 1994.
Vertical bars represent standard error (n=12).

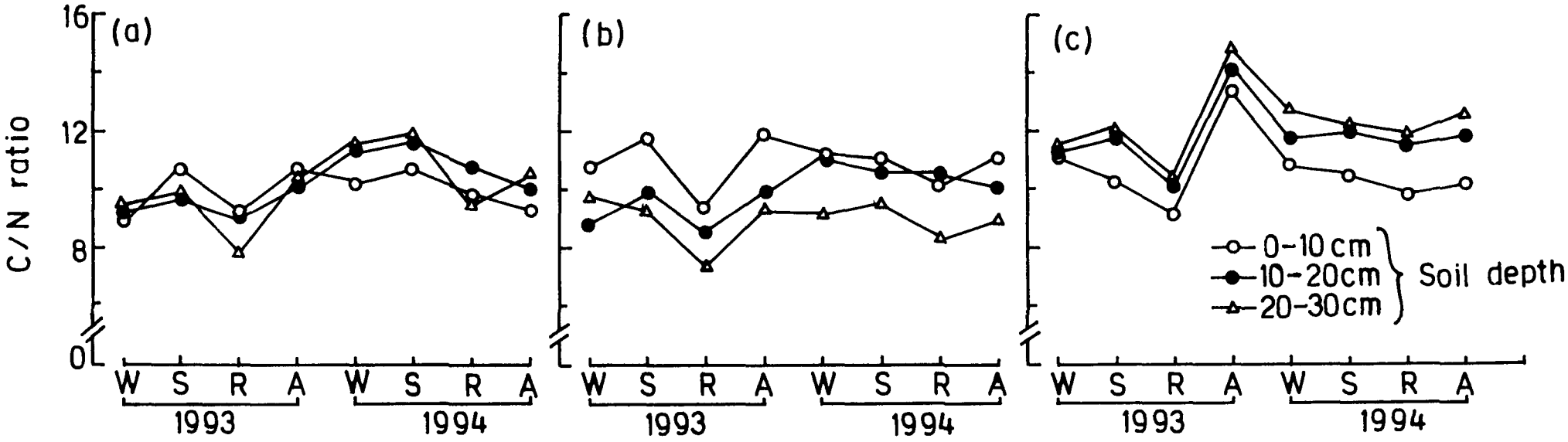


Figure 4.8. Seasonal variations in the C/N ratio of soils at (a) 7, (b) 13 and (c) 16 year old stands.

insignificant. TKN concentration in the surface layer was higher than the subsurface layers. TKN concentration was maximum in the 16-year old stand (0.39-0.61%), followed by 13-year (0.29-0.51%) and 7-year (0.20-0.39%) old stands (Table 4.4). The nitrogen content in soil increased markedly with the progression of vegetation regrowth from the 7-year old stand ($4.1x10^3$ kg ha^{-1}) to the 16-year old stand ($7.5x10^3$ kg ha^{-1}).

C/N ratio: The carbon to nitrogen (C/N) ratio in soil varied significantly ($P<0.01$) between season, depth and stand age in both the years. The top soil layer had higher C/N ratio in 7- and 13- year old stands (8.92-10.77 and 9.38-11.95, respectively), while, the lower soil layer (10-20 and 20-30 cm) had higher values (11.74-12.31%) in the 16-year old stand. Despite inconsistent seasonal trend, the C/N ratio generally increased with the increase in stand age (Figure 4.8).

Soil phosphorus: The concentration of total phosphorus (TP) in soil was maximum during rainy season and minimum during spring season in all the three stands. The seasonal difference was more clear in the surface soil layer than the subsurface layers. There was a significant increase ($P<0.01$) in the concentration of TP from the 7-year old to the 16-year old stand (Table 4.5). In all the three stands the concentration of available-P in soil was maximum during rainy season and minimum during winter season and it showed a declining trend with soil depth in all stands. It increased significantly ($P<0.05$) with the increase in age of the stand (Table 4.6).

In the 7 year old stand, total P content in 10-20 cm soil layer (600 kg ha^{-1}) was higher than the 0-10 and 20-30 cm soil layers, which had more or less the same amount of P (500 kg ha^{-1}) (Figure 4.9). However, in the 13- and 16-year old stands, the amount of TP showed a decreasing trend with the soil depth (Figure 4.9). The total stock of available-P in the soil followed the trend of TP. Available-P was significantly higher ($P<0.05$) during 1994 (10-20 kg ha^{-1}) than during 1993 (7-12 kg ha^{-1}) (Figure 4.10).

Table 4.5. Seasonal variation in total soil phosphorus (%) in different forest regrowths.

Age of the forest stand	Soil depth (cm)	1993					1994				
		W	S	R	A	Mean	W	S	R	A	Mean
7-yr	0-10	0.46 ±5	0.25 ±10	0.50 ±30	0.42 ±28	0.41	0.43 ±21	0.33 ±11	0.47 ±21	0.32 ±11	0.39
	10-20	0.48 ±11	0.36 ±15	0.65 ±16	0.52 ±16	0.50	0.42 ±12	0.31 ±10	0.41 ±11	0.41 ±11	0.39
	20-30	0.48 ±15	0.19 ±4	0.32 ±30	0.45 ±15	0.36	0.45 ±4	0.29 ±15	0.31 ±10	0.27 ±8	0.33
	Mean	**0.47**	**0.27**	**0.49**	**0.46**	**0.42**	**0.43**	**0.31**	**0.40**	**0.34**	**0.37**
13-yr	0-10	0.56 ±15	0.36 ±5	0.63 ±20	0.74 ±15	0.57	0.48 ±11	0.47 ±15	0.51 ±12	0.42 ±10	0.47
	10-20	0.30 ±15	0.33 ±10	0.65 ±5	0.48 ±15	0.44	0.32 ±1	0.37 ±12	0.41 ±31	0.39 ±15	0.37
	20-30	0.26 ±21	0.41 ±5	0.58 ±30	0.50 ±15	0.44	0.37 ±31	0.31 ±12	0.37 ±41	0.32 ±6	0.34
	Mean	**0.37**	**0.37**	**0.62**	**0.57**	**0.48**	**0.39**	**0.38**	**0.43**	**0.38**	**0.39**
16-yr	0-10	0.57 ±13	0.43 ±20	0.99 ±30	0.89 ±24	0.72	0.67 ±21	0.40 ±22	0.61 ±15	0.40 ±8	0.52
	10-20	0.26 ±22	0.38 ±11	1.07 ±20	0.59 ±50	0.58	0.36 ±14	0.41 ±12	0.49 ±10	0.39 ±11	0.42
	20-30	0.26 ±5	0.37 ±20	0.62 ±30	0.50 ±5	0.44	0.41 ±15	0.39 ±17	0.39 ±12	0.36 ±17	0.39
	Mean	**0.36**	**0.39**	**0.89**	**0.66**	**0.58**	**0.48**	**0.40**	**0.50**	**0.39**	**0.44**

W-winter, S-spring,R-rainy, A-autumn

± SEM (n=3)

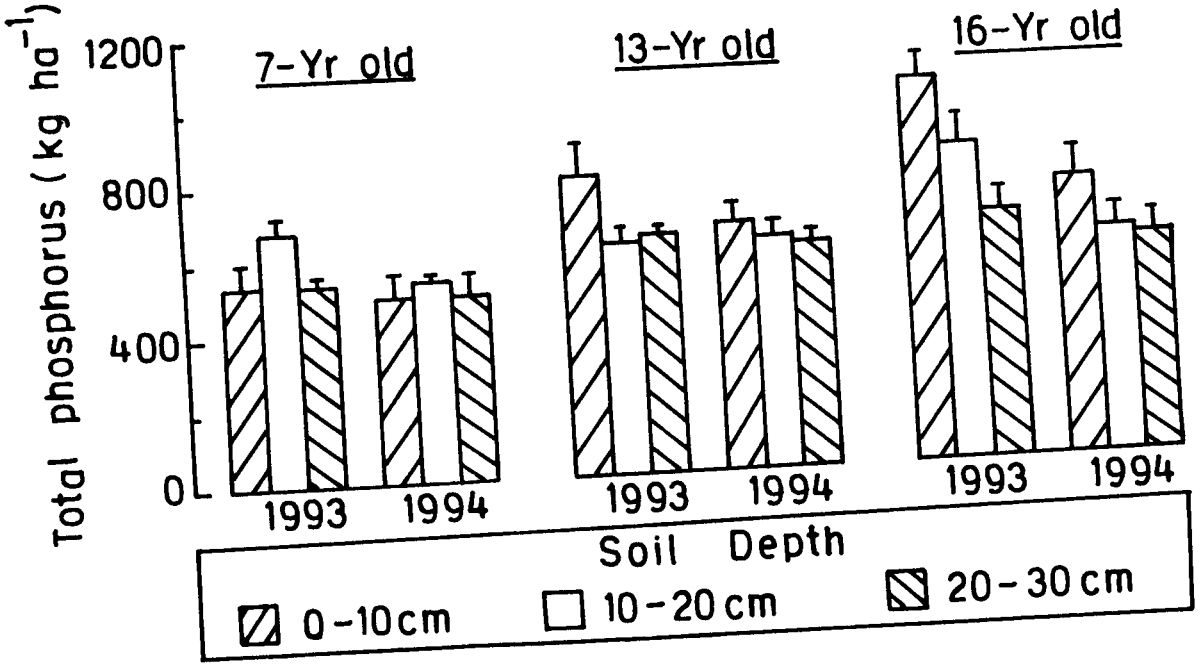


Figure 4.9. Mean total phosphorus stock in the top 0-30 cm soil in forest regrowths of three different ages. Vertical bars represent standard error (n=12).

Table 4.6. Seasonal variation in soil available phosphorus ($\mu g\ g^{-1}$) in different forest regrowths.

Age of the forest stand	Soil depth (cm)	1993					1994				
		W	S	R	A	Mean	W	S	R	A	Mean
7-yr	0-10	2.66 ±0.03	7.64 ±0.59	8.15 ±0.51	5.15 ±0.49	5.90	4.88 ±0.08	6.15 ±0.15	10.17 ±0.11	10.89 ±0.09	8.02
	10-20	1.76 ±0.07	7.06 ±0.17	7.24 ±0.05	3.06 ±0.04	4.78	3.44 ±0.14	6.41 ±0.18	9.72 ±0.02	7.34 ±0.04	6.73
	20-30	1.63 ±0.03	6.57 ±0.09	6.48 ±0.17	2.16 ±0.03	4.21	2.50 ±0.11	5.25 ±0.25	8.41 ±0.03	6.78 ±0.07	5.74
	Mean	**2.02**	**7.09**	**7.29**	**3.46**	**4.96**	**3.61**	**5.94**	**9.43**	**8.34**	**6.83**
13-yr	0-10	10.30 ±0.06	11.94 ±0.35	12.11 ±0.53	6.61 ±0.03	10.24	14.09 ±0.41	13.44 ±1.37	14.70 ±0.12	12.78 ±0.21	13.75
	10-20	4.96 ±0.02	7.74 ±0.50	8.24 ±0.14	3.74 ±0.37	6.17	12.08 ±0.12	12.02 ±0.42	10.72 ±0.31	11.45 ±0.18	11.57
	20-30	4.70 ±0.05	6.13 ±0.09	8.17 ±0.13	3.60 ±0.20	5.65	11.01 ±0.31	11.17 ±1.89	9.71 ±0.04	7.11 ±0.07	9.75
	Mean	**6.65**	**8.60**	**9.51**	**4.65**	**7.35**	**12.39**	**12.21**	**11.71**	**10.45**	**11.69**
16-yr	0-10	10.13 ±0.03	11.23 ±0.09	11.28 ±0.14	7.01 ±0.06	9.91	15.36 ±0.84	18.98 ±0.50	19.90 ±0.03	19.60 ±0.20	18.46
	10-20	6.90 ±0.02	9.88 ±0.42	10.22 ±0.43	4.73 ±0.11	7.93	13.02 ±0.15	18.06 ±0.34	16.20 ±0.06	10.32 ±0.13	14.40
	20-30	6.67 ±0.03	9.14 ±0.29	11.44 ±0.21	4.53 ±0.38	7.95	11.76 ±0.27	18.14 ±0.34	12.20 ±0.09	9.02 ±0.17	12.78
	Mean	**7.90**	**10.08**	**10.98**	**5.42**	**8.59**	**13.38**	**18.39**	**16.10**	**12.98**	**15.21**

W-winter, S-spring,R-rainy, A-autumn

± SEM (n=3)

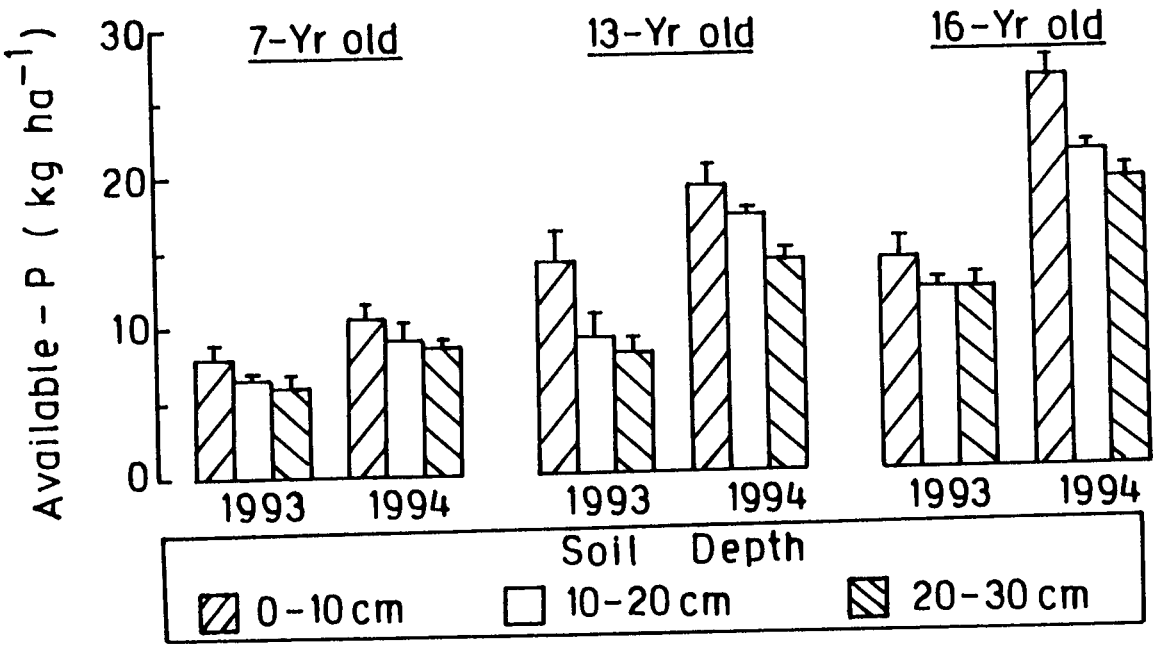


Figure 4.10. Mean stock of available-P in soils of forest regrowths of three different ages.
Vertical bars represent standard error (n=12).

DISCUSSION

CHANGES IN FOREST MICROCLIMATE

Analysis of microclimatic data in the three stands revealed that due to regrowth of vegetation, particularly the woody components in the community, the light intensity and air temperature near the ground decreased gradually from 7- to 16- year old stand. Contrary to this, relative humidity registered *ca.* 20% increase during the same period. Gradual closing of canopy due to growth of large number of sprouts from the cut trees of *Quercus dealbata*, *Quercus griffithii*, *Rhododendron arboreum* and *Schima* spp., etc. was responsible for such a change in the forest microclimate. Marked seasonal fluctuation in the microclimatic variables, as observed in all the three stands, is in confirmity with the findings of Schultz (1960), Lee (1978) and Barik *et al.* (1992) in various degraded forest ecosystems. Seasonal changes in microclimate within the forest community depends on a number of external and internal factors, notable among them are duration of sunshine and cloudiness, tree canopy architecture and phenological stage of the constituent plant species *etc.* (Lal 1987). Temperature of the surface soil layer is influenced by the fluctuations in air temperature near the ground, while the decline in soil temperature with increasing soil depth depends to some extent on the metabolic activities of plant roots (especially, fine roots) and microbes inhabiting this layer (Kaspar and Bland 1992).

EDAPHIC CHANGES DURING FOREST REGROWTH

As a result of canopy opening by way of tree cutting in forests, there occurs erosion of the top soil due to extreme rainfall events (Greacen and Sands 1980, Scholes *et al.* 1994). Loss of finer soil particles, especially the clay component, increases the proportion of sand in the soil during the early developmental stages after disturbance (Eyre 1968). This could be one

of the reasons for lower proportion of finer soil particles in the 7-year old regrowth than the 13- and 16-year old stands. A strong positive correlation was observed between the clay percentage and bulk density (Figure 4.11 a). Similar finding has been reported by Scholes *et al.* (1994). The increasing trend in bulk density from 7- to 16-year old stand and with soil depth indicates gradual soil compaction. Low bulk density of the surface soil in forest fallows has been attributed to the greater concentration of roots which loosen the soil (Aweto 1981). Manual harvesting on clay soils of a tropical rain forest may cause 23% increase (from 0.82 to 1.01 g cm^{-3}) in soil bulk density of the surface layer (0-5 cm) compared with 56% increase (from 0.82 to 1.28 g cm^{-3}) by logging with tractors. There is, however, some evidence to suggest that bulk density can recover, especially in the surface soils (Gayoso and Iroume 1991), depending upon the degree of compaction and soil type. Hatchell *et al.* (1970) estimated that recovery in bulk density to pre-disturbance levels may take 18 years in loblolly pine forest. Malmer and Grip (1990) found that the bulk density in a 6-year old stand (1.16 g cm^{-3}) was 41% more than an undisturbed forest. Wert and Thomas (1981) reported that soil compaction may cause significant decrease in the productivity of the regenerating vegetation.

Congdon and Herbohn (1993), Scholes *et al.* (1994) and Lyngdoh (1995) have reported a positive correlation between clay content and WHC. In the present study, similar relationship was partly true, since higher proportion of clay in the lower soil depths, WHC was more in the surface soil layer which had greater accumulation of organic matter. Thereby indicating a stronger influence of SOM on WHC than the clay particles (Lyngdoh 1995). Depletion of clay particles and low SOM content could be the possible reasons for the lower soil moisture content in the 7-year old stand, whereas, the reverse was true for the 13- and 16-year old stands.

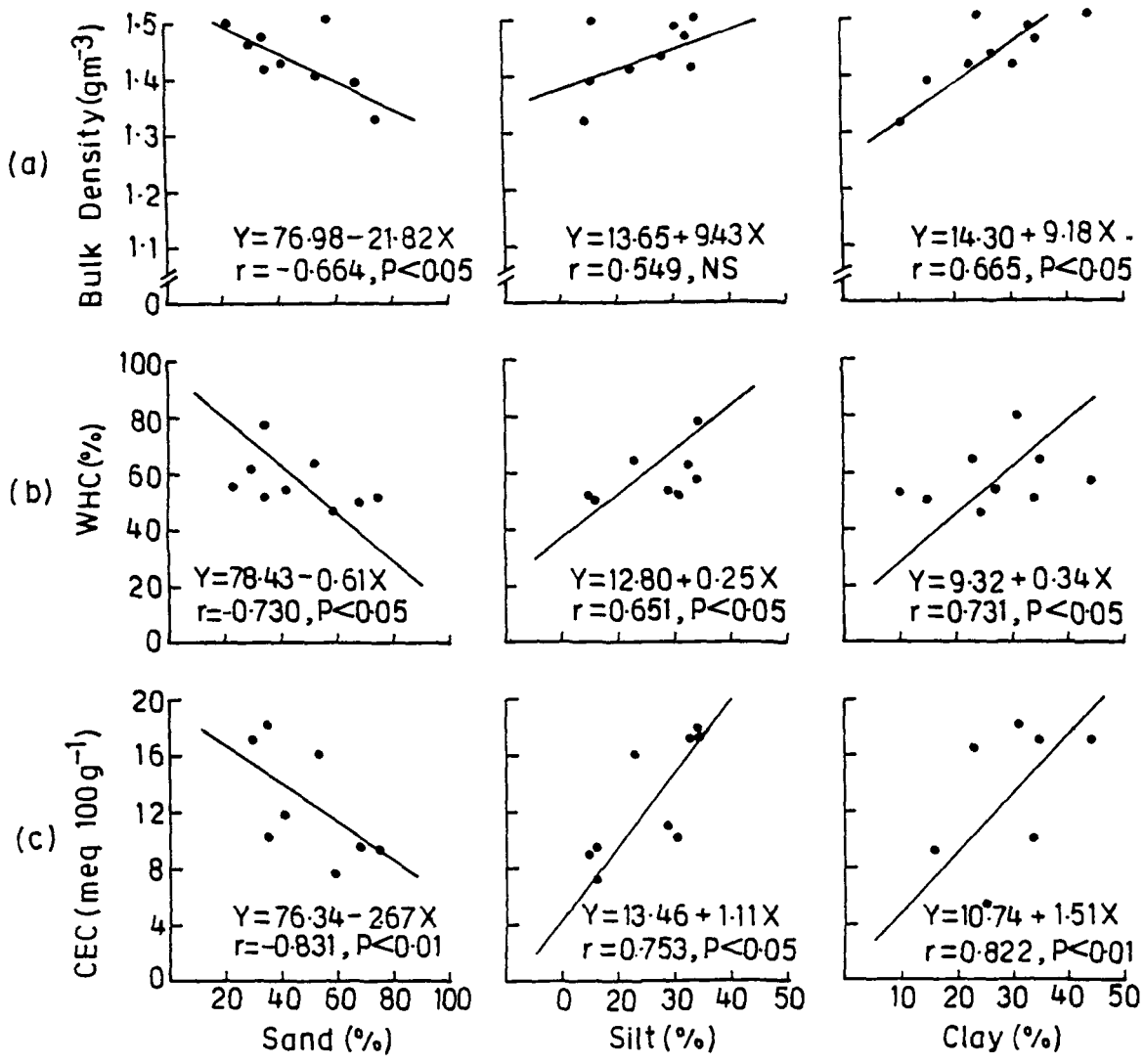


Figure 4.11. Relationship between soil particles and CEC, WHC and bulk density in the three regrowing forest stands. The replicate (n=3) values of all the above-said properties, irrespective of stand age were taken in to consideration for plotting.

The relationship between mean seasonal soil moisture content (SMC) and rainfall (irrespective of stand age) tested through linear regression analysis resulted in the following relationship:

$$Y = 95.63 + 0.85X \quad (r = 0.422, df. = 22, P < 0.05)$$

This also explains the higher SMC during the first year of the study when rainfall was more than the succeeding year. Lower SMC during spring is attributed to higher evaporation losses due to high air and soil temperatures and scanty rainfall. Maximum retention of moisture in the surface soil layer might be due to greater accumulation of litter on the forest floor (see Chapter 6) and higher soil organic matter content in this layer. On the other hand, lower SMC in surface layer during dry winter and spring seasons could be the result of higher evapotranspiration from the soil surface and percolation and infiltration of water to the lower depths (Tiwari *et al.* 1992).

CEC was negatively correlated with the percentage of sand particles and positively correlated with the clay content of the soil (Figure 4.11 c). This explains the low CEC in the 7-year old stand and high CEC in the older stands. This corroborates the findings of Scholes *et al.* (1994) who found a linear relationship between clay particles and CEC. Nonetheless a decline in CEC with the increase in soil depth where proportion of clay was higher than the surface soil layer suggested that CEC was strongly influenced by organic colloidal particles in the soil (Scholes *et al.* 1994).

The soils of the study area were acidic (pH 4.4-5.8). Low pH is detrimental to plant growth in extreme conditions (Sutton 1970), but, tolerance to acidity varies from species to species (Bannister 1976). The pH as such may not be the main factor associated with the revegetation of acidic soils (Pandey and Singh 1984/1985). Results of Berg and Vogel (1973) and Inerson and Wali (1992) suggest that the availability of iron,

aluminium and manganese to plants increases as the soil pH decreases, and therefore under very acidic conditions these elements become more toxic to plants. The decrease in soil pH during spring in the regrowing forest stands could be due to higher soil temperatures and lower rate of leaching leading to greater accumulation of reaction products in soil (Williams and Chadwick 1977). Low concentration of cations such as Ca, Mg etc. may also cause acidity (Eyre 1968). Besides seasonal variation, the soil pH showed a declining trend with stand age. Similar temporal change in soil pH has been reported by Mishra and Ramakrishnan (1983) in 'jhum' fallows of different ages in this region.

The concentration of organic matter and nutrients in the soil increased from their minimum level in the 7-year old stand to the maximum level in the 16-year old stand. In the studies carried out by Odum (1960) and Juo and Lal (1977) soil organic matter concentration in regenerating forest decreased during first 3 years of fallow period, thereafter it increased in 7- and 10-year old stands. According to Odum (1960) and Aweto (1981), the organic matter content in the top soil approaches to the level of mature forest by the end of the tenth year of secondary succession in the forest ecosystems. In the present study, SOM and TKN and available-P in the 16-year stand is comparable to the values reported by Das *et al.* (Unpublished data) from a mature broadleaved forest of this region.

Thus the WHC, SMC, SOM, TKN and available-P increased with the increase in the age of the stand, while, percentage sand and pH showed a reverse trend. The study also indicates that intrinsic difference between the sites in regard to soil physical properties, particularly the texture may have a confounding effect on other physico-chemical properties of the soil.

CHAPTER 5

COMMUNITY STRUCTURE AND DYNAMICS

INTRODUCTION

The structure of plant community is often influenced by frequent natural and man-induced disturbances (White 1979, Vogl 1980, Armesto and Pickett 1985). Clements (1936) viewed disturbance as a negative force that destroys climax assemblages and brings instability in the system, while Paine (1966), Lubchenco (1978), Connell (1978), Grime (1979), Armesto and Pickett (1985), Messier and Kimmins (1991) considered it as a positive force that might increase plant species richness in the community and augment species diversity by preventing competitive exclusion by dominant species. In terrestrial environment, grazing, burning, cutting, mining, etc., are major human-related activities that cause disturbance in the forest communities. Each of the above activities cause different effect on the vegetation (Loucks *et al.* 1980, Pandey and Singh 1984/1985).

Recovery of a disturbed forest ecosystem largely depends on the regrowth of vegetation (Likens *et al.* 1970) which in turn is influenced by a large number of factors. Notable among them are size, intensity and frequency of the disturbance (Dryness 1973, Halpern 1988), fertility of the site (Boring *et al.* 1981, Gholz *et al.* 1985, Hamilton and Yearsley 1988), the amount, availability and establishment success of off-site seeds (Hamilton and Yearsley 1988), type of the understorey vegetation present during disturbance (Bormann and Likens 1979, Halpern 1988) and their regrowth and competitive ability (Stewart *et al.* 1984).

Our understanding of the revegetation process, following disturbance in forest ecosystems is based mainly on the works done by Ewel (1976), Bormann and Likens (1979), Uhl (1987), Guarighuata (1990), and Herbohn and Congdon (1993) who have studied the vegetation recovery process after tree cutting in different temperate and tropical forest ecosystems of the world. In India, similar studies have been carried out by Pandey and Singh (1984/1985) in moist temperate oak forest ecosystem in Central Himalaya. In the subtropical humid forests of north-east India studies on the effects of tree cutting are limited to the population structure (Khan *et al.* 1987, Rao *et al.* 1991) and regeneration behaviour of certain dominant tree species (Khan 1986). This chapter presents data related to the community structure after 7, 13 and 16 years of human disturbance in a subtropical humid forest.

METHODS

COMMUNITY ANALYSIS

The structure of plant community in 7-, 13- and 16-year old stands was analysed during August-September, 1993 and 1994 when majority of the plants were at the peak of their growth. An area of 2.5 ha was demarcated in each

stand and ten quadrats each of 10 m x 10 m size were laid randomly to study the woody vegetation. The ground vegetation (herbs, tree seedlings and saplings) was studied by laying 20 quadarts of 1 m x 1 m size. In case of tree species, three categories *viz.* seedlings (height <20 cm and basal diameter <10 cm), saplings (height 20-150 cm and basal diameter <10 cm) and trees (DBH >10 cm) were recognized. The tree component was further divided into six DBH classes *viz.*, 10-15, 15-20, 20-25, 25-30, 30-35 and 35-40 cm. Nomenclature of the plant species follows Hooker (1972-1897). Density, frequency, abundance, basal cover and importance value of all species were determined according to the methods given by Misra (1968). Density-diameter distribution curve, and dominance distribution curve in terms of IVI, were drawn for the tree species in all the stands (Muller-Dombois and Ellenberg 1974, Magurran 1988).

COMMUNITY INDICES

Sorensen's similarity index (Sorensen 1948), Pielou's evenness index (Pielou 1966), species richness index (Magurran 1988) and Shannon's diversity index (Shannon-Wiener 1963) were computed as follows:

Similarity index : $\frac{2\,C}{A + B} \times 100$

where, A = Number of species in stand A
B = Number of species in stand B
C = Number of species common to both stand A and B.

Evenness index : $\frac{-\sum \left(\frac{n_i}{N}\right) \log_e \left(\frac{n_i}{N}\right)}{\log_e S}$

where, n_i = Importance value for each species
N = Total importance value
S = Number of species.

Species richness index : $\frac{S-1}{\log_e N}$

where, S = Number of species
N = Number of individuals.

Diversity index : $$-\sum \left(\frac{n_i}{N}\right) \log_e \left(\frac{n_i}{N}\right)$$

where, n_i = Importance value for each species
N = Total importance value.

Regeneration potential of each stand was evaluated by computing relative sprout growth (RSG) in the following manner:

$$\text{(i) RSG (B)} = \frac{\text{Basal area of SS}}{\text{Total basal area (SS + NS)}} \times 100$$

$$\text{(ii) RSG (N)} = \frac{\text{No. of SS}}{\text{Total no. of stumps (SS + NS)}} \times 100$$

where, SS is the sprouting stumps and NS is the non-sprouting stumps.

STATISTICAL ANALYSIS

The data were subjected to one-way ANOVA (fixed efects model) to test their variability over time. Wherever necessary linear regressions were worked out following Zar (1974).

RESULTS

FLORISTIC COMPOSITION AND DENSITY

Trees: Among the ten species of trees that were identified, *Pinus kesiya* and *Quercus dealbata* were present in all the three stands (Table 5.1). In the 7-year old stand *Q. dealbata* was represented only by saplings. In 13- and 16-year old stands, species were distributed in 3 distinct strata, whereas, in the 7-year old stand there were only two layers. The canopy layer in the 7-year old stand comprised of a few sparsely distributed trees of *P. kesiya, Schima wallichii, S. khasiana* and *Corylopsis himalayana*. The dense herbaceous vegetation was composed of tree seedlings and saplings and a few young regenerating trees (<2 m height) of the above-said broadleaved species. In the 13-year old stand the broken canopy was composed of

Table 5.1. Analytical characters of tree species in three forest stands undergoing recovery after tree cutting (measurements were made during August-September).

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	1994	Basal area (m^2 ha^{-1}) 1993	1994
7-yr	*Corylopsis himalayana* Griff.[4]	17.8 ±0.1	22.2 ±0.2	0.16 ±0.01	0.21 ±0.01
	Pinus kesiya Royle Ex. Gordon[1]	94.9 ±1.2	105.1 ±1.1	1.24 +0.09	1.42 +0.10
	Schima khasiana Dyer[3]	40.0 ±0.2	40.0 ±0.2	0.98 ±0.01	0.98 ±0.01
	Schima wallichii Chois[2]	17.5 ±0.6	22.5 ±0.3	0.54 ±0.01	0.66 ±0.02
13-yr	*Castonopsis kurzii* (Hance).B.[2]	78.4 ±0.5	81.6 ±0.3	2.25 ±0.90	2.36 ±0.10
	Litsea khasiana Bl.[5]	40.0 ±0.1	40.0 ±0.2	0.36 ±0.03	0.36 +0.01
	Myrica esculenta Buch. Hans[4]	40.0 ±0.3	40.0 ±0.6	1.56 ±0.1	1.59 ±0.1
	Pinus kesiya Royle Ex. Gordon[3]	60.0 ±0.6	60.0 ±0.5	1.10 ±0.1	1.10 ±0.1
	Quercus dealbata Hook f. & Th'1	256.0 ±2.7	264.0 ±2.1	13.79 ±0.31	15.22 ±0.92
16-yr	*Castonopsis kurzii* (Hance).B.[6]	60.0 ±0.9	60.0 ±1.2	1.25 ±0.1	1.25 ±0.3
	Corylopsis himalayana Griff.[7]	60.0 ±0.5	60.0 ±0.9	1.00 ±0.2	1.00 ±0.1
	Lindera caudata Benth.[8]	60.0 ±1.3	60.0 ±1.3	0.58 ±0.2	0.58 ±0.1
	Litsea khasiana Bl.[10]	40.0 ±0.9	40.0 ±0.7	0.38 ±0.01	0.38 +0.01
	Pinus kesiya Royle Ex. Gordon.[5]	125.0 ±2.7	115.0 ±5.1	2.80 ±0.1	2.59 ±0.1
	Quercus dealbata Hook f. & Th.[1]	270.0 ±3.2	290.0 ±7.1	13.59 ±0.12	14.34 +0.91

Table 5.1 continued

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	Density (Plants ha^{-1}) 1994	Basal area (m^2 ha^{-1}) 1993	Basal area (m^2 ha^{-1}) 1994
	Quercus griffithii Hook f. & Th.[3]	136.0 ±3.9	144.0 ±1.2	5.12 ±0.1	5.44 ±0.6
	Rhododendron arboreum Sm.[2]	200.0 ±5.2	200.0 ±4.8	13.11 ±1.7	13.11 ±0.6
	Schima khasiana Dyer[4]	114.0 ±4.1	126.0 ±1.4	4.45 ±0.6	5.01 ±1.1
	Schima wallichii Chois[9]	60.0 ±3.1	60.0 ±1.7	1.22 ±0.1	1.22 ±0.1

Values as superscript are species ranking based on IVI.

± SEM (n=10)

Table 5.2. Density and Basal area of saplings of dominant tree species in the three forest stands.

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	1994	Basal area (m^2 ha^{-1}) 1993	1994
7-yr	*Corylopsis himalayana*	63.1 ±0.2	56.8 ±0.5	0.08 ±0.01	0.07 ±0.01
	Pinus kesiya	403.4 ±1.3	396.6 ±1.2	1.70 ±0.13	1.72 ±0.14
	Quercus dealbata	120.0 ±2.1	120.0 ±1.9	0.45 ±0.01	0.45 ±0.01
	Schima khasiana	40.0 ±0.9	40.0 ±2.1	0.08 ±0.01	0.08 ±0.02
	Schima wallichii	57.3 ±1.1	62.7 ±0.9	0.13 ±0.01	0.14 ±0.01
13-yr	*Castonopsis kurzii*	21.0 ±1.1	19.0 ±0.7	0.06 ±0.01	0.06 ±0.01
	Litsea khasiana	200.0 ±5.3	200.0 ±3.1	0.44 ±0.01	0.44 ±0.09
	Quercus dealbata	88.0 ±1.1	72.0 ±2.1	0.37 ±0.02	0.33 ±0.01
16-yr	*Castonopsis kurzii*	20.0 ±0.3	20.0 ±0.1	0.06 ±0.01	0.06 ±0.01
	Quercus dealbata	130.0 ±3.7	110.0 ±1.1	0.56 ±0.09	0.51 ±0.05
	Quercus griffithii	77.0 ±0.9	83.0 ±1.1	0.29 ±0.01	0.31 ±0.01
	Rhododendron arboreum	18.0 ±2.1	22.0 ±1.3	0.07 ±0.01	0.09 ±0.02
	Schima khasiana	147.0 ±3.9	133.0 ±4.1	0.47 ±0.01	0.43 ±0.02
	Schima wallichii	20.0 ±0.9	20.0 ±1.3	0.07 ±0.01	0.07 ±0.01

± SEM (n=20)

Table 5.3. Density and Basal area of seedlings of dominant tree species in the three forest stands.

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	Density (Plants ha^{-1}) 1994	Basal area (m^2 ha^{-1}) 1993	Basal area (m^2 ha^{-1}) 1994
7-yr	*Corylopsis himalayana*	2.1 ±0.3	1.9 ±0.4	0.06 ±0.01	0.05 ±0.01
	Pinus kesiya	43.2 ±2.1	44.8 ±1.7	0.82 ±0.06	0.73 ±0.04
	Quercus dealbata	5.8 ±1.1	6.2 ±1.0	0.08 ±0.01	0.10 ±0.02
	Schima khasiana	12.0 ±3.1	12.0 ±1.1	0.38 ±0.01	0.38 ±0.06
	Schima wallichii	2.3 ±0.9	1.7 ±0.4	0.04 ±0.01	0.03 ±0.00
13-yr	*Castonopsis kurzii*	6.3 ±1.1	5.7 ±0.9	0.09 ±0.03	0.11 ±0.02
	Myrica esculenta	2.0 ±0.5	2.0 ±0.2	0.06 ±0.01	0.06 ±0.01
	Pinus kesiya	3.8 ±1.7	4.2 ±0.2	0.17 ±0.01	0.18 ±0.01
	Quercus dealbata	7.6 ±1.3	8.4 ±1.2	0.38 ±0.12	0.42 ±0.01
16-yr	*Pinus kesiya*	3.3 ±1.1	4.7 ±0.6	0.12 ±0.01	0.18 ±0.01
	Quercus dealbata	7.7 ±1.1	8.3 ±0.9	0.32 ±0.05	0.34 ±0.09
	Quercus griffithii	5.8 ±0.9	6.2 ±1.7	0.21 ±0.01	0.22 ±0.02
	Rhododendron arboreum	6.3 ±2.1	5.7 ±1.8	0.30 ±0.03	0.27 ±0.02
	Schima khasiana	1.0 ±0.2	14.0 ±0.9	0.02 ±0.00	0.04 ±0.01
	Schima wallichii	2.0 ±0.3	2.0 ±0.3	0.04 ±0.01	0.04 ±0.01

± SEM (n=20)

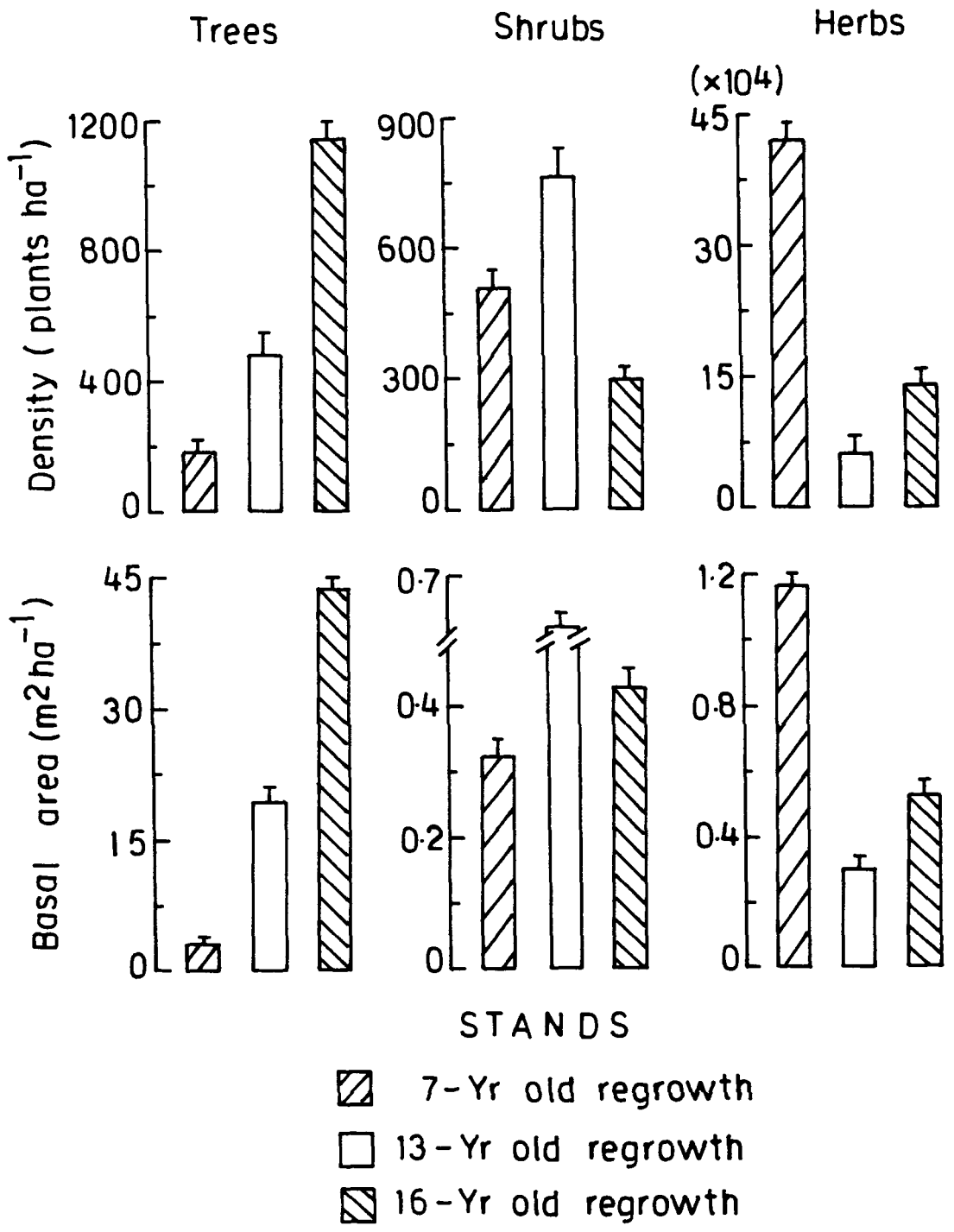


Figure 5.1. Density and basal area of (a) trees, (b) shrubs and (c) herbs in forest stands of three different ages.

scattered trees of *Q. dealbata*, while in the 16-year old stand, alongwith *Q. dealbata*, *Rhododendron arboreum*, *Quercus griffithi* and *S. khasiana* were also present in the canopy layer. The sprouts of *Q. dealbata*, *Q. griffithii*, *S. khasiana* and *R. arboreum* ranging between 3 and 7 m height formed the sub-canopy layer in the 13- and 16-year old stands.

P. kesiya, a secondary successional species had a density of 100 trees ha^{-1} in the 7-year old stand. Its density declined in the older stands. Conversely, density of *Q. dealbata* increased with stand age. The total tree density and basal area increased significantly ($P<0.05$) from 180 trees ha^{-1} and 3.1 m^2 ha^{-1} in the 7-year old stand to 1140 trees ha^{-1} and 44.2 m^2 ha^{-1}, respectively in the 16-year old stand (Figure 5.1). Density of seedlings and saplings were maximum in the 7-year old stand, where *P. kesiya* alone constituted more than 60% of the total seedling and/or sapling density. Seedlings of *C. himalayana*, *Q. dealbata* and *S. khasiana* were abundant in the 13- and 16-year old stands (Tables 5.2 and 5.3).

On the basis of IVI, *P. kesiya* was the dominant species among the trees in the 7-year old stand. In 13- and 16-year old stands, however, *Q. dealbata* was the dominant species, sharing about 71% dominance among five tree species in the former stand and 72% dominance among ten tree species in the latter stand (Figure 5.2a).

Shrubs: There were 4, 9 and 3 shrub species in 7-, 13- and 16-year old stands, respectively. *Litsea elongata* and *Rhus semi-alata* were commonly present in all the three regrowths (Table 5.4). Shrub density was lowest in the 16-year old stand (300 plants ha^{-1}) and highest (780 plants ha^{-1}) in the 13-year old stand. Their basal area was also maximum (0.62m^2 ha^{-1}) in the 13-year old stand but the minimum value (0.34 m^2 ha^{-1}) was recorded in the 7-year old stand (Figure 5.1).

Herbs: The number of herbaceous species declined sharply from 33 in the 7-year old stand to 12 in the 16-year old stand (Table 5.5). Perennial

Table 5.4. Analytical characteristics of shrub species in the three forest stands.

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	Density (Plants ha^{-1}) 1994	Basal area (m^2 ha^{-1}) 1993	Basal area (m^2 ha^{-1}) 1994
7-yr	*Litsea elongata* Benth & Hook.f.[1]	158 ±12	162 ±11	0.14 ±0.02	0.14 ±0.01
	Osbeckia stellata Ham.[2]	180 ±18	180 ±9	0.05 ±0.01	0.05 ±0.01
	Rhus semi-alata Murry[4]	97 ±11	103 ±13	0.04 ±0.01	0.05 ±0.02
	Rubus ellipticus Sm.[3]	60 ±5	60 ±7	0.07 ±0.01	0.07 ±0.01
13-yr	*Breynia retusa* (Dennst) Alst.[7]	60 ±3	60 ±7	0.02 ±0.00	0.02 ±0.00
	Eurya japonica[6]	93 ±9	107 ±11	0.03 ±0.00	0.03 ±0.00
	Gaultheria fragrantissima Wall.[2]	109 ±11	131 ±12	0.07 ±0.01	0.08 ±0.02
	Lonicera macrantha Dc.[8]	40 ±2	40 ±7	0.003 ±0.00	0.003 ±0.00
	Litsea elongata Benth & Hook.f.[1]	231 ±11	249 ±13	0.38 ±0.10	0.42 ±0.09
	Osbeckia stellata Ham.[3]	121 ±11	119 ±12	0.04 ±0.01	0.04 ±0.01
	Rhus semi-alata Murry[5]	105 ±9	95 ±3	0.04 ±0.01	0.04 ±0.01
	Symplocos spicata Roxb.[4]	20 ±3	20 ±4	0.01 ±0.00	0.01 ±0.00
	Symplocos sismuntia Ham.[9]	22 ±3	18 ±6	0.002 ±0.00	0.002 ±0.00
16-yr	*Litsea elongata* Benth & Hook.f.[1]	112 ±13	128 ±9	0.26 ±0.07	0.30 ±0.06
	Rhus semi-alata Murry[3]	81 ±12	79 ±6	0.08 ±0.01	0.07 ±0.01
	Viburnum foetidum Wall.[2]	96 ±13	104 ±21	0.07 ±0.01	0.07 ±0.01

Values as superscripts are species ranking based on IVI

± SEM (n=20)

Table 5.5. Analytical characteristics of herbaceous species in the three forest stands.

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	1994	Basal area (m^2 ha^{-1}) 1993	1994
7-yr	*Anaphilis araneusa* Dc[7]	14.3 ±0.3	15.7 ±0.3	0.03 ±0.01	0.04 ±0.01
	Anaphilis adnata Dc[12]	12.3 ±0.9	11.7 ±0.7	0.02 ±0.001	0.02 ±0.001
	Anemone rivularisltam[3]	33.2 ±1.3	32.8 ±1.5	0.07 ±0.01	0.07 ±0.01
	Ambrossia artimissifolia[16]	10.0 ±0.2	10.0 ±0.1	0.02 ±0.001	0.02 ±0.001
	Arundinella bengalensis[2] (Spreng) Druce	68.9 ±1.3	71.1 ±2.1	0.18 ±0.02	0.18 ±0.02
	Asparagus racemosus Willd[32]	2.0 ±0.2	2.0 ±0.1	0.003 ±0.001	0.003 ±0.001
	Brachiaria sp.[24]	4.8 ±0.3	5.2 ±0.7	0.006 ±0.001	0.007 ±0.002
	Brunella vulgaris Linn[6]	19.0 ±1.1	19.0 ±1.3	0.03 ±0.001	0.03 ±0.001
	Commelina benghalensis Linn[10]	13.2 ±2.9	12.8 ±1.7	0.02 ±0.001	0.02 ±0.001
	Cassia mimosoides Linn[22]	12.1 ±0.9	11.9 ±0.8	0.02 ±0.001	0.02 ±0.001
	Desmodium heterophyllum Dc[18]	7.0 ±0.9	7.0 ±0.3	0.02 ±0.001	0.02 ±0.001
	Erigeron pusillus[15]	9.8 ±0.9	10.2 ±1.2	0.02 ±0.001	0.02 ±0.002
	Eupatorium adenophorum[4]	21.8 ±0.2	20.7 ±0.3	0.11 ±0.03	0.10 ±0.09
	Erigeron canadensis Linn[21]	7.0 ±0.9	7.0 ±0.3	0.01 ±0.001	0.01 ±0.002

Table 5.5 continued

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	1994	Basal area (m^2 ha^{-1}) 1993	1994
	Erigeron bunariensis[20]	5.1 ±0.3	4.9 ±0.1	0.02 ±0.001	0.01 ±0.001
	Galium rotundifolium Linn[23]	5.2 ±0.1	4.8 ±0.3	0.01 ±0.0001	0.01 ±0.001
	Gleichenia longissima[8]	12.8 ±0.7	13.2 ±0.6	0.05 ±0.001	0.05 ±0.001
	Hemiphragma heterophylla Wall[26]	3.0 ±0.5	3.0 ±0.7	0.01 ±0.001	0.01 ±0.001
	Hypericum japonicum Thumb[19]	7.2 ±1.3	6.8 ±0.3	0.02 ±0.001	0.02 ±0.002
	Hypocharis radicata[11]	10.1 ±1.3	9.9 ±0.9	0.04 ±0.01	0.03 ±0.01
	Imperata cylindrica[1] (Linn) P.Beauv	81.3 ±3.9	82.7 ±1.3	0.21 ±0.01	0.21 ±0.01
	Neillia thyrisiflora D.Don[24]	5.0 ±0.03	5.0 ±0.1	0.01 ±0.001	0.01 ±0.001
	Oplismenus undulatifolium[30]	2.0 ±0.02	2.0 ±0.01	0.01 ±0.001	0.01 ±0.001
	Osbeckia crinata Benth[17]	5.9 ±1.2	6.1 ±1.2	0.04 ±0.001	0.04 ±0.001
	Panax sp.[28]	4.0 ±0.2	4.0 ±0.3	0.006 ±0.001	0.006 ±0.001
	Ranunculus diffusus Dc[5]	23.0 ±1.3	23.0 ±1.3	0.08 ±0.01	0.08 ±0.02
	Rubia cordifolia Linn[14]	7.0 ±0.3	7.0 ±1.2	0.02 ±0.001	0.02 ±0.001
	Rubus moluccans Linn[13]	9.0 ±1.1	9.0 ±1.3	0.04 ±0.001	0.04 ±0.001

Table 5.5 continued

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	1994	Basal area (m^2 ha^{-1}) 1993	1994
	Salix criophylla Ander[27]	4.0 ±0.3	4.0 ±0.2	0.01 ±0.001	0.01 ±0.001
	Oxalis corniculata[9]	11.8 ±1.3	12.2 ±0.9	0.02 ±0.001	0.03 ±0.002
	Tetrastigma lanceolarium[29] (Roxb) Planch	3.0 ±0.5	3.0 ±0.3	0.01 ±0.001	0.01 ±0.001
	Teucrium quadrifolium Ham[31]	2.1 ±0.1	1.9 ±0.3	0.01 ±0.001	0.01 ±0.001
	Vitis sp.[33]	1.0 ±0.001	1.0 ±0.001	0.003 ±0.001	0.003 ±0.001
13-yr	*Asparagus racemosus* Willd[7]	2.0 ±0.2	2.0 ±0.3	0.01 ±0.001	0.01 ±0.001
	Dumania villosa[8]	1.8 ±0.3	2.2 ±0.4	0.01 ±0.001	0.01 ±0.001
	Hedyotis oricinella Hook.f[6]	5.1 ±1.0	4.9 ±0.3	0.02 ±0.001	0.02 ±0.005
	Hemiphragma heterophylla Wall[2]	13.3 ±1.3	12.7 ±1.3	0.06 ±0.01	0.05 ±0.01
	Oplimenus undulatifolium[9]	1.0 ±0.2	1.0 ±0.1	0.005 ±0.001	0.006 ±0.001
	Osbeckia crinata Benth[3]	9.2 ±1.3	8.8 ±0.9	0.07 ±0.01	0.06 ±0.01
	Pteridium quilinum (Linn) Kuhn[1]	10.6 ±1.1	11.4 ±0.9	0.07 ±0.01	0.06 ±0.01
	Rubus acuminatus[4]	6.3 ±1.1	7.7 ±0.3	0.05 ±0.001	0.07 ±0.001
	Smilax blumei Dc[5]	5.0 ±0.2	5.0 ±0.1	0.01 ±0.001	0.01 ±0.001

Table 5.5 continued

Age of the Stand	Species	Density (Plants ha^{-1}) 1993	1994	Basal area (m^2 ha^{-1}) 1993	1994
16-yr	*Commelina benghalensis* Linn[2]	22.6 ±3.2	23.4 ±1.1	0.10 ±0.02	0.10 ±0.01
	Gleichenia longissima[5]	9.2 ±1.1	8.8 ±1.1	0.03 ±0.01	0.03 ±0.01
	Hedyotis oricinella Hook.f[8]	7.0 ±0.1	7.0 ±0.3	0.02 ±0.001	0.02 ±0.001
	Hypericum japonicum Thumb[10]	5.8 ±0.3	6.2 ±0.7	0.02 ±0.001	0.02 ±0.001
	Plantago major Linn[11]	4.1 ±0.3	3.9 ±0.1	0.01 ±0.001	0.01 ±0.001
	Polygonum hydropiper Linn[12]	5.0 ±0.2	5.0 ±0.07	0.02 ±0.001	0.02 ±0.001
	Pteridium quilinum (Linn) Kuhn[9]	6.0 ±0.2	6.0 ±1.3	0.04 ±0.01	0.04 ±0.01
	Ranunculus diffusus Dc[6]	8.8 ±0.3	9.2 ±1.3	0.05 ±0.01	0.05 ±0.01
	Rubia cordifolia Linn[7]	7.3 ±1.1	8.7 ±0.3	0.03 ±0.002	0.03 ±0.001
	Selaginella bisculata Spreng[3]	25.0 ±2.3	25.0 ±1.9	0.05 ±0.02	0.05 ±0.01
	Oxalis corniculata[4]	14.0 ±2.1	14.0 ±1.3	0.07 ±0.01	0.07 ±0.02
	Lycopodium clavatum[1]	31.8 ±0.3	32.2 ±6.3	0.08 ±0.01	0.08 ±0.01

Values as superscripts are species ranking based on IVI.

± SEM (n=20)

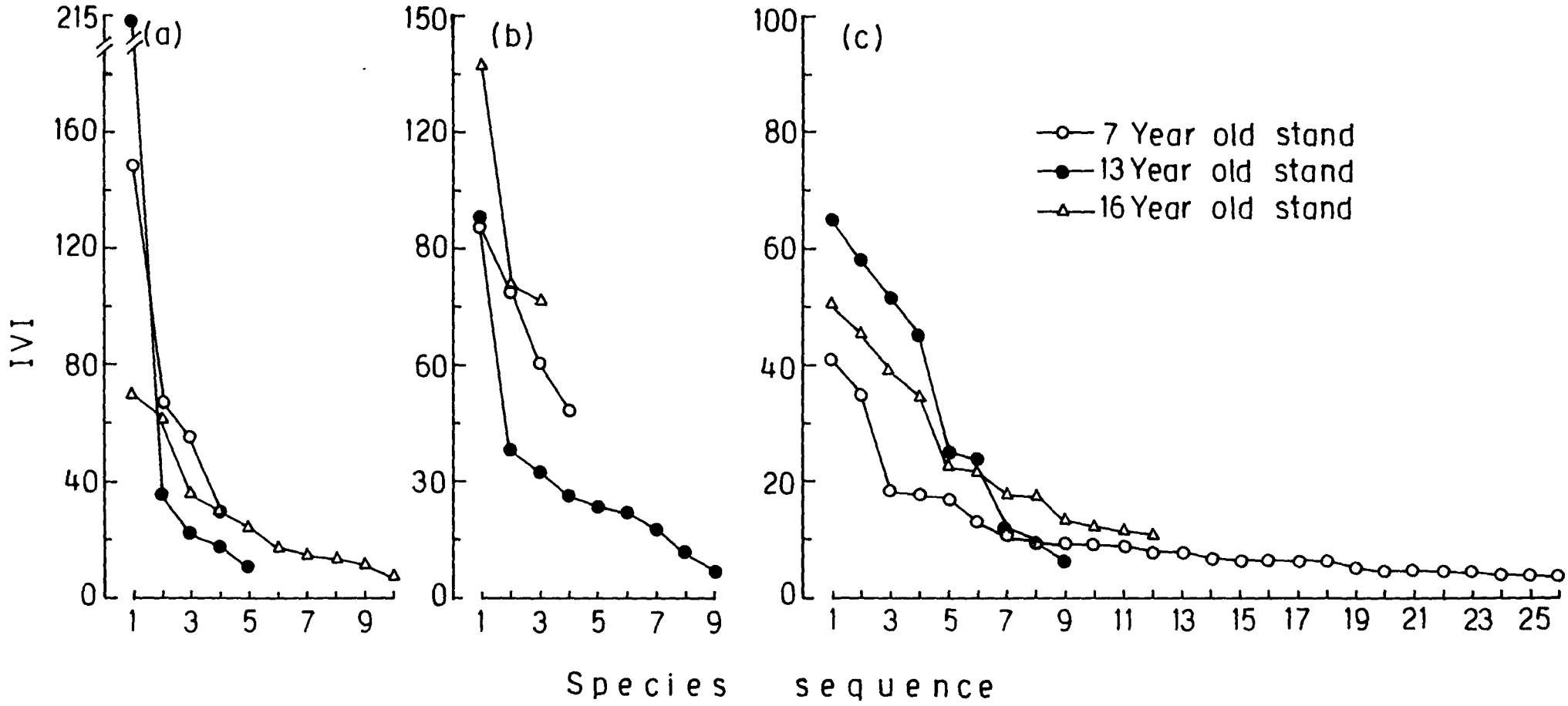


Figure 5.2. Dominance curves for (a) tree, (b) shrub and (c) herbaceous species in the three forest stands.

grasses like *Imperata cylindrica* (IVI=41), *Arundinella bengalensis* (IVI=36) and early successional weed like *Eupatorium adenophorum* (IVI=18) were dominant in the 7-year old stand. *Pteridium aquilinum* (IVI=65) and *Osbeckia crinata* (IVI=54) were dominant in the 13-year old stand (Figure 5.2c). *Commelina benghalensis* and *Lycopodium clavatum* had the maximum IVI (52) in the ground vegetation of the 16-year old stand. Density and basal area of herbaceous vegetation was maximum in the 7-year old stand and minimum in the 13-year old stand (Figure 5.1).

In terms of Sorensen's similarity index, trees and herbaceous components were less similar in 7- and 13-year old stands as compared to the 13- and 16-year old stands. The shrubs showed greater similarity between 7- and 13-year old stands (Table 5.6).

SPECIES RICHNESS

The number of species sharply declined from 41 in the 7-year old stand to 25 in the 16-year old stand (Table 5.7). But the number of tree species as well as its richness index showed marked increase from 7- to 16-year old stands (Table 5.8). The shrub and herb species richness, however, declined with the regrowth of the forest.

SPECIES ABUNDANCE

Rank abundance curves of woody species (trees plus shrubs) in the three forest stands presented in Figure 5.3 indicate high dominance in the 7-year old stand compared to 13- and 16-year old stands. In the 7-year old stand, four species *viz. Litsea elongata, Rhus javonica, Osbeckia stellata* and *Pinus kesiya* together shared 68.4% dominance and the rest 31.6% was shared by remaining four species, while in 13-year old stand, four species *viz. Litsea khasiana, P. kesiya, Quercus dealbata* and *R. javonica* together had only 39.04% dominance and the rest 60.96% was distributed among ten other species. Out of 13 woody species in the 16-year old stand, first four rank holding species *viz. Q. dealbata, R. arboreum, S. khasiana* and *P.*

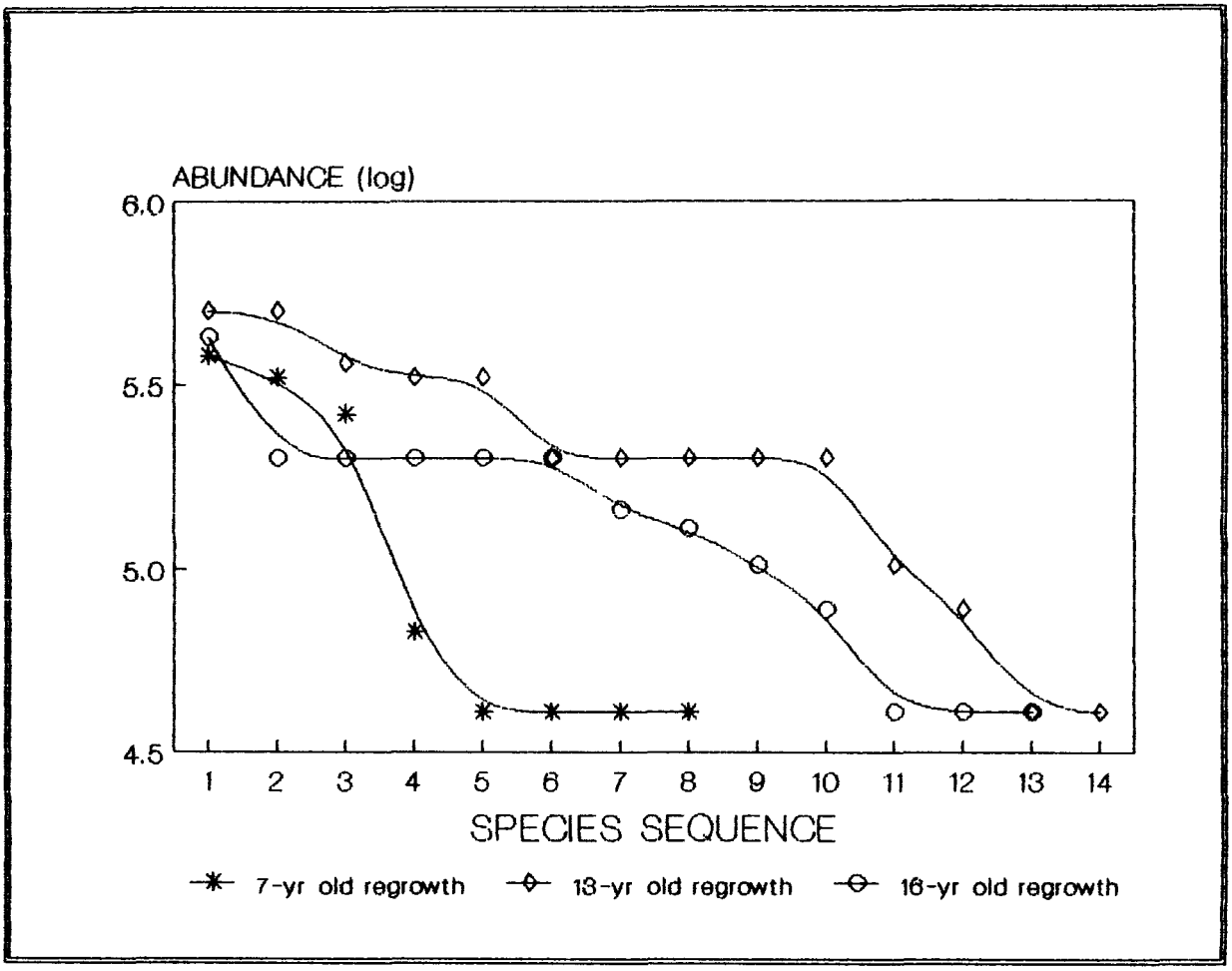


Figure 5.3. Rank-abundance curve of woody species in the three regrowing forest stands.

Table 5.6. Comparison of Sorensen's simalarity index of tree, shrub and herbaceous species in the forest stands of three different ages.

Vegetation components	7-year old vs 13-year old	13-year old vs 16-year old
Tree species	22.22	53.33
Shrub species	46.15	33.33
Herbaceous species	19.10	20.00
Total woody species	36.36	44.44
Total vegetation	25.40	33.33

Table 5.7. Species content of the three forest stands.

Vegetation components	Age of the forest stand		
	7-yr	13-yr	16-yr
Tree species	4	5	10
Shrub species	4	9	3
Herbaceous species	33	9	12
Total woody species	8	14	13
Total no. of species	41	23	25

Table 5.8. Comparison of species richness index in three forest stands.

Vegetation components	Age of the forest stand		
	7-yr	13-yr	16-yr
Tree species	0.58	0.65	1.28
Shrub species	0.48	0.01	0.33
Herbaceous species	0.07	0.13	0.07
Total woody species	1.07	1.82	1.64
Total vegetation	3.08	2.01	2.01

Table 5.9. Comparison of Pielou's evenness index in three forest stands.

Vegetation components	Age of the forest stand		
	7-yr	13-yr	16-yr
Tree species	0.881	0.606	0.909
Shrub species	0.972	0.875	0.966
Herbaceous species	0.842	0.572	0.735
Total woody species	1.236	0.701	1.230
Total vegetation	0.560	0.406	0.610

Table 5.10. Comparison of Shannon's diversity index of community components among the three forest stands.

Vegetation components	Age of the forest stand		
	7-yr	13-yr	16-yr
Tree species	1.22	0.98	2.09
Shrub species	1.35	1.92	1.06
Herbaceous species	2.94	1.26	1.83
Total woody species	1.29	1.45	1.32
Total vegetation	2.11	1.35	1.57

kesiya shared 39.93% of the total abundance and the rest 60.07% was distributed among the 7 species. This trend of abundance distribution in the three stands was further clear from a high (0.61) Pielou's evenness index in the 16-year old stand as compared to the 7- (0.56) and 13-year (0.40) old regrowths (Table 5.9).

SPECIES DIVERSITY

Shannon's diversity index for the tree component showed maximum diversity in the 16 year old stand and minimum in the 7-year old stand (Table 5.10). The index for herbaceous species was maximum (2.94) in the 7-year old stand and minimum in the 13-year old stand. Shrub species diversity was highest (1.9) in the 13-year old stand. The overall diversity for the community vegetation was maximum in the 7-year old stand and minimum in the 13-year old stand.

DENSITY-DIAMETER DISTRIBUTION OF TREE SPECIES

An overall straight-line negative relationship was obtained between density and diameter of trees in all the three stands (Figure 5.4a). Trees of lower DBH class were more frequent in the younger regrowths. While in the 16-year old stand, apart from the younger trees, older trees (25-30 cm DBH) also showed hihger frequency (15-25 cm DBH) (Figure 5.4b).

The density-diameter distribution within different tree species (Figure 5.5) indicated that except for *Quercus griffithii*, *Rhododendron arboreum* and *Schima wallichii*, population was mainly composed of young individuals having 10-15 cm DBH. In case of *Q. griffithii*, *R. arboreum* and *S. wallichii* relatively older trees (DBH 15-20 or 20-25 cm) were abundant in the 16-year old stand. *Q. dealbata* in the 13-year old stand had a DBH range of 10-30 cm, while in the 16-year old stand, the range was 10-40 cm. In the 7-year old stand, its population was composed mainly of saplings. The population of *R. arboreum* had a greater proportion of individuals in the intermediate DBH class (e.g. 20-25 cm) in the 16-year old stand. In both 7-

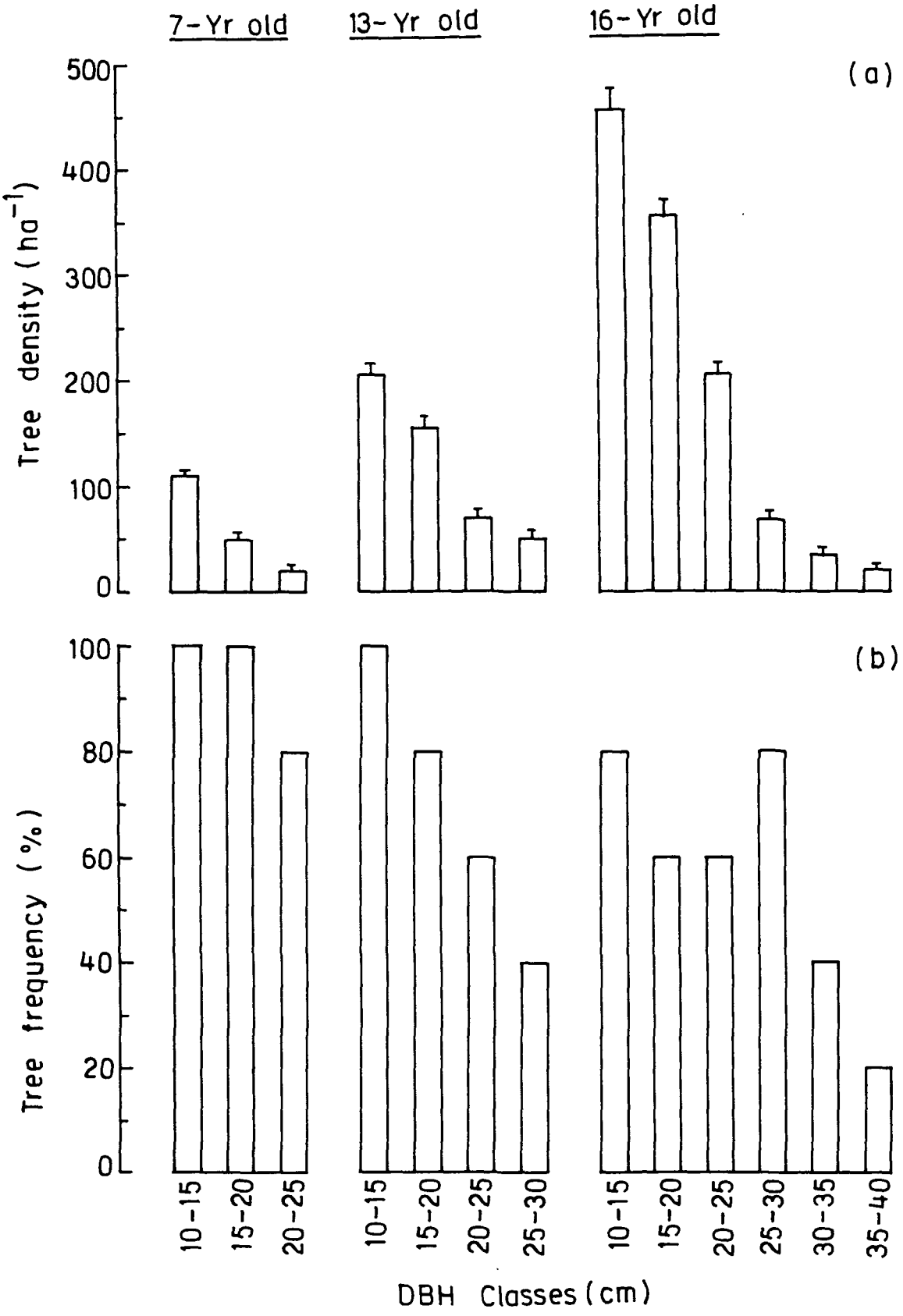


Figure 5.4. Density-diameter distribution (a) and respective frequency (b) of trees in the regrowing forest communities of three different ages.

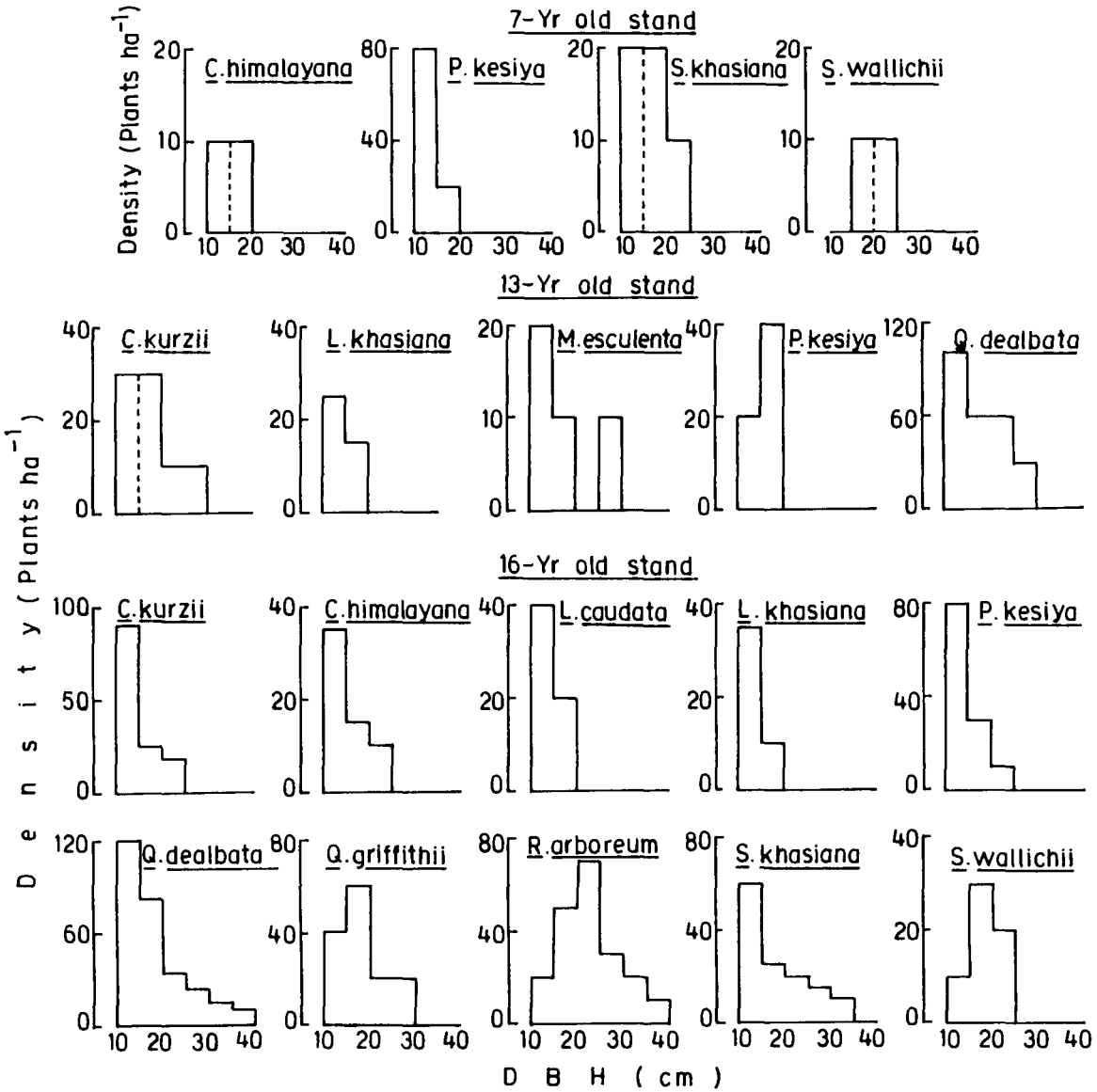


Figure 5.5. Population structure of the tree species in the three forest communities.

and 16-year old stands, *P. kesiya* was represented mostly by young (DBH 10-15 cm) individuals. Trees above 20 cm DBH were represented by *S. khasiana* in the 7-year old stand, by *C. kurzii*, *M. esculenta* and *Q. dealbata* in the 13-year old stand, and by *C. kurzii*, *C. himalayana*, *P. kesiya*, *Q. dealbata*, *Q. griffithii*, *R. arboreum*, *S. khasiana* and *S. wallichii* in the 16-year old stand.

GROWTH OF CUT TREES

The broadleaved species regenerated both through coppice and seeds, while, *P. kesiya* regenerated only through seeds. The density of sprouting stumps varied from 275 ha^{-1} in the 16-year old stand to 180 ha^{-1} in the 13-year old stand and 60 ha^{-1} in the 7-year old stand (Figure 5.6). The sprouting stumps constituted 42.9. 75.0 and 87.3% of the total stump density in 7-, 13- and 16-year old stands, respectively. The variation in sprouting stumps density was significant ($P<0.05$) between the three stands. The average diameter of the sprouting stumps was 24.6, 25.3 and 25.9 cm in 7-, 13- and 16-year old stands, respectively (Figure 5.7), while the diameter of non-sprouting stumps averged 26.1, 29.2 and 29.5 cm, respectively.

The total sprout density increased from 220 ha^{-1} in the 7-year old stand to 760 ha^{-1} in the 13-year old stand and 1350 ha^{-1} in the 16-year old stand. The sprout density of *Q. dealbata* alone represented 63.4, 71.1 and 37.4% of the total sprout density in the 7-, 13- and 16-year old stands, respectively. On an average there were 5 sprouts per stump in 7- and 13-year old stands, and 6 sprouts per stump in 16-year old stand (Table 5.11).

Ratio between the number and basal area of sprouting stumps to the total number and basal area of stumps, respectively served as useful indices to express the regrowth potential of trees in disturbed forest stands. Both these indices increased from 7- to 16-year old stand (Table 5.12).

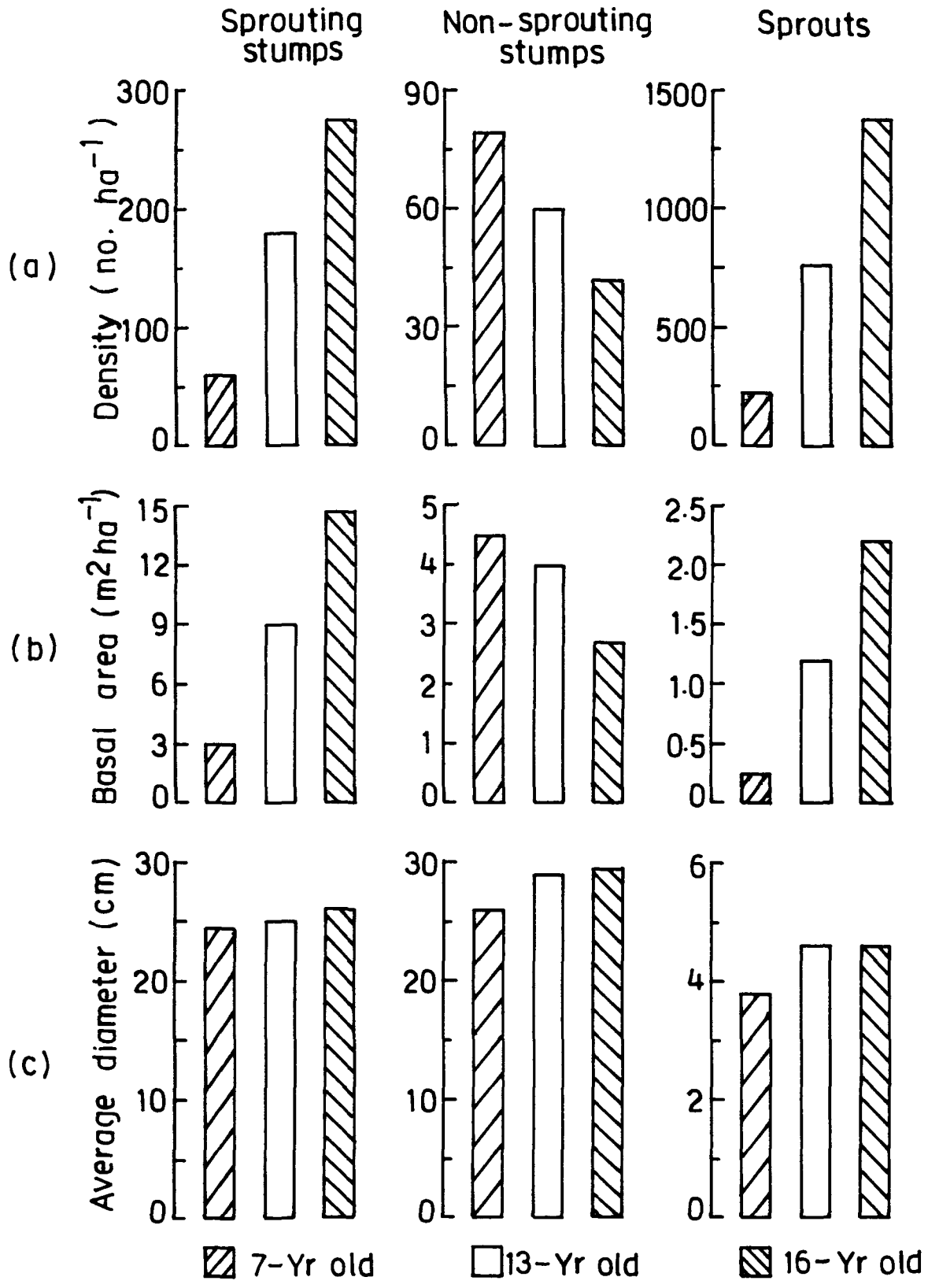


Figure 5.6. Density (a), basal area (b) and average basal diameter (c) of stumps and sprouts in forest stands of three different ages.

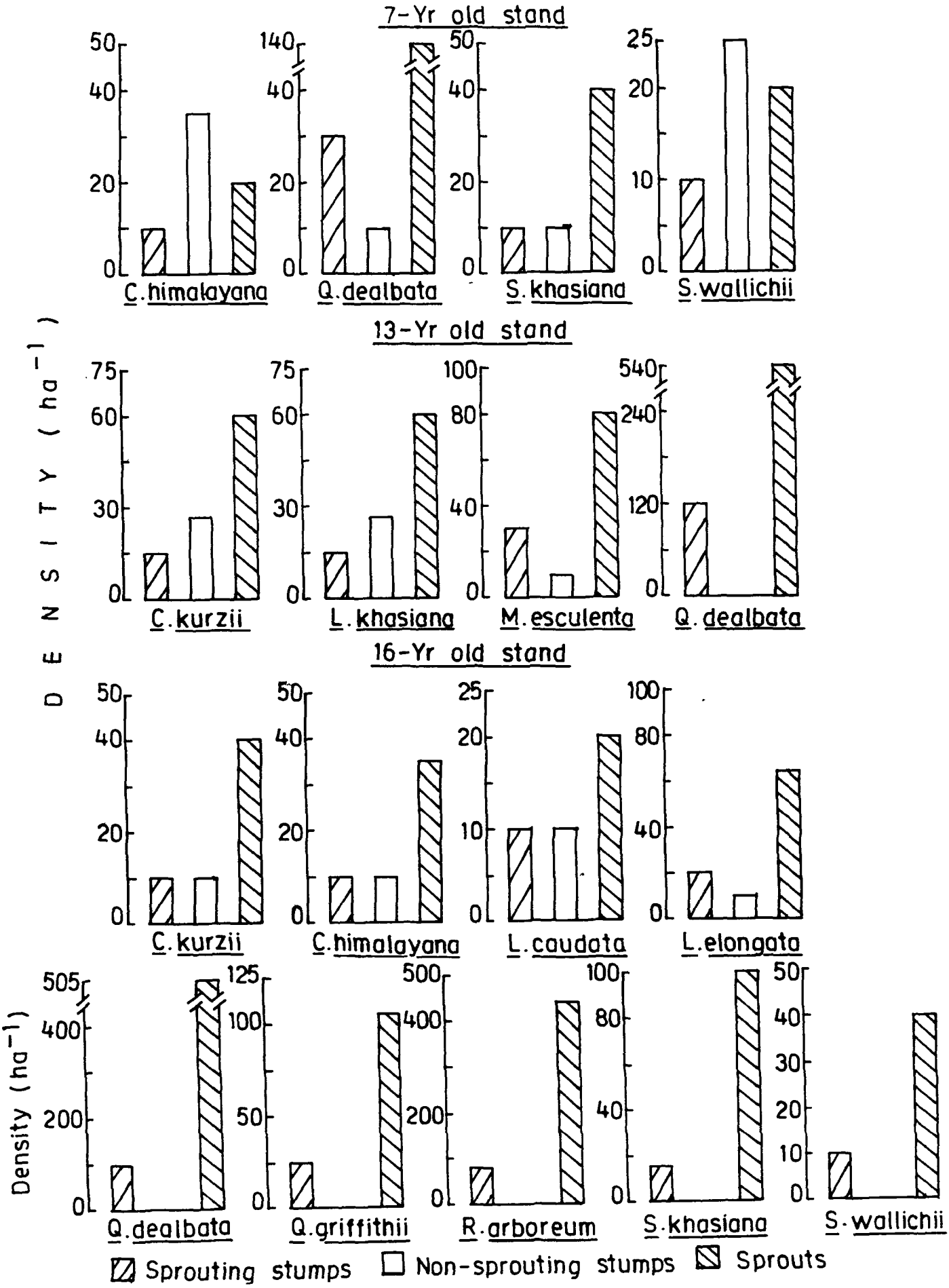


Figure 5.7. Stumps and sprout densities of the tree species in the three regrowing forest communities.

Table 5.11. Average number of sprouts per stump of the dominant tree species in the three forest stands.

Species	Age of the forest stand		
	7-yr old	13-yr old	16-yr old
Castonopsis kurzii	-	4±0.53	4±0.01
Corylopsis himalayana	2±0.30	-	4±0.61
Lindera caudata	-	-	2±0.31
Litsea khasiana	-	4±0.61	3±0.27
Myrica esculenta	-	3±0.21	-
Quercus dealbata	5±0.50	5±0.05	6±0.21
Quercus griffithii	-	-	4±0.12
Rhododendron arboreum	-	-	6±0.05
Schima khasiana	4±0.01	-	6±0.05
Schima wallichii	2±0.50	-	4±0.3

- absent

± SEM (n=10)

Table 5.12. Relative sprout growth (RSG) in terms of basal area (B) and number (N) in the three forest stands.

Formula used	Age of the forest regrowth		
	7-yr old	13-yr old	16-yr old
RSG (B)	41.1	71.8	90.7
RSG (N)	42.9	75.0	87.3

Note: Formulae (B and N) are given in the Methods.

DISCUSSION

COMMUNITY COMPOSITION AND SPECIES DYNAMICS

Community characteristics like species composition, density, dominance and species diversity showed marked differences among the three regrowing forest stands. The young stand was characterised by the predominance of grasses, with a large number of seedlings and saplings of *Pinus kesiya* in the stand. Since the vegetation in the surrounding area is mostly composed of secondary *P. kesiya* forests, large number of pine seeds could reach the newly created open habitat after partial harvesting of the overhead canopy and colonize the area. Role of site history and seed rain in determining the stand composition during early succession has been discussed by Christensen and Peet (1984). With the gradual closing of the canopy due to growth of sprouts from the cut trees, the dominance of shade intolerant pine declined in the older regrowths. In the 16-year old stand it was present only in the periphery.

According to Bormann and Likens (1979), disturbance triggers germination of the buried seeds, and the mechanism which synchronize the germination of such seeds with disturbance is a paramount control feature in ecosystem dynamics. In the 7-year old stand, prevailing high light intensity and relative dryness favoured growth and establishment of shade intolerant grasses, weeds and a few shrubs. Species richness in the community normally increases during the course of succession (Nicholson and Monk 1974, Peet and Christensen 1980). In the present study this trend was observed only in case of tree species, the herbaceous species showed a marked reduction from 7- to 16-year old stand. This could be explained on the basis of alteration in microenvironmental condition within the forest community due to significant reduction in the light intensity and accompanying increase in moisture content and detrital matter on the forest

floor from 7- to 16-year old stand. Total tree density in a protected broadleaved climax forest adjacent to the present study site was reported to be 2134 trees ha^{-1} (Khan 1986). Considering this as control, the tree density in 7-, 13- and 16-year old stands was about 8.4, 22.5 and 53.1%, respectively. Evidently, the tree density increased by *ca.* 14% from 7- to 13-year old stand, and by *ca.* 31% from 13- to 16-year old stand, indicating a faster rate of recovery from 13- to 16-year old stand than from 7- to 13-year old stand.

Pandey and Singh (1984/1985) reported a dense growth of seedlings and saplings, and sparse growth of young trees of climax species after 21 years of succession in a moist temperate oak forest. Compared to this situation, presence of seedlings and saplings of the climax oak (*Q. dealbata*) in the 7-year old stand indicate the faster rate of vegetation recovery in this part of the country, probably due to favourable climatic conditions prevailing in the area. A dense herbaceous cover might have also contributed to the recruitments and regeneration of the climax species by ameliorating the extreme conditions created by soil exposure to direct solar insolation. Shrubs appeared on the disturbed sites after 6 years in a moist temperate forest of India (Pandey and Singh 1984/1985). In the present study also, perennial herbs and shrubs were abundant in the 7-year old stand, but their populations could not stabilize. However *Litsea khasiana* and *Rhus semi-alata* persisted until 16 years, indicating their wider ecological amplitude compared to other shrub species.

Connell and Slatyer (1977) have proposed three models *viz.* facilitation model, tolerance model and inhibition model to explain the mechanism that brings about successional change after perturbation. A marked decline in the dominance of *P. kesiya* from 7- to 16-year old stand and its replacement by broadleaved tree species was related mainly to a significant reduction in light intensity which inhibited the growth and

establishment of shade intolerant *P. kesiya*. Therefore the sequence of at least few species in the successional community after partial tree harvesting in the subtropical humid forest of the area could be explained on the basis of inhibition model proposed by Connell and Slatyer (1977).

Bornkamm (1981) used community coefficient to calculate the rates of secondary succession. Low similarity was considered to be an indicative of high rate of change, and *vice versa*. Thus, the lower similarity between 7- and 13-year old stands indicated a faster rate of change in the community until 13 years of forest regrowth. A higher community coefficient between 13- and 16-year old stands suggested a decline in the pace of development after 13 years of disturbance. Aweto (1981) reported that major structural changes in forest fallows take place during first ten years of succession.

DOMINANCE AND DIVERSITY

Keeley *et al.* (1981) studied the post-fire succession of the herbaceous flora in southern California chaparral and reported that total species richness was positively related to the herb cover. In the present study also, a significant positive correlation between the herb cover and total number of species ($Y=0.68+0.05X$, $df=4$, $r=0.985$, $P<0.01$) was observed. The number of tree species increased over time until 16 years reaching to the level of an undisturbed forest of this region (Rao *et al.* 1990). This could occur due to the recruitment of shade tolerant tree species such as *R. arboreum*, *Q. griffithii* and *C. kurzii* after 7-13 years of canopy growth.

Magurran (1988) has discussed four major species abundance models: (i) geometric series (May 1975), (ii) log series (Fisher *et al.* 1943), (iii) log normal (Sugihara 1980), and (iv) broken stick (MacArthur 1957) model, to explain the ecological diversity patterns in forest communities. Rank abundance curves of woody vegetation (trees plus shrubs) obtained in the present study fitted to the log series model in case of the 7-year old stand and log normal model in the 13- and 16-year old stands. The log

series model in the younger stand indicates that the intervals between the arrival of any two species into the system were random (Boswell and Patil 1971). While the log normal pattern in the older stands indicates the regular distribution of species owing to a large number of favourable environmental factors (May 1975, Connell 1978). The temporal variation in species diversity index as observed in the three forest stands fully corroborates the hypothesis of Bormann and Likens (1979) who reported that in a secondary successional forest community species diversity after an initial increase, declines and again increases as the climax is approached.

POPULATION STRUCTURE OF TREE SPECIES

The configuration and slope of density-diameter curves have often been correlated with the age structure of the forest stand, character of the vegetation and successional status of the forest (Goff and West 1975, Saxena *et al.* 1984). In the present study, all the three forest stands have an overall straightline negative relationship between density and diameter confirming the observations of Schmeiz and Lindsey (1965) in uneven aged mixed stands and Kruchel (1953) in predominantly coniferous stands. In the 16-year old stand, high density of young trees and their fast growth were responsible for the predominance of intermediate DBH classes. Similar findings have been reported by West *et al.* (1981) in moist deciduous forest ecosystems. Density-diameter distribution patterns obtained for various species may be used to characterize the response of species populations to disturbance. Relatively higher density of the lower or intermediate DBH classes in all the three stands indicated high regeneration potential of the constituent tree species in the stands. A normal distribution curve shows preponderance of individuals in lower or intermediate DBH classes. This could be due to infrequent seedling recruitment and selective felling of trees of higher DBH classes. According to Benton and Werner (1976), the population is on the way to extinction if such a trend continues. A

comparison of the density-diameter distribution of *Q.dealbata*, which was present in all the three forest stands, also revealed normal distribution of individuals in a wide range of DBH classes from 10 to 40 cm in the 16-year old stand unlike the 13-year old stand, where the individuals ranged between 10 and 30 cm DBH class. In the 7-yr old stand the species was represented only by seedlings and saplings.

REGENERTION STATUS OF THE FOREST STANDS

Since the 7-year old stand provided favourable conditions for seed germination of shade-intolerant species, large number of seedlings of *P. kesiya* and *S. knasiana* were recruited in this stand leading to maximum tree seedling density in the stand. Higher sapling density in the young stand further indicated a comparatively better success of recruited seedlings in this stand than in the older stands. Decline in tree seedling and sapling density in the older stands could be the result of competition for various resources among the seedlings populations, especially for light and space which hamper the success of recruited seedlings (Whitmore 1974). In the older stands, role of sprouts in the regrowth of vegetation was more important than the seedlings.

An assessment of the sprouting behaviour of different species in terms of sprout numbers per cut-stump indicated that *Q. dealbata*, *R. arboreum*, *Q. griffitnii* and *S. khasiana* were good sprouters (5-6). Other species like *M. esculenta*, *Litsea khasiana* and *C. kurzii* were poor sprouters (2-4).

The ratios between the basal area and density of sprouting stumps and total stump basal area and density, respectively (Table 5.12) served as useful indices of regrowth potential. Both the ratios increased steadily from 7-to 16-year old stand attaining a value of about 90% in the 16-year old stand. This clearly indicated that both in terms of basal area and density there was 90% recovery after 16 years of disturbance in the forest.

CHAPTER 6

LITTER DYNAMICS

INTRODUCTION

Litterfall and decomposition processes maintain nutrient pool in soil, influences primary productivity and regulate energy flow, and nutrient cycling in forest ecosystems (Waring and Schlesinger 1985). The decay rate of litter is particularly important in the nutrient budget of the tropical forest ecosystems where vegetation depends mainly on the recycling of nutrients contained in the plant detritus (Vogt *et al.* 1986).

Studies concerning litter and litter-mediated nutrient dynamics in forest ecosystems are many both in natural forests and tree plantations

(Singh and Gupta 1977, Vogt *et al.* 1986, Couteaux *et al.* 1995). In natural forests species composition, density, basal area, age structure (Stohlgren 1988), altitude (Reiners and Lang 1987), latitude (Bray and Gorham 1964) and season (Luizao and Schubart 1987) strongly influence litterfall.

Litter decomposition is strongly influenced by the climatic conditions and its chemical composition. Among the environmental conditions air temperature and soil moisture supply play a more critical role in the decay process than other factors (Singh and Gupta 1977, Vogt *et al.* 1986, Couteaux *et al.* 1995). A strong negative linear relationship between initial lignin/N ratio and the disappearance rates of leaf litter was reported by Aber and Melillo (1982) and Melillo *et al.* (1982). Results of several other workers indicate that nitrogen (Heal and French 1974, Schlesinger and Hasey 1981) and lignin concentrations (Meentemeyer 1978) and C/N ratio (Taylor *et al.* 1989) in litter influences decay rate.

Variability in litterfall and accumulation pattern in successional forest communities have been studied by Odum (1960), Swift *et al.* (1981), Muller and Martin 1983, Toky and Ramkrishnan (1983) and Das and Ramakrishnan (1985). Data on these aspects from disturbed forest ecosystems are limited (Richards 1952, Hall and Okali 1979, Herbohn and Congdon 1993). In this chapter, data on litter accumulation, production and decomposition have been presented. These are discussed to understand the role of litter in N and P dynamics in soils supporting forest regrowths of different ages in a humid subtropical region of north-east India.

METHODS

FOREST-FLOOR LITTER MASS AND LITTER PRODUCTION

Forest-floor litter: Litter was collected over a period of two years (from January, 1993 to October, 1994) in ten 1 m x 1 m quadrats randomly laid on

the forest floor in all three stands during January, April, July and October which corresponded with the winter, spring, rainy and autumn seasons, respectively (Rout and Gupta 1990a).

Litterfall: Litterfall was measured on a monthly basis from January, 1993 to December 1994 in all three forest stands. In the month of January'93, ten 1 m x 1 m permanent quadrats were laid randomly on the forest floor, exclusively for this purpose. The quadrats were demarcated using bamboo and the litter was cleaved from each. One of them prior to the commencement of the sampling. Prescribed litter traps (Proctor *et al.* 1983) could not be used because of human and live-stock interferences. Litter samples were collected during first week of every month and brought to the laboratory for separation and further processing.

PROCESSING AND SORTATION OF DIFFERENT LITTER COMPONENTS

The litter samples (both forest-floor litter and litterfall) were brought to the laboratory in polythene bags, and were sorted into, (i) leaf (including needles) litter, woody litter (<20 mm in diameter) and miscellaneous litter (flowers, fruits, bark and other unidentified plant detritus). The separated samples were washed under a fine jet of water for removing the adhered soil particles. These were weighed after oven-drying at 80°C for 48 h. Samples of a given category of the litter from all quadrats were pooled, ground in a CYCLOTEC (Tecator) and stored at a dry place for chemical analyses.

LEAF LITTER DECOMPOSITION

Leaf litter decomposition of dominant tree species in the respective was studied by litter bag technique (Gilbert and Bocock 1960). The litter bags (20 cm x 20 cm) made of nylon mesh (2 mm) were used for the study. Freshly fallen needles of *Pinus kesiya*, leaves of *Quercus dealbata*, *Quercus griffithii*, *Rhododendron arboreum* and *Schima khasiana* were collected during peak litterfall period (March), and air-dried in the laboratory. 10 g of

air-dried material was kept in each bag and it was stiched with nylon threads. Sub-samples were taken for determining oven-dry mass. For each species 36 bags were prepared. The bags containing litter of the above-mentioned species were kept randomly on the forest floor in the month of May 1993 in their respective stands. At each sampling date *i.e.* 60, 120, 180, 240, 300, 360, 420, 480, 540 and 600 days, three bags for each species were brought to the laboratory carefully avoiding loss of material from the litter bags. The litter was washed under gently flowing tap water to remove extraneous matter, dried at 80° C for 48 h and weighed. The samples were powdered and used for chemical analyses.

NUTRIENT ANALYSIS

The ash content in the litter samples was determined by igniting the oven-dried material at 550° C for 6 h in a muffle furnace and carbon (C) content was calculated as 50% of the ash-free weight (Allen *et al.* 1974). Total Kjeldahl nitrogen (TKN) was determined by the micro-Kjeldahl procedure using Kjeltec Auto 1030 Analyser and total phosphorus (TP) was analysed colorimetrically (Allen *et al.* 1974). Lignin and cellulose contents were determined according to Peach and Tracey (1956).

LITTER TURNOVER

Litter turnover rate (K) was calculated using mathematical model of Reiners and Reiners (1970): $K_L = L/X_L+L$, where, L = annual litterfall and X_L = mean annual standing crop. Similarly, the nutrient rate turnover was calculated by substituting the dry mass values with nutrient content figures.

Turnover time (T) was calculated as a reciprocal of turnover rate:

$$T = 1/K_L, \text{ where, } T = \text{time in year.}$$

The data obtained from the litter bag experiment was used to compute the decay and mineralization constants of leaf litter using a negative exponential decay model, of Olson (1963): $X/X_o = e^{-kt}$, where, X = weight

remaining at time t, X_0 = original weight, e = base of natural logarithm, k = decay rate coefficient, and t = time. N and P mineralization constants (k_N and k_P) were calculated by substituting dry weight with N and P contents in the above formula (Singh and Shekhar 1989b). Further, the time required for 50% (t_{50}) and 99% (t_{99}) decay was calculated as, $t_{50} = 0.693/k$ and $t_{99} = 5/k$.

STATISTICAL ANALYSIS

One-, two- and three-way analysis of variance (ANOVA, fixed effects model) tests were applied to the litter mass and litter production data to study the effect of sampling period and stand age. Linear regressions were worked out following Zar (1974) to study the relationship between community characteristics and litterfall and accumulation patterns. Similar regressions were also worked out to evaluate the importance of climatic variables (rainfall and air temperature) on litter production and accumulation in the regrowing forest stands.

Multiple regressions were worked out using dummy factors (0 or 1) as the indicator variables, to distinguish between different phases in the weight loss pattern during decomposition of leaf litter. The composite linear decay model used for this purpose was as follows: $Y = a+bX_1+cX_2+dX_3$ is the rate of change in Y with respect to time, c is shift parameter for adjustment of the Y intercept in phase-II and d is the shift parameter for adjustment of the Y intercept in phase-III. The values of c and d were taken as zero, if decay was slow, and/or equal to one, if the decay was fast. The effect of initial litter chemistry and a few soil characteristics on the decomposition rate of leaf litter was assessed using simple linear regression function, $Y = a+bX$.

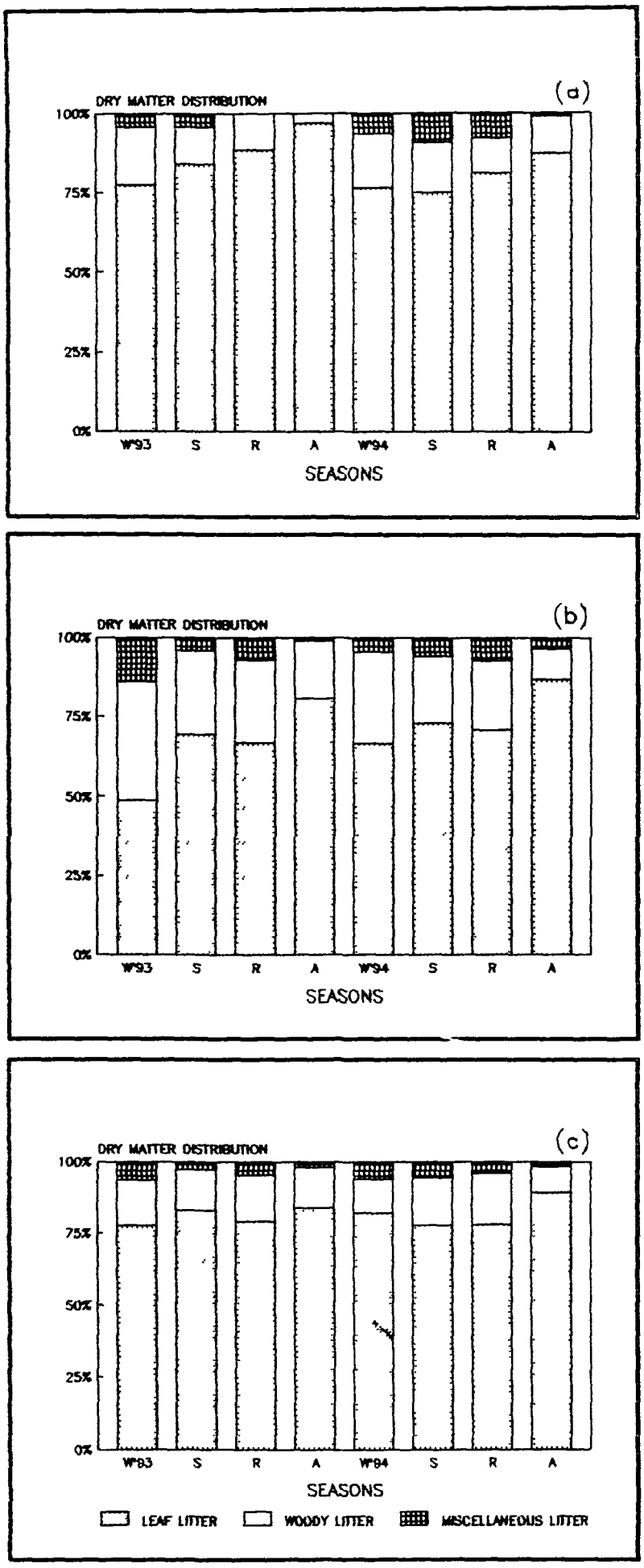


Figure 6.1. Partitioning of litter mass into leaf, woody and miscellaneous fractions on the forest floor in (a) 7-, (b) 13- and (c) 16-year old regrowths. W-winter, S-spring, R-rainy and A-autumn seasons.

Table 6.1 Seasonal variation in forest-floor litter mass (kg ha-1) in forest regrowths of three different ages.

Year/season	Age of the forest regrowth		
	7-yr old	13-yr old	16-yr old
1993 winter	1939.4 ±23.1	3241.9 ±138.4	2840.7 ±97.2
spring	1617.3 ±102.7	2535.9 ±201.5	2117.3 ±87.8
rainy	1083.4 ±98.3	1498.6 ±111.1	1411.6 ±213.4
autumn	899.6 ±21.2	1207.1 ±87.1	1054.9 ±34.9
1994 winter	1093.4 ±131.2	2365.4 ±211.8	2107.4 ±99.8
spring	1326.9 ±120.6	2177.0 ±202.3	2449.2 ±117.1
rainy	1040.5 ±96.2	1647.4 ±112.5	1938.5 ±32.9
autumn	1003.2 ±108.9	1386.2 ±251.8	1622.1 ±96.2

± SEM (n=10)

Table 6.2 Mean dry weight (kg ha^{-1}) of different fractions of forest-floor litter in the three forest regrowths.

Age of the forest regrowth	Year	Litter fractions			
		Leaf	Woody	Miscellaneous	Total
7-yr	1993	1177.5 (82.4)	172.9 (12.1)	78.8 (5.5)	1429.2
	1994	888.0 (79.6)	156.3 (14.0)	72.5 (6.4)	1116.8
13-yr	1993	1327.5 (62.6)	623.2 (29.4)	170.0 (8.0)	2120.8
	1994	1382.6 (72.9)	408.4 (21.6)	103.0 (5.5)	1894.0
16-yr	1993	1491.2 (80.3)	280.0 (15.1)	84.8 (4.6)	1856.1
	1994	1659.8 (81.2)	286.8 (14.1)	95.1 (4.7)	2029.3

Note: Values in parentheses are percentages of total.

RESULTS

FOREST-FLOOR LITTER MASS

In all regrowths, winter or ensuing spring season was the peak periods of litter accumulation on the forest floor. Litter accumulation was minimum during autumn in all the stands (Table 6.1). The total litter mass on the forest floor increased significantly ($P<0.01$) from 7- to 13-year old regrowth, but the difference between 13- and 16-year old regrowths was insignificant. Two-way ANOVA revealed significant ($P<0.01$) difference in litter accumulation due to season ($F=4.91-39.44$). The leaf litter increased steadily with the progression of vegetation recovery (Table 6.2). Woody as well as miscellaneous litter was, however, more in the 13-year old regrowth, followed by the 16-and 7-year old regrowths (Table 6.2). The seasonality in woody litter mass was similar to leaf litter (Figure 6.1).

The proportion of leaf litter ranged between 62 and 82% of the total litter mass on the forest floor (Figure 6.1), while the woody and miscellaneous fractions accounted for 12-29% and 4-8%, respectively. The proportion of woody litter was maximum (*ca.* 29%) in the 13-year old regrowth, where leaf litter contributed only *ca.* 62% to the total litter. On the other hand, in the 7-year old regrowth leaf litter constituted the major fraction (81%) of the forest floor (Figure 6.1).

LITTERFALL

Litterfall in the three regrowths exhibited a marked seasonality with peaks occurring between February and April (Figure 6.2). In the 13-year old regrowth, small peaks were also observed during October and December (Figure 6.2). Season-wise litterfall was maximum during spring (4623-7666 kg ha^{-1}) followed by winter (2847-5245 kg ha^{-1}), rainy (1996-4442 kg ha^{-1}) and autumn (1304-2585 kg ha^{-1}). Leaf, woody and miscellaneous fractions showed more or less a similar seasonal pattern.

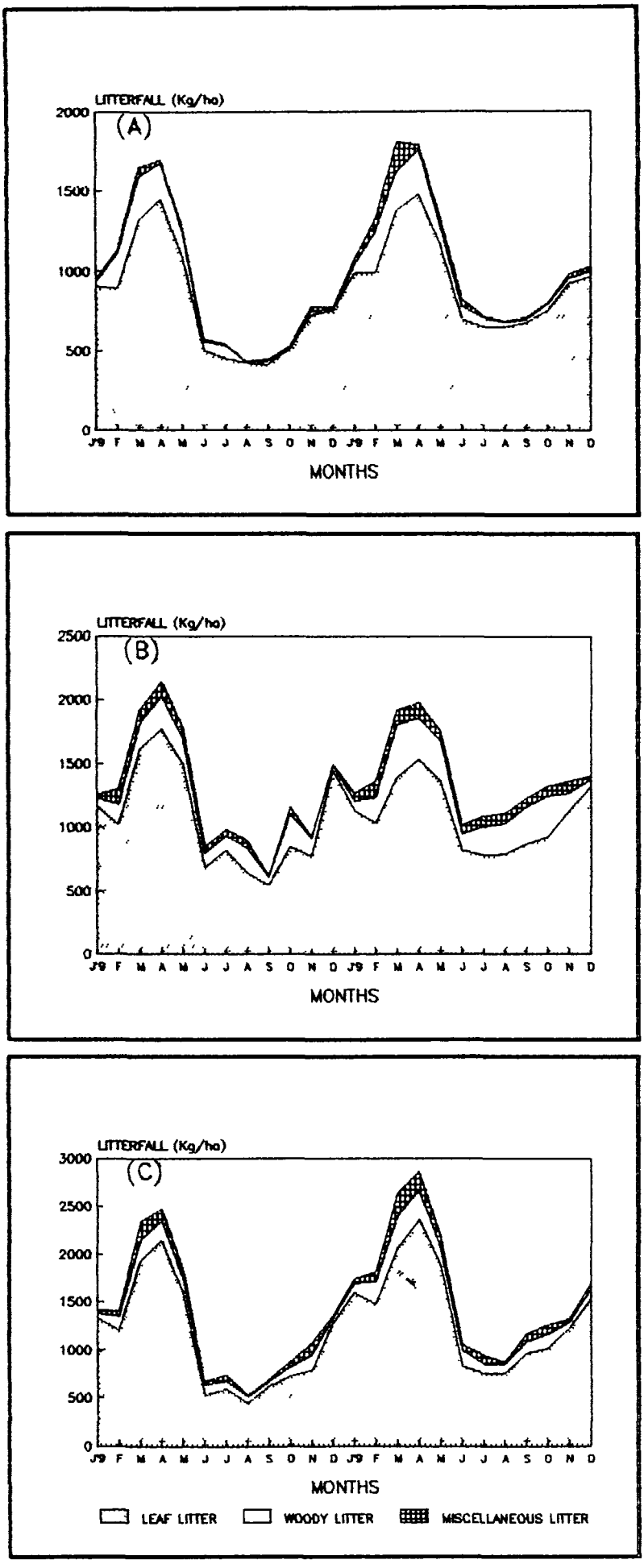


Figure 6.2. Litterfall pattern in (A) 7-, (B) 13- and (C) 16-year old regrowths.

Table 6.3 Annual litter production (kg ha^{-1}) in the three forest regrowths.

Age of the forest regrowth	Year	Litter fractions			
		Leaf	Woody	Miscellaneous	Total
7-yr	1993	9443.9 (87.7)	1108.9 (10.3)	217.4 (2.0)	10770.2
	1994	11271.5 (86.5)	1236.4 (9.5)	526.7 (4.0)	13034.6
13-yr	1993	12820.3 (83.7)	1780.8 (11.6)	715.0 (4.7)	15316.1
	1994	13078.1 (77.8)	2737.9 (16.3)	986.0 (5.9)	16802.0
16-yr	1993	13210.7 (85.6)	1397.7 (9.1)	830.1 (5.4)	15438.5
	1994	16440.8 (84.1)	1941.7 (9.9)	1163.2 (6.0)	19545.7

Note: Values in parentheses are percentages of total.

The annual litter production averaged 11902 kg ha-1 in the 7-year old regrowth, 16059 kg ha^{-1} in the 13-year old regrowth and 17402 kg ha^{-1} in the 16-year old regrowth (Table 6.3). The corresponding values for leaf litter production were 10358, 12949 and 14826 kg ha^{-1}, respectively. The woody litterfall was significantly ($P<0.01$) higher in the 13-year old regrowth than 7- and 16-year old regrowths (Table 6.3). However, production of miscellaneous litter increased steadily from 372 to 997 kg ha^{-1} with the progression of vegetation recovery.

Leaves constituted about 78-88% of litterfall in all the three forest regrowths. The woody litter made only a minor contribution (9-16%) to the total litterfall, although in certain months its proportion went up to 30%. The peak period of woody litterfall was similar to the leaf-fall pattern.

The miscellaneous fraction mainly composed of reproductive parts and bark, exhibited a seasonal pattern in all regrowths. About 60% of the total annual production of this fraction was recorded during post-rainy season (Figure 6.2). In all stands, it made only a small contribution (2 - 6%) to the total litter production (Table 6.3). During peak litterfall, its proportion increased up to 10%, but during rainy season it was negligible (0.5%).

NUTRIENT CONCENTRATION IN FOREST-FLOOR LITTER

Nitrogen: In all three forest regrowths, N concentration in the litter showed a marked seasonality. N concentration was maximum during autumn or winter, and minimum during rainy season (Table 6.4). In the 7-year old regrowth, leaf litter had significantly ($F=17.29$, $P<0.01$) higher concentration of N (averaging 0.9%) than the miscellaneous litter (averaging 0.6%) and the fine woody litter (averaging 0.5%); the difference between the latter two fractions was not significant. Year-to-year variation in N concentration in various fractions of litter was also insignificant (Figure 6.3). In the 13-year old regrowth, leaf (0.8-1.5%)

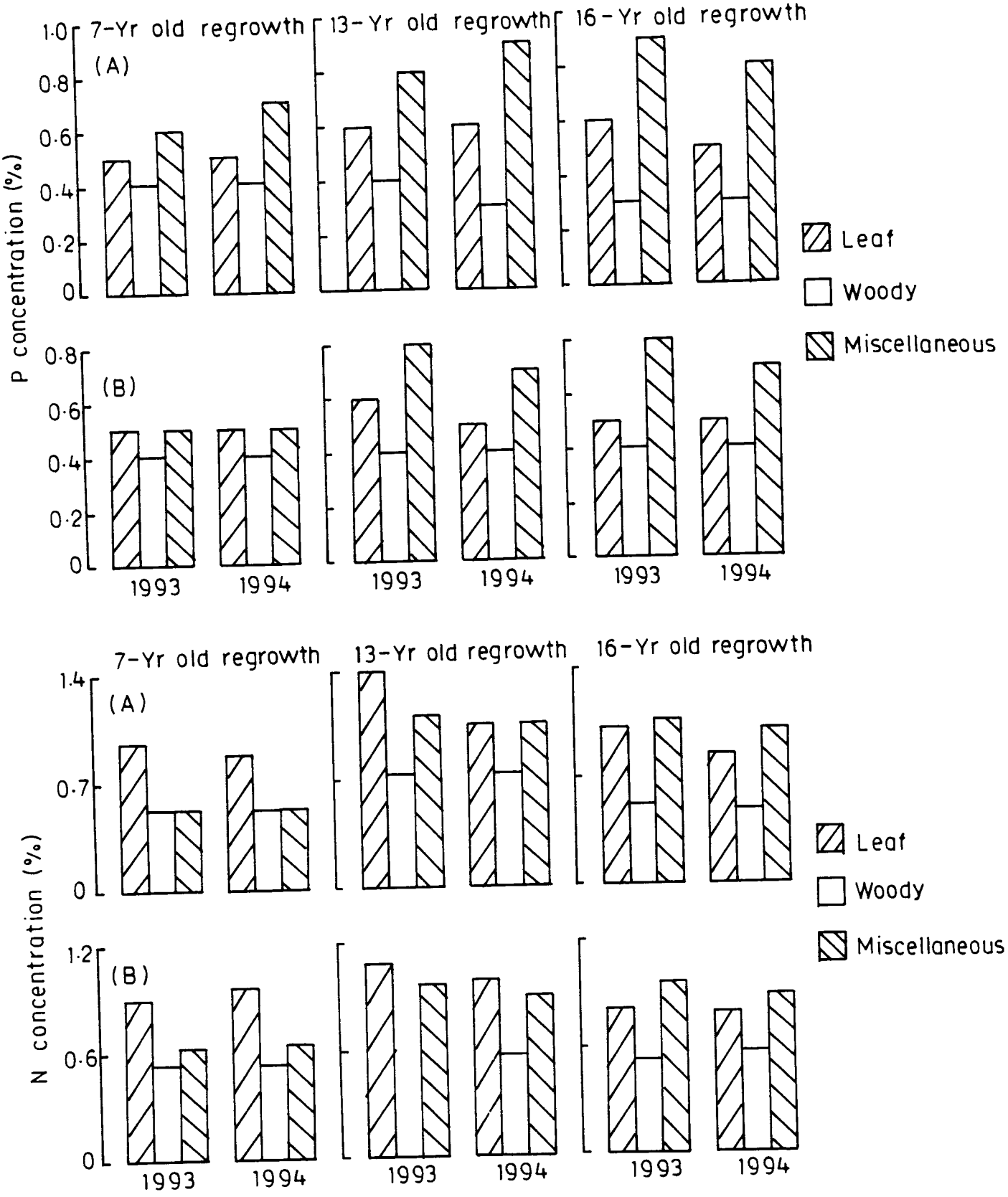


Figure 6.3. Mean concentration (%) of N and P in different fractions of (A) forest-floor litter and (B) fresh litter in the three forest regrowths during 1993 and 1994.

Table 6.4 Seasonal variation in nitrogen concentration (%) in different fractions of forest-floor litter in the three forest regrowths.

Year/Season	Forest regrowths								
	7-yr old			13-yr old			16-yr old		
	L	W	Mis	L	W	Mis	L	W	Mis
1993 winter	0.97 ±0.17	0.49 ±0.07	0.53 ±0.15	1.43 ±0.17	0.83 ±0.17	1.18 ±0.01	0.96 ±0.04	0.55 ±0.15	1.11 ±0.02
spring	0.98 ±0.10	0.55 ±0.15	0.55 ±0.01	1.34 ±0.09	0.76 ±0.03	1.23 ±0.03	0.92 ±0.05	0.55 ±0.15	1.07 ±0.02
rainy	0.62 ±0.02	0.39 ±0.01	-	1.25 ±0.01	0.68 ±0.03	1.11 ±0.01	0.88 ±0.02	0.39 ±0.02	1.03 ±0.01
autumn	1.17 ±0.09	0.62 ±0.01	-	1.49 ±0.07	0.86 ±0.02	1.18 ±0.01	0.98 ±0.02	0.61 ±0.01	1.11 ±0.01
1994 winter	0.89 ±0.11	0.51 ±0.02	0.41 ±0.02	1.19 ±0.17	0.78 ±0.11	1.03 ±0.03	0.90 ±0.04	0.51 ±0.09	1.09 ±0.01
spring	1.00 ±0.09	0.59 ±0.03	0.57 ±0.01	1.08 ±0.17	0.81 ±0.21	1.11 ±0.04	0.79 ±0.06	0.50 ±0.10	0.99 ±0.02
rainy	0.69 ±0.05	0.44 ±0.44	0.59 ±0.00	0.80 ±0.06	0.66 ±0.16	1.09 ±0.00	0.71 ±0.07	0.46 ±0.05	0.92 ±0.01
autumn	0.88 ±0.05	0.63 ±0.07	0.61 ±0.01	1.14 ±0.15	0.74 ±0.15	1.01 ±0.01	0.84 ±0.08	0.56 ±0.05	0.97 ±0.01

L-Leaf litter, W-Woody litter and Mis-Miscellaneous litter.

± SEM (n=3)

- absent

Table 6.5 Seasonal variation in phosphorus concentration (%) in different fractions of forest-floor litter in the three forest regrowths.

Year/Season	Forest Regrowths								
	7-yr old			13-yr old			16-yr old		
	L	W	Mis	L	W	Mis	L	W	Mis
1993 winter	0.05 ±0.01	0.05 ±0.01	0.06 ±0.00	0.06 ±0.00	0.04 ±0.01	0.08 ±0.01	0.06 ±0.01	0.02 ±0.00	0.09 ±0.01
spring	0.04 ±0.00	0.04 ±0.00	0.05 ±0.01	0.06 ±0.01	0.04 ±0.00	0.08 ±0.00	0.05 ±0.01	0.03 ±0.01	0.09 ±0.00
rainy	0.05 ±0.00	0.04 ±0.00	-	0.06 ±0.01	0.04 ±0.00	0.08 ±0.01	0.05 ±0.00	0.04 ±0.00	0.08 ±0.00
autumn	0.05 ±0.00	0.05 ±0.01	-	0.06 ±0.01	0.04 ±0.00	0.08 ±0.01	0.06 ±0.01	0.04 ±0.00	0.09 ±0.01
1994 winter	0.05 ±0.01	0.03 ±0.00	0.07 ±0.01	0.05 ±0.01	0.03 ±0.00	0.08 ±0.01	0.05 ±0.01	0.03 ±0.01	0.08 ±0.01
spring	0.05 ±0.01	0.03 ±0.00	0.06 ±0.01	0.05 ±0.01	0.02 ±0.00	0.07 ±0.01	0.05 ±0.01	0.03 ±0.00	0.07 ±0.01
rainy	0.04 ±0.01	0.03 ±0.00	0.06 ±0.01	0.04 ±0.00	0.02 ±0.00	0.07 ±0.01	0.04 ±0.01	0.02 ±0.00	0.07 ±0.01
autumn	0.05 ±0.00	0.04 ±0.00	0.08 ±0.02	0.06 ±0.01	0.04 ±0.01	0.08 ±0.01	0.06 ±0.02	0.04 ±0.00	0.08 ±0.01

L-Leaf litter, W-Woody litter and Mis-Miscellaneous litter.

± SEM (n=3)

- absent

and miscellaneous (1.0-1.2%) litter had significantly higher (F=139.16, P<0.01) N concentration than the woody litter (0.7-0.9%). Seasonal (F=8.40, P<0.05) and yearly (F=45.98, P<0.01) variations in all three litter components were also significant. In the 16 year old regrowth, N concentration was relatively lower than the 13-year old regrowth (Table 6.4). The miscellaneous fraction of the litter had significantly higher (F=404.12, P<0.01) concentration of N (0.9-1.1%) than the leaf (0.7-0.98%) and woody litter (0.4-0.6%). The variation due to season (F=13.23) and year (F=25.26) was also significant at P<0.01.

Phosphorus: Generally, P concentration in the litter lacked seasonality (Table 6.5), but it varied markedly between different fractions. It did not vary appreciably between the stands and years as well. The miscellaneous fraction usually had higher concentration, followed by the leaf and woody litter (Figure 6.3).

NUTRIENT CONCENTRATION IN FRESH LITTER

Nitrogen: N concentration varied significantly (P<0.01) between sites (F=41.3) and litter fractions (F=140.16). In 7- and 13-year old regrowths, N concentration was generally higher in the leaf litter than the miscellaneous and woody litter (Figure 6.3). In contrast, the miscellaneous litter had relatively higher values (0.87-0.96%) than the leaf (0.77-0.88%) and woody litter (0.51-0.55%) in the 16 year old regrowth (Figure 6.3). Yearwise variation was significant (P<0.05) in the 7-year (F=5.99) and 13-year (F=175.49) old regrowths. Seasonal as well as annual variations were insignificant in the 16-year old regrowth. Generally, the concentration of N was maximum during autumn (0.6-1.3%) and minimum during rainy season (0.4-0.9%) in all forest regrowths (Table 6.6).

Phosphorus: P concentration in the fresh litter varied significantly between leaf, woody and miscellaneous litter fractions (F=551.01, P<0.01) in all the three forest regrowths. But the differences due to season and

Table 6.6 Seasonal variation in nitrogen concentration (%) in different fractions of fresh litter in the three forest regrowths.

Year/Season	Forest Regrowths								
	7-yr old			13-yr old			16-yr old		
	L	W	Mis	L	W	Mis	L	W	Mis
1993 winter	0.97 ±0.01	0.49 ±0.02	0.53 ±0.01	1.43 ±0.06	0.83 ±0.09	1.18 ±0.12	0.96 ±0.06	0.55 ±0.04	1.11 ±0.01
spring	0.82 ±0.11	0.47 ±0.03	0.66 ±0.12	0.94 ±0.12	0.65 ±0.06	1.02 ±0.11	0.69 ±0.09	0.50 ±0.12	0.92 ±0.01
rainy	0.61 ±0.01	0.54 ±0.06	0.59 ±0.09	0.88 ±0.12	0.64 ±0.01	0.92 ±0.12	0.61 ±0.05	0.40 ±0.01	0.73 ±0.10
autumn	1.19 ±0.01	0.61 ±0.01	0.68 ±0.01	1.29 ±0.03	0.81 ±0.07	1.17 ±0.01	0.95 ±0.05	0.60 ±0.05	1.06 ±0.05
1994 winter	1.08 ±0.11	0.56 ±0.04	0.68 ±0.03	1.21 ±0.09	0.54 ±0.10	0.81 ±0.01	0.83 ±0.03	0.53 ±0.01	0.91 ±0.02
spring	0.99 ±0.12	0.52 ±0.01	0.59 ±0.01	1.01 ±0.09	0.53 ±0.09	0.91 ±0.04	0.69 ±0.05	0.47 ±0.04	0.81 ±0.05
rainy	0.80 ±0.12	0.41 ±0.17	0.60 ±0.06	0.89 ±0.01	0.48 ±0.01	0.81 ±0.03	0.62 ±0.12	0.41 ±0.11	0.81 ±0.09
autumn	1.29 ±0.11	0.69 ±0.12	0.71 ±0.09	1.26 ±0.01	0.69 ±0.01	1.01 ±0.01	0.92 ±0.11	0.64 ±0.01	0.93 ±0.21

L-Leaf litter, W-Woody litter, Mis-Miscellaneous litter.

± SEM (n=3)

- absent

Table 6.7 Seasonal variation in phosphorus concentration (%) in different fractions of fresh litter in the three forest regrowths.

Year/Season	Forest Regrowths								
	7-yr old			13-yr old			16-yr old		
	L	W	Mis	L	W	Mis	L	W	Mis
1993 winter	0.05 ±0.01	0.05 ±0.01	0.06 ±0.01	0.06 ±0.01	0.04 ±0.00	0.09 ±0.01	0.06 ±0.00	0.02 ±0.00	0.09 ±0.01
spring	0.05 ±0.01	0.04 ±0.01	0.05 ±0.01	0.06 ±0.01	0.05 ±0.01	0.08 ±0.01	0.05 ±0.01	0.05 ±0.01	0.08 ±0.01
rainy	0.04 ±0.00	0.03 ±0.00	0.04 ±0.00	0.05 ±0.01	0.04 ±0.00	0.07 ±0.02	0.05 ±0.00	0.04 ±0.00	0.07 ±0.01
autumn	0.05 ±0.01	0.04 ±0.00	0.06 ±0.01	0.06 ±0.01	0.04 ±0.00	0.08 ±0.02	0.05 ±0.01	0.04 ±0.00	0.08 ±0.02
1994 winter	0.05 ±0.01	0.04 ±0.00	0.05 ±0.00	0.05 ±0.01	0.04 ±0.00	0.08 ±0.01	0.05 ±0.01	0.04 ±0.01	0.07 ±0.02
spring	0.04 ±0.00	0.03 ±0.00	0.04 ±0.00	0.05 ±0.01	0.04 ±0.00	0.07 ±0.01	0.05 ±0.00	0.04 ±0.00	0.07 ±0.01
rainy	0.04 ±0.00	0.03 ±0.00	0.04 ±0.01	0.05 ±0.01	0.04 ±0.00	0.06 ±0.01	0.04 ±0.00	0.04 ±0.00	0.07 ±0.01
autumn	0.05 ±0.01	0.04 ±0.00	0.05 ±0.01	0.06 ±0.01	0.04 ±0.00	0.08 ±0.01	0.05 ±0.01	0.04 ±0.00	0.07 ±0.01

L-Leaf litter, W-Woody litter, Mis-Miscellaneous litter.

± SEM (n=3)

Table 6.8 Annual input (kg ha^{-1}) of N and P through different fractions of litter and its mean accumulation (kg ha^{-1}) in the forest-floor litter in the three forest regrowths.

Age of the forest regrowth/ Year	Litter fractions							
	Leaf		Woody		Miscellaneous		Total	
	N	P	N	P	N	P	N	P
7-yr old								
1993	82.08	4.58	5.47	0.45	1.31	0.10	88.43	4.74
	11.05	**0.56**	**0.85**	**0.08**	**0.42**	**0.05**	**12.11**	**0.66**
1994	114.16	4.93	6.48	0.41	3.31	0.23	123.94	5.56
	7.73	**0.42**	**0.85**	**0.06**	**0.39**	**0.06**	**8.97**	**0.54**
13-yr old								
1993	142.36	7.96	12.63	0.77	7.48	0.56	162.47	8.64
	18.29	**0.79**	**4.92**	**0.25**	**2.00**	**0.13**	**25.21**	**1.17**
1993	140.30	6.74	14.84	1.07	8.73	0.90	144.39	8.52
	14.74	**0.71**	**3.09**	**0.11**	**1.10**	**0.08**	**18.93**	**0.90**
16-yr old								
1993	103.61	6.78	7.07	0.54	7.85	0.66	118.53	7.99
	13.89	**0.83**	**1.47**	**0.08**	**0.92**	**0.07**	**16.28**	**0.98**
1994	119.19	7.80	9.46	0.72	9.79	0.82	138.44	9.32
	13.46	**0.79**	**1.43**	**0.08**	**0.96**	**0.07**	**15.85**	**0.94**

Note: Bold values are corresponding N or P accumulation in the forest-floor litter.

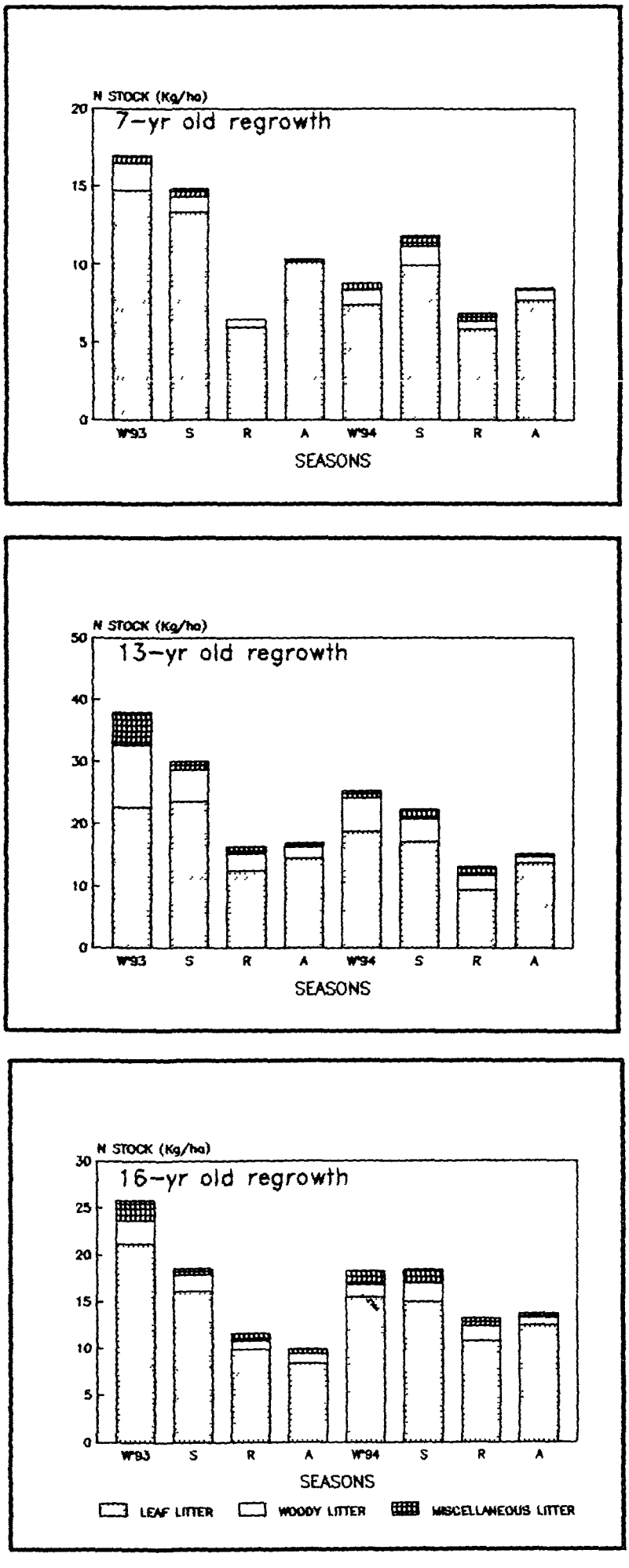


Figure 6.4. Seasonal variation in N stock in different fractions of forest-floor litter (W-winter, S-spring, R-rainy, A-autumn) in the three forest regrowths.

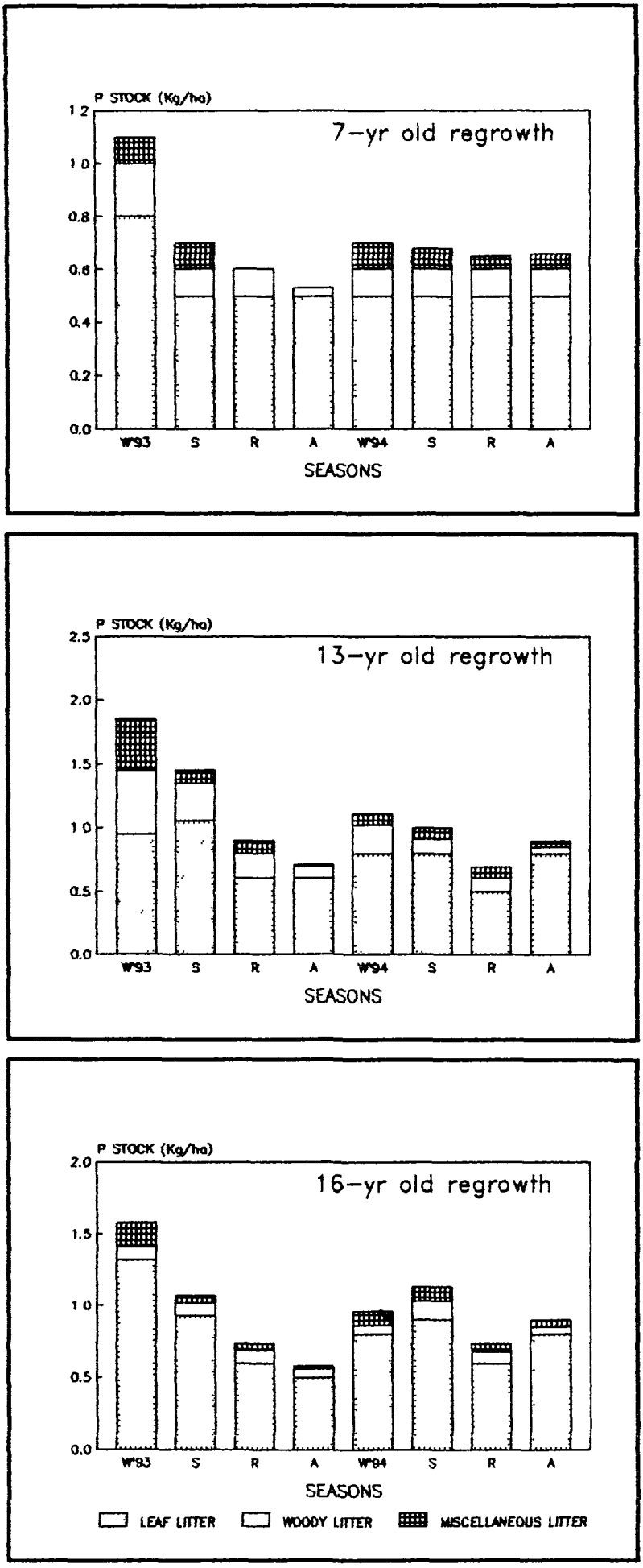


Figure 6.5. P stock in different fractions of forest-floor litter during different seasons (W-winter, S-spring, R-rainy, A-autumn) in the three forest regrowths.

year were significant (P<0.01) only in case of 7-and 13-year old regrowths (Table 6.7). The concentration during autumn (0.035-0.08%) was significantly higher than the spring and rainy seasons (Table 6.7). The lowest concentration was observed during the rainy season.

NUTRIENT ACCUMULATION IN FOREST-FLOOR LITTER

Nitrogen: Peak accumulation of N in the forest-floor litter observed generally during winter season declined gradually until rainy season in all the three stands (Figure 6.4). The amount of N accumulated in the forest-floor litter varied significantly (P<0.01) between leaf, woody and miscellaneous fractions (Table 6.8). The total amount ranging between 8.5 and 16.9 kg ha^{-1} in the youngest regrowth increased up to 13-year old stand (13.1-37.9 kg ha^{-1}) and then declined in the 16-year old regrowth (11.4-25.7 kg ha^{-1}) (Figure 6.4). The variation between sites was highly significant (F=183.01, P<0.01). Leaf litter accumulated significantly higher amount of N (F=183.01, P<0.01) on the forest floor compared to the other two fractions. Seasonal difference was significant (P<0.05) in 7- (F=5.31) and 13-year (F=32.13) old regrowths. Generally, N stock in litter was lower during 1994 than 1993 in all regrowths (Table 6.8).

Phosphorus: P stock in the forest-floor litter was almost the same in 13- and 16-year old regrowths (Figure 6.5). Compared to these two stands, 7-year old stand had significantly lower amount of P (F=28.50, P<0.01) in the forest-floor litter. Accumulation of P in different fractions of litter varied significantly (P<0.01) in all stands. Seasonal variation was significant only in the 13-year old regrowth (F=11.75, P<0.01). Generally, P stock was maximum (0.05-1.32 kg ha^{-1}) during winter and minimum (0.05-0.64 kg ha^{-1}) during rainy season in all the stands (Figures 6.5).

The mean stock of N in the forest-floor litter was always higher than P (Table 6.12). The difference between N and P stocks was 17-18 times in 7- and 16-year old regrowths and 22 times in the 13-year old regrowth.

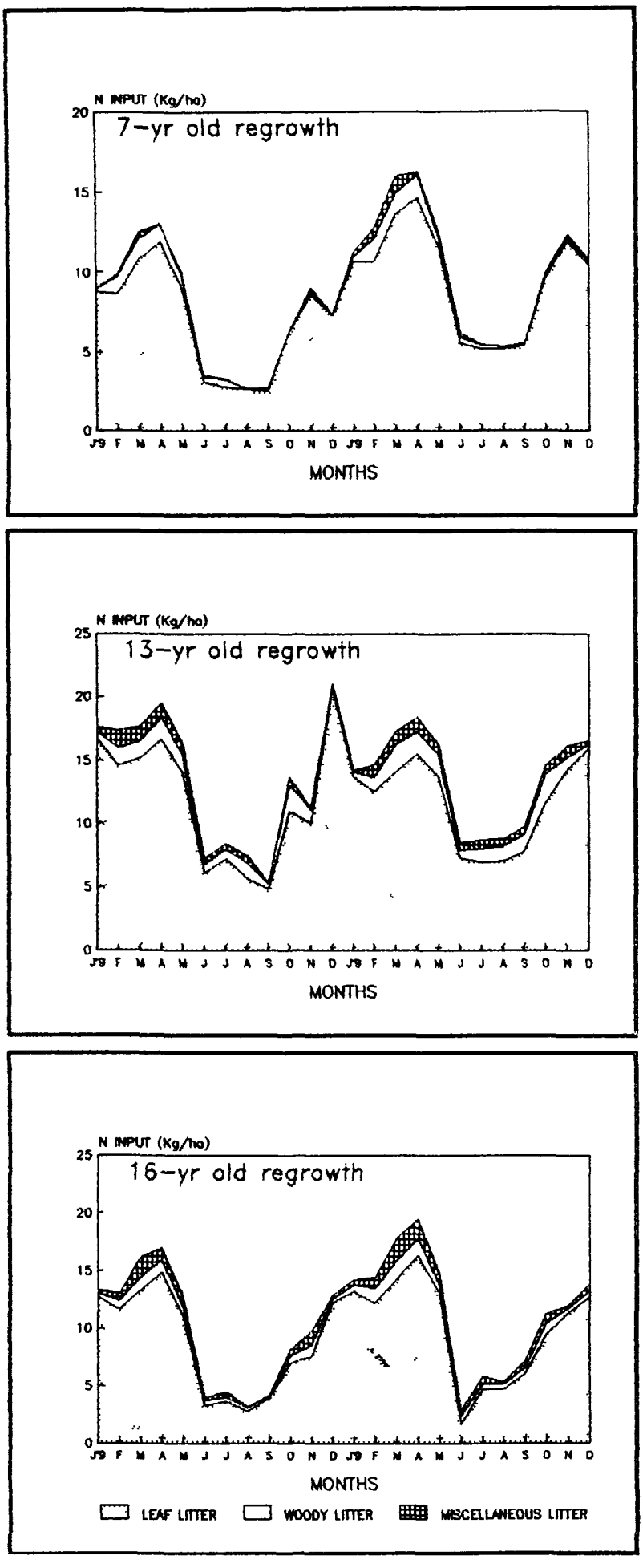


Figure 6.6. Monthly variation in N input through litterfall in the three forest regrwoths.

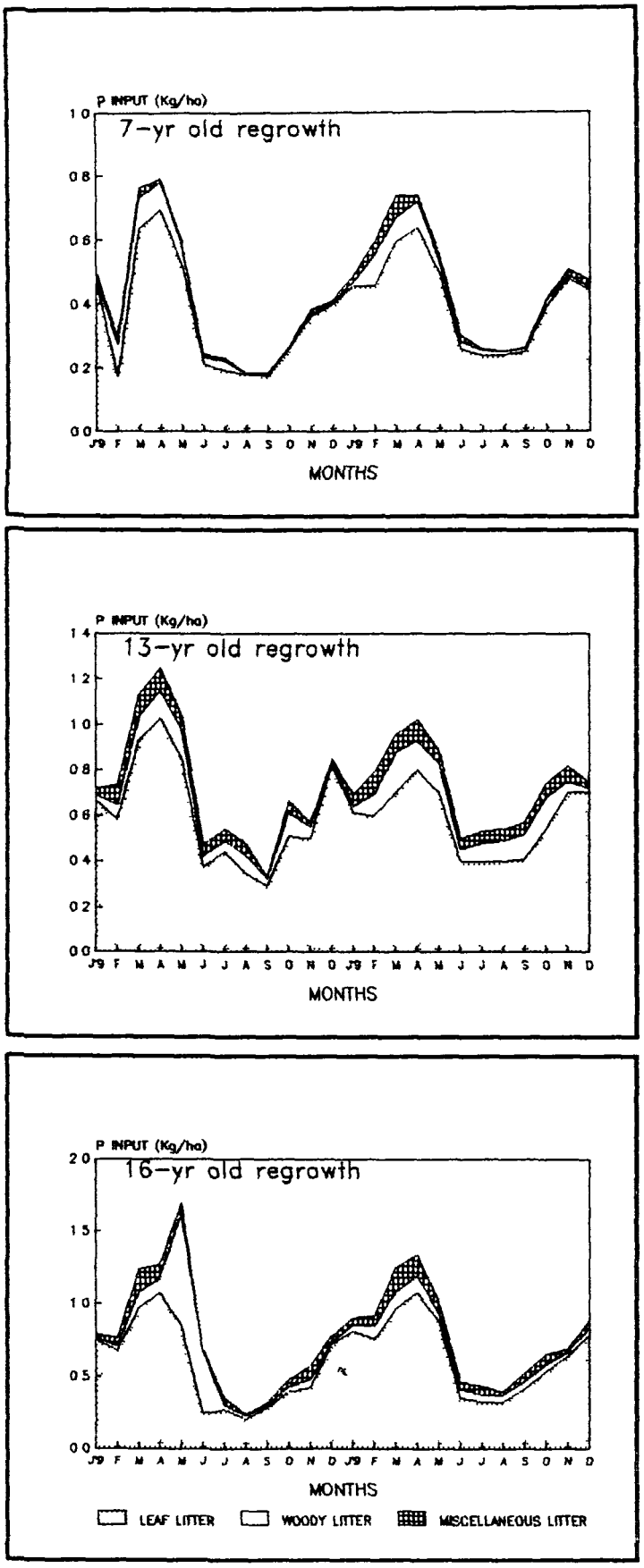


Figure 6.7. Monthly variation in P input through litterfall in the three forest regrowths.

Table 6.9 Seasonal input of N and P (kg ha^{-1}) to the forest floor through litterfall in the 7 year old regrowth.

Year/Season	Litter fractions							
	Leaf		Woody		Miscellaneous		Total	
	N	P	N	P	N	P	N	P
1993 winter	24.70 ±1.31	1.35 ±0.91	1.24 ±0.12	0.12 ±0.01	0.25 ±0.09	0.03 ±0.00	26.19 ±0.91	1.13 ±0.11
spring	31.66 ±3.12	1.85 ±0.11	3.09 ±0.17	0.26 ±0.06	0.68 ±0.07	0.05 ±0.01	35.43 ±0.18	2.14 ±1.00
rainy	10.93 ±2.12	0.75 ±0.01	0.89 ±0.01	0.05 ±0.01	0.20 ±0.03	0.01 ±0.00	11.59 ±0.99	0.82 ±0.09
autumn	14.79 ±7.01	0.62 ±0.03	0.25 ±0.01	0.02 ±0.00	0.02 ±0.00	0.01 ±0.00	15.22 ±1.11	0.65 ±0.09
1994 winter	31.68 ±6.43	1.35 ±0.31	1.90 ±0.33	0.13 ±0.01	1.01 ±0.09	0.04 ±0.01	34.59 ±3.11	1.55 ±0.62
spring	39.73 ±1.72	1.73 ±0.21	3.33 ±0.42	0.19 ±0.02	1.59 ±0.44	0.11 ±0.05	44.65 ±0.98	2.03 ±0.13
rainy	21.26 ±3.62	0.98 ±0.01	0.77 ±0.01	0.05 ±0.01	0.42 ±0.02	0.03 ±0.00	22.45 ±1.31	1.07 ±0.11
autumn	21.49 ±3.11	0.87 ±0.31	0.48 ±0.14	0.03 ±0.00	0.28 ±0.02	0.02 ±0.00	22.24 ±0.91	0.92 ±0.01

± SEM (n=10)

Table 6.10 Seasonal input of N and P (kg ha^{-1}) to the forest floor through litterfall in the 13 year old regrowth.

Year/Season	Litter fractions							
	Leaf		Woody		Miscellaneous		Total	
	N	P	N	P	N	P	N	P
1993 winter	51.93 ±3.11	2.73 ±0.91	2.17 ±0.01	0.09 ±0.01	1.86 ±0.06	0.12 ±0.01	55.95 ±1.11	2.29 ±0.09
spring	45.78 ±3.11	2.81 ±0.61	4.28 ±1.11	0.34 ±0.03	3.30 ±0.01	0.26 ±0.01	53.36 ±1.11	3.41 ±0.91
rainy	23.70 ±6.11	1.45 ±0.11	3.03 ±0.11	0.19 ±0.01	1.56 ±0.61	0.12 ±0.01	28.29 ±1.02	1.76 ±0.09
autumn	20.95 ±0.01	0.98 ±0.11	3.15 ±1.11	0.16 ±0.06	0.77 ±0.02	0.06 ±0.03	24.87 ±1.11	1.19 ±0.09
1994 winter	42.19 ±3.11	1.88 ±0.91	1.78 ±0.02	0.14 ±0.06	1.72 ±0.11	0.17 ±0.01	45.69 ±4.44	2.19 ±1.00
spring	43.28 ±7.11	2.14 ±0.64	5.59 ±1.11	0.42 ±0.03	2.88 ±0.11	0.23 ±0.02	51.75 ±3.11	2.79 ±0.44
rainy	28.94 ±3.22	1.53 ±0.09	4.30 ±0.03	0.32 ±0.01	2.49 ±0.09	0.18 ±0.02	16.24 ±1.11	2.03 ±1.31
autumn	25.89 ±5.31	1.19 ±0.32	3.18 ±0.71	0.19 ±0.07	1.64 ±0.02	0.31 ±0.03	30.71 ±3.11	1.51 ±0.02

± SEM (n=10)

Table 6.11 Seasonal input of N and P (kg ha^{-1}) through litterfall to the forest floor in the 16 year old regrowth.

Year/Season	Litter fractions							
	Leaf		Woody		Miscellaneous		Total	
	N	P	N	P	N	P	N	P
1993 winter	36.56 ±6.11	2.13 ±0.91	1.32 ±0.02	0.05 ±0.01	1.33 ±0.07	0.11 ±0.01	39.21	2.29
spring	39.16 ±3.11	2.84 ±0.61	2.93 ±0.51	0.28 ±0.01	3.70 ±1.11	0.32 ±0.01	46.80	3.44
rainy	13.47 ±1.31	0.99 ±0.01	1.24 ±0.09	0.12 ±0.02	0.99 ±0.11	0.09 ±0.01	15.70 ±1.11	1.21 ±0.22
autumn	14.43 ±2.11	0.82 ±0.02	1.58 ±0.22	0.09 ±0.01	1.82 ±0.11	0.13 ±0.01	17.83 ±1.31	1.05 ±0.01
1994 winter	38.08 ±0.51	2.34 ±0.11	2.35 ±0.02	0.17 ±0.01	1.94 ±0.01	0.15 ±0.02	42.37 ±2.11	2.66 ±1.11
spring	43.42 ±3.11	2.90 ±1.02	3.79 ±0.11	0.29 ±0.11	4.59 ±2.11	0.39 ±0.11	51.80 ±2.11	3.58 ±0.31
rainy	17.05 ±3.11	1.39 ±0.72	1.98 ±0.32	0.18 ±0.01	2.05 ±0.91	0.18 ±0.11	21.08	1.75
autumn	20.64 ±7.01	1.17 ±0.21	1.34 ±0.21	0.08 ±0.01	1.21 ±0.31	0.09 ±0.03	23.18	1.34

± SEM (n=10)

NUTRIENT INPUT THROUGH LITTERFALL

Nitrogen: N return to the forest floor through litterfall followed a marked seasonal pattern by showing maximum input during February-April and minimum during June-September (Figure 6.6) and different fractions such as leaf, woody and miscellaneous litter also showed a similar trend. N input was significantly ($P<0.01$) influenced by months ($F=87.00$), years ($F=33.99$) and stand age ($F=104.42$).

N input during 1994 was greater (123.9-144.4 kg ha^{-1}) than 1993 (88.43-162.5 kg ha^{-1}). Total annual input of N to the forest floor through litterfall was 153.43 kg ha^{-1} in the 13-year old regrowth, while the corresponding values for the 7- and 16-year old regrowths were 106.19 and 128.49 kg ha^{-1}, respectively (Table 6.12). The amount of N returned annually by the woody and miscellaneous litter was also greater in the 13-year old regrowth (*ca.* 22 kg ha^{-1}) than the 16-year (*ca.* 17 kg ha^{-1}) and 7-year (*ca.* 8 kg ha^{-1}) old regrowths. The maxima of the N input through non-leaf litter generally coincided the peak leaf-fall period. Leaf litter added 87-92% of the total N to the forest floor, and the rest was contributed by the non-leaf litter. In certain months *e.g.* August-September, the contribution of non-leaf litter was negligible (Figure 6.6).

Phosphorus: P input through litter attained a peak during March and April, and a trough during June-September in all the three regrowths (Figure 6.7). Leaf litter contributed 70-80% of the total P added to the forest floor. Contribution made by the non-leaf litter to the total P input was about 20% during the peak period. In all the three regrowths, there were small peaks either during October or December. P input through litter varied significantly ($P<0.01$) due to months, year and stand age.

Seasonal variation in P input to the forest floor was similar to N (Tables 6.9-6.11). P input was relatively higher during 1994 than 1993, and it increased gradually from 5.14 kg ha^{-1} yr^{-1} in the 7-year old regrowth to

Table 6.12 Mean annual input (dry weight, Kg ha^{-1}) and mean accumulation (dry weight, Kg ha^{-1}) of litter mass (OM), N and P on the forest floor of the forest regrowths.

Variables		Age of the forest regrowth		
		7-year old	13-year old	16-year old
Input				
OM	Leaf	10357.7	12949.2	14825.8
	Total	11902.4	16059.1	17492.1
N	Leaf	98.1	141.3	111.4
	Total	106.2	153.4	128.5
P	Leaf	4.8	7.4	7.3
	Total	5.2	8.6	8.7
Accumulation				
OM	Leaf	1033.0	1355.1	1575.5
	Total	1231.4	2007.4	1942.7
N	Leaf	9.4	16.5	13.9
	Total	10.5	22.1	16.1
P	Leaf	0.5	0.8	0.8
	Total	0.6	1.0	1.0

Note: Values are the means of two year (1993-94) samplings.

Table 6.13 Chemical composition of leaf litter of dominant tree species used for decomposition study by litter bag method.

Species	C (%)	N (%)	P (%)	Lignin (%)	Cellulose (%)	C/N	Lignin/N
Pinus kesiya	47.3 ±1.2	0.98 ±0.01	0.05 ±0.004	43.2 ±1.1	7.4 ±0.9	48.27	44.08
Quercus dealbata	47.6 ±0.3	0.89 ±0.01	0.06 ±0.01	24.4 ±1.4	7.1 ±1.9	53.48	27.42
Quercus griffithii	46.4 ±2.1	0.73 ±0.05	0.05 ±0.001	23.7 ±0.9	11.9 ±0.3	63.56	32.47
Rhododendron arboreum	45.6 ±3.6	0.59 ±0.06	0.03 ±0.001	37.3 ±3.1	9.3 ±0.7	77.29	63.22
Schima khasiana	47.3 ±1.0	1.03 ±0.03	0.04 ±0.001	25.1 ±3.1	5.1 ±0.1	45.92	24.37

± SEM (n=3)

8.66 kg ha-1 yr-1 in the 16-year old regrowth. The contribution of leaf litter, however, declined from about 93 to 84% during this period. The woody litter added 0.4-0.9 kg P ha^{-1} yr^{-1} to the forest floor, the maximum being in the 13-year old regrowth. The amount of P in the miscellaneous litter increased from 0.15 kg ha^{-1} yr^{-1} in the 7-year old regrowth to 0.74 kg ha^{-1} yr^{-1} in the 16-year old stand.

LITTER TURNOVER

The annual turnover rates of dry mass, N and P were almost the same for leaf as well as total litter. The decomoposition coefficients (K) for dry matter, nitrogen and phosphorus averaged *ca.* 0.9 in all the three forest regrowths without showing any definite successional trend.

RESOURCE QUALITY OF FRESH LEAF LITTER

Mean N concentration in the leaf litter of 5 dominant species varied from a minimum of 0.59% in *Rhododendron arboreum* to a maximum of 1.03% in *Schima khasiana*. P concentration was relatively low, varying between 0.03% and 0.06% in different species. Lignin concentration was maximum (43.2%) in the coniferous species, *P. kesiya*. Among the broadleaved species, *R. arboreum* had the highest concentration of lignin (37.3%). In other species the values varied from 23.7 to 25.1%. Cellulose concentration was relatively high (11.9%) in *Quercus griffithii*, followed by *R. arboreum* (9.3%) and other species (5.1-7.4%). Lignin and cellulose concentrations were minimum in *Q. griffithii* and *S. khasiana*, respectively (Table 6.13).

DECOMPOSITION OF LEAF LITTER

Weight loss pattern: The decay pattern of leaf litter was different for different species and it also varied between the stands (Figures 6.8, 6.9). Needles of *Pinus kesiya* decomposed in a three-phased manner (Figure 6.8). The first phase lasting for about 60 days, was characterised by a slow rate (0.05% weight loss day^{-1}) of decay. This was followed by a period of rapid weight loss (0.76% weight loss day^{-1}) upto 120 days (Table 6.14). During

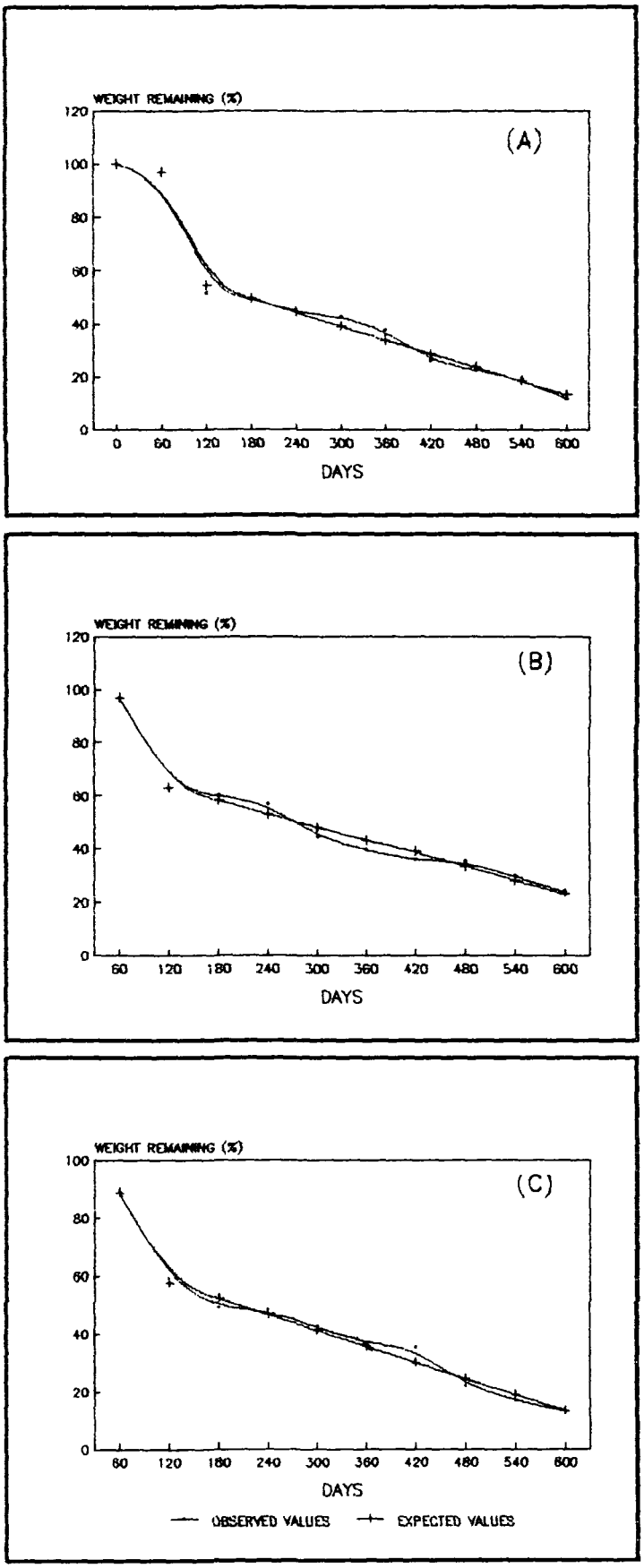


Figure 6.8. Decay pattern of (A) *Pinus kesiya* needles in the 7-yr old regrowth, (B) and (C) *Quercus dealbata* leaves in 13- and 16-yr old regrowths, respectively.

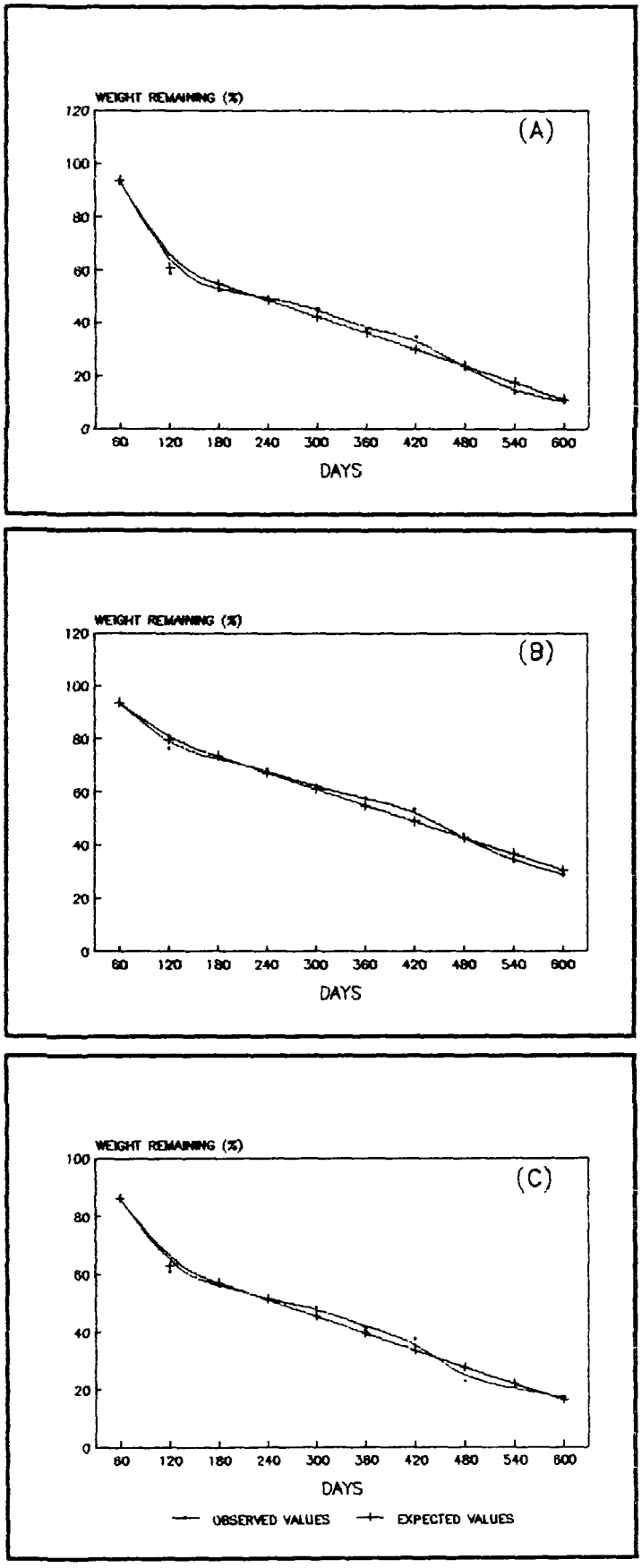


Figure 6.9. Decay pattern of leaf litter of *Q. griffithii*, *R. arboreum* and *S. khasiana* in the 16-yr old regrowth.

Table 6.14 Relative decay/nutrient mineralization rates (mean weight loss/nutrient release (mg and %) day^{-1}) during different phases of leaf litter decomposition.

Species	k		k_N		k_P	
	mg	%	mg	%	mg	%
(7-yr old regrowth)						
Pinus kesiya						
I phase	4.63	0.05	0.58	0.64	0.008	0.17
II phase	67.2	0.75	0.15	0.27	0.022	0.51
III phase	3.82	0.08	0.03	0.07	0.003	0.09
(13-yr old regrowth)						
Quercus dealbata						
I phase	26.20	0.31	0.20	0.26	0.026	0.54
II phase	6.54	0.08	0.05	0.09	0.001	0.04
(16-yr old regrowth)						
Quercus dealbata						
I phase	29.54	0.35	0.17	0.23	0.012	0.24
II phase	6.73	0.09	0.06	0.12	0.004	0.12
Quercus griffithii						
I phase	30.45	0.35	0.17	0.27	0.014	0.35
II phase	8.14	0.10	0.05	0.11	0.002	0.10
Rhododendron arboreum						
I phase	9.75	0.11	0.08	0.16	0.002	0.07
Schima khasiana						
I phase	29.11	0.33	0.31	0.35	0.018	0.45
II phase	6.89	0.09	0.04	0.08	0.001	0.05

k-decay constant, k_N-N mineralization constant and

k_P-P mineralization constant.

Table 6.15 Annual decay and mineralization constants of leaf litter of the study speciese and their t_{50} and t_{99} in the three forest regrowths.

Decay/Mineralization	*P. kesiya*[a]	*Q. dealbata*[b]	*Q. dealbata*[c]	*Q. griffithii*[c]	*R. arboreum*[c]	*S. khasiana*[c]
Dry mass						
k	1.28	0.88	1.24	1.39	0.77	1.06
t_{50}	0.50	0.80	0.60	0.50	0.90	0.70
t_{99}	3.90	5.70	4.00	3.60	6.50	4.70
Nitrogen						
k_N	1.24	0.69	1.24	1.28	0.62	1.02
t_{50}	0.60	1.00	0.60	0.54	1.12	0.71
t_{99}	4.00	7.20	4.00	3.90	8.10	4.90
Phosphorus						
k_P	1.20	0.80	1.13	1.28	0.37	0.92
t_{50}	0.56	0.90	0.61	0.54	1.90	0.76
t_{99}	4.20	6.23	4.42	3.91	13.70	5.48

[a] In 7-year old regrowth, [b] In 13-year old regrowth, [c] In 16-year old regrowth.

k is the decay constant, k_N and k_P are N and P mineralization constants.

the third phase (*i.e.* 120-600 days) the decay process continued more or less at a constant rate (0.08% weight loss day^{-1}). *Quercus dealbata*, *Quercus griffithii* and *Schima khasiana* followed a two-phased decay pattern (Figures 6.8, 6.9). The first phase lasting for about 120 days, was characterized by a rapid weight loss, followed by a slow rate of decay until 600 days (Table 6.14). Leaves of *Rhododendron arboreum* followed a uniform pattern of weight loss from the beginning to the end of the experiment (Figure 6.9). The dry mass remaining (% of initial) at the end of the experiment were, 11.9%-*P. kesiya* in 7-year old regrowth, 23.8%-*Q. dealbata* in 13-year old regrowth, 13.3%-*Q. dealbata* in 16-year old regrowth, 10.3%-*Q. griffithii*, 28.9%-*R. arboreum* and 17.1%-*S. khasiana.*

Based on the annual decay constants (Table 6.15) the study species were grouped into three categories. First, the fast decomposing species (*e.g. Q. griffithii*, k=1.39). Second, species decomposing at a moderate rate (*e.g. P. kesiya*-1.28, *Q. dealbata*-1.24 and *S. khasiana*-1.02), and third, species decomposing at a slow rate (*e.g. R. arboreum*, k=0.77). The pine needles required 3.9 years for 99% decay. The corresponding value for *Q. dealbata* was 5.7 years in the 13-year old regrowth and 4.0 years in the 16-year old regrowth. The t_{99} was 3.6 years for *Q. griffithii*, 4.7 years for *S. khasiana* and 6.5 years for *R. arboreum.*

A composite linear decay model, $Y = a+bX_1+cX_2+dX_3$ showed a good fit for the weight loss pattern in *P. kesiya.* The multiple regression equation, $Y = a+bX_1+cX_2$ fitted well for the observed decay pattern in the case of all broadleaved species except for *R. arboreum.* In the latter case expected values calculated through a simple linear regression function, $Y = a+bX$ was the best fit. The regressions describing the decay rates over time were highly significant ($P<0.001$, r^2 ranged from 0.937 to 0.987). Similarly, the difference in the decay coefficients (k) were statistically significant between different species ($F=25.46$, $P<0.01$).

Table 6.16 Leaf litter decomposition rate (% weight loss day $^{-1}$) as influenced by climatic variables, soil characteristics and initial leaf chemistry.

Variable	Regression equation	df	r	P
Weight loss vs climatic variables				
*Rainfall (mm)	Y=44.64+1.15X	40	0.992	0.001
**Air temperature (°C)	Y=11.28+0.33X	40	0.691	0.001
Weight loss vs soil characteristics*				
Temperature (°C)	Y=17.10+0.04X	40	0.155	NS
Moisture content (%)	Y=57.40+0.25X	40	0.743	0.001
pH	Y=4.84+0.006X	40	0.502	0.001
Organic matter (%)	Y=9.76+0.005X	40	0.144	NS
TKN (%)	Y=0.55+0.0003X	40	0.443	0.01
Available-P (ug g^{-1})	Y=10.87+0.05X	40	0.246	NS
Weight loss vs initial chemistry				
Lignin (%)	Y=41.62-0.17X	16	-0.712	0.001
C (%)	Y=47.48-0.01X	16	-0.318	NS
N (%)	Y=1.03-0.003X	16	-0.533	0.05
P (%)	Y=0.05-0.0001X	16	-0.275	NS
Cellulose (%)	Y=6.74+0.02X	16	0.268	NS
Lignin/N	Y=45.16-0.17X	16	-0.510	0.05
C/N	Y=40.05-0.05X	16	-0.120	NS

NS-Not Significant

*mean daily rainfall

**mean monthly air temperature

***indicate the soil depth whose values have been used in the computation

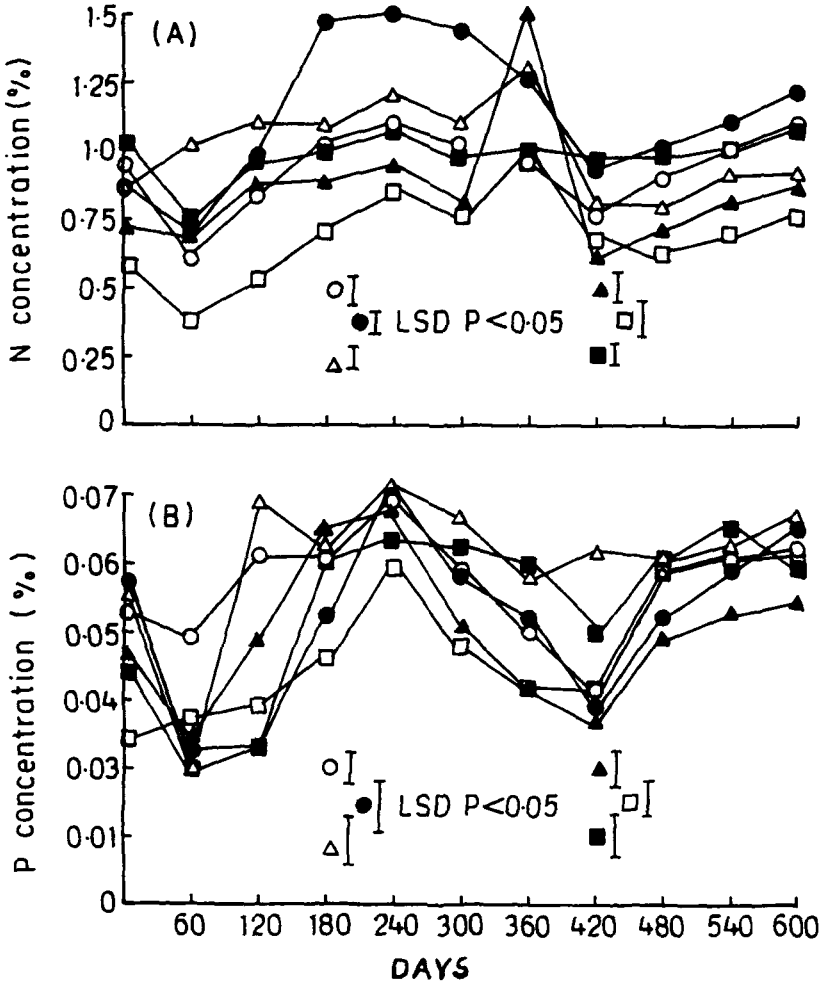


Figure 6.10. Variation in (A) N and (B) P concentrations in the decomposing leaf litter through time. -o- *P. kesiya*, -●- *Q. dealbata* (13-yr old regrowth), -Δ- *Q. dealbata* (16-yr old regrowth), -▲- *Q. griffithii*, -□- *R. arboreum*, -■- *S. khasiana*.

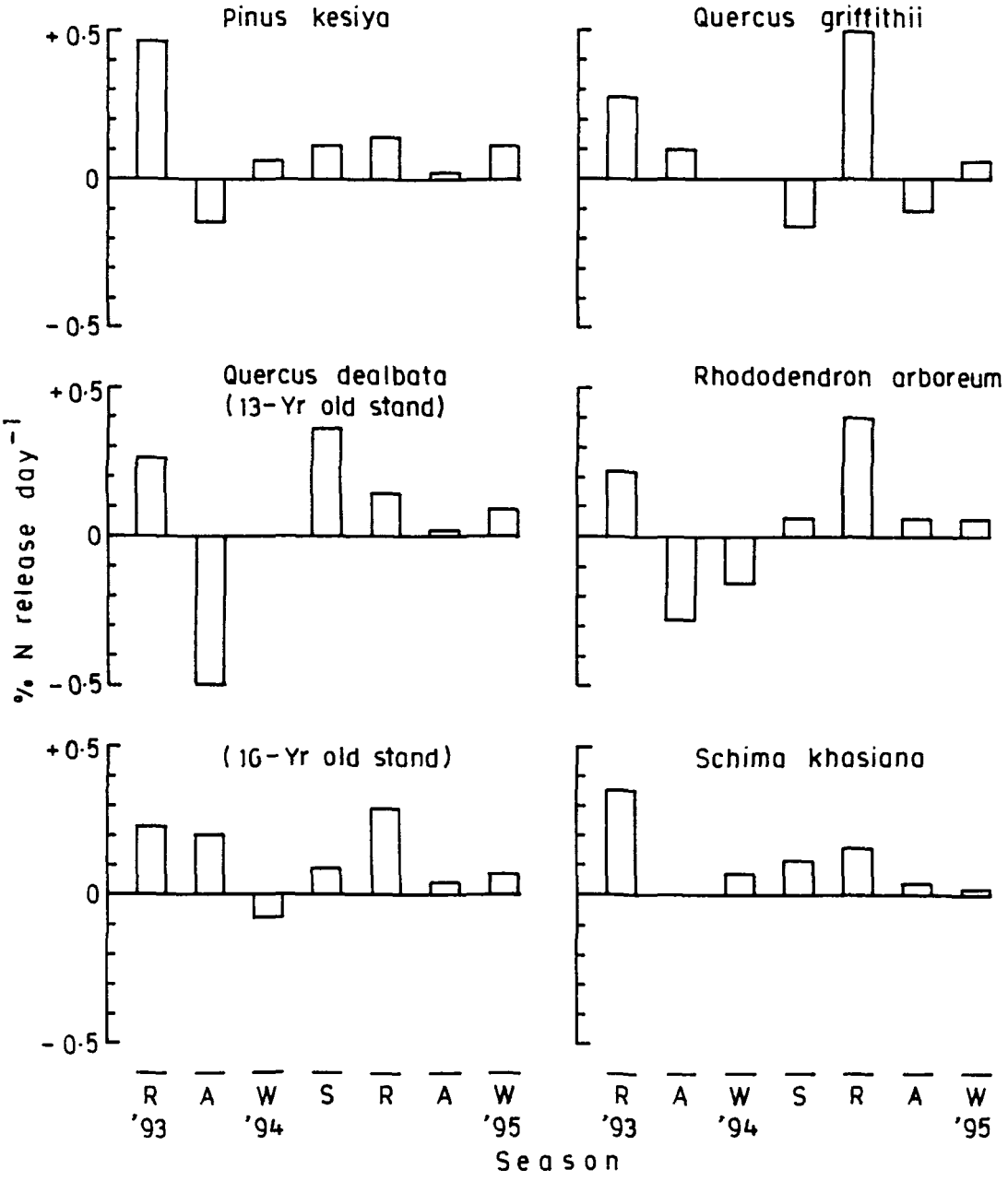


Figure 6.11. N mineralization rate (% release day^{-1}) in the decomposing leaf litter of the study species during different seasons (R-rainy, A-autumn, W-winter and S-spring seasons).

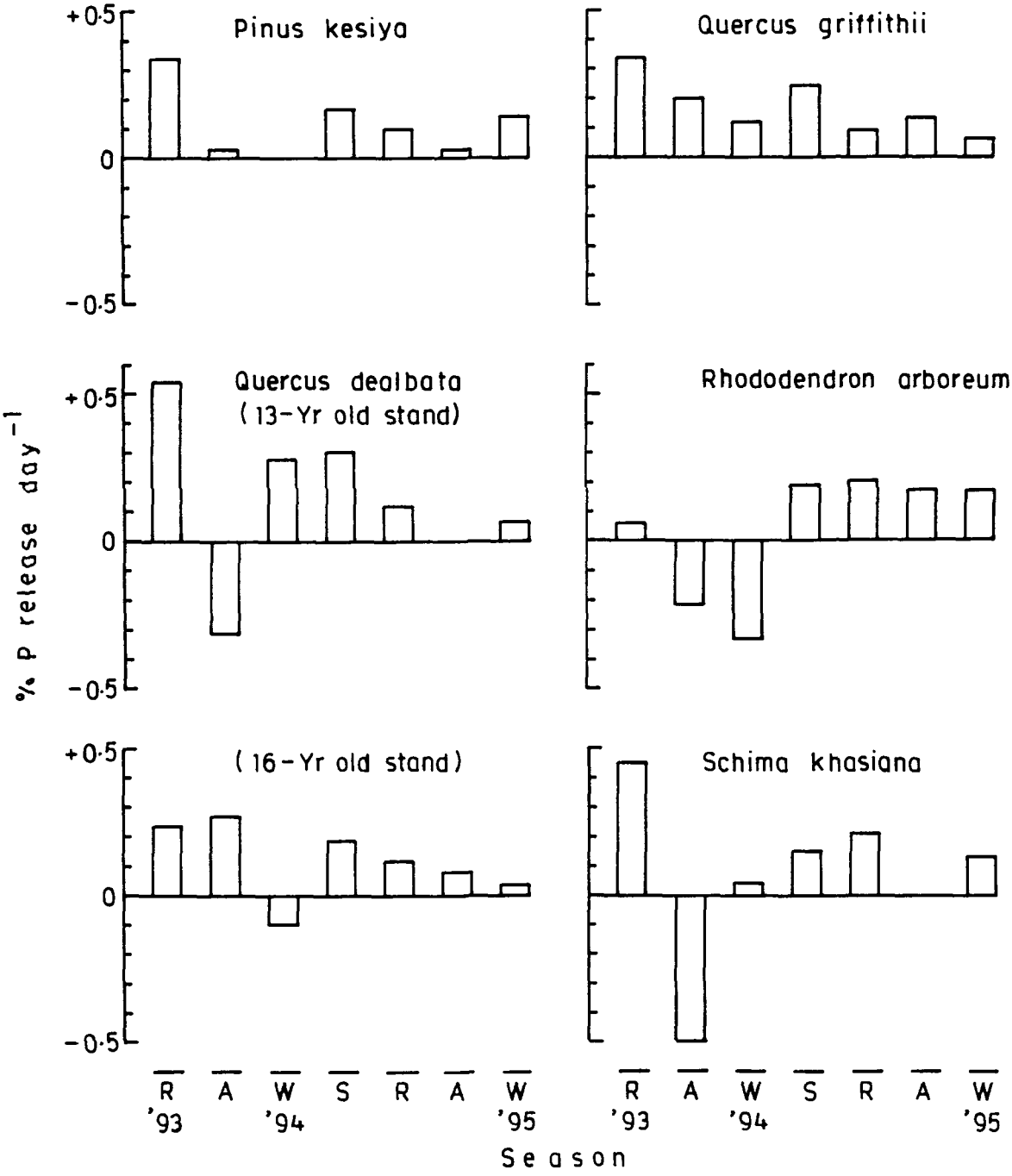


Figure 6.12. P mineralization rate (% release day-1) in the decomposing leaf litter of the study species during different seasons (R-rainy, A-autumn, W-winter and S-spring seasons).

Simple linear regression analysis between mean daily rate of weight loss and fifteen intrinsic and extrinsic variables yielded significant correlations only with eight of them *viz.*, initial lignin and N concentrations and lignin/N ratio in the litter, and mean seasonal soil moisture content, soil pH and soil-TKN, mean daily rainfall and mean monthly air temperature (Table 6.16).

Nutrient mineralization: N and P concentrations in the decomposing leaf litter of various tree species broadly followed a similar temporal pattern. After showing an initial drop at 60 days, the nutrient concentration in the decaying leaves gradually increased up to 240 days and then declined until 420 days to rise again till the termination of the experiment (Figure 6.10). One-way ANOVA revealed significant ($P<0.01$) differences in the N and P concentrations between species ($F=5.48$) and sampling time ($F=10.52$). In all species, rates of N and P mineralization were at its peak during rainy season, followed by a phase of immobilization or slowest release during autumn and winter seasons (Figures 6.11, 6.12). Generally, the mineralization rate was lower during second year of the study. *Rhododendron arboreum*, however, had faster rate of N and P release during the second year.

The N mineralization constants (k_N) of *P. kesiya*, *Q. dealbata* (in the 16-year old regrowth), *Q. griffithii* and *S. khasiana* ranged from 1.02 to 1.28. *Q. dealbata* of the 13-year old regrowth and *R. arboreum* registered lower k_N (0.62-0.69). *R. arboreum* also had the lowest P mineralization constant ($k_P=0.37$), while for the other study species the k_P varied between 0.80 and 1.28 (Table 6.16). Despite these variations in the N and P mineralization constants, their stocks in decomposing leaf litter were positively correlated ($P<0.001$) with the corresponding dry weight (Figure 6.13).

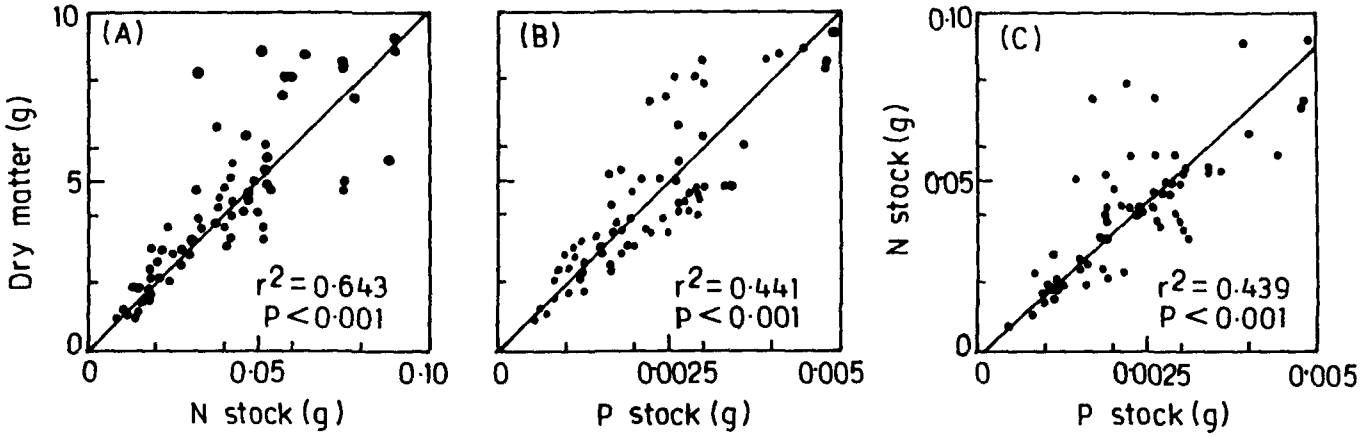


Figure 6.13. Relationship of dry matter content of decomposing leaf litter with (A) N stock and (B) P stock, and the relationship among (C) N and P stocks in the regrowing forest stands.

DISCUSSION

LITTER ACCUMULATION PATTERN

Maximum accumulation of litter on the forest floor during winter (January) and spring (April) corresponded to the period of peak litterfall and lower decomposition rate (Singh and Gupta 1977, Swift *et al.* 1981). In contrast, the rainy and autumn seasons which were characterized by high soil microbial activity, had minimum litter mass on the forest floor. Similar findings have been reported by Swift *et al.* (1981) from the tropical rain forests, Pandey and Singh (1981) from a mixed oak-conifer forest, and by Visalakshi (1993) from the tropical evergreen forests.

The average litter mass although increased steadily with the age of the forest regrowth from 1231.4 to 2007.4 kg ha^{-1}, the values are very less compared to the range (2170-2257 kg ha^{-1}) reported by Vogt et al. (1986) for various tropical and subtropical forests of the world. There could be many reasons for low forest-floor litter mass obtained in this study. The notable among them are the degree of initial disturbance caused to the original forest vegetation, and characteristics of successional community *viz.* species composition, density and age of the regenerating forest and a variety of climatic and edaphic factors which influence litter production and decomposition on the forest floor. Rapid decomposition of litter in the humid tropics (Vogt *et al.* 1986, Mohankumar and Deepu 1992, Couteaux *et al.* 1995) has been attributed as an important cause of lower accumulation of litter on the forest floor of wet tropical forests. Conversely, slower rate of decomposition help accumulation of litter in the temperate and montane forests (Bray and Gorham 1964).

Higher litter accumlation in the 13- and 16-year old regrowths (Plates 6.1 b&c) compared to the 7-year old regrowth (Plate 6.1a) was positively correlated with soil and vegetation characteristics (Table 6.17).

Plate 6.1. Status of forest-floor litter in (a) 7-, (b) 13- and (c) 16-year old regrowths.

Table 6.17 Relationship between soil, vegetation and litter characteristics in the three forest regrowths.

Variable	Accumulation	Litterfall
Macroclimatic variables		
Rainfall (mm)	0.295^{ns}	0.500^{ns}
Maximum temperature (°C)	0.624^{ns}	0.009^{ns}
Minimum temperature (°C)	$0.718^{0.05}$	0.193^{ns}
Soil characteristics		
pH	-0.988^{**}	-0.997^{**}
Soil organic matter (%)	0.889^{*}	0.991^{**}
Soil total N (%)	0.866^{*}	0.980^{**}
Available-P ($\mu g\ g^{-1}$)	0.930^{**}	0.999^{**}
Vegetation characteristics		
Total no. of woody species	0.997^{**}	0.919^{*}
Density of woody species	0.954^{*}	0.999^{**}
Basal area of woody species	0.766^{ns}	0.931^{*}
Diversity of woody species	-0.572^{ns}	-0.280^{ns}

Note: Rainfall and maximum and minimum air temperatures were monthly means.

** Significant at P<0.001 level

* Significant at P<0.01 level

ns Not significant

Throughout the study period leaf litter was the major component (63-82%) of the forest-floor litter. This proportion is comparable to majority of the tropical forests (UNESCO report 1978). The relative contribution of woody litter, however, followed some what seasonal trend as its proportion increased up to 30% during rainy season when the decomposition activity was at its peak. The proportion of leaf litter increased by 30% from 7- to 16-year old regrowth. While, the proportion of woody litter was two- to three-times higher in the 13-year old regrowth than the 16- (283 kg ha^{-1}) and 7-year (165 kg ha^{-1}) old regrowths.

LITTER PRODUCTION

In the tropical forest ecosystems maximum litterfall has been observed in wet season (Cornforth 1970, Jackson 1978, Brassel *et al.* 1980, Rai and Proctor 1986). Pascal (1988) reported that the rhythm of leaf shedding in wet evergreen forests of Attapadi region, leaf shedding was characterized by a heavy fall during warm and dry summer season. In evergreen *Acacia nilotica* and *Eucalyptus tereticornis*, the litterfall peaked during cool and dry winter months (Gill *et al.* 1987). In tree plantations of deciduous species maximum litter falls during early summer months (Gholz *et al.* 1985).

In the present study leaf shedding was maximum during dry period of the year ranging from November to April in all the three forest regrowths. Low soil moisture level during these seasons could be the possible reason for heavy leaf-fall as suggested by Moore (1980). He reported that the water stress triggers *de novo* synthesis of abscissic acid in the foliage of plants, which in turn, can stimulate senescence of leaves and other parts. The prolonged litterfall upto early-May in the present study could be attributed to the prevailing high-speed wind during these months in this region (Khiewtam and Ramakrishnan 1993, Uma Shankar *et al.* 1993). There was little variation in the timing of minimum litterfall which occurred mostly

during June to September (rainy season), when the decomposition rate is at its peak.

Annual litter production in the youngest stand is comparable to the values reported by William and Gray (1974) for equatorial forests (5500-15300 kg ha^{-1} yr^{-1}), and by Laudelot and Meyer (1954) for semi-evergreen secondary forests (12300 kg ha^{-1} yr^{-1}). But, the values obtained for 13-and 16-year old regrowths are greater than most values reported for the tropical forests elsewhere and in India (UNESCO report 1978, Vogt *et al.* 1986). Gholz and Fisher (1982) reported an average total annual litterfall of 5000 kg ha^{-1} yr^{-1} for five stands of 15-35 year old slash pine (*Pinus elliottii*) plantations in northern Dakota. Litterfall in the 7-year old regrowth, which mainly consisted of young khasi pines (*Pinus kesiya*) is higher than the above-mentioned litterfall estimates as well as from a 70-year old lodgepole pine (*Pinus contorta* spp. *latifolia*) forest, which had 2080 kg ha^{-1} yr^{-1} litterfall (Fahey 1983). The values are comparable to a 240-year old lodgepole pine forest (12500 kg ha^{-1} yr^{-1}, Fahey 1983). The favourable temperature and rainfall conditions prevailing in the region, and the concomitant higher primary productivity can account for higher litter production in the humid subtropical pine forest (Bray and Gorham 1964, Das and Ramakrishnan 1985).

Annual litter production in the three regrowing forest stands was directly related to the density and basal area of woody vegetation (Table 6.17). Thus, a small difference in the basal area of woody species from 24 to 41 m^2 ha^{-1}) as noticed in the three forest regrowths could manifest itself in terms of litterfall. Similar findings have been reported by Gaur & Pandey (1978) in two tropical dry deciduous forests at Varanasi, India. However, recent studies have failed to establish the cause-effect relationship between basal area and litterfall in a close canopied temperate forest ecosystem (Stohlgren 1988) and in a tropical moist

deciduous forest ecosystem (Mohankumar and Deepu 1992). Litter production was also strongly related to the age of the forest regrowth ($Y=6.89+0.001X$, $r=0.997$, $P<0.05$). Similar relationship has also been observed by Odum (1960) in old-field successional communities, Das and Ramakrishnan (1985) in *Pinus kesiya* forests, O'Connell and Menage (1982) in *Eucalyptus diversicolor* forests, Toky and Ramakrishnan (1983) in 'jhum' fallows and Singh (1990) in degraded forests.

Year-to-year variation in litter production have been reported by several workers (Bray and Gorham 1964, Bernhard 1970, Rai and Proctor 1986, Rout and Gupta 1990b). It has been reported that in the tropical forests where litterfall has been measured over two year, the value in the first year is within 88% of the second year (UNESCO 1978). The ratio between the first and second year of the study ranged from 1:1.2 to 1:1.3 in all three stands. These ratios are comparable to the ratios (1:1.1-1.3) reported for various tropical rain forests of the world (Bray and Gorham 1964, Bernhard 1970, Spain 1984).

The proportion of leaf litter to total litterfall in the forest regrowths ranged from 78-88%. These values are comparable to the results of other studies, on the basis of which, Meentemeyer *et al.* (1982) calculated an average leaf-fall contributes *ca.* 70% to the total annual litterfall. Woody litter accounted for 9-16% of the total annual litterfall. These values were very less compared to those reported by Bray and Gorham (1964) (21.23%), Christensen (1978) (19-36%) and Fahey (1983) (17-46%). This is, however, similar to those reported by Mehra *et al.* (1985) from Central Himalayan forests (9-20%). The obvious reason for the low values are non-inclusion of branches beyond 20 mm diameter. The average proportion of miscellaneous litter to total annual litterfall in the 7-year old regrowth was extremely low compared to 5.3-5.7% in the older regrowths, which fall in the lower limit of the range (5-27%) reported by Mehra *et al.* (1985).

NUTRIENT DYNAMICS OF LITTER

N and P concentrations in fresh litter was generally higher during autumn and lower during rainy season. Such a seasonal variation in mineral elements concentration may occur due to nutrient translocation within the plant, and differences in nutrient solubility and leaching (Van Cleve and Noonan 1975, Gosz *et al.* 1976). In this context, Tukey (1970) reported that the leaching of soluble organic and inorganic consituents from leaf tissues may affect the nutrient content of senescing foliage. Heavy leaching losses of N during rainy season might be the reason for its low concentration, compared to P, which is a relatively less mobile element.

Generally, the woody litter had lower N and P concentrations than the foliage, and it did not show marked temporal variation. These results are in agreement with the observations of Gosz *et al.* (1972) and Rout and Gupta (1990a,b), who reported that perennial tissues had lower concentration of nutrients, especially N and P. Relatively higher concentration in the miscellaneous litter could be attributed to the presence of floral parts, fruits and bark. Nutrient concentration in different litter fractions in the pine-dominated 7-year old regrowth was relatively lower than the oak-dominated 13- and 16-year old regrowths. This is in conformity with the findings of Brassel *et al.* (1980) and Rout and Gupta (1990a), who reported higher concentration of N and P in tropical rain forest litter than the conifer litter. Similar observations have also been made by Metz (1952) and Kramer and Kozlowski (1960) in the temperate regions.

Maximum nutrient input during winter and spring seasons in the three forest regrowths coincided with the periods of peak litterfall. Seasonal pulses of nutrient return to the forest floor generally reflected the trends of leaf-litterfall and accumulation on the forest floor. In all three regrowths quantitative and qualitative variation in litterfall influenced the amount of nutrients returned to the soil as well as their

stock on the forest floor. Annual input of N was maximum in the 13-year old regrowth, followed by the 16-year old regrowth and minimum in the 7-year old regrowth. High concentration of N in the litter of the 13-year old regrowth, as compared to the 16- and 7-year old regrowths, was the main reason for greater N input to the forest floor in this stand. On the other nand, P input and accumulation pattern was similar in the 13-and 16-year old regrowths, due to similar P concentration in different components of the litter. Thus, a relatively lower annual litter production was balanced by higher N concentration in the 13-year old regrowth. In all stands, the amount of N returned to the soil through litterfall and its stock in the forest-floor litter mass was greater than P. This agrees with the findings of Gosz *et al.* (1972) and Rai and Proctor (1986).

LITTER AND NUTRIENT TURNOVER

The litter turnover rate (K) varied within in a narrow range of 0.889-0.905 and failed to show a clear successional trend. It appears that a more detailed investigation covering a wide range of gradient is required to understand the litter turnover pattern during vegetation recovery after disturbance. Nonetheless, the leaf litter higher turnover rate than the non-leaf litter materials in all stands. This has been explained by many workers on the basis of resource quality of litter. Leaves being devoid of much of the sclerophyllous cells have low lignin and high N concentrations than the woody litter (Singh and Gupta 1977, Swift *et al.* 1981, Vogt *et al.* 1991), therefore they decompose faster than the woody material.

On the basis of fractional annual turnover rates, several workers have determined the mobility of nutrient elements in different forest ecosystems (Reiners and Reiners 1970, Gosz *et al.* 1972, Van Cleve and Noonan 1975). Gosz *et al.* (1976) reported that N and P has long residence time on the forest floor as a result of relatively faster translocation, and greater immobilization by decomposers. Relatively longer residence time (1.13 yr.)

of N in the older regrowths indicated its greater immobilization in the forest-floor detrital mass compared to the young regrowth. In contrast, a slightly rapid turnover of P in the older regrowths suggested their relatively faster mobility within the system.

Chemical composition of the litter determines the rate of turnover of organically bound nutrients. Initial N (0.59-1.03%) and lignin (23.7-43.2%) concentrations of leaf litter of dominant tree sepcies are well within the range (0.36-3.90% and 4.5-46.4%, respectively) reported by Vogt *et al.* (1986, 1991), Van Vuuren *et al.* (1993) and Myers *et al.* (1994) for various tropical and temperate tree species. Species having more sclerophyllous cells (*e.g. R. arboreum, P. kesiya*) had greater lignin concentration and low nutrient level. The concentration of cellulose (5.1-11.9%) in freshly fallen leaves was very less compared to the values (21.3-31.7%) reported by Bloomfield *et al.* (1993) for a few tropical species. This may be related partly to the difference in species composition, and partly due to difference in the method used for its estimation.

The low quality materials having high C/N ratio immobilizes N at a faster rate, while the high-quality litter releases nutrients at a faster rate during decomposition (Myers *et al.* 1994). In the light of the above hypothesis, leaf litter of *Q. dealbata, Q. griffithii, S. khasiana* and *P. kesiya* belong to high quality and that of *R. arboreum* belongs to low quality.

DECAY PATTERN OF LEAF LITTER

Decomposition of *P. kesiya* needles followed a slightly different pattern than other broadleaved species by showing slow rate of weight loss during initial stage of decay. This could be attributed to the time-lag in the colonization and establishment of the microbes on the litter (Alexander 1977) on account of its toughness due to low moisture, and high lignin content in the needles. The rapid rate of decay after an initial lag-phase

was the net effect of a large number of processes such as utilization of readily available energy sources by microbes, loss of water soluble components and non-structural carbohydrates from the leaf litter (Bloomfield *et al.* 1993), and removal of leaf litter particles by animals, especially termites (Swift *et al.* 1979) operating on the freshly fallen litter on the forest floor. A decline in the rate of weight loss after rapid phase of decay may be attributed to higher percentage of recalcitrant fractions like cellulose, lignin and tannin during the advanced stage of leaf decay. These substances are known to control decay rate by showing resistance to enzymatic attack and by physically interfering with the degradation of other chemical fractions of the cell wall (Bloomfield *et al.* 1993).

Within the overall weight loss pattern, a relatively higher rate (24-48% of initial weight) of weight loss during the rainy season could be tne effect of physical determinants such as temperature and soil moisture content (Rochow 1974, Bhatt *et al.* 1985), while a relatively slow rate (12-21% of initial weight) during post-rainy seasons could be due to low soil moisture and reduced microbial activity.

Influence of initial N and lignin concentration on the decomposition of leaf litter has been emphasized by a large number of workers both in the tropics and temperate climates (Singh and Gupta 1977, Meentemeyer 1978, Melillo *et al.* 1982, Vogt *et al.* 1991, Okeke and Omaliko 1992, Bloomfield *et al.* 1993). In the present study, *R. arboreum* leaves having high lignin and low N concentration decomposed at a slow rate, while *Pinus kesiya* needles with high lignin and N concentrations (Table 6.13) decomposed at a faster rate than the broadleaved species. Initial C/N ratio did not show any relationship with the decay rate, but lignin/N ratio showed a significant negative correlation with the decay rate (Table 6.15). This finding is in accordance to Melillo *et al.* (1982) who have reported a

significant inverse relationship between initial lignin/N ratio and net decay rate. Relatively slow rate of release of N and P from decomposing leaf litter of *R. arboreum* is attributed to its relatively tough and sclerophyllous nature with low N and high lignin content.

Initial faster decay rate of leaf litter of *Q. griffithii* and *Q. dealbata* appears to be related to high N concentration. Aber and Melillo (1982) reported that species adapted to higher N availability are expected to have faster rate of organic matter turnover and such species exhibit low immobilization rates also. Berg (1984) and Taylor *et al.* (1989) have, however, suggested that as the decomposition proceeds the influence of N decreases while that of lignin increases. Hence, the reduction in decomposition rate with time may be due in part to the slow breakdown of residual refractory materials.

N AND P MINERALIZATION DURING LEAF LITTER DECOMPOSITION

A marked decline in N and P concentrations in the decomposing leaf litter of the study species during initial phase of decay (until 60 days) may be ascribed to leaching losses due to heavy rainfall during that period (Figure 3.2). Subsequent steady increase in nutrient concentration could be the result of microbial immobilization (Anderson 1973), nutrient inputs from throughfall and atmospheric precipitation (Bocock 1963), and/or atmospheric N_2 fixation (Wood 1974). Despite variations in N and P concentration in decaying leaf litter due to mineralization and immobilization, N and P stocks in the decomposing leaf litter were positively correlated with its dry mass (Figure 6.13). Similar trend has also been reported by Prescott *et al.* (1993) for conifer litter. Warm-humid rainy season being more favourable for mineralization, was characterized by rapid rate of N and P release from decomposing leaf litter contrary to the dry-winter season when immobilization was the dominant process on the forest floor .

Pastor and Post (1986) have reported an increase in litter decay rates owing to disturbances in forest ecosytems and contemporary changes in the external environmental conditions. In the present study, rapid decay of *Q. dealbata* leaves in the 16-year old regrowth than the 13-year old regrowth may be attributed to the favourable changes in microclimatic factors leading to better growth and activity of soil microbial population. The climax species, *Q. dealbata, Q. griffithii* and *R. arboreum* registered slow decay rates (k=0.77-1.39) in the present study when compared to the rates reported by Laishram and Yadava (1988) for the same species (0.18-0.56) in an undisturbed subtropical forest at Shiroy hills in north-east India. They also reported faster decay and nutrient turnover in bigger leaves than the narrow ones. Probably this was the reason why comparatively bigger *Q. griffithii* leaves had faster decay and nutrient release rates than other studied species. Thus, a relatively rapid release of N and P in the 7-year old regrowth could be considered as an influence of disturbance which inturn may be useful in meeting N and P requirements of regrowing vegetation following disturbance.

CHAPTER 7

FINE AND COARSE ROOT DYNAMICS

INTRODUCTION

Roots are the connecting link between plant and soil. In many ways, growth of the root system plays a decisive role both in the development of shoot and in soil formation. During the past two decades quantitative estimations of the roots in the forest ecosystem were mainly confined to the individual trees (Leith 1968, Newbould 1967, Hermann 1977). These studies have broadly classified the belowground plant system into structural coarse roots and physiologically active fine roots. The distinction between these two types of roots have been made by an

arbitrarily chosen diameter limit, which generally range from <1 to 2 mm diameter for the fine roots and >2-<15 mm diameter for the coarse roots (Ulrich *et al.* 1981, Vogt *et al.* 1986, 1991; Fahey and Hughes 1994). In the tropical moist forests, the fine roots are found either in the form of a superficial root-mat or they are concentrated in the upper 0-30 cm layer of mineral soil. They play a major role in nutrient absorption in forest ecosystem (Nambiar 1987) and contribute substantially to organic matter pool and profile development of the soil (Vogt *et al.* 1991).

The importance of fine roots in functioning of the forest ecosystem has been recognized only recently (Persson 1983, Singh *et al.* 1984, Vogt *et al.* 1982, 1983). As a result, a large number of studies have been conducted both in the tropical (Jordan and Escalante 1980, Ramakrishnan and Singh 1983, Srivastava *et al.* 1986, Nambiar 1987, Parrotta and Lodge 1991, Silver and Vogt 1992, Visalakshi 1994) and temperate (Persson 1979, Keyes and Grier 1981, Vogt *et al.* 1983, Gale and Grigal 1987, Fahey and Hughes 1994) forest ecosystems. The fine roots represent a large and dynamic portion of the belowground biomass and nutrient capital, and they may account upto 50% of the net primary production in the forest ecosystems (Santantonio *et al.* 1977, Srivastava 1985). Meier *et al.* (1985) reported that N and P concentrations in fine roots and their turnover rates can be considerably higher than the nutrient concentration and turnover rates of leaf litter. Vogt *et al.* (1983) supported this hypothesis and further suggested that depending upon the age of the stand, internal redistribution of nutrients in the belowground parts may meet 40-55% N and 45-70% P requirements of the fine roots. Contrary to this finding, McClaugherty *et al.* (1982) and Nadelhoffer *et al.* (1985) reported that the retranslocation of N and P from senescent fine roots is small.

Fine roots are in constant flux, with death and replacement taking place simultaneously (Persson 1983, Vogt *et al.* 1986). These processes have not been studied accurately mainly due to practical difficulties involved in such studies. McClaugherty *et al.* (1982), however, suggested that together with the aboveground litter, fine root necromass provide the main bulk of organic materials for tne complex decomposition cycles in the soil system. In spite of its importance, only a few workers have studied the decomposition dynamics and nutrient mineralization patterns of the fine roots in the forest ecosystem (McClaugherty *et al.* 1984, Bloomfield *et al.* 1993).

In the tropical forests, studies focusing on the influence of natural disturbance on community structure and function in general and fine root dynamics in particular are limited (Harrington 1986, Marchand *et al.* 1986, Parrotta and Lodge 1991). Futhermore, the role of fine roots in soil processes and vegetation regrowth following major human disturbances such as tree cutting in the natural forest ecosystem is not fully understood. Nevertheless, some data are available on the growth and development of fine roots and their dynamics in successional forests on fallow agricultural land (Uhl *et al.* 1982), and in the subtropical forests following hurricane disturbance and gap formation (Parrotta and Lodge 1991, Silver and Vogt 1993).

Data presented in this chapter aims to analyze some of the major aspects of fine root dynamics such as growth periodicity, spatial distribution pattern, accumulation and allocation of dry mass, production, turnover and decay pattern, and nutrient release in forest stands representing three different stages of vegetation recovery after selective tree felling in a subtropical humid forest. The objective of the study was to assess the relative importance of fine roots in N, P and organic matter enrichment of the soil during secondary succession after disturbance.

METHODS

ROOT SAMPLING

In each of the three stands, ten randomly located soil cores were taken on a monthly basis (during first week of every month) from January 1993 to December 1994 using a long tubiform steel corer (40 cm length, 6.5 cm inner diameter). They were sliced into three sections *viz.* 0-10, 10-20 and 20-30 cm, starting from the soil surface. The cores were taken to the laboratory in polythene bags and stored in a deep freeze at -20°C before root separation. Roots were retrieved from the soil cores by wet-sieving method outlined by Bohm (1979), and processing of all samples was completed within 21 days as suggested by Parrotta and Lodge (1991).

The roots were separated into three diameter classes: <1, 1-2 and 2-15 mm using a Vernier-caliper. In each diameter class, live and dead roots were distinguished on the basis of pliability and degree of cohesion between cortex and periderm. Live roots were much more resistant than the dead ones, and they did not break easily when bent. Dead roots were often wrinkled and dark in colour in contrast to the smooth and light coloured live roots (Persson 1983). Fine roots (<1+1-2 mm diameter classes) as well as coarse roots (2-15 mm diameter class) were washed twice to ensure removal of all external mineral matter and soil particles adhered to the roots.

The terms and abbreviations used throughout the thesis to denote different categories of roots are as under:
Biomass-live roots, Necromass-dead roots, FRB-fine root biomass, FRN-fine root necromass, FRM-fine root mass (FRB+FRN), CRB-coarse root biomass, CRN-coarse root necromass, CRM-coarse root mass (CRB+CRN), TRB-total root biomass, TRN-total root necromass and TRM-total root mass.

DRY MATTER AND PRODUCTION OF ROOTS

The cleaned root samples were dried to a constant weight at 80°C for 48 h and weighed to get the dry matter content. Annual root production by diameter class was determined by summing up the significant positive increments in the root biomass and concurrent increment, if any, in the necromass during successive samplings in a given diameter class (Sims and Singh 1978, Uma Shankar *et al.* 1993). The monthly data on biomass were pooled to get an average for winter (December-February), spring (March-May), rainy (June-September) and autumn (October-November) seasons.

FINE ROOT DECOMPOSITION

Roots in top 0-10 cm soil layer were collected in bulk from all three stands during April, 1993. They were carefully washed under a gentle flow of tap water to remove adhering soil and accompanying organic debris and separated into live and dead portions according to Persson (1982). Due to difficulty in collecting sufficient amount of newly senesced fine roots, live roots measuring <2 mm in diameter were separated, air-dried and used for decomposition studies by litter bag technique (McClaugherty *et al.* 1984).

Five grams air-dried root material was placed in each nylon bag (1 mm mesh, size 15 cm x 15 cm). Sixty such bags were buried in surface (0-10 cm) soil layer during May, 1993 in each stand. Subsamples of air-dried materials were taken in triplicate from each stand for dry weight determination. Five bags were retrieved from each stand at 60, 120, 180, 240, 300, 360, 420, 480, 540 and 600 days. The sample from each bag was cleaned of adhering plant parts and soil particles, oven-dried at 80° C for 48 h. and weighed. The dried samples were ground in a grinding mill (Cyclotec-Tecator) and used for chemical analysis.

CHEMICAL ANALYSIS OF ROOT SAMPLES

The ash content was determined by igniting the oven-dried material at 550° C for 6 hours in a muffle furnace. Carbon (C) content was calculated as 50% of the ash free weight (Upadhyay, 1993). Total Kjeldahl nitrogen (TKN) was determined by the micro-Kjeldahl procedure using Kjeltec Auto 1030 Analyzer and total phosphorus was analysed colorimetrically (Allen et al., 1974). Lignin and cellulose contents were determined following the methods outlined by Peach and Tracey (1956). N and P contents in biomass and necromass fractions of the fine and coarse roots were calculated by multiplying dry mass with their respective element concentration.

ROOT TURNOVER

Turnover rate (K) of fine roots was calculated using the mathematical model of Reiners and Reiners (1970): $K = P/X_m+P$, where P = annual fine root production and X_m = mean annual dry weight. Similarly the N and P turnover through fine roots were calculated by substituting the dry mass with the values of mineral elements. Turnover time (T) was calculated as reciprocal of turnover rate: T=1/K, where T=time in year.

Annual decay constant (k) was calculated with the data obtained from the litter bag experiment using the negative exponential decay model of Olson (1963): $k=\ln(X/X_o)/t_1$, where X_o is the initial dry weight, X is the dry weight remaining at the end of the investigation, and t is the time interval. N and P mineralization constants, k_N and k_P, respectively, were calculated by substituting dry weight with the amount of N and P in the above formula. The time (years) required for 50% (t_{50}) and 99% (t_{99}) decay or nutrient mineralization was calculated as, $t_{50}=0.693/k$, and $t_{99}=5/k$.

STATISTICAL ANALYSIS

Data was analyzed using one-, two- and three-way ANOVA (fixed effects model) to test the effect of variations between sampling periods, stands and different diameter classes on biomass, production, decomposition, and

nutrient content of fine roots. Tukey's test was carried to compare the mean values across the regrowth age. Simple and multiple regression analyses were conducted on fine root data considering them as dependent variables and climatic (monthly/daily rainfall, mean monthly maximum and minimum air temperatures) and edaphic (soil temperature, soil moisture, soil pH, soil organic matter, total nitrogen and available-P) parameters as independent variables. A few community characteristics such as density and basal area of woody vegetation were also used as independent variables to study the relationships between forest regrowth and accumulation of dry matter and nutrients in the fine roots. Regression analyses were also carried out to assess the effect of initial root chemistry on decomposition.

A composite linear regression model, $Y=a+bX_1+cX_2+dX_3$ was constructed using dummy factors as the indicator variables (Zar 1974) to distinguish different phases of root decomposition. In this equation, Y is the mass remaining, a is the constant (Y intercept), b is the rate of change in Y with respect to time or slope of the line with respect to time, and c is shift parameter for adjustment of the Y intercept in phase-II and d is the shift parameter for adjustment of the Y intercept in phase-III. The shift parameters used are the dummy factors equivalent to zero, if the decay was slow, and/or 1 if the decay was fast. By using this equation an expected decay curve was drawn and fitted to the observed weight loss pattern in the decomposition study.

RESULTS

TEMPORAL VARIATION IN ROOT MASS

Fine roots: Monthly variation in the dry weight of the fine roots in 7-, 13- and 16-year old regrowths are shown in Figure 7.1. The fine root mass (FRM)

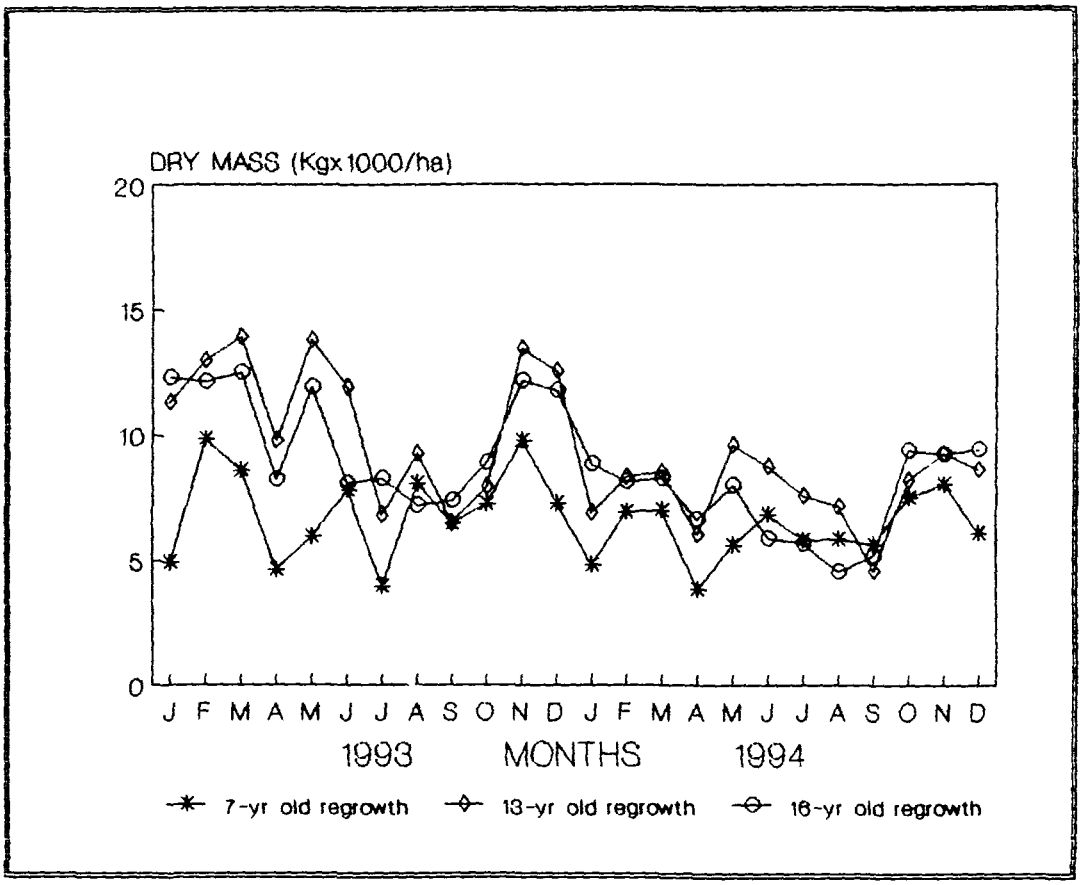


Figure 7.1. Monthly variations in fine-root mass in three forest regrowths.

Table 7.1 Depthwise variation in biomass (BM) and necromass (NM) fractions of fine roots (kg ha^{-1}) during different seasons in the 7-year old regrowth.

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
Root diameter class (<1 mm)						
1993 Winter	2171.3 ±111.3	712.4 ±62.1	599.1 ±15.1	265.1 ±20.1	366.5 ±11.1	130.3 ±12.3
Spring	1750.8 ±120.1	887.2 ±11.1	464.9 ±32.6	233.2 ±47.1	376.1 ±11.6	103.5 ±18.2
Rainy	1832.2 ±231.3	793.6 ±23.4	506.2 ±12.2	349.9 ±11.9	515.7 ±23.9	151.5 ±11.9
Autumn	3034.9 ±394.1	996.5 ±69.4	597.1 ±11.9	292.2 ±20.9	700.9 ±11.0	176.1 ±10.9
Mean	**2197.3**	**847.3**	**541.8**	**284.1**	**489.8**	**140.4**
1994 Winter	2104.3 ±420.9	667.5 ±61.8	374.1 ±18.9	329.3 ±11.6	340.5 ±60.2	300.2 ±11.1
Spring	1632.2 ±325.1	1707.6 ±90.9	303.5 ±18.2	289.3 ±21.8	226.1 ±51.7	281.4 ±15.6
Rainy	1621.4 ±153.3	1429.4 ±110.8	2829.7 ±126.7	418.5 ±12.9	325.3 ±18.7	339.4 ±64.1
Autumn	2740.3 ±328.1	1506.0 ±180.1	404.1 ±20.9	269.9 ±93.1	356.9 ±12.9	510.6 ±11.9
Mean	**2024.6**	**1327.6**	**341.2**	**326.8**	**312.2**	**357.9**
Root diameter class (1-2 mm)						
1993 Winter	1338.5 ±122.9	395.4 ±62.8	368.5 ±42.1	307.5 ±12.9	692.3 ±38.1	98.1 ±12.1
Spring	622.8 ±11.2	302.4 ±40.4	331.6 ±62.0	204.8 ±43.1	754.9 ±73.1	142.4 ±11.0
Rainy	830.3 ±92.0	547.8 ±62.3	187.1 ±23.9	145.6 ±48.3	587.4 ±60.1	140.8 ±14.3
Autumn	1026.7 ±18.1	315.1 ±11.9	410.2 ±30.9	291.4 ±81.3	532.1 ±41.3	163.0 ±43.1
Mean	**954.6**	**390.2**	**324.4**	**237.3**	**639.4**	**136.1**

Table 7.1 continued

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	548.1 ±68.1	289.6 ±32.8	326.9 ±12.6	239.5 ±19.4	320.9 ±42.3	110.6 ±12.6
Spring	264.3 ±36.9	218.1 ±92.1	145.5 ±23.4	117.8 ±31.9	165.3 ±18.6	143.3 ±11.3
Rainy	478.1 ±23.1	515.5 ±50.1	158.9 ±35.8	148.5 ±11.9	178.9 ±10.0	144.9 ±9.9
Autumn	481.9 ±10.9	266.7 ±32.4	453.1 ±44.1	441.7 ±18.1	162.8 ±13.2	188.7 ±12.1
Mean	**443.1**	**322.5**	**271.1**	**236.9**	**206.9**	**146.9**

± SEM (n=20 for autumn, 30 for spring and winter, 40 for rainy season)

Table 7.2 Depthwise variation in biomass (BM) and necromass (NM) fractions of fine roots (kg ha^{-1}) during different seasons in the 13-year old regrowth.

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
	Root diameter class (<1 mm)					
1993 Winter	3518.8 ±112.1	984.7 ±65.1	1213.1 ±98.9	198.1 ±32.6	647.2 ±43.1	310.8 ±29.3
Spring	3107.3 ±431.2	1222.9 ±231.1	1042.7 ±232.1	192.5 ±32.6	688.5 ±48.3	361.4 ±32.9
Rainy	2366.5 ±545.6	1057.0 ±126.9	792.5 ±69.1	203.7 ±23.8	386.5 ±45.9	354.8 ±12.1
Autumn	2441.5 ±325.1	880.5 ±79.1	1635.9 ±234.5	278.8 ±23.9	613.2 ±43.6	402.5 ±39.5
Mean	**2858.5**	**1036.3**	**1171.1**	**218.3**	**583.9**	**357.4**

Table 7.2 continued

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	2583.3 ±482.7	843.9 ±98.6	762.5 ±48.1	463.1 ±36.1	250.8 ±23.9	313.9 ±43.6
Spring	1754.8 ±325.9	1503.5 ±236.4	498.5 ±79.3	656.3 ±56.1	334.7 ±43.2	470.4 ±32.3
Rainy	1559.6 ±236.5	1330.6 ±146.8	440.8 ±32.6	655.1 ±56.8	194.2 ±32.9	308.4 ±29.1
Autumn	1589.6 ±258.1	1105.3 ±231.3	808.3 ±54.9	571.8 ±65.1	387.1 ±23.6	597.3 ±32.6
Mean	**1871.8**	**1195.8**	**627.5**	**611.6**	**291.7**	**422.5**
	Root diameter class (1-2 mm)					
1993 Winter	2712.6 ±356.4	905.4 ±56.8	723.7 ±32.8	370.5 ±18.9	363.1 ±25.8	349.4 ±15.1
Spring	3505.5 ±881.8	745.7 ±56.9	573.9 ±63.9	182.8 ±23.9	435.3 ±43.4	451.5 ±32.9
Rainy	1236.3 ±154.6	1074.2 ±200.1	413.4 ±43.1	233.1 ±19.2	196.5 ±10.3	316.2 ±18.9
Autumn	1922.8 ±235.9	735.4 ±53.6	793.9 ±33.9	375.8 ±43.6	281.3 ±23.9	359.8 ±41.9
Mean	**2345.1**	**865.2**	**627.5**	**290.6**	**319.1**	**369.2**
1994 Winter	940.4 ±56.9	549.6 ±12.9	425.3 ±23.9	364.9 ±47.7	295.4 ±53.3	170.6 ±16.9
Spring	1223.1 ±120.9	523.6 ±53.1	399.0 ±41.1	170.8 ±23.9	323.6 ±74.1	222.1 ±12.9
Rainy	555.7 ±99.1	959.7 ±12.9	392.0 ±62.6	303.2 ±87.1	175.5 ±12.9	146.2 ±13.6
Autumn	861.2 ±52.6	786.0 ±23.9	628.5 ±41.1	644.6 ±23.9	345.9 ±14.5	325.5 ±29.9
Mean	**895.1**	**704.7**	**461.2**	**370.9**	**285.9**	**216.1**

± SEM (n=20-40)

Table 7.3 Depthwise variation in biomass (BM) and necromass (NM) fractions of fine roots (kg ha^{-1}) during different seasons in the 16-year old regrowth.

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
Root diameter class (<1 mm)						
1993 Winter	3012.9 ±650.1	1247.7 ±120.9	1083.5 ±119.1	629.8 ±12.1	631.6 ±11.9	133.1 ±12.9
Spring	2698.9 ±543.4	622.1 ±32.9	993.5 ±63.9	455.0 ±45.6	895.1 ±32.9	213.7 ±23.9
Rainy	2135.7 ±358.4	657.9 ±98.9	884.3 ±42.8	381.7 ±21.9	491.9 ±18.7	156.4 ±12.0
Autumn	3240.6 ±455.0	951.3 ±96.1	899.0 ±15.9	430.6 ±10.6	692.2 ±12.9	366.8 ±15.9
Mean	**2772.0**	**869.8**	**965.1**	**474.3**	**677.7**	**217.5**
1994 Winter	2250.2 ±155.4	1453.4 ±215.9	766.2 ±45.6	504.8 ±33.6	362.6 ±42.1	369.2 ±12.3
Spring	1587.9 ±234.9	1462.3 ±101.2	573.9 ±53.6	568.9 ±41.1	382.9 ±12.1	434.2 ±10.0
Rainy	928.9 ±54.9	999.0 ±56.9	451.1 ±15.9	527.1 ±12.4	279.6 ±23.3	369.8 ±15.2
Autumn	1614.9 ±101.0	1909.4 ±99.1	597.1 ±12.6	661.1 ±65.1	502.1 ±15.8	782.4 ±51.6
Mean	**1595.5**	**1456.0**	**597.1**	**572.9**	**381.8**	**488.9**
Root diameter class (1-2 mm)						
1993 Winter	2239.7 ±235.6	654.6 ±43.6	1404.3 ±98.1	431.8 ±12.9	396.5 ±29.9	372.6 ±10.1
Spring	1644.1 ±84.6	437.6 ±12.6	1350.2 ±54.8	439.9 ±10.9	664.4 ±12.1	398.2 ±14.3
Rainy	1092.2 ±104.9	359.2 ±23.9	587.2 ±43.7	435.3 ±21.9	284.7 ±18.9	274.4 ±17.7
Autumn	1390.6 ±71.1	537.2 ±18.9	901.1 ±18.4	243.0 ±65.1	563.9 ±45.1	324.2 ±12.1
Mean	**1591.7**	**497.2**	**1060.7**	**412.5**	**477.4**	**342.4**

Table 7.3 continued

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	1319.0 ±104.6	771.6 ±12.9	446.8 ±36.9	193.9 ±17.9	178.9 ±35.6	191.1 ±32.9
Spring	882.4 ±58.8	520.8 ±48.1	469.9 ±15.5	248.2 ±16.6	288.4 ±12.1	215.1 ±12.9
Rainy	595.4 ±36.1	499.4 ±10.1	248.8 ±12.9	235.1 ±16.6	143.8 ±9.4	220.6 ±12.6
Autumn	991.5 ±65.1	944.2 ±35.6	352.8 ±15.9	396.0 ±11.9	299.1 ±12.3	270.9 ±36.9
Mean	**947.1**	**684.0**	**379.6**	**261.7**	**227.6**	**224.4**

± SEM (n=20-40)

Table 7.4 Seasonal variation in biomass to necromass and fine root to coarse root mass ratios in the three forest regrowths.

Year/Season	1993				1994			
	W	S	R	A	W	S	R	A
7 year old regrowth								
FRB/FRN	3.33	2.12	2.09	2.82	2.07	0.99	1.02	1.44
CRB/CRN	1.31	1.41	1.53	2.17	1.89	1.73	1.47	2.72
FRM/CRM	11.09	17.00	8.79	7.16	3.62	6.99	5.99	4.42
13 year old regrowth								
FRB/FRN	2.94	2.96	1.66	2.54	1.94	1.28	0.90	1.12
CRB/CRN	1.78	2.15	1.49	2.28	2.16	1.65	1.20	1.60
FRM/CRM	4.94	3.00	4.70	2.38	1.83	1.56	1.32	1.79
16 year old regrowth								
FRB/FRN	2.65	3.07	2.42	2.69	1.52	1.21	0.93	0.88
CRB/CRN	1.58	3.63	1.98	2.15	2.11	2.12	1.38	1.78
FRM/CRM	7.14	3.19	2.18	3.33	2.72	1.39	1.21	1.76

FRB-Fine root biomass, FRN-Fine root necromass, CRB-Coarse root biomass, CRN-Coarse root necromass, FRM-Fine root mass, CRM-Coarse root mass.

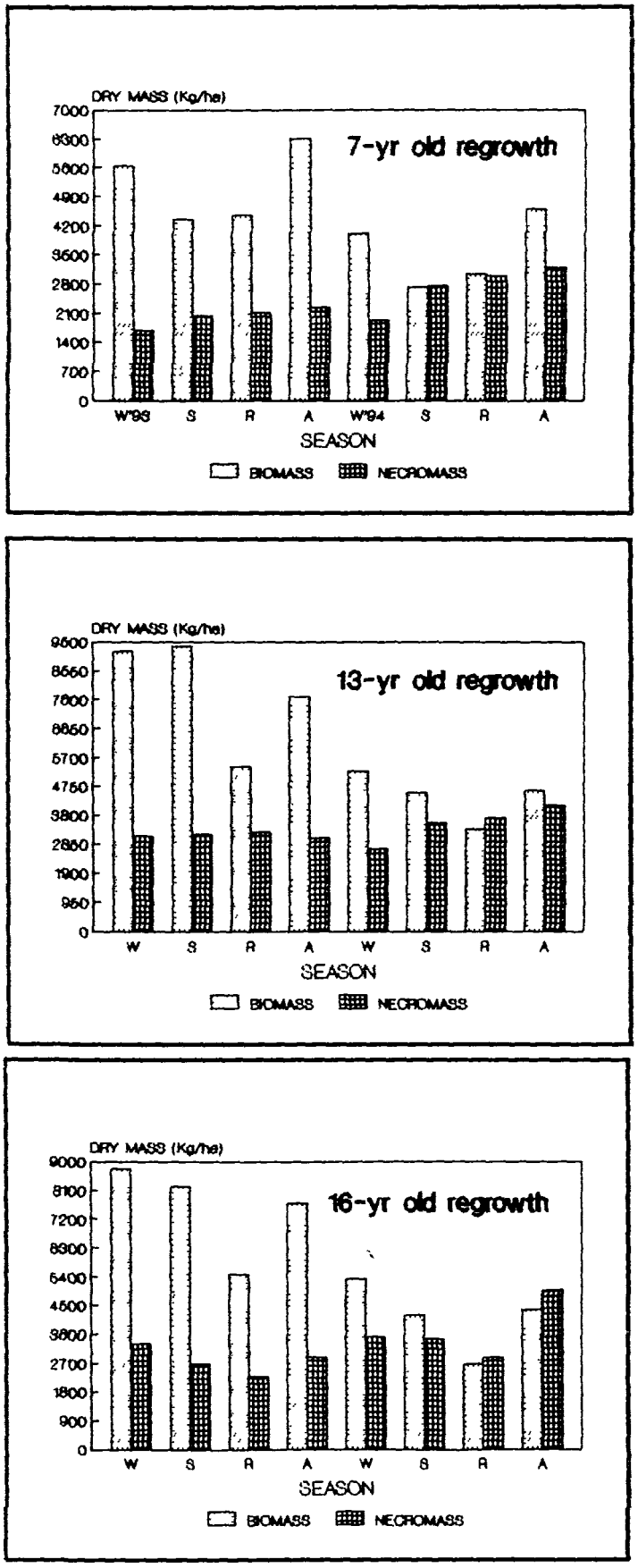


Figure 7.2. Seasonal variation in biomass and necromass of fine roots in the three forest regrowths. W-winter, S-spring, R-rainy, A-autumn.

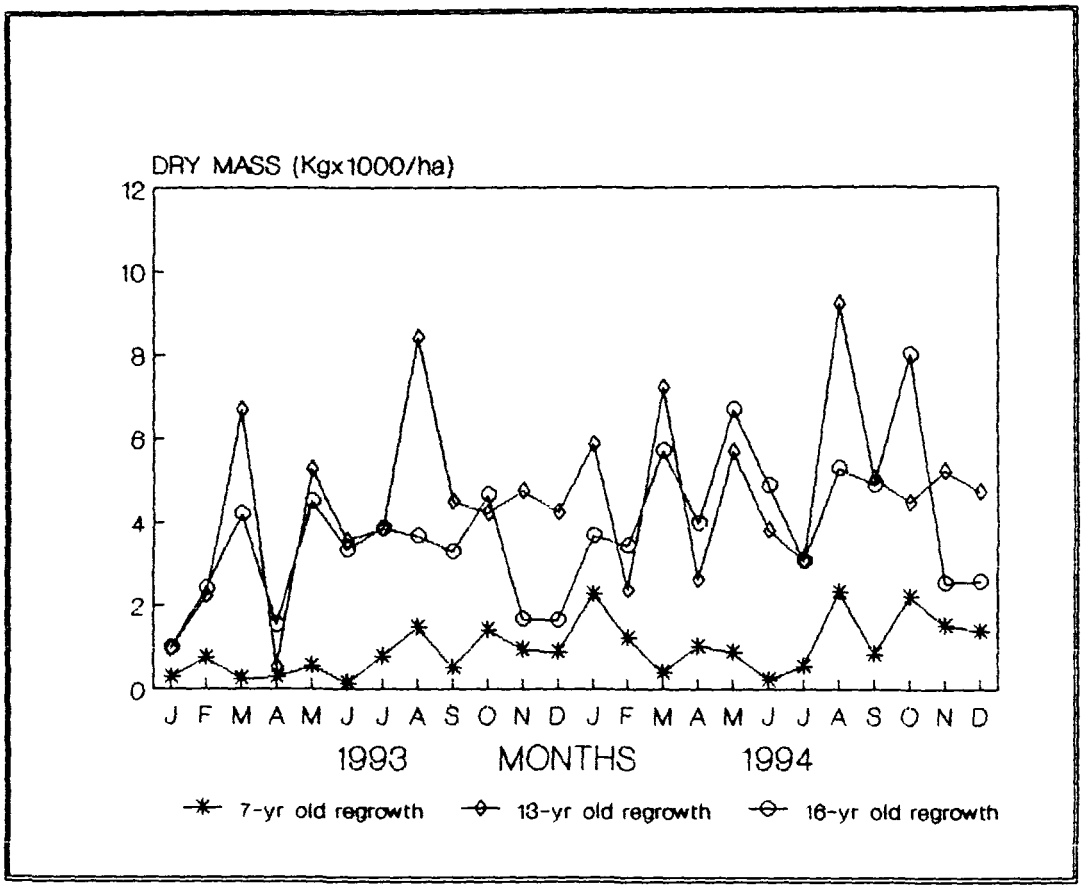


Figure 7.3. Monthly variation in coarse root mass in the three forest regrowths.

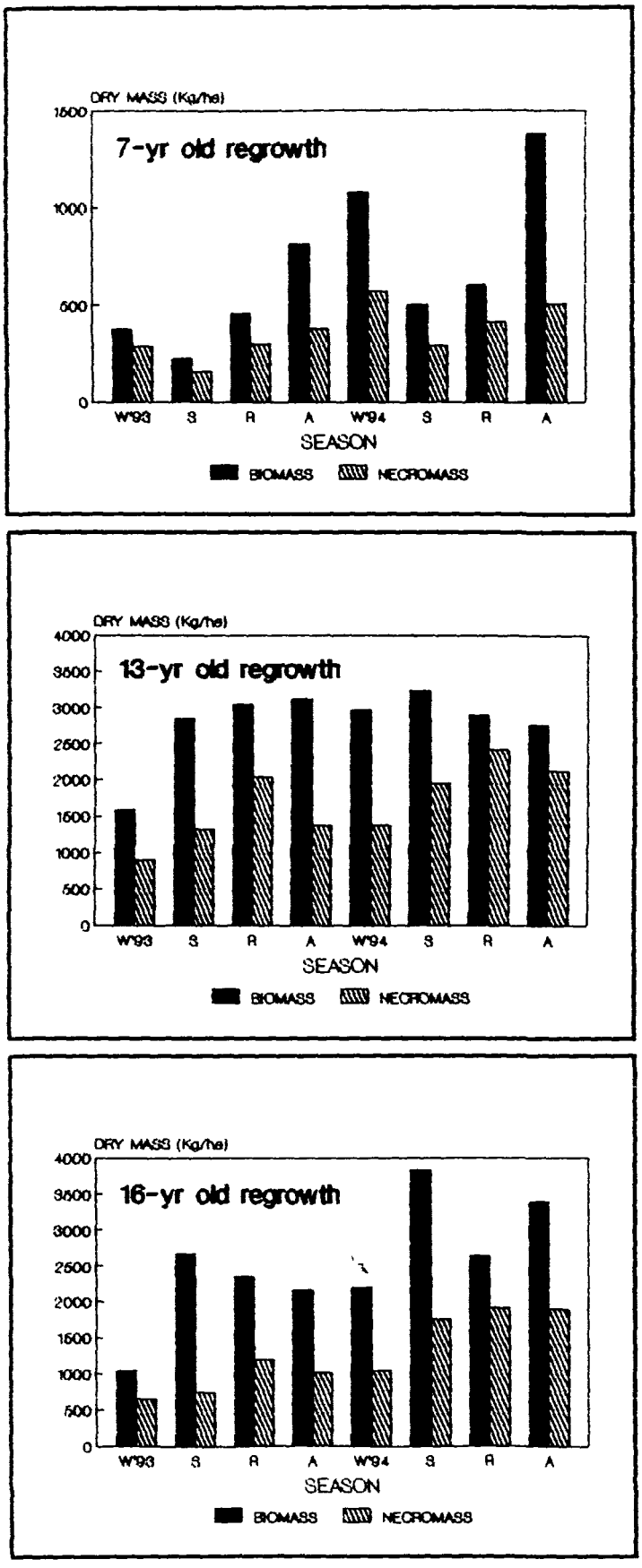


Figure 7.4. Seasonal variation in biomass and necromass of coarse roots in the three forest regrowths. W-winter, S-spring, R-rainy, A-autumn.

showed wide monthly fluctuation in all regrowths without any definite seasonal trend. Nonetheless, the peak values were generally obtained either during autumn or winter seasons and the trough was obtained during rainy season. Monthly and yearly variations were highly significant (Table 7.1). Biomass of very fine roots (<1 mm diameter) peaked during autumn in the 7-year old regrowth and during winter in the 13- and 16-year old regrowths (Figure 7.2). The minimum value was obtained during spring in the 7-year old regrowth and during rainy season in the other two regrowths. Dry weight of 1-2 mm diameter roots was maximum either during winter or spring and minimum during rainy season in all regrowths (Tables 7.1-7.3). Seasonal and standwise variations in FRM was significant in all the three forest regrowths (Table 7.5). FRB was significantly higher ($F=61.79$, $P<0.01$) than the FRN in all regrowths. FRB/FRN ratio was highest (1.5-3.3) during winter and lowest (0.9-2.4) during rainy season (Table 7.4). The mean FRM registered a significant ($P<0.01$) increase from 6751 kg ha^{-1} in the 7-year old regrowth to 9088 and 9499 kg ha^{-1} in the 16- and 13-year old regrowths, respectively (Table 7.16).

Coarse roots: Monthly and seasonal variation in coarse root biomass (CRB) and necromass (CRN) in the three forest regrowths are given in Figures 7.3 and 7.4 respectively. Total coarse root mass (CRM) varied significantly ($P<0.01$) between months, years and stands (Table 7.5). In the 7-year old regrowth, the CRM was maximum during autumn (1192-1887 kg ha^{-1}) and minimum during spring (376-786 kg ha^{-1}), whereas in 13- and 16-year old regrowths it peaked during spring and rainy seasons and showed lower value during winter (Figure 7.4).

In general, all three stands had higher CRB during October-January, and lower value during March-April. The amount of CRB was significantly higher ($F=8.84$, $P<0.01$) than the CRN in all three regrowths. Standwise difference in CRB/CRN ratio was insignificant. Generally, the ratio was

Table 7.5 Three-way ANOVA showing effects of temporal and spatial variations on fine and coarse root mass (kg ha^{-1}) in the three forest regrowths.

Interactions	df	MSS	F	P
		Fine root mass (FRM)		
Month	11	7125440.0	23.42	0.01
Season	3	1756629.0	8.56	0.05
Year	1	9949216.0	11.73	0.01
Soil depth	2	22507730.0	6.26	0.01
Regrowths	2	28856510.0	140.53	0.01
Regrowths x Year	2	8694336.0	42.34	0.01
Regrowths x Seasons	7	1754528.0	8.54	0.01
Regrowths x Months	23	694487.3	2.28	0.05
Regrowths x Soil depths	2	739123.0	7.25	0.01
		Coarse root mass (CRM)		
Month	11	24.0	2.74	0.05
Season	3	872777.1	11.16	0.01
Year	1	3298808.0	16.16	0.01
Regrowths	2	13368190.0	65.47	0.01
Regrowths x Year	2	325688.0	1.60	0.00
Regrowths x Seasons	7	229373.7	2.93	0.05
Regrowths x Months	23	732761.5	3.04	0.01

BM-Biomass, NM-Necromass.

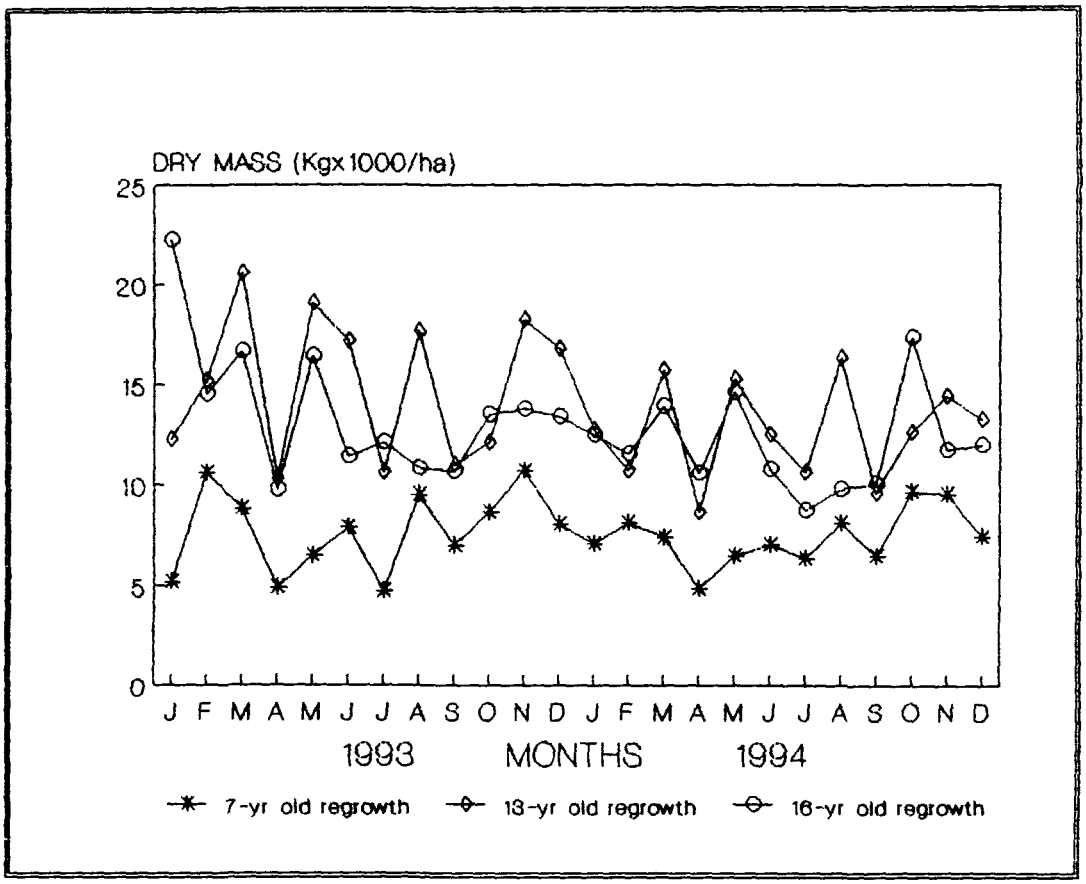


Figure 7.5. Monthly variation in total root mass (TRM) in (A) 7-year, (B) 13-year and (C) 16-year old regrowths.

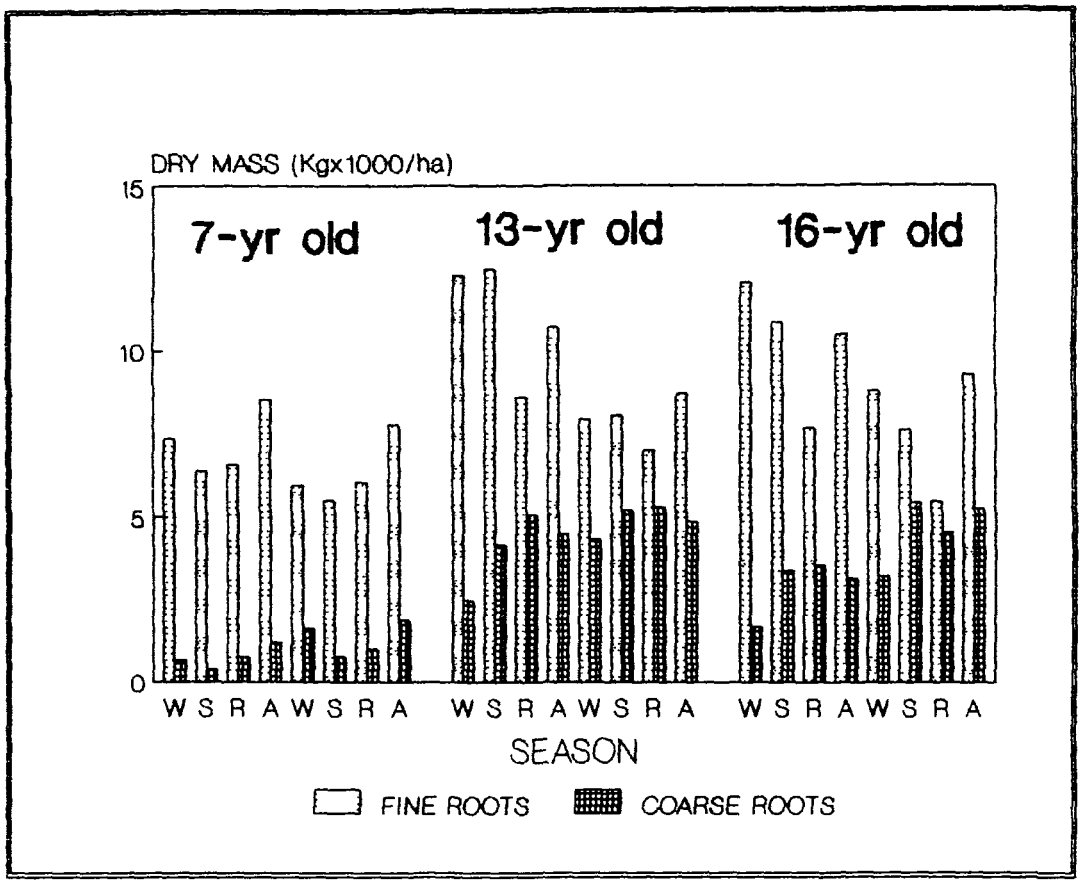


Figure 7.6. Seasonal variation in fine and coarse root mass in forest regrowths of three different ages. W-winter, S-spring, R-rainy, A-autumn.

lower during rainy season and higher during post-rainy months in all three regrowths. The mean annual CRM during 1993 was significantly lower (18.44%) than 1994 (Table 7.16). In both the years, 13-year old regrowth showed greater accumulation of dry matter in CRM (4059-4931 kg ha^{-1}) than 7- and 16-year old regrowths. The CRM was minimum (744-1332 kg ha^{-1}) in the 7-year old regrowth.

Total roots: Monthly and seasonal variations in total root mass (TRM) were similar to FRM (Figure 7.5). The TRM varied significantly between stands, years and diameter classes (Table 7.5). None of the three stands showed seasonal trend in TRM during the course of investigation (Figure 7.6). In the 7-year old regrowth, fine roots represented about 87% of the total roots, while, in 13- and 16-year old regrowths their proportion declined to about 70%. Consequently, FRM/CRM ratio was 3-times higher in the 7-year old regrowth compared to the older regrowths. In all regrowths, the ratio was generally higher during winter (1.83-11.09) and lower during rainy season (1.21-8.79) (Table 7.4).

The mean annual standing crop of the roots in all three stands was 4- to 15-times greater during 1993 than 1994. The variation in TRM between 7- and 13-year old regrowths was significant ($F=58.51$, $P<0.01$), but the difference between the 13- and 16-year old regrowths was insignificant.

VERTICAL DISTRIBUTION OF FINE ROOT MASS

Major portion (upto 65%) of fine roots was present in the surface soil layer (0-10 cm) in all three regrowths. The subsurface layer (10-20 cm) had only about 19% of the total fine root mass. Further down in the 20-30 cm soil layer the value was 15% only (Figure 7.7). The decrease in FRB with increasing depth was significant ($F=35.20$, $P<0.05$) in all three regrowths. Accumulation of fine roots in the surface soil layer increased significantly ($P<0.05$) from 7- to 13-year old regrowths, beyond this age the difference was not significant. The proportion of fine roots to the

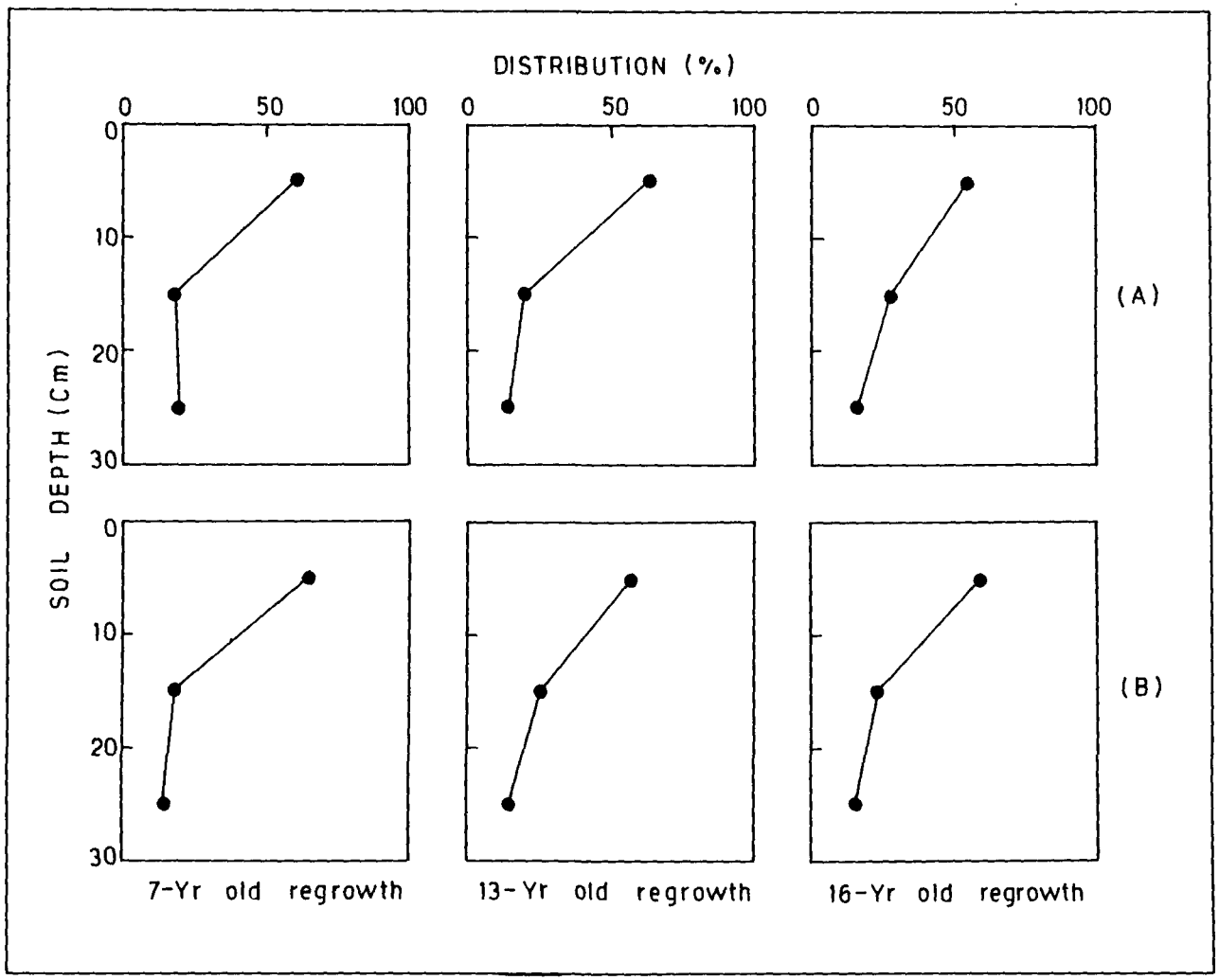


Figure 7.7. Vertical distribution of fine roots in mineral soil (0-30 cm depth) in three forest regrowths during (A) 1993 and (B) 1994.

Table 7.6 Seasonal and annual production (kg ha-1 day-1) of fine roots of different diameter classes in three forest regrowths.

Year/season	Soil Depth (cm)			
	0-10	10-20	20-30	0-30
(7-YEAR OLD REGROWTH)				
	<1 mm diameter class			
1993 Winter	21.52	4.99	6.97	33.48
Spring	23.81	6.57	1.88	32.26
Rainy	12.99	4.52	4.94	22.45
Autumn	17.08	4.52	0.86	22.46
Mean	**18.85**	**5.15**	**3.66**	**27.66**
1994 Winter	22.48	3.23	2.35	28.06
Spring	22.28	4.86	2.45	29.59
Rainy	13.02	3.08	4.44	20.54
Autumn	15.76	2.58	1.34	19.68
Mean	**18.39**	**3.44**	**2.65**	**24.47**
	1-2 mm diameter class			
1993 Winter	23.99	1.30	12.93	38.22
Spring	20.76	4.96	0.33	26.05
Rainy	22.20	5.02	16.61	43.83
Autumn	7.93	8.96	14.02	30.91
Mean	**18.72**	**5.06**	**10.97**	**34.75**
1994 Winter	8.96	0.97	4.16	14.09
Spring	9.71	2.14	0.68	12.54
Rainy	8.02	9.33	6.56	23.90
Autumn	2.67	0.06	2.81	5.54
Mean	**7.34**	**3.13**	**3.55**	**14.02**
(13-YEAR OLD REGROWTH)				
	<1 mm diameter class			
1993 Winter	20.71	3.85	9.49	34.05
Spring	28.27	5.06	6.01	39.34
Rainy	11.38	12.04	1.87	25.29
Autumn	22.11	9.23	17.47	48.81
Mean	**20.62**	**7.55**	**8.71**	**36.87**
1994 Winter	9.16	5.88	8.72	23.76
Spring	28.90	6.26	1.04	36.20
Rainy	26.15	9.72	4.11	39.98
Autumn	11.67	10.21	3.17	25.05
Mean	**18.97**	**8.02**	**4.26**	**31.25**

Table 7.6 continued

Year/season	Soil Depth (cm)			
	0-10	10-20	20-30	0-30
	1-2 mm diameter class			
1993 Winter	37.29	2.11	3.47	42.87
Spring	34.75	6.74	4.21	45.70
Rainy	11.69	10.07	0.90	22.66
Autumn	39.53	10.69	6.09	59.31
Mean	**30.82**	**7.40**	**3.67**	**42.64**
1994 Winter	18.16	0.46	2.32	20.94
Spring	22.63	4.56	2.04	29.23
Rainy	5.16	12.39	3.84	21.39
Autumn	6.36	2.10	0.33	8.79
Mean	**13.08**	**4.88**	**2.13**	**20.09**
(16-YEAR OLD REGROWTH)				
	<1 mm diameter class			
1993 Winter	19.56	4.89	8.33	32.78
Spring	6.14	5.53	3.47	15.14
Rainy	35.82	2.91	4.14	42.87
Autumn	19.55	7.78	2.81	30.14
Mean	**20.27**	**5.28**	**4.69**	**30.23**
1994 Winter	6.41	5.73	4.91	17.05
Spring	14.71	4.39	8.61	27.71
Rainy	17.12	4.92	6.86	28.89
Autumn	15.82	2.22	1.27	19.31
Mean	**13.52**	**4.31**	**5.41**	**23.24**
	1-2 mm diameter class			
1993 Winter	10.39	2.07	8.25	20.71
Spring	4.69	22.71	8.01	35.41
Rainy	5.14	8.44	10.69	24.27
Autumn	21.64	28.92	4.89	55.45
Mean	**10.47**	**15.54**	**7.96**	**33.96**
1994 Winter	4.78	1.58	4.48	10.84
Spring	5.99	9.43	5.46	20.88
Rainy	11.08	6.93	5.55	23.56
Autumn	5.59	6.95	0.21	12.75
Mean	**6.86**	**6.22**	**3.93**	**17.01**

total root mass in this layer declined from 63% in the 7-year old to 57% in the 16-year old regrowth.

ROOT PRODUCTION

Seasonal and depthwise productivity data of very fine roots (<1 mm diameter) is given in Table 7.6. The production declined significantly ($F=6.0-37.6$, $P<0.01$) during autumn compared to the preceding rainy season in all three regrowths. Production data for 1993 and 1994 was significantly ($P<0.05$) different in 13- and 16-year old regrowths; the variation was insignificant in the 7-year old regrowth. Generally, the productivity declined with increase in the soil depth.

The next larger diameter class (1-2 mm) roots showed maximum production rate during the rainy season and minimum during autumn in the 7-year old regrowth (Table 7.6). In other regrowths, the seasonal trend was not clear. Three-way ANOVA revealed significant ($P<0.01$) difference in fine root production between seasons, years and stands.

Production of coarse roots was maximum during rainy season and minimum during autumn in the 7-year old regrowth while in other two stands peak was observed during winter but minimum ramained in autumn (Figure 7.8). This trend was also reflected in the total root production data which varied significantly ($P<0.05$) due to seasons, years and stands. The ratio between fine and coarse root production was high in the 7-year old regrowth (2.0) than in 13- and 16-year old regrowths (1.3 and 1.5).

The production of fine roots decreased significantly ($F=18.55$, $P<0.01$) with the increase in soil depth (Figure 7.9). In the surface soil layer fine root production increased from 11588 kg ha-1 yr^{-1} in the 7-year old regrowth to 13432 kg ha^{-1} yr^{-1} in the 13-year old regrowth and then it declined to 9299 kg ha^{-1} yr^{-1} in the 16-year old regrowth. Similarly, the total root production increased significantly ($F=39.04$, $P<0.01$) from 23029 kg ha^{-1} yr^{-1} in the 7-year old regrowth to 39060 in 13-year old regrowth

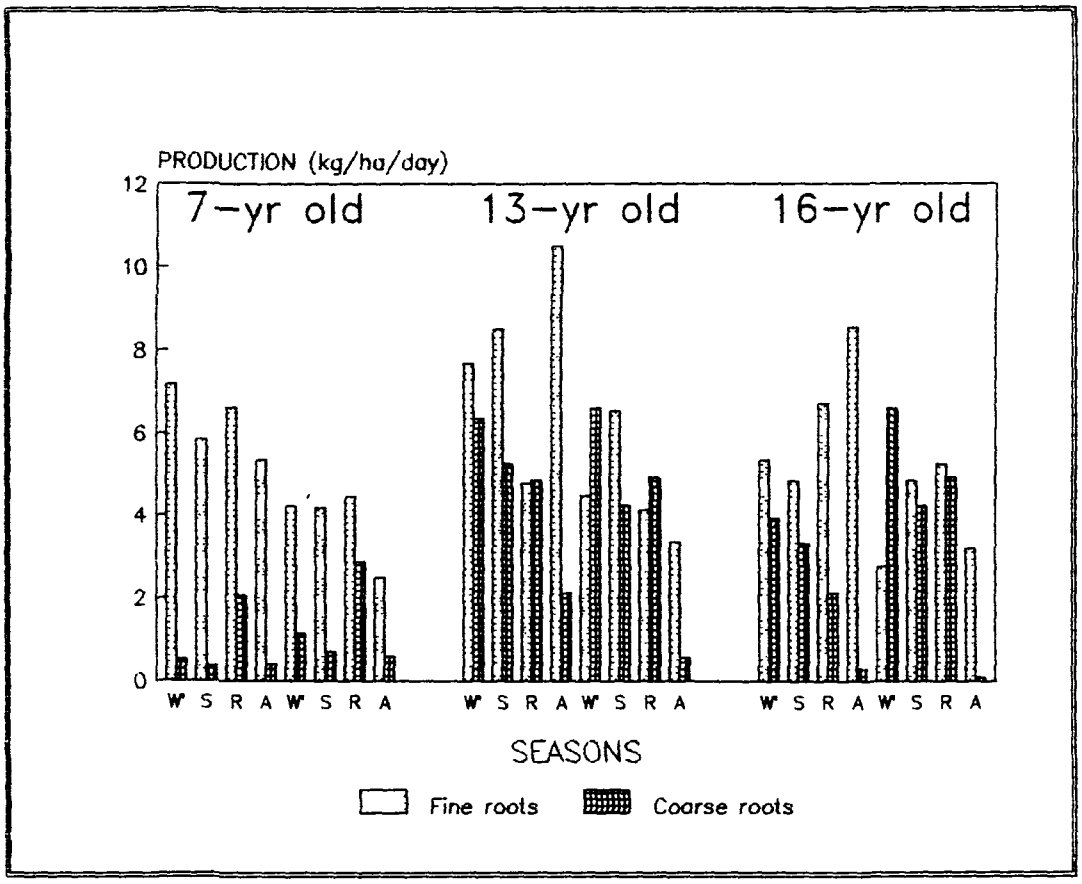


Figure 7.8. Daily production of fine and coarse roots during different seasons (W-winter, S-spring, R-rainy, A-autumn) in forest regrowths of three different ages.

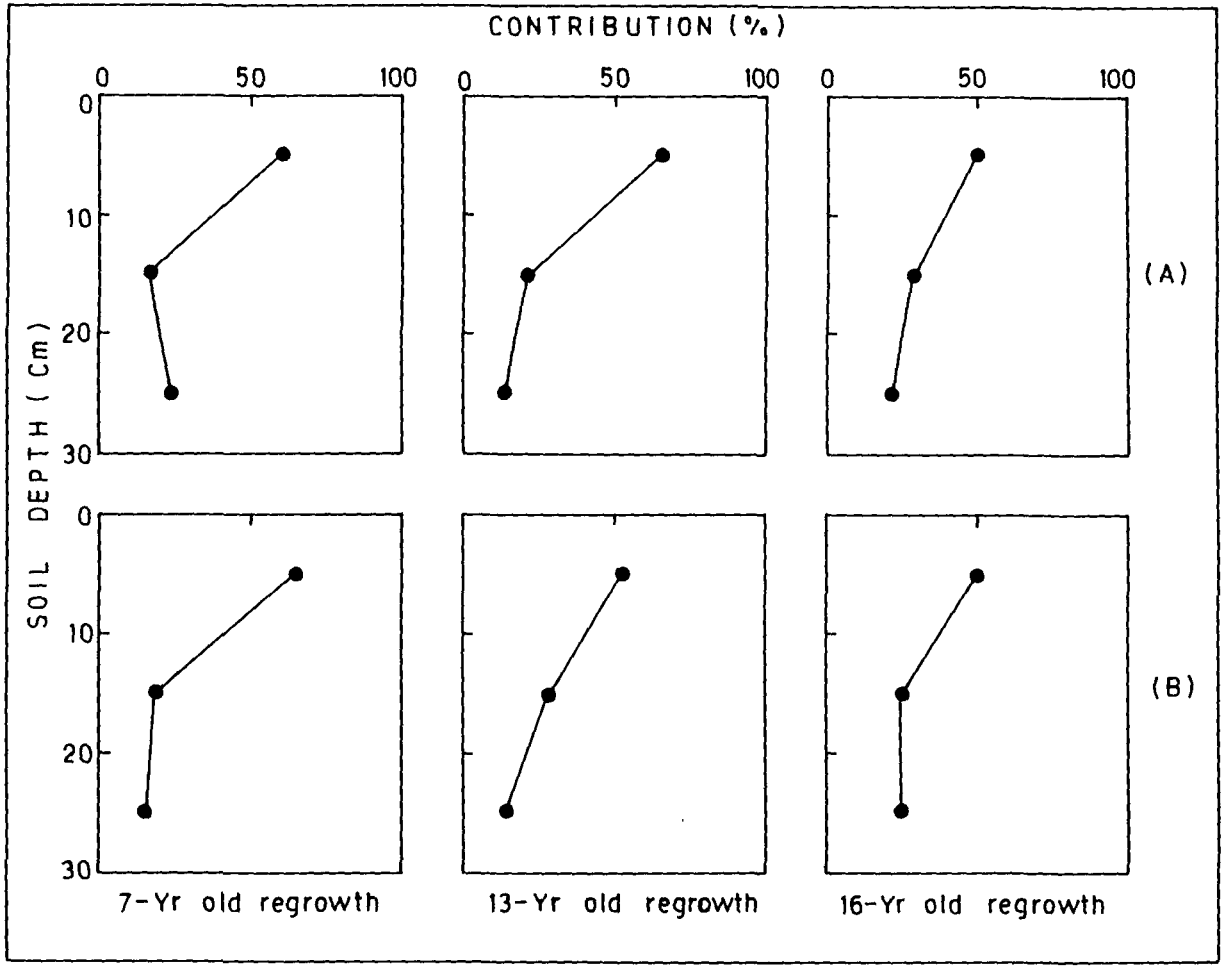


Figure 7.9. Contribution of fine roots to total fine root production in three forest regrowths during (A) 1993 and (B) 1994.

Table 7.7 Correlation coefficients (r) showing relationships of mean seasonal fine root mass (kg ha^{-1}) and production (kg ha^{-1} day^{-1}) with climatic (n=8), soil (0-30 cm depth) (n=8) and vegetation (n=6) characteristics.

Variable	Fine root mass	Fine root production
Climatic variables		
Rainfall (mm)	0.662^{ns}	$0.761^{0.05}$
Maximum temperature (°C)	0.662^{ns}	$0.761^{0.05}$
Minimum temperature (°C)	0.420^{ns}	$0.761^{0.05}$
Soil characteristics		
pH	$-0.960^{0.001}$	$-0.988^{0.001}$
Organic matter (%)	$0.915^{0.002}$	$0.995^{0.001}$
Total N (%)	$0.972^{0.001}$	$0.932^{0.001}$
Available-P (µg g^{-1})	$0.952^{0.001}$	$0.928^{0.001}$
Vegetation characteristics		
Total no. of woody species	$0.904^{0.05}$	$0.953^{0.005}$
Density of woody species (Plants ha^{-1})	$0.998^{0.001}$	$0.997^{0.001}$
Basal area of woody species (m^2 ha^{-1})	$0.943^{0.005}$	$0.891^{0.05}$

Note: (1) Values as superfixes indicate significance levels, ns-not significant.

(2) Mean daily rainfall, mean monthly maximum and minimum air temperatures were used for regression analysis.

and then declined to 30886 kg ha-1 yr-1 in the 16-year old regrowth, the difference between latter two stands being insignificant. The contribution of fine roots to total root production was 88, 65 and 50% in 7-, 13- and 16- year old regrowths, respectively.

INFLUENCE OF CLIMATE, SOIL AND VEGETATION ON PRODUCTION AND ACCUMULATION OF FINE ROOTS

Fine root production was positively correlated with mean seasonal rainfall and mean monthly maximum and minimum temperatures. Soil organic matter, total-N and available-P strongly favoured production and accumulation of the fine roots. Fine root production and accumulation were also positively correlated with the total number of woody species, their density, and basal area (Table 7.7).

N AND P CONCENTRATIONS IN FINE AND COARSE ROOTS

N concentration: In all three regrowths, N concentration was minimum during spring. It increased during winter in 13- and 16-year old regrowths, except in the 7-year old regrowth, where the concentration was more during the rainy season (Table 7.8). Two-way ANOVA revealed significant ($P<0.01$) difference in N concentration due to season and year, except in the 16-year old regrowth where seasonal difference was insignificant. Biomass had significantly ($F=109.92, P<0.01$) higher N concentration than the necromass. Similarly, very fine roots (<1 mm in diameter) had significantly higher ($F=35.81$, $P<0.01$) N concentration than the fine roots (1-2 mm diameter). Standwise variation was not significant.

Seasonal trend in N concentration of coarse roots was not observed during two years of the study (Table 7.8). One-way ANOVA, however, revealed significant difference between biomass and necromass fractions ($F=30.26, P<0.01$). Yearwise variation was also significant ($F=13.29$, $P<0.01$).

P concentration: Biomass and necromass fractions of the fine roots did not

Table 7.8 Seasonal variation in N concentration (%) in fine and coarse roots in the 7-, 13- and 16-year old regrowths.

Year/Seasons	Fine roots				Coarse roots	
	< 1 mm		1-2 mm		2-15 mm	
	BM	NM	BM	NM	BM	NM
			(7-YEAR OLD REGROWTH)			
1993 Winter	0.92 ±0.01	0.71 ±0.01	0.66 ±0.02	0.71 ±0.08	0.56 ±0.03	0.51 ±0.03
Spring	1.02 ±0.09	0.59 ±0.01	0.55 ±0.01	0.63 ±0.03	0.48 ±0.03	1.07 ±0.03
Rainy	1.09 ±0.01	0.58 ±0.01	0.73 ±0.03	0.66 ±0.03	0.57 ±0.05	0.68 ±0.01
Autumn	1.06 ±0.03	0.60 ±0.09	0.71 ±0.03	0.56 ±0.07	0.31 ±0.01	0.38 ±0.01
1994 Winter	1.21 ±0.09	0.81 ±0.03	0.76 ±0.03	0.69 ±0.01	0.57 ±0.01	0.53 ±0.02
Spring	1.06 ±0.03	0.71 ±0.05	0.61 ±0.03	0.52 ±0.02	0.60 ±0.01	0.49 ±0.01
Rainy	1.45 ±0.09	0.90 ±0.03	0.79 ±0.01	0.63 ±0.01	0.61 ±0.03	0.65 ±0.03
Autumn	1.39 ±0.09	1.02 ±0.09	0.90 ±0.01	0.77 ±0.01	0.60 ±0.03	0.64 ±0.02
			(13-YEAR OLD REGROWTH)			
1993 Winter	1.10 ±0.01	0.77 ±0.01	0.79 ±0.02	0.52 ±0.01	0.57 ±0.09	0.62 ±0.01
Spring	1.03 ±0.01	0.75 ±0.01	0.57 ±0.03	0.56 ±0.04	0.43 ±0.01	0.45 ±0.01
Rainy	1.10 ±0.03	0.80 ±0.09	0.65 ±0.09	0.54 ±0.01	0.58 ±0.01	0.69 ±0.01
Autumn	1.08 ±0.09	0.73 ±0.01	0.65 ±0.03	0.54 ±0.04	0.30 ±0.02	0.34 ±0.01
1994 Winter	1.51 ±0.09	1.09 ±0.03	1.00 ±0.03	0.92 ±0.01	0.71 ±0.01	0.67 ±0.01
Spring	1.02 ±0.09	0.91 ±0.03	0.82 ±0.01	0.80 ±0.02	0.60 ±0.01	0.57 ±0.01

Table 7.8 continued

Year/Seasons	Fine roots				Coarse roots	
	< 1 mm		1-2 mm		2-15 mm	
	BM	NM	BM	NM	BM	NM
Rainy	1.04 ±0.01	1.00 ±0.01	0.91 ±0.03	0.89 ±0.03	0.61 ±0.03	0.54 ±0.01
Autumn	1.23 ±0.01	1.01 ±0.09	0.97 ±0.01	0.90 ±0.04	0.67 ±0.01	0.60 ±0.03
	(16-YEAR OLD REGROWTH)					
1993 Winter	1.07 ±0.01	0.87 ±0.01	0.67 ±0.03	0.58 ±0.03	0.43 ±0.03	0.82 ±0.01
Spring	1.11 ±0.03	0.72 ±0.09	0.56 ±0.01	0.49 ±0.01	0.36 ±0.03	0.43 ±0.02
Rainy	1.16 ±0.01	0.76 ±0.09	0.59 ±0.03	0.48 ±0.01	0.47 ±0.01	0.46 ±0.04
Autumn	1.03 ±0.03	0.79 ±0.01	0.49 ±0.01	0.46 ±0.03	0.34 ±0.05	0.43 ±0.05
1994 Winter	1.50 ±0.09	1.00 ±0.01	1.01 ±0.01	0.92 ±0.03	0.80 ±0.07	0.71 ±0.01
Spring	1.07 ±0.01	1.00 ±0.03	0.82 ±0.01	0.89 ±0.03	0.68 ±0.03	0.67 ±0.04
Rainy	1.10 ±0.06	0.90 ±0.03	1.00 ±0.03	0.90 ±0.01	0.72 ±0.03	0.67 ±0.01
Autumn	1.24 ±0.03	0.93 ±0.05	1.00 ±0.09	1.00 ±0.03	0.76 ±0.03	0.69 ±0.02

± SEM (n=3)

Table 7.9 Seasonal variation in P concentration (%) in fine and coarse roots in 7-, 13- and 16-year old regrowths.

Year/Seasons	Fine roots				Coarse roots	
	< 1 mm		1-2 mm		2-15 mm	
	BM	NM	BM	NM	BM	NM
	(7-YEAR OLD REGROWTH)					
1993 Winter	0.084 ±0.001	0.038 ±0.001	0.049 ±0.002	0.051 ±0.001	0.044 ±0.004	0.075 ±0.009
Spring	0.079 ±0.001	0.056 ±0.001	0.047 ±0.001	0.054 ±0.010	0.075 ±0.001	0.100 ±0.009
Rainy	0.080 ±0.010	0.060 ±0.009	0.050 ±0.001	0.060 ±0.003	0.075 ±0.010	0.065 ±0.008
Autumn	0.060 ±0.003	0.060 ±0.003	0.042 ±0.004	0.042 ±0.003	0.037 ±0.008	0.053 ±0.001
1994 Winter	0.082 ±0.003	0.043 ±0.009	0.043 ±0.001	0.051 ±0.001	0.042 ±0.003	0.039 ±0.001
Spring	0.077 ±0.001	0.056 ±0.001	0.043 ±0.010	0.041 ±0.009	0.052 ±0.010	0.039 ±0.008
Rainy	0.084 ±0.011	0.066 ±0.001	0.047 ±0.003	0.055 ±0.005	0.057 ±0.012	0.041 ±0.009
Autumn	0.088 ±0.012	0.059 ±0.010	0.051 ±0.009	0.051 ±0.007	0.052 ±0.001	0.043 ±0.003
	(13-YEAR OLD REGROWTH)					
1993 Winter	0.072 ±0.003	0.045 ±0.009	0.053 ±0.009	0.043 ±0.006	0.048 ±0.001	0.041 ±0.001
Spring	0.068 ±0.001	0.045 ±0.002	0.046 ±0.003	0.054 ±0.002	0.048 ±0.003	0.052 ±0.003
Rainy	0.070 ±0.003	0.046 ±0.001	0.050 ±0.013	0.050 ±0.009	0.056 ±0.007	0.046 ±0.001
Autumn	0.060 ±0.003	0.050 ±0.009	0.040 ±0.009	0.040 ±0.006	0.056 ±0.005	0.037 ±0.009
1994 Winter	0.090 ±0.009	0.054 ±0.005	0.055 ±0.005	0.049 ±0.003	0.046 ±0.001	0.045 ±0.001
Spring	0.080 ±0.001	0.051 ±0.003	0.050 ±0.003	0.043 ±0.006	0.043 ±0.005	0.037 ±0.001

Table 7.9 continued

Year/Seasons	Fine roots				Coarse roots	
	< 1 mm		1-2 mm		2-15 mm	
	BM	NM	BM	NM	BM	NM
Rainy	0.083 ±0.003	0.064 ±0.001	0.050 ±0.003	0.047 ±0.003	0.045 ±0.009	0.041 ±0.001
Autumn	0.084 ±0.003	0.050 ±0.009	0.051 ±0.009	0.042 ±0.003	0.045 ±0.001	0.042 ±0.003
(16-YEAR OLD REGROWTH)						
1993 Winter	0.088 ±0.009	0.060 ±0.001	0.046 ±0.004	0.056 ±0.002	0.061 ±0.001	0.075 ±0.001
Spring	0.088 ±0.009	0.066 ±0.006	0.045 ±0.001	0.041 ±0.001	0.050 ±0.001	0.056 ±0.003
Rainy	0.090 ±0.010	0.070 ±0.010	0.050 ±0.009	0.040 ±0.001	0.063 ±0.003	0.059 ±0.002
Autumn	0.070 ±0.003	0.050 ±0.007	0.040 ±0.001	0.040 ±0.003	0.032 ±0.006	0.043 ±0.009
1994 Winter	0.093 ±0.003	0.061 ±0.009	0.050 ±0.003	0.046 ±0.002	0.050 ±0.006	0.049 ±0.007
Spring	0.084 ±0.001	0.050 ±0.005	0.040 ±0.006	0.040 ±0.005	0.047 ±0.006	0.041 ±0.006
Rainy	0.088 ±0.003	0.066 ±0.001	0.041 ±0.001	0.040 ±0.006	0.047 ±0.005	0.041 ±0.003
Autumn	0.088 ±0.003	0.060 ±0.010	0.045 ±0.003	0.042 ±0.002	0.048 ±0.003	0.048 ±0.001

± SEM (n=3)

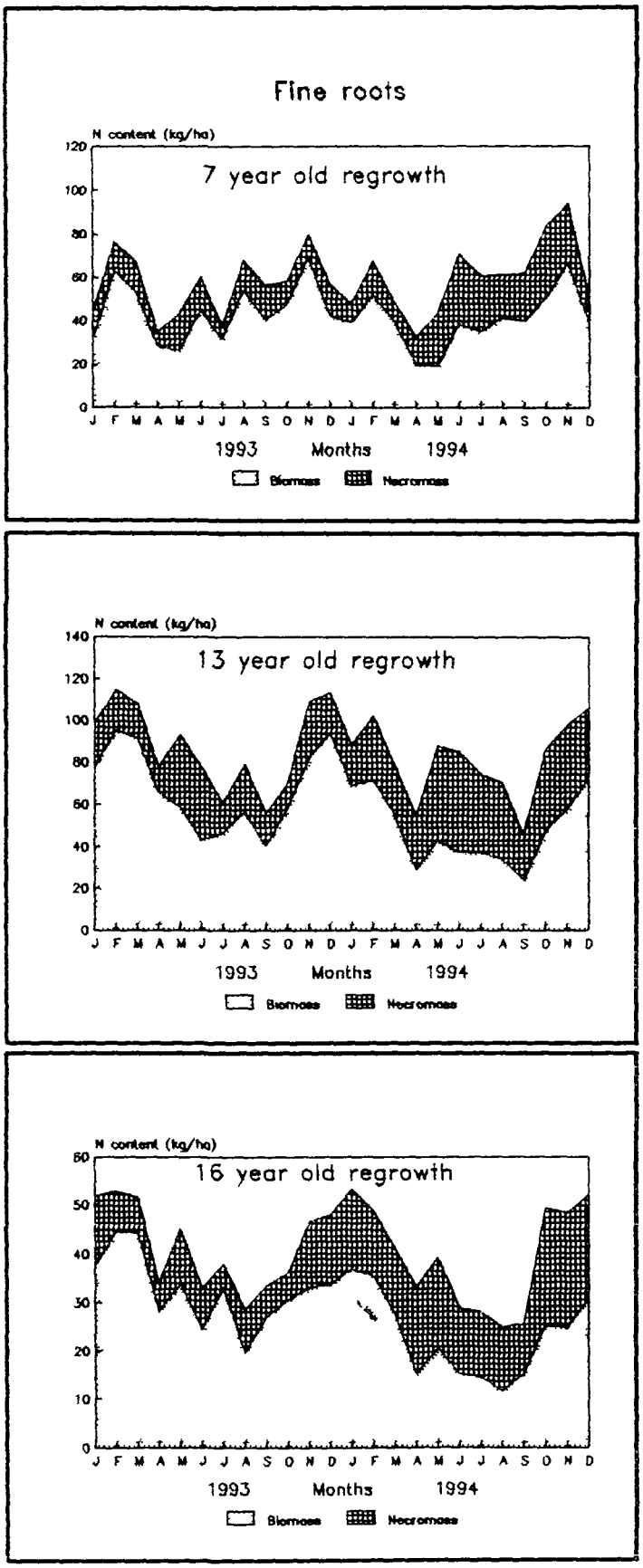


Figure 7.10. N accumulation pattern in biomass and necromass fractions of fine roots in soil (0-30 cm depth) in the three forest regrowths.

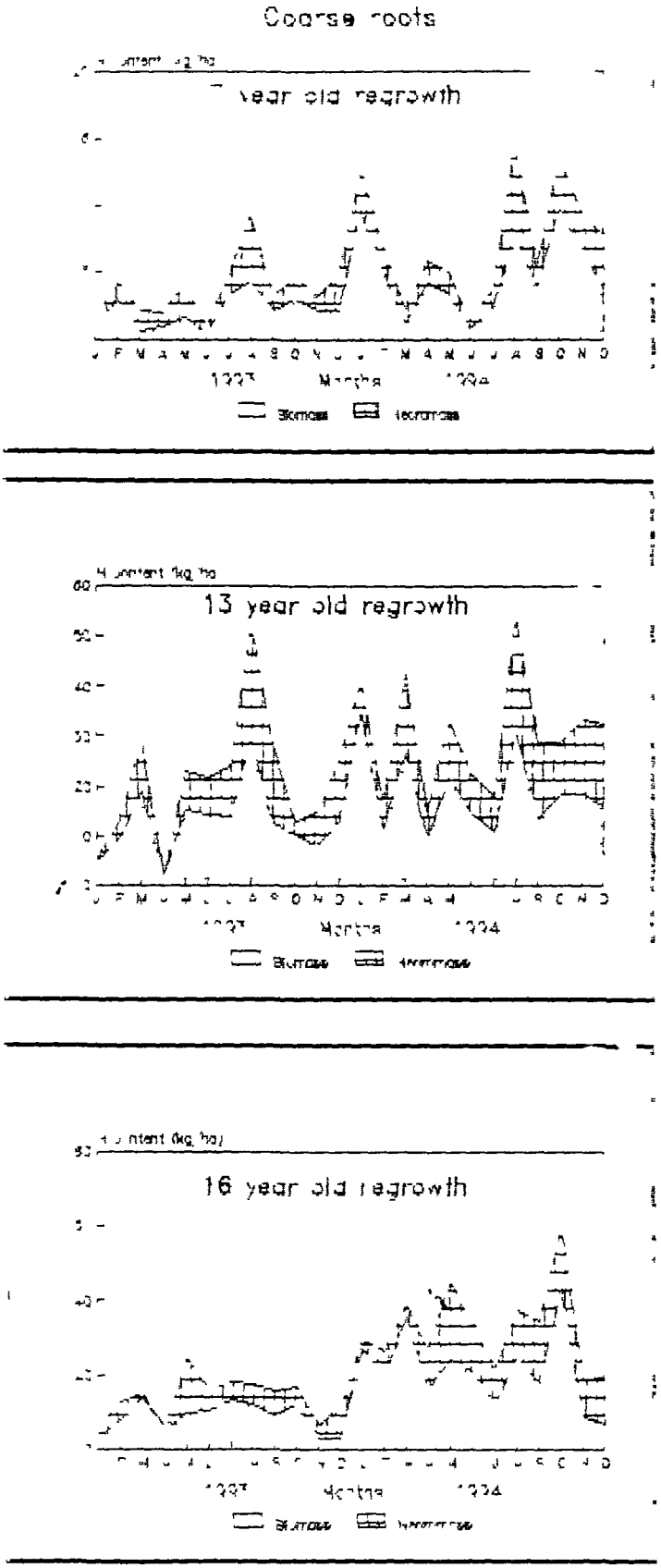


Figure 7.11. Standing state of N in coarse root biomass and necromass in soil (0-30 cm depth) in the three forest regrowths.

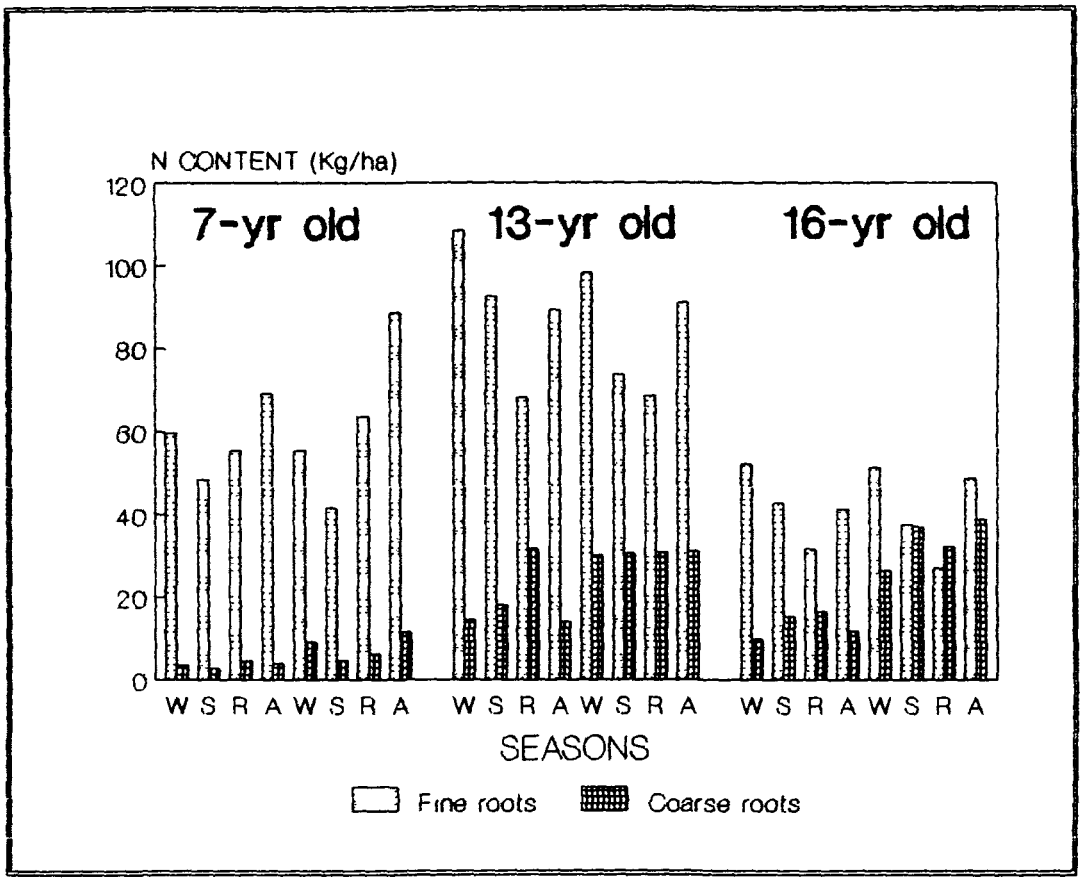


Figure 7.12. Seasonal variation in N accumulation in fine and coarse roots in forest regrowths of three different ages. W-winter, S-spring, R-rainy, A-autumn.

show marked seasonality in P concentration (Table 7.9), however the former had significantly ($P<0.05$) higher concentration than the latter. In all regrowths, very fine roots had significantly higher ($F=66.32$, $P<0.01$) concentration than the fine roots (1-2 mm diameter). Yearwise and standwise variations in P concentration of fine roots was insignificant. P concentration in coarse roots varied significantly ($P<0.01$) between years ($F=13.88$), stands ($F=32.70$) and biomass/necromass fractions ($F=71.84$). Generally, P concentration was maximum during rainy season and minimum either during autumn or spring (Table 7.9).

N AND P ACCUMULATION IN FINE AND COARSE ROOTS

N Stock: Figure 7.10 presents the monthly variation in N content of fine roots in three regrowths. Though there was no clear seasonal trend, the values were generally higher during autumn in the 7-year old regrowth and during winter in 13- and 16-year old regrowths. Spring recorded minimum value in the 7-year old regrowth while in other stands minima was observed during rainy season (Figure 7.12). During this season FRN accumulated upto 50% of the total N in the fine roots. In the surface soil layer (0-10 cm) fine roots had significantly ($P<0.01$) greater N content than the subsurface layers in all regrowths. Monthly ($F=6.15$) and standwise ($F=13.88$) variations in N accumulation in fine roots were also significant ($P<0.01$). N accumulation in fine roots averaged 59, 83 and 79 kg ha^{-1} in 7-, 13-and 16-year old regrowths, respectively. Generally, very fine roots accumulated more N than the next larger diameter class roots (Tables 7.10-7.12).

N accumulation in coarse roots showed wide monthly variation (Figure 7.11). Seasonal pattern of N accumulation in the coarse roots was not distinct as fine roots (Figure 7.12). The CRB shared 50-90% of the total N accumulation in the coarse roots. The contribution of coarse roots to total N stock in roots increased from 10% in the 7-year old regrowth to 40% in the older regrowths. N accumulation in root mass was much higher in the

Table 7.10 Seasonal variation in N accumulation (kg ha-1) in fine roots in the 7-year old regrowth.

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
	(<1 mm root diameter)					
1993 Winter	19.91 ±1.21	5.07 ±0.90	5.49 ±0.12	1.89 ±0.01	4.28 ±0.11	0.70 ±0.09
Spring	17.91 ±3.14	6.27 ±2.11	4.76 ±0.32	1.38 ±0.12	3.85 ±0.60	0.62 ±0.12
Rainy	19.97 ±1.11	4.66 ±0.92	5.52 ±0.32	1.83 ±0.22	5.62 ±0.11	0.88 ±0.12
Autumn	32.17 ±3.12	3.59 ±0.62	6.33 ±0.11	1.75 ±0.32	7.43 ±0.11	1.07 ±0.01
Mean	**22.49**	**4.90**	**5.53**	**1.71**	**5.29**	**0.82**
1994 Winter	25.50 ±1.19	2.71 ±0.92	4.53 ±0.32	2.67 ±0.11	4.13 ±0.09	2.44 ±0.71
Spring	17.32 ±0.32	8.71 ±1.11	3.22 ±0.92	2.06 ±0.03	2.40 ±0.09	2.00 ±0.11
Rainy	23.53 ±3.11	12.89 ±4.09	4.11 ±1.01	3.78 ±0.12	4.72 ±0.92	3.06 ±0.81
Autumn	38.12 ±0.92	15.38 ±1.11	5.62 ±0.09	2.76 ±0.12	4.96 ±0.52	5.22 ±0.63
Mean	**26.12**	**9.92**	**4.37**	**2.82**	**4.05**	**3.18**
	(1-2 mm root diameter)					
1993 Winter	8.83 ±0.01	3.43 ±0.91	2.43 ±1.01	2.19 ±0.01	4.57 ±0.54	0.70 ±0.06
Spring	3.69 ±0.92	1.92 ±0.23	1.83 ±0.03	1.30 ±0.69	4.11 ±0.06	0.90 ±0.12
Rainy	6.06 ±0.06	8.06 ±1.23	1.37 ±0.06	0.96 ±0.04	4.29 ±0.09	0.93 ±0.17
Autumn	5.75 ±1.32	1.77 ±0.63	2.92 ±0.81	1.64 ±0.72	3.78 ±0.54	0.91 ±0.09
Mean	**6.08**	**3.80**	**2.14**	**1.52**	**4.19**	**0.86**

Table 7.10 continued

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	4.18 ±0.31	2.00 ±0.12	2.49 ±0.92	1.66 ±0.06	2.45 ±0.05	0.76 ±0.02
Spring	1.62 ±0.03	1.14 ±0.09	1.69 ±0.32	0.62 ±0.16	1.01 ±0.84	0.75 ±0.68
Rainy	3.78 ±0.95	3.25 ±0.83	1.26 ±0.63	0.94 ±0.63	1.41 ±0.36	0.92 ±0.12
Autumn	4.35 ±1.01	2.06 ±0.36	4.09 ±0.69	3.41 ±0.32	1.98 ±0.36	1.46 ±0.56
Mean	**3.48**	**2.11**	**2.38**	**1.66**	**1.71**	**0.97**

BM-Biomass, NM-Necromass
± SEM (n=20-40)

Table 7.11 Seasonal variation in N accumulation (kg ha^{-1}) in fine roots in the 13-year old regrowth.

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
	(<1 mm root diameter)					
1993 Winter	38.53 ±3.54	7.59 ±1.12	13.28 ±2.12	1.44 ±0.63	7.09 ±0.12	2.40 ±0.13
Spring	31.94 ±1.12	9.17 ±0.63	10.72 ±1.12	1.44 ±0.62	7.08 ±1.65	2.71 ±1.11
Rainy	26.01 ±5.12	8.46 ±1.30	8.71 ±0.06	1.63 ±0.13	4.25 ±0.56	2.84 ±0.51
Autumn	26.37 ±3.12	6.62 ±0.62	17.67 ±1.11	2.04 ±0.62	6.63 ±0.12	2.94 ±0.09
Mean	**30.71**	**7.96**	**12.60**	**1.64**	**6.26**	**2.72**

Table 7.11 continued

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	39.03 ±4.11	9.21 ±0.62	11.52 ±1.11	4.96 ±0.62	3.79 ±0.11	3.43 ±0.32
Spring	17.92 ±1.11	13.69 ±3.12	5.09 ±1.03	5.98 ±0.99	3.42 ±0.62	4.31 ±0.99
Rainy	16.24 ±1.41	13.35 ±2.32	4.59 ±0.92	6.56 ±1.11	2.02 ±0.92	3.09 ±0.32
Autumn	19.58 ±4.52	11.19 ±3.12	7.96 ±1.12	6.80 ±0.32	4.77 ±1.13	6.05 ±0.62
Mean	**23.19**	**11.86**	**7.79**	**6.08**	**3.50**	**4.22**
	(1-2 mm root diameter)					
1993 Winter	21.35 ±6.31	4.69 ±0.62	5.70 ±1.01	1.92 ±0.92	2.86 ±0.11	1.81 ±0.23
Spring	16.18 ±2.31	4.19 ±0.52	3.27 ±0.23	1.03 ±0.09	2.48 ±0.13	2.53 ±0.32
Rainy	8.04 ±2.10	5.80 ±0.99	2.69 ±0.07	1.26 ±0.99	1.28 ±0.92	1.71 ±0.55
Autumn	12.50 ±3.11	3.97 ±1.01	5.16 ±0.99	2.03 ±0.55	1.83 ±0.23	1.94 ±0.56
Mean	**14.52**	**4.89**	**4.21**	**1.56**	**2.11**	**1.99**
1994 Winter	9.39 ±2.12	5.04 ±1.01	4.25 ±0.96	3.35 ±0.09	2.95 ±0.62	1.56 ±0.62
Spring	9.99 ±0.55	4.20 ±0.66	3.26 ±0.11	1.37 ±0.09	2.60 ±0.07	1.78 ±0.01
Rainy	5.07 ±0.52	8.55 ±1.13	3.58 ±1.03	2.70 ±0.99	1.60 ±0.12	1.31 ±0.13
Autumn	8.38 ±0.23	7.08 ±1.01	6.12 ±0.99	5.81 ±1.11	3.37 ±0.92	2.85 ±0.09
Mean	**8.21**	**6.22**	**4.80**	**3.31**	**2.63**	**1.88**

BM-Biomass, NM-Necromass
± SEM (n=20-40)

Table 7.12 Seasonal variation in N accumulation (kg ha-1) in fine roots in the 16-year old regrowth.

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
	(<1 mm root diameter)					
1993 Winter	32.12 ±6.12	10.82 ±1.12	11.55 ±0.96	4.06 ±2.11	6.73 ±1.99	1.15 ±0.99
Spring	29.88 ±2.12	4.49 ±1.11	10.99 ±0.11	3.44 ±0.18	9.91 ±1.09	1.54 ±0.39
Rainy	24.77 ±3.11	5.00 ±1.82	10.26 ±0.99	2.90 ±0.60	5.71 ±0.09	1.19 ±0.09
Autumn	33.38 ±1.06	7.52 ±1.00	9.26 ±0.09	3.40 ±1.11	7.13 ±1.09	2.90 ±0.09
Mean	**30.03**	**6.96**	**10.52**	**3.45**	**7.37**	**1.70**
1994 Winter	33.73 ±3.39	14.52 ±1.12	11.49 ±0.92	5.04 ±0.12	4.03 ±0.30	3.69 ±0.60
Spring	16.01 ±3.05	14.65 ±1.11	6.15 ±0.09	5.70 ±0.56	4.10 ±0.63	4.35 ±0.93
Rainy	10.26 ±0.99	9.01 ±1.01	4.98 ±1.18	4.75 ±0.82	3.08 ±0.23	3.34 ±0.73
Autumn	20.04 ±1.01	17.78 ±2.32	7.41 ±1.92	6.16 ±1.42	6.23 ±0.99	7.29 ±0.12
Mean	**20.01**	**13.99**	**7.51**	**5.41**	**4.36**	**4.67**
	(1-2 mm root diameter)					
1993 Winter	14.94 ±3.11	3.76 ±1.01	9.37 ±0.99	2.48 ±0.32	2.64 ±0.11	2.14 ±0.32
Spring	9.22 ±0.32	2.14 ±0.32	6.00 ±0.12	2.58 ±0.99	3.53 ±0.82	1.95 ±0.83
Rainy	6.44 ±1.02	1.73 ±0.99	3.47 ±0.82	2.09 ±1.32	1.68 ±0.15	1.32 ±0.09
Autumn	6.82 ±1.32	2.48 ±0.09	4.42 ±0.09	1.12 ±0.32	2.76 ±0.99	1.49 ±0.44
Mean	**9.36**	**2.53**	**5.82**	**2.07**	**2.65**	**1.73**

Table 7.12 continued

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	13.35 ±2.13	7.12 ±1.32	4.52 ±0.99	1.79 ±0.04	1.81 ±0.44	1.77 ±0.23
Spring	8.15 ±0.99	4.64 ±1.01	4.34 ±0.62	2.14 ±0.63	2.66 ±0.93	1.92 ±0.05
Rainy	5.95 ±0.99	4.42 ±1.06	2.49 ±0.99	2.12 ±0.23	1.44 ±0.39	1.99 ±0.64
Autumn	9.94 ±2.12	9.43 ±3.17	3.54 ±0.62	3.96 ±0.62	3.00 ±1.12	2.71 ±0.32
Mean	**9.35**	**6.40**	**3.72**	**2.50**	**2.23**	**2.10**

BM-Biomass, NM-Necromass
± SEM (n=20-40)

Table 7.13 Seasonal variation in P accumulation (kg ha^{-1}) in fine roots in the 7-year old regrowth.

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
	(<1 mm root diameter)					
1993 Winter	1.82 ±0.01	0.27 ±0.01	0.50 ±0.09	0.10 ±0.01	0.39 ±0.06	0.05 ±0.01
Spring	1.60 ±0.62	0.60 ±0.21	0.37 ±0.01	0.13 ±0.02	0.30 ±0.05	0.06 ±0.01
Rainy	1.47 ±0.32	0.48 ±0.11	0.41 ±0.09	0.21 ±0.02	0.41 ±0.03	0.09 ±0.03
Autumn	1.82 ±0.32	0.60 ±0.01	0.36 ±0.03	0.18 ±0.01	0.42 ±0.08	0.11 ±0.02
Mean	**1.65**	**0.49**	**0.41**	**0.16**	**0.38**	**0.08**

Table 7.13 continued

Year/Season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	1.72 ±0.08	0.29 ±0.05	0.31 ±0.06	0.14 ±0.01	0.28 ±0.01	0.13 ±0.01
Spring	1.26 ±0.63	0.96 ±0.12	0.23 ±0.05	0.16 ±0.03	0.17 ±0.07	0.16 ±0.01
Rainy	1.36 ±0.32	0.95 ±0.23	0.24 ±0.09	0.28 ±0.12	0.27 ±0.06	0.22 ±0.08
Autumn	2.42 ±0.12	0.89 ±0.12	0.36 ±0.06	0.16 ±0.01	0.32 ±0.06	0.30 ±0.05
Mean	**1.69**	**0.77**	**0.29**	**0.19**	**0.26**	**0.20**
(1-2 mm root diameter)						
1993 Winter	0.66 ±0.01	0.20 ±0.09	0.18 ±0.02	0.16 ±0.05	0.34 ±0.06	0.05 ±0.01
Spring	0.32 ±0.01	0.16 ±0.02	0.16 ±0.03	0.11 ±0.03	0.35 ±0.01	0.08 ±0.01
Rainy	0.42 ±0.01	0.33 ±0.06	0.09 ±0.02	0.09 ±0.01	0.07 ±0.01	0.09 ±0.02
Autumn	0.43 ±0.09	0.14 ±0.06	0.17 ±0.01	0.12 ±0.02	0.05 ±0.01	0.07 ±0.01
Mean	**0.46**	**0.21**	**0.15**	**0.12**	**0.20**	**0.07**
1994 Winter	0.54 ±0.11	0.15 ±0.03	0.14 ±0.02	0.12 ±0.01	0.14 ±0.01	0.06 ±0.01
Spring	0.11 ±0.03	0.09 ±0.03	0.06 ±0.01	0.05 ±0.01	0.07 ±0.01	0.06 ±0.01
Rainy	0.23 ±0.07	0.28 ±0.03	0.08 ±0.02	0.08 ±0.01	0.09 ±0.03	0.08 ±0.01
Autumn	0.25 ±0.03	0.14 ±0.05	0.23 ±0.05	0.23 ±0.05	0.09 ±0.01	0.10 ±0.02
Mean	**0.21**	**0.17**	**0.13**	**0.12**	**0.10**	**0.08**

BM-Biomass, NM-Necromass
± SEM (n=20-40)

Table 7.14 Seasonal variation in P accumulation (kg ha-1) in fine roots in the 13-year old regrowth.

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
	(<1 mm root diameter)					
1993 Winter	2.53 ±0.09	0.44 ±0.05	0.65 ±0.11	0.09 ±0.01	0.47 ±0.06	0.14 ±0.06
Spring	2.11 ±0.06	0.55 ±0.05	0.67 ±0.06	0.09 ±0.01	0.47 ±0.23	0.16 ±0.09
Rainy	1.66 ±0.03	0.48 ±0.11	0.56 ±0.17	0.09 ±0.03	0.27 ±0.05	0.17 ±0.06
Autumn	1.47 ±0.11	0.44 ±0.11	0.98 ±0.25	0.14 ±0.05	0.37 ±0.06	0.37 ±0.12
Mean	**1.94**	**0.48**	**0.72**	**0.10**	**0.40**	**0.21**
1994 Winter	2.32 ±0.99	0.45 ±0.11	0.69 ±0.19	0.25 ±0.03	0.22 ±0.05	0.17 ±0.09
Spring	2.07 ±0.09	0.77 ±0.09	0.40 ±0.06	0.33 ±0.11	0.27 ±0.09	0.24 ±0.05
Rainy	1.30 ±0.03	0.85 ±0.23	0.37 ±0.09	0.42 ±0.10	0.16 ±0.09	0.20 ±0.01
Autumn	1.34 ±0.01	0.56 ±0.11	0.68 ±0.03	0.34 ±0.09	0.33 ±0.03	0.25 ±0.09
Mean	**1.78**	**0.66**	**0.54**	**0.34**	**0.25**	**0.22**
	(1-2 mm root diameter)					
1993 Winter	1.44 ±0.11	0.39 ±0.12	0.38 ±0.11	0.16 ±0.09	0.19 ±0.09	0.15 ±0.02
Spring	1.61 ±0.03	0.40 ±0.11	0.27 ±0.09	0.10 ±0.01	0.20 ±0.03	0.25 ±0.05
Rainy	0.62 ±0.06	0.79 ±0.08	0.51 ±0.06	0.12 ±0.01	0.10 ±0.01	0.16 ±0.05
Autumn	0.77 ±0.11	0.30 ±0.01	0.32 ±0.06	0.15 ±0.03	0.11 ±0.01	0.15 ±0.02
Mean	**1.11**	**0.45**	**0.30**	**0.13**	**0.15**	**0.18**

Table 7.14 continued

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	0.52 ±0.12	0.27 ±0.09	0.23 ±0.03	0.18 ±0.06	0.16 ±0.06	0.08 ±0.02
Spring	0.61 ±0.11	0.20 ±0.08	0.20 ±0.05	0.07 ±0.01	0.16 ±0.03	0.10 ±0.01
Rainy	0.36 ±0.10	0.45 ±0.02	0.25 ±0.05	0.14 ±0.01	0.11 ±0.01	0.07 ±0.02
Autumn	0.44 ±0.06	0.33 ±0.03	0.32 ±0.04	0.27 ±0.02	0.18 ±0.03	0.13 ±0.02
Mean	**0.48**	**0.24**	**0.25**	**0.17**	**0.15**	**0.09**

BM-Biomass, NM-Necromass
± SEM (n=20-40)

Table 7.15 Seasonal variation in P accumulation (kg ha^{-1}) in fine roots in the 16-year old regrowth.

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
	(<1 mm root diameter)					
1993 Winter	2.65 ±1.01	0.75 ±0.11	0.95 ±0.09	0.28 ±0.06	0.55 ±0.06	0.08 ±0.01
Spring	2.38 ±0.99	0.41 ±0.06	0.87 ±0.06	0.31 ±0.06	0.79 ±0.05	0.14 ±0.01
Rainy	1.92 ±0.01	0.46 ±0.06	0.50 ±0.05	0.27 ±0.08	0.44 ±0.09	0.11 ±0.01
Autumn	2.27 ±0.99	0.48 ±0.11	0.63 ±0.12	0.22 ±0.09	0.49 ±0.03	0.19 ±0.02
Mean	**2.31**	**0.53**	**0.81**	**0.27**	**0.57**	**0.13**

Table 7.15 continued

Year/season	Soil Depth (cm)					
	0-10		10-20		20-30	
	BM	NM	BM	NM	BM	NM
1994 Winter	2.09 ±0.12	0.89 ±0.11	0.71 ±0.23	0.31 ±0.11	0.34 ±0.09	0.23 ±0.02
Spring	1.34 ±0.01	0.73 ±0.06	0.48 ±0.06	0.29 ±0.06	0.32 ±0.01	0.22 ±0.01
Rainy	0.82 ±0.11	0.66 ±0.09	0.40 ±0.03	0.35 ±0.05	0.25 ±0.09	0.25 ±0.09
Autumn	1.43 ±0.06	1.15 ±0.05	0.53 ±0.09	0.40 ±0.02	0.44 ±0.03	0.47 ±0.06
Mean	**1.42**	**0.86**	**0.53**	**0.34**	**0.34**	**0.29**
	(1-2 mm root diameter)					
1993 Winter	1.03 ±0.01	0.37 ±0.11	0.64 ±0.23	0.24 ±0.11	0.18 ±0.096	0.21 ±0.06
Spring	0.74 ±0.09	0.18 ±0.01	0.61 ±0.12	0.21 ±0.06	0.29 ±0.07	0.17 ±0.06
Rainy	0.55 ±0.03	0.14 ±0.06	0.29 ±0.02	0.18 ±0.09	0.14 ±0.09	0.11 ±0.02
Autumn	0.56 ±0.21	0.22 ±0.09	0.36 ±0.06	0.10 ±0.02	0.23 ±0.03	0.13 ±0.05
Mean	**0.72**	**0.23**	**0.51**	**0.18**	**0.21**	**0.16**
1994 Winter	0.66 ±0.11	0.35 ±0.09	0.22 ±0.02	0.09 ±0.01	0.09 ±0.01	0.09 ±0.02
Spring	0.36 ±0.06	0.21 ±0.06	0.19 ±0.03	0.10 ±0.02	0.11 ±0.01	0.08 ±0.01
Rainy	0.25 ±0.03	0.20 ±0.02	0.10 ±0.01	0.10 ±0.01	0.06 ±0.01	0.09 ±0.01
Autumn	0.45 ±0.11	0.40 ±0.09	0.16 ±0.09	0.17 ±0.02	0.14 ±0.02	0.12 ±0.01
Mean	**0.43**	**0.29**	**0.17**	**0.12**	**0.10**	**0.10**

BM-Biomass, NM-Necromass
± SEM (n=20-40)

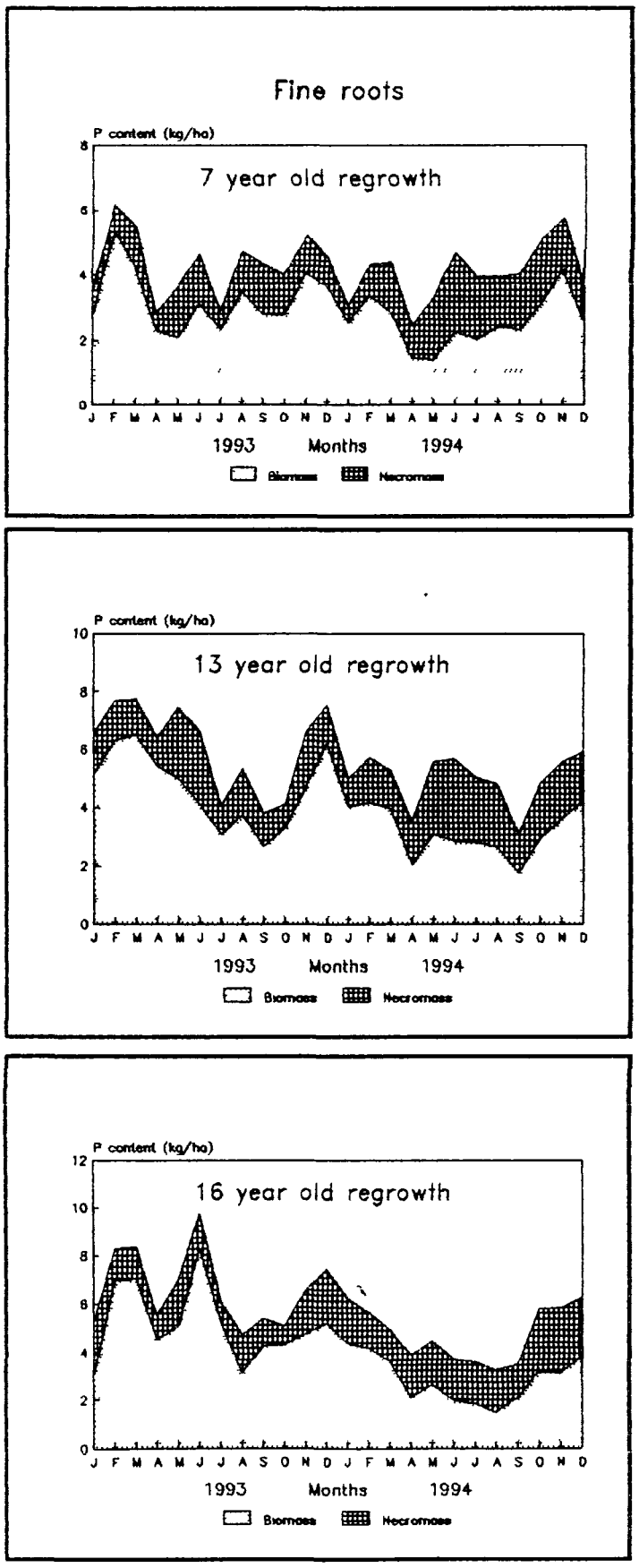


Figure 7.13. Standing state of P in fine roots (biomass and necromass) in soil down to 30 cm depth in the three regrowing forest stands.

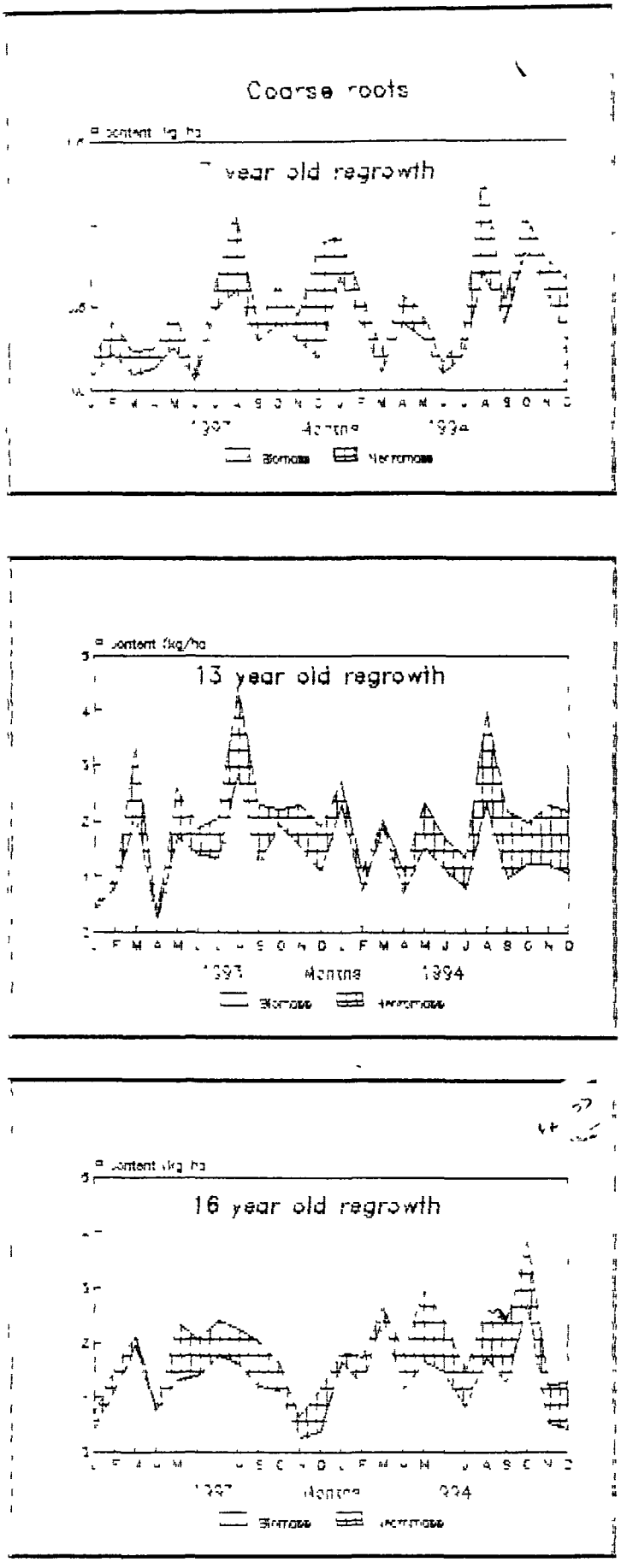


Figure 7.14. Standing state of P in biomass and necromass of coarse roots in soil (0-30 cm depth) in the three forest regrowths.

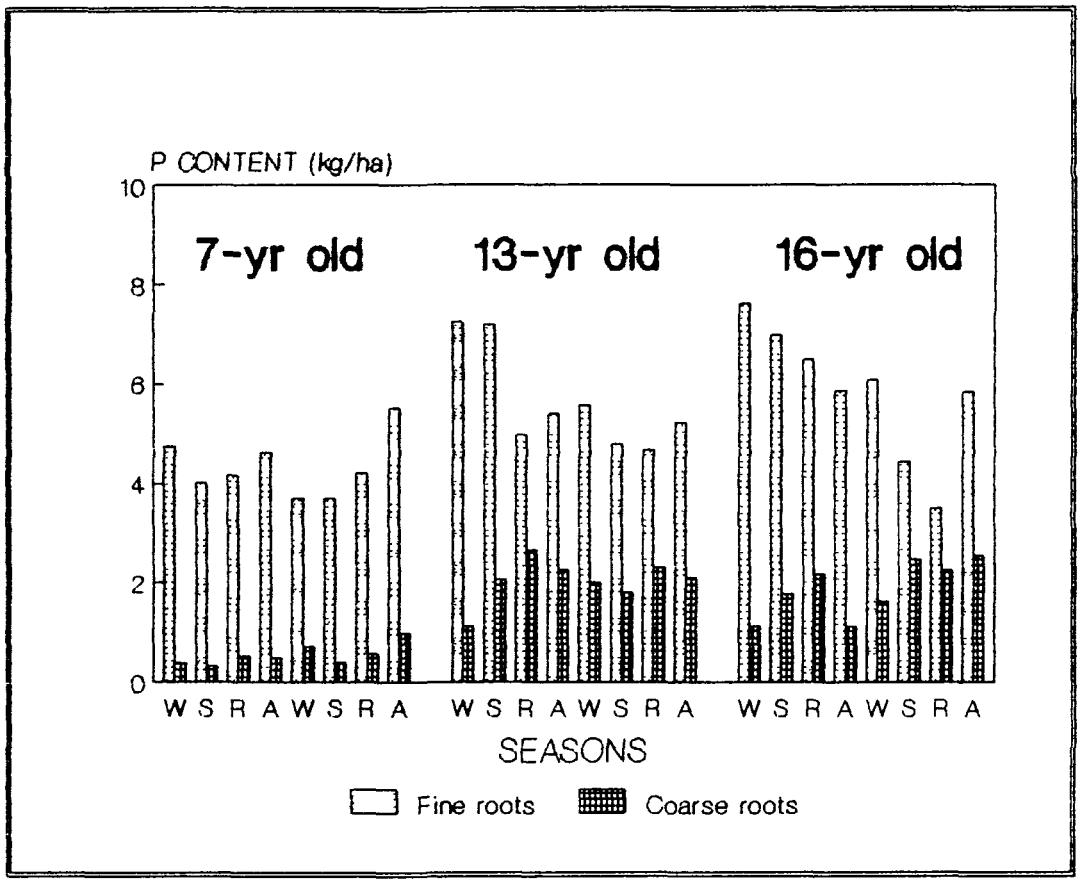


Figure 7.15. Seasonal variation in P accumulation in soil through fine and coarse roots in forest regrowths of three *different ages.*

older regrowths than in the 7-year old regrowth (Table 7.16); the difference between 13-and 16-year old regrowths was, however insignificant. *P Stock*: Monthly and seasonal variations in P accumulation in the fine roots are shown in Figures 7.13 and 7.15 and the spatial data are given in Tables 7.13-7.15. P accumulation was similar to the N in both diameter classes. The FRB had significantly greater ($P<0.01$) amount of P in the top soil layer than in the subsurface layers. Seasonal ($F=3.86$) and standwise ($F=186.13$) variations were also significant ($P<0.01$). The standing state of P in the fine roots averaged 3.9, 5.2 and 4.6 kg ha^{-1} in the 7-, 13- and 16-year old regrowths, respectively. In each stand, very fine roots had more than 50% of the total P stock in roots. The P stock in coarse roots was very less (0.69 kg ha^{-1}) in the 7-year old regrowth compared to the 13-year (2.04 kg ha^{-1}) and 16-year (1.93 kg ha^{-1}) old regrowths (Table 7.16); the difference between the latter two regrowths was not significant. The necromass contributed upto 50% to the total P stock in coarse roots.

N AND P INPUT IN SOIL THROUGH ROOTS

Total N and P input to the soil by roots (fine plus coarse roots) was maximum in the 13-year old regrowth (275.09 kg N ha^{-1}, 19.61 kg P ha^{-1}) and minimum in the 7-year old stand (Table 7.16). Most of these inputs were confined to the top layer of the soil profile.

ROOT TURNOVER

The annual decomposition coefficient (K) calculated according to Reiners and Reiners (1970) revealed little variation between fine and coarse roots, soil depths and stands (Table 7.16). Annually, about 67% fine roots and 77% coarse roots were recycled in all three regrowths. N and P turnover through coarse roots was faster than the fine roots (Table 7.16).

FINE ROOT CHEMISTRY

C and lignin concentrations in the fine roots did not vary significantly between stands, while C/N and lignin/N ratios increased from

Table 7.16 Input of organic matter, N and P (kg ha-1 yr-1) through fine and coarse roots and their accumulation (kg ha^{-1}) and turnover (years) in the three forest regrowths.

Variable/ Soil depth (cm)		7-year old regrowth			13-year old regrowth			16-year old regrowth		
		1993	1994	Mean	1993	1994	Mean	1993	1994	Mean
I. Input and turnover of fine root mass										
Mass	0-10	4389.5	4117.8	4253.8	7105.1	4667.4	5886.4	5730.7	4682.6	5206.7
	10-20	1388.6	1176.0	1282.4	2307.5	2071.2	2189.5	2912.6	1811.4	2362.0
	20-30	1405.7	1023.9	1214.9	1629.8	1216.2	1423.0	1715.0	1322.7	1518.9
	0-30	7183.8	6317.8	6751.1	11042.2	7954.8	9798.9	10358.3	7816.7	9087.8
Input	0-10	13836.6	9339.6	11588.1	17329.1	9535.5	13432.3	11057.9	7539.5	9298.7
	10-20	3559.7	2655.1	3107.4	5625.7	4925.6	5275.6	6393.4	3792.0	5092.7
	20-30	5469.0	2436.5	3952.8	3832.0	2435.4	3133.7	4766.5	3689.6	4228.1
	0-30	22866.3	14431.2	18648.3	26786.8	17779.8	22283.3	22217.8	15021.1	18619.5
K	0-10	0.76	0.69	0.73	0.71	0.67	0.70	0.66	0.62	0.64
	10-20	0.72	0.69	0.71	0.71	0.70	0.71	0.69	0.68	0.68
	20-30	0.79	0.70	0.77	0.70	0.67	0.69	0.74	0.74	0.74
	0-30	0.76	0.70	0.73	0.71	0.69	0.70	0.68	0.66	0.67
N Input and turnover										
Stock	0-10	32.35	42.00	37.18	54.14	48.07	51.11	42.35	48.69	45.52
	10-20	10.23	11.99	11.11	17.58	21.33	19.46	21.52	18.84	20.18
	20-30	10.36	10.44	10.44	12.42	12.53	12.48	12.67	13.76	13.22
	0-30	52.94	64.43	58.69	84.14	81.93	83.05	76.54	81.29	78.92
Input	0-10	101.98	95.26	98.62	132.05	98.22	115.14	81.72	78.41	80.07
	10-20	26.23	27.08	26.66	42.87	50.73	46.80	47.25	39.44	43.35
	20-30	40.31	24.85	32.58	29.20	25.08	27.14	35.22	38.37	36.80
	0-30	171.52	147.19	157.86	204.12	174.03	189.08	164.19	156.22	160.22
K_N	0-10	0.76	0.69	0.73	0.71	0.67	0.69	0.66	0.62	0.64
	10-20	0.72	0.69	0.71	0.71	0.70	0.71	0.69	0.68	0.68
	20-30	0.80	0.70	0.75	0.70	0.68	0.69	0.74	0.74	0.74
	0-30	0.76	0.70	0.73	0.71	0.68	0.70	0.66	0.66	0.67
P input and turnover										
Stock	0-10	2.55	2.43	2.49	3.69	2.75	3.22	2.29	2.72	2.51
	10-20	0.81	0.69	0.75	1.20	1.22	1.21	1.51	1.05	1.28
	20-30	0.82	0.60	0.71	0.85	0.72	0.79	0.89	0.77	0.83
	0-30	4.18	3.72	3.95	5.74	4.69	5.22	4.69	4.54	4.62
Input	0-10	8.03	5.51	6.77	9.01	5.63	7.32	4.42	4.37	4.40
	10-20	2.06	1.57	1.82	2.93	2.91	2.92	2.56	2.20	2.38
	20-30	3.17	1.44	2.31	1.99	1.44	1.72	1.91	2.14	2.03
	0-30	13.26	8.52	10.90	13.93	9.98	11.96	8.89	8.71	8.81
K_P	0-10	0.76	0.69	0.73	0.71	0.67	0.69	0.66	0.62	0.64
	10-20	0.72	0.70	0.71	0.71	0.71	0.71	0.63	0.68	0.66
	20-30	0.79	0.70	0.77	0.70	0.67	0.69	0.68	0.74	0.71
	0-30	0.76	0.70	0.73	0.71	0.68	0.70	0.66	0.66	0.66

Table 7.16 continued

Variable/ Soil depth (cm)	7-year old regrowth			13-year old regrowth			16-year old regrowth		
	1993	1994	Mean	1993	1994	Mean	1993	1994	Mean
II. *Coarse root production and turnover*									
Standing crop	744.4	1331.9	1028.2	4058.9	4930.8	4495.0	2954.7	4641.5	3798.2
Production	3281.9	5479.1	4380.5	17569.2	15984.7	16776.9	9279.5	15703.4	12491.5
K	0.82	0.80	0.81	0.81	0.76	0.79	0.76	0.77	0.77
N input and turnover									
Stock	3.48	7.80	5.64	16.84	30.57	23.71	11.91	33.05	2.48
Input	15.36	32.11	23.74	72.91	99.11	86.01	37.39	111.81	74.60
K_N	0.82	0.80	0.81	0.81	0.76	0.78	0.76	0.77	0.77
P input and turnover									
Stock	0.49	0.88	0.69	1.95	2.12	2.04	1.63	2.23	1.93
Input	2.17	2.52	2.35	8.43	6.87	7.65	5.10	7.54	6.32
K_P	0.82	0.74	0.78	0.81	0.76	0.79	0.77	0.77	0.77
III. *Total root production and turnover*									
Standing crop	7928.2	7649.7	7779.3	15101.2	12885.6	13993.9	13313.0	12458.2	12885.8
Production	26147.2	19910.3	23028.8	44356.0	33764.5	39060.3	31497.3	30274.5	30885.9
K	0.77	0.72	0.75	0.75	0.72	0.74	0.70	0.71	0.71
N input and turnover									
Stock	56.42	72.23	64.33	100.98	112.50	106.76	88.45	114.34	101.40
Input	186.88	179.30	181.60	277.03	273.14	275.09	201.58	268.03	234.82
K_N	0.77	0.71	0.74	0.73	0.71	0.72	0.70	0.70	0.70
P input and turnover									
Stock	4.67	4.60	4.64	7.69	6.81	7.26	6.32	6.77	6.55
Input	15.43	11.04	13.25	22.36	16.85	19.61	13.99	16.25	15.13
K_P	0.77	0.71	0.74	0.74	0.71	0.73	0.69	0.71	0.70

K-Dry matter turnover rate (in year)

K_N-Nitrogen turnover rate (in year)

K_P-Phosphorus turnover (in year)

Note: 1. Dry matter, N and P content of fine and coarse roots are the means of 12 months across two year of sampling.

2. Data on coarse as well as total roots are summed-up irrespective of soil depths (0-30 cm).

Table 7.17. Chemical composition of fine roots used in the decomposition study.

Age of the forest regrowth	C (%)	N (%)	P (%)	Lignin (%)	Cellulose (%)	C/N	Lignin/N
7-yr	47.1 ±0.3	1.18 ±0.09	0.036 ±0.001	25.91 ±1.31	29.4 ±0.9	39.92	21.95
13-yr	44.4 ±1.3	0.95 ±0.02	0.048 ±0.001	22.93 ±0.93	33.4 ±0.1	46.74	24.14
16-yr	44.6 ±1.0	0.74 ±0.01	0.088 ±0.002	22.32 ±1.02	37.4 ±0.3	60.27	30.16

± SEM (n=3)

Table 7.18. Decay and nutrient release rates (mg day^{-1}) during three phases of fine root decomposition.

Variable	Phase I (0-60 days)	Phase II (60-120 days)	Phase III (120-600 days)
7-year old regrowth			
Weight loss	3.83 (0.09)	22.57 (0.56)	2.34 (0.09)
N release	0.39 (0.77)	0.08 (0.30)	0.01 (0.04)
P release	-0.02 (-1.0)	0.03 (1.24)	0.001 (0.1)
13-year old regrowth			
Weight loss	0.87 (0.02)	22.84 (0.53)	2.93 (0.10)
N release	0.27 (0.66)	0.02 (0.08)	0.02 (0.08)
P release	-0.003 (-0.16)	0.01 (0.63)	0.001 (0.09)
16-year old regrowth			
Weight loss	1.73 (0.04)	23.21 (0.55)	2.80 (0.10)
N release	0.13 (0.42)	0.11 (0.47)	0.01 (0.05)
P release	0.03 (0.83)	0.004 (0.22)	0.001 (0.04)

Note: Values in parentheses represent percent weight loss.

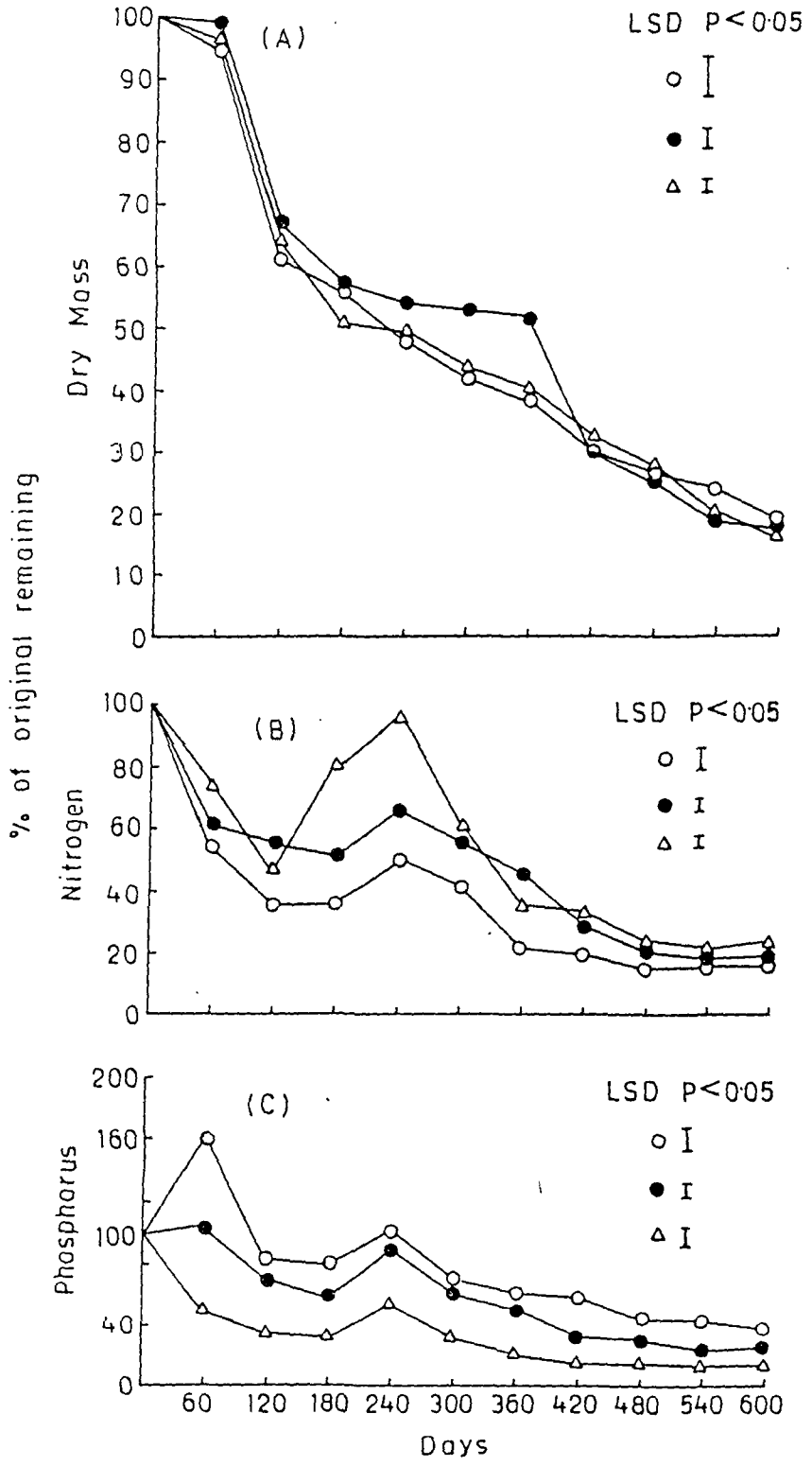


Figure 7.16. Mean dry weight (a), and N (b) and P (c) remaining (% of initial) in the fine roots during decomposition in the 7- (o), 13- (●) and 16-year(△) old regrowths.

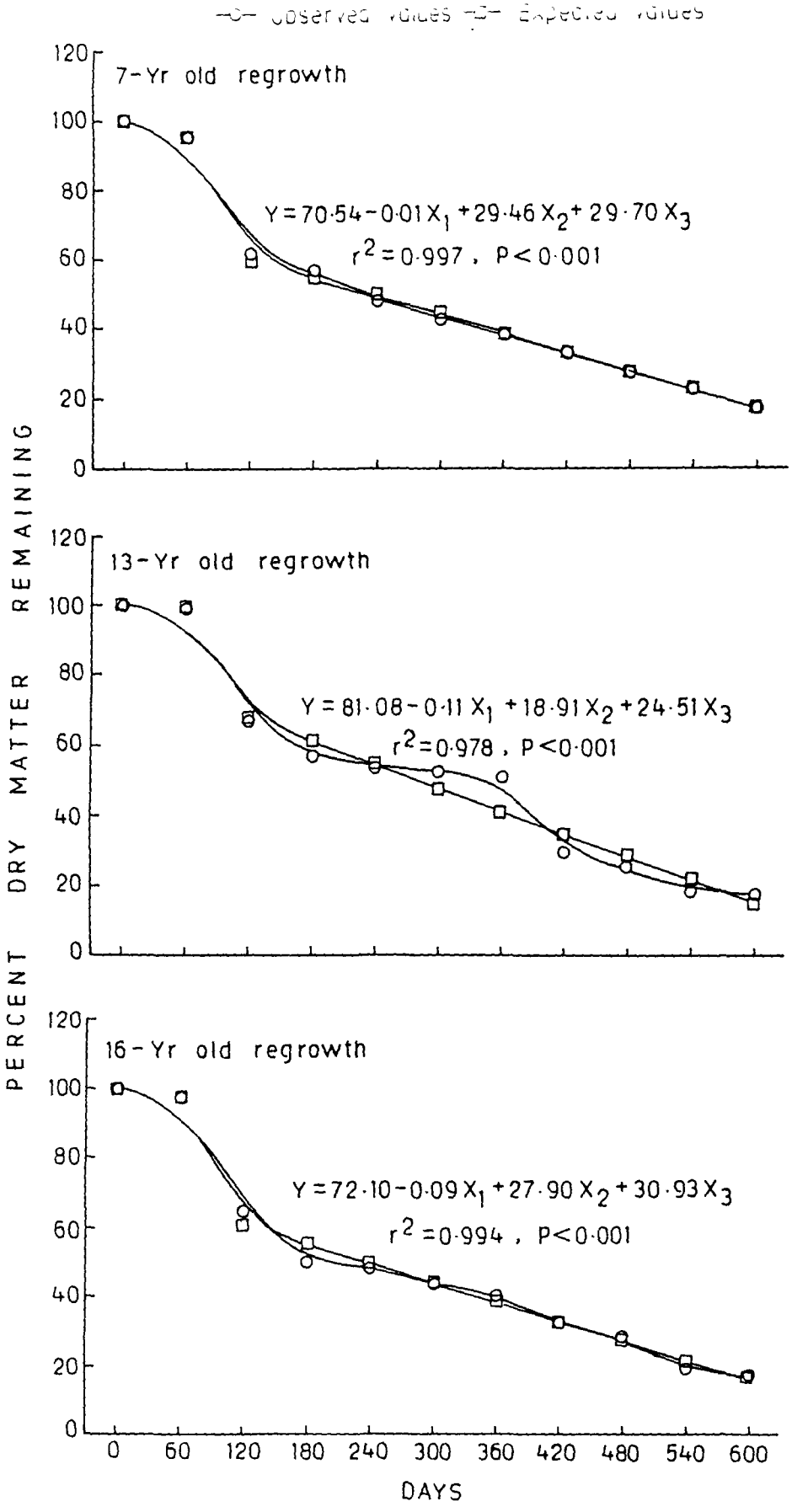


Figure 7.17. Decay pattern of fine roots in the three forest regrowths. (—o—) Observed values and (—□—) expected values calculated using the composite linear equation.

7-yr to 16-yr old regrowth (Table 7.17). Concentrations of P and cellulose increased significantly ($P<0.05$) from 7-yr to 16-yr old stand, while N followed a reverse trend.

DECOMPOSITION OF FINE ROOTS

Weight loss pattern: Fine roots showed three distinct phases of decomposition (Figure 7.16). The first phase lasting for about 60 days was characterized by a slow rate of decomposition during which 0.09, 0.02 and 0.04% day^{-1} weight loss were observed in the 7-, 13- and 16-year old regrowths, respectively (Table 7.18). This was followed by a period of rapid weight loss (0.53-0.56% weight loss day^{-1}) lasting for the next 60 days. During the third phase *i.e.*, between 120 and 600 days, fine roots decomposed at an average rate of 0.10% weight loss day^{-1} in all the three forest regrowths. About 18% of initial root mass remained undecomposed at the end of the study in all regrowths. A composite linear equation showed a good fit for the three-phased decay pattern and the regressions were highly significant ($P<0.001$, $r^2=0.978-0.997$) (Figure 7.17). The decay constant (k) varied from 1.62 in the 7-year old regrowth to 1.74 in the 16-year old regrowth. The time required for 99% decay of the fine roots varied between 4.72 and 5.07 years (Table 7.19).

Correlation analysis between the rate of weight loss per day and fifteen intrinsic and extrinsic independent variables yielded significant results with only seven variables *viz.*, initial lignin content, lignin/N and C/N ratios in fine roots, and seasonal means of soil moisture content and soil pH, and mean daily rainfall and mean monthly air temperature (Table 7.20).

N and P dynamics: N concentration in fine roots decreased during the first phase of decomposition, followed by a sharp increase until 240 days, and then by a decrease again (Figure 7.18). The difference in N concentration between 7- and 13-year old stands was insignificant, but the variation

Table 7.19. Annual decay (k)/mineralization (k_N and k_P) constants and turnover time (year) of fine roots in the three forest regrowths.

Decay parameters	Age of the forest regrowth		
	7-yr	13-yr	16-yr
Root decay			
% mass loss yr^{-1}	49.12	49.79	50.30
k	1.62	1.68	1.74
t_{50}	0.70	0.68	0.65
t_{99}	5.07	4.89	4.72
N mineralization			
% release yr^{-1}	50.86	49.21	46.42
k_N	1.10	1.02	0.88
t_{50}	0.63	0.68	0.79
t_{99}	4.57	4.89	5.71
P mineralization			
% release yr^{-1}	37.29	44.59	51.40
k_P	0.58	0.80	1.13
t_{50}	1.19	0.86	0.61
t_{99}	8.56	6.23	4.42

Table 7.20. Relationships of fine root decomposition rate (% weight loss day^{-1}) with climatic variables, soil characteristics and root chemistry.

Variable	Regression equation	df	r	P
Weight loss vs Climatic variables				
Daily Rainfall (mm)	Y=33.86+0.24X	19	0.721	0.001
Monthly air temperature (°C)	Y=11.28+0.20X	19	0.631	0.01
Weight loss vs Soil characteristics				
Temperature (°C)	Y=17.75+0.03X	19	0.138	NS
Moisture content (%)	Y=54.86+0.25X	19	0.601	0.01
pH	Y=4.92+0.01X	19	0.531	0.05
Organic matter (%)	Y=8.65+0.003X	19	0.249	NS
TKN (%)	Y=0.43+0.001X	19	0.216	NS
Available-P ($\mu g\ g^{-1}$)	Y=8.75+0.04X	19	0.185	NS
Weight loss vs Initial root chemistry				
Lignin (%)	Y=19.83-0.064X	7	-0.619	0.05
Carbon (%)	Y=46.84-0.034X	7	-0.354	NS
Nitrogen (%)	Y=1.10-0.003X	7	-0.282	NS
Phosphorus (%)	Y=0.035-0.0005X	7	-0.360	NS
Cellulose (%)	Y=29.20-0.095X	7	-0.450	NS
Lignin/N	Y=21.91+0.11X	7	0.714	0.05
C/N	Y=39.83+0.28X	7	0.765	0.05

r=correlation coefficient; P-significance level.

NS-Not significant

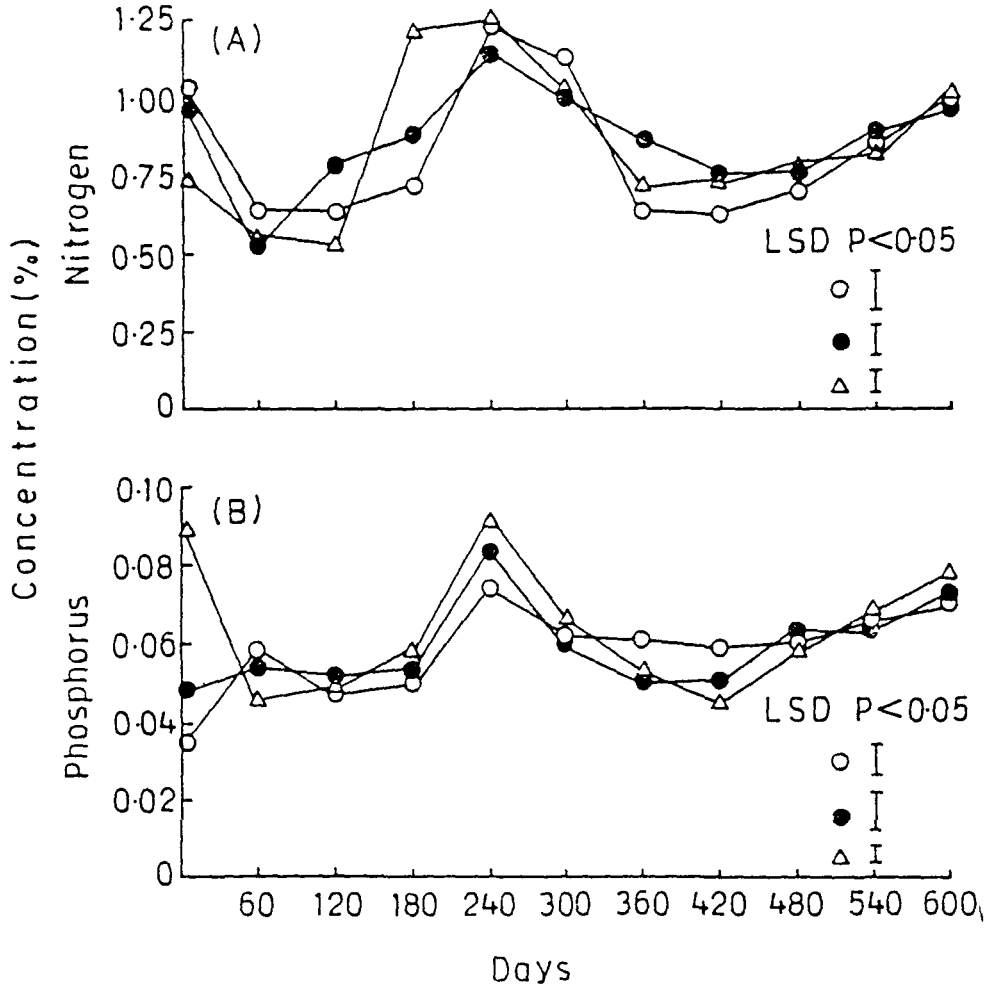


Figure 7.18. Nitrogen (a) and phosphorus (b) concentrations (%) in the decomposing fine roots in the 7- (○), 13-(●) and 16-year (△) old regrowths.

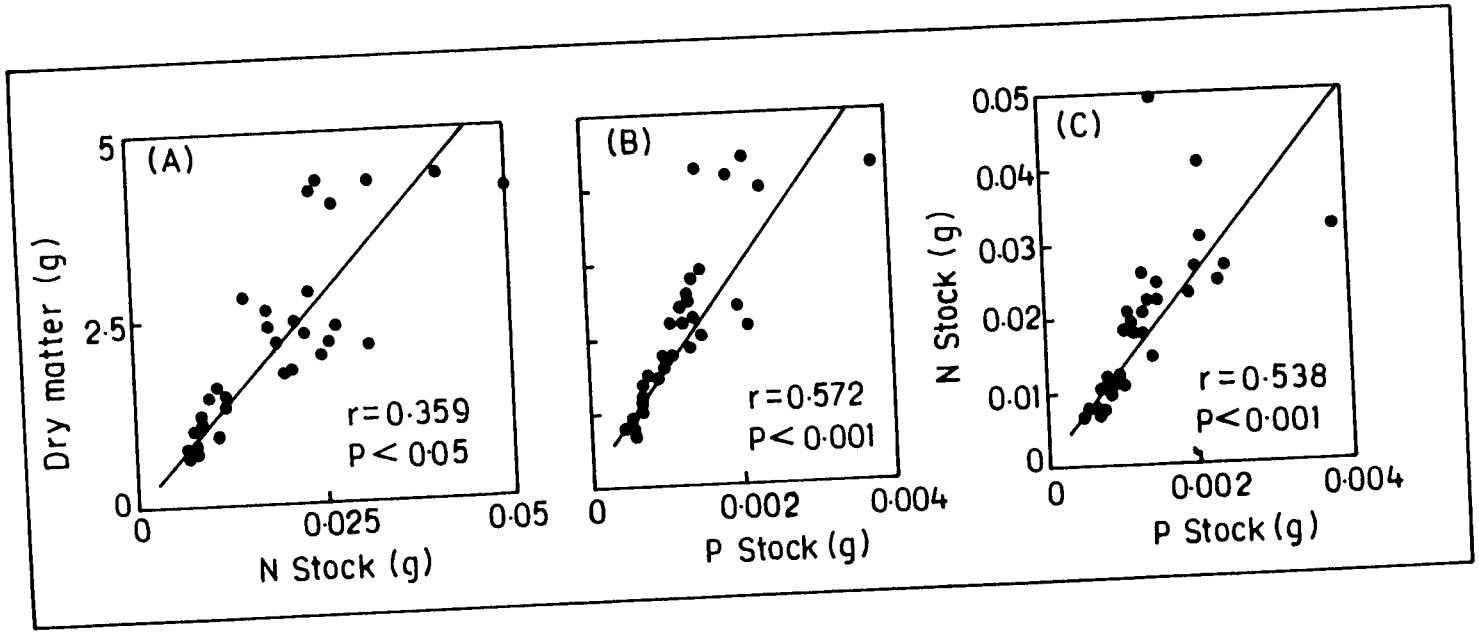


Figure 7.19. Relationships between (a) dry-weight and N, (b) dry-weight and P and (c) between N and P stocks in the decomposing fine roots. Data points were plotted irrespective of stand age.

between 7- and 16-year old stands was significant ($P<0.05$). In 7- and 13-yr old regrowths the rapid rate of N mineralization (0.66 and 0.77% day^{-1}, respectively) during the initial 60 days, decreased during II phase and remained constant. In the 16-year old stand, N mineralization continued more or less at a constant rate (0.42-0.47% day^{-1}) until 120 days (Table 7.18). In all three stands, mineralization was almost negligible during winter (180-240 days), rather N content increased (19-28%) over the preceding autumn (Figure 7.16). N mineralization decreased with increase in the age of the stand. As a result, 16.4, 19.0 and 23.8% N remained unmineralized after 600 days of root decomposition in the 7-, 13- and 16-year old regrowths, respectively. The N mineralization constant (k_N) was highest in the 7-year old regrowth and lowest in the 16-year old regrowth (Table 7.19).

P concentration in decaying roots increased until 60 days, except in the 16-yr old regrowth, where it recorded a sharp decrease (Figure 7.18). P concentration increased during winter over the preceding autumn and then decreased. During the first phase of decomposition 0.03-0.15% P was immobilized in the two younger regrowths, while in the 16-year old regrowth P was mineralized at the rate of 0.03 mg P day^{-1} (Table 7.18). A small peak in P content of the root mass during winter (240 days) in all the three stands indicated the period of P immobilization. At the end of the study, about 39, 27 and 16% of the initial P content remained unmineralized in the 7-, 13- and 16-year old regrowths, respectively (Figure 7.16). The annual rate of P mineralization increased from 37.3% in the 7-year old regrowth to 51.4% in the 16-year old regrowth. A similar trend was observed in case of P mineralization constant (k_P) (Table 7.19).

During decay N and P stocks in fine roots were positively correlated ($P<0.01$) with its dry weight. Similarly, the N and P stocks in the fine roots were also correlated (Figure 7.19).

DISCUSSION

BIOMASS AND PRODUCTION

The mean annual fine root mass in the 7-year old regrowth is close to the value reported from a dry deciduous forest (Singh and Singh 1981), while those obtained in the 13- and 16-year old regrowths are higher than majority of estimates in tne tropical and temperate forests (Visalakshi 1994). However, the fine root production in the three forest regrowths are comparable to the values (15900-23300 kg ha^{-1} yr^{-1}) reported by Medina and Cuevas (1989) for the San Carlos forests.

Studies show that tree roots are mainly found in the upper 50 cm soil, while, majority of the fine roots are confined within top 20 cm layer of the soil profile (Kozlowski 1971, Hermann 1977, Persson 1983). Findings of tne present study, wherein top 20 cm layer of the soil profile had 82-84% of the fine root mass confirm the results of earlier workers. Safford and Bell (1972) have reported a similar distribution pattern in top 15 cm soil layer in a 39 year old spruce plantation. In *Pinus taeda* (Harris *et al.* 1977) and *Abies amabilis* (Vogt *et al.* 1981) stands, 60-71% of the fine roots were concentrated in the top 20 cm of soil. A relatively higher proportion of fine roots in the top soil layer (0-20 cm) in the present study as compared to the values reported by other workers may be attributed to extensive coppicing of the residual root stocks in the disturbed stands and in part due to abundance of herbaceous species, especially grasses in the early stages of succession (Berish 1982).

The total fine root mass in the upper 10 cm soil layer that averaged 4254, 5886 and 5207 kg ha^{-1} in 7-, 13- and 16-year old regrowths, respectively, fall within the range reported from a secondary forest at Luquillo, USA (Cuevas *et al.* 1991), premontane forest in Costa Rica (Berish 1982) and in a hurricane-disturbed subtropical wet forest in Puerto Rico

(Parrotta and Lodge 1991). Presence of a large proportion of fine roots in the top soil layer might have helped in faster recovery of the disturbed ecosystem through efficient recycling of nutrients released during decomposition of detrital material on the forest floor.

The fine root mass in forests changes both seasonally and annually. The seasonal periodicity of fine root growth is known both in the tropical and temperate forests (Persson 1978, Srivastava *et al.* 1986, Parthasarathy 1987, Fahey and Hughes 1994). Wide monthly fluctuations in fine root mass data in tne present study did not permit us to conclude about its seasonal behaviour. However, when the data were pooled on seasonal basis, a unimodal growth pattern with a trough during spring or rainy season and a peak either during autumn (in 7-year old regrowth) or during ensuing winter (in 13- and 16-year old regrowths) was observed particularly in the surface layer (0-10 cm) of the soil. Similar findings have been reported by Srivastava *et al.* (1986) from dry tropical teak forests and by Khiewtam and Ramakrishnan (1993) from a subtropical climax forest. The autumn peak in the belowground biomass obtained in the grassland ecosystems has been attributed to the translocation of large amount of organic matter from shoot to the belowground parts (Sims and Singh 1978). This seems to be true in the case of the 7-year old regrowth which looked like a savanna due to abundance of perennial grasses such as *Imperata cylindrica* and *Arundinella bengalensis* in the open spaces between sparsely growing young regenerating trees of pine, *Quercus dealbata*, *Castanopsis kurzii* and *Schima khasiana*. In the other two regrowths, where woody elements were abundant, the peak in fine roots coincided with the period of leaf senescence and fall. Low spring biomass coincided with the period of active shoot growth. The seasonal changes in fine root mass also reflected the variations in production and decomposition processes through seasons (Ford and Deans 1977, Srivastava *et al.* 1986). For instance, low fine root mass in July

coincided with the peak period of decomposition process due to high temperature and humid conditions. While, high standing crop during post-rainy season was obtained when the rate of decomposition declines due to fall in soil moisture level and atmospheric temperature.

Production estimates are usually based on time series data of root biomass collected during a growing season by sequential coring method. Many authors have reported that estimates of total root production from biomass data can be a serious underestimation due to unaccountable losses by root respiration, decomposition and exudation. On the other hand, Singh *et al.* (1984) suggested that variations in the root mass can lead to extremely large estimations of root production if all positive increments of root mass during successive samplings are summed up. According to Sims and Singh (1978), the summing up of significant positive increases in root mass during successive samplings appears to give reliable results. In the present study, the production estimates of fine roots are based on the latter method.

In most of the fine root production studies, it has been suggested that a large flux of belowground organic matter takes place through this component. The contribution of fine roots to the total root that varied between 57 and 81% in the three forest regrowths, is higher than those reported by Harris *et al.* (1977) for a mixed temperate deciduous forest, and Persson (1978) for Scots pine stands. Similarly, root production in the 7-year old regrowth was higher than a 7-year old 'jhum' fallow (8719-9611 kg ha^{-1} yr^{-1}) located at a lower altitude (950 m asl, Barapani), about 30 km away from the study area (Boral 1993). Relatively higher proportion of fine roots in the 7-year old regrowth compared to the older stands is attributed to the dominance of perennial grasses and evergreen *Pinus kesiya* saplings, both of which have the tendency of accumulating more organic matter in the belowground parts (Persson 1979, Vogt *et al.* 1991). The

results from the older regrowths agree with the findings of Ford and Deans (1977) who hypothesized that high concentration and production of fine roots in the surface soil layers of Sitka spruce (*Picea sitchensis*) plantations were related to higher nutrient concentrations and greater moisture retention due to accumulation of plant litter on the soil surface. Persson (1983) reported that better soil conditions promote faster development of fine roots. The results obtained in the present study do not agree fully with the findings of several workers who suggested that low availability of water in soil, and low light and nutrients in forest ecosystems increases the contribution of roots to the forest-floor detrital pool (Vogt *et al.* 1991), since root production was positively correlated with WHC, organic-C, TKN and available-P. A decline (*ca.* 20%) in fine root production from 1993 to 1994 was related to low annual rainfall thereby low soil moisture during 1994 (1565 mm) as compared to the preceding year (2094 mm).

Changes in fine root mass with increasing stand age have been examined by several workers in forest ecosystems (Scholtes 1953, Karizumi 1968, Vogt *et al.* 1981). In a comprehensive review article on root mass, Santantonio *et al.* (1977) concluded that complete occupation of the forest site by fine roots occur early in stand development, it peaks and levels off as physiological and ecological factors limit fine root mass per hectare at some upper limit. In the present study, the fine root mass as well as production peaked after 12 years of regrowth and then leveled off. In the temperate region, Karizumi (1968) and Vogt *et al.* (1983) recorded peak fine root mass in 20-year old stands of *Cryptomeria japonica* and *Abies amabilis* forests, respectively, while Scholtes (1953) obtained similar results in 25-year old loblolly pine and short-leaf pine stands. In a dry tropical area, Singh and Srivastava (1984) reported peak fine root mass in a 20-year old *Tectona grandis* forest.

Plate 7.1. Status of fine roots on the soil surface in (a) 7-, (b) 13- and (c) 16-year old regrowths.

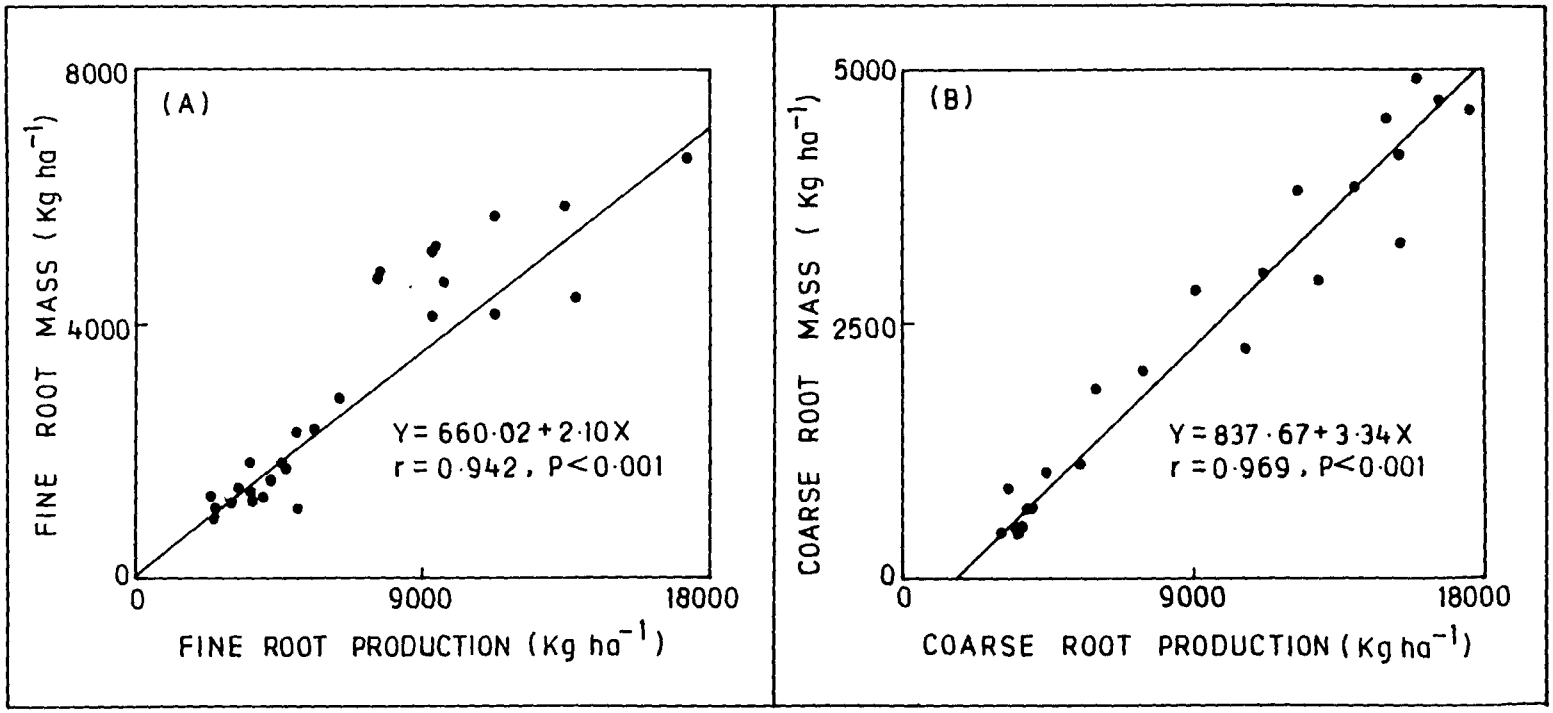


Figure 7.20. Relationship between production and standing crop of (A) fine and (B) coarse roots in the regrowing forest stands. Data points were plotted irrespective of stand age.

Ehrenfeld *et al.* (1992) and Visalakshi (1994) suggested that plant density and basal area may influence the root mass. The findings of the present study corroborate their view, as there were significant positive correlations between fine root mass and the above-said vegetation characteristics (Table 7.7).

Vogt *et al.* (1981) suggested that organic matter accumulation during stand development provides increased habitat space for root growth, and therefore, the root biomass expands to fill the available space. Our data support this contention, since both fine root mass and litter accumulation on the forest floor increased simultaneously during the course of vegetation recovery. The litter layer increases nutrient availability in the top soil (0-10 cm) layer by reducing leaching and translocation of particles (Ehrenfeld *et al.* 1992) and gives shelter to the surface roots and provides a moist microclimate for the development of new roots. This was observed in case of 13- and 16- year old regrowths where numerous fresh roots formed a dense root mat on the soil surface (Plate 7.1).

A significant positive correlation between root production and accumulation (Figure 7.20) indicated a positive feed-back mechanism in the fine root dynamics during the course of vegetation recovery after disturbance. Similar relationships have also been established by Srivastava *et al.* (1986) in *Tectona grandis* forests, and by Lamotte (1975) in savanna stands.

NUTRIENT ACCUMULATION

Fine roots play an important role by accumulating detritus and redistributing nutrients into the soil profile (Persson 1990). The nutrients that are released during decomposition of both above and belowground litter are mostly transferred directly to the surface feeding roots (Walter 1971).

McClaugherty *et al.* (1982) on the basis of their study on fine root dynamics in a mixed hardwood forest and red pine plantation reported small seasonal fluctuation in N concentration in fine roots. Similar findings have been reported from *Picea sitchensis* (Alexander 1985) and *Pinus radiata* (Nambiar 1987) plantations. Coutts and Phillipson (1976) suggested that nutrients could be internally translocated within the roots from nutrient rich area to nutrient poor zones resulting in similar concentration throughout the root system, despite environmental heterogenieties. In the present study, nutrient concentration in fine roots was influenced more strongly by the species composition of the stand than by the seasonal cycle. Other factors which influenced nutrient concentration in roots was the relative proportion of dead tissue or necromass and larger roots which had invariably lower concentration than the live and smaller roots. Nambiar (1987) attributed low concentrations of N and P in the root necromass to their translocation to the live tissues during senescence. Newman and Eason (1989) and Khiewtam and Ramakrishnan (1993) assigned the reduction in nutrient concentration with increasing root diameter to the increase of dead woody tissues containing fewer nutrients.

Concentration alongwith root mass influenced N and P accumulation in fine and coarse roots. Thus high nutrient concentration (N = 0.90%, P = 0.06%) and greater root mass in the 13-year old regrowth resulted in higher nutrient accumulation in this stand than in the 16- and 7-year old regrowths. In all three forest regrowths, the relative abundance of N and P in fine and coarse roots was in the order of N>P, agreeing with the findings of Nambiar (1987), Khiewtam and Ramakrishnan (1993) and Visalakshi (1994).

DRY MATTER AND NUTRIENT TURNOVER

Turnover estimates for fine roots are available from a mixed hardwood forest and *Pinus resinosa* plantation (McClaugherty *et al.* 1982) and *Tectona grandis* forests (Srivastava *et al.* 1986). The turnover rate obtained in the present study, are high compared to the values reported in the above studies. But they are comparable to a wet heathland ecosystem in the Netherlands (Aerts *et al.* 1992). A decreasing trend in both biomass and nutrient turnover rates in fine and coarse roots from 7- to 16-year old regrowth suggests a gradual development of organic matter and nutrient conservation mechanisms during secondary succession (Grime 1979, Chapin 1980, Aerts 1990). Higher turnover rates of fine and coarse roots in the subsoil layers (10-30 cm depth) is in confirmity with the findings of Nilson (1970) who reported greater root turnover in deeper soil layers of hay-meadow. Lower turnover values for fine roots than the coarse roots do not agree with the results obtained by Srivastava *et al.* (1986) and Vogt *et al.* (1986) who reported higher turnover rates for fine roots.

Dominance of *Pinus kesiya*, a species with high potential growth rate (Das and Ramakrishnan 1985) and abundance of herbaceous plants, especially grasses whose roots decompose at a faster rate than the tree roots (Vogt *et al.* 1986), might have resulted in a higher rate of root turnover in the 7-year old regrowth (Table 7.16). On the contrary, relative stability in the physical environment (soil moisture, soil temperature, air temperature and relative humidity) which favours greater accumulation of fine roots (Berish 1982) might have reduced the turnover rates in 13- and 16-year old regrowths. Persson (1983) also observed similar trend in fine root turnover in *Pinus sylvestris* forest along an age sequence.

ROOT CHEMISTRY AND DECAY DYNAMICS

N and lignin concentrations of fine roots in the present study are well within the range (0.25-1.67% N and 20.8-59.1% lignin) reported for

various forest ecosystems of the world (Persson 1982, McClaugherty *et al.* 1984, Vogt *et al.* 1991). However, these values are relatively higher than those obtained for leaf litter both in this study and other studies carried out in various forest ecosystems (Laishram and Yadava 1988, Upadhyay 1993, Bloomfield *et al.* 1993). Cellulose concentration in fine roots (29.4-37.4%) was very low compared to a dry tropical bamboo savanna (64.1%, Tripathi and Singh 1992).

Decomposition pattern of fine roots was characterized by three distinct phases of weight loss in all three forest regrowths. The initial slow rate of decay until 60 days could be attributed to the time-lag in colonization and establishment of microbes on the root mass (Alexander 1977). The next rapid phase of weight loss may be ascribed to the utilization of readily available energy sources by microbes and loss of water-soluble components and non-structural carbohydrates from the fine roots (Bloomfield et al., 1993). A marked reduction in the decay rate during the third phase might be related to the relatively higher percentage of recalcitrant fractions like cellulose, lignin and tannin in the decaying root tissue. These materials are known to control decomposition rate through their own resistance to enzymatic attack and by physically interfering with the decay of other chemical fractions of the cell wall (Alexander, 1977).

Within the three-phased decay pattern, seasonal fluctuations were observed in all three stands. For instance, the rate of decay was faster during rainy than winter season. Seasonality in litter decomposition observed by many workers in the tropical forest ecosystems and has been attributed to the soil moisture condition (Rochow, 1974; Bhatt et al., 1985), ambient temperature (Swift et al., 1979) and microbial activity (Singh and Gupta, 1977). Significant ($P<0.01$) positive correlations between the rate of weight loss and rainfall and soil moisture content revealed

that these factors also influenced the root decay. Apart from edaphic and climatic factors, initial N and lignin concentrations also influenced decomposition rate of fine roots (Vogt et al., 1991; Bloomfield et al., 1993). Thus, relatively faster rate of weight loss during the first phase of decomposition in the 7-year old regrowth than in the older regrowths could be ascribed to higher initial N concentration and lower cellulose content. Pandey and Singh (1981) noted that high nitrogen concentration in litter enhanced decomposition in an oak-conifer forest. Tripathi and Singh (1992) found that roots having low cellulose contents decomposed at a faster rate. A significant negative correlation between initial lignin content and decomposition rate confirms the findings of Meentemeyer (1978) and Swift et al. (1979).

The annual decay constants (k) for fine roots in the 7-, 13- and 16-year old regrowths (1.62-1.74) are comparable to those reported for dry tropical bamboo savanna (1.71; Tripathi and Singh, 1992), teak forests (0.55-1.94; Singh et al., 1984) and 'jhum' fallow in subtropical climate (1.56; Boral, 1993).

N AND P MINERALIZATION DURING DECOMPOSITION

The initial decrease in N and P concentration in the decomposing fine roots might be the result of leaching during the rainy season. Subsequent, short-term increase during autumn and winter could be attributed to microbial immobilization (Anderson*, 1973), nutrient inputs from throughfall and atmospheric precipitation (Bocock, 1963) and atmospheric N_2 fixation (Wood, 1974).

In all three stands, N and P release was influenced by the seasonal cycle of immobilization and mineralization. The rainy season being more favourable for mineralization, was marked by a rapid rate of release of N and P, contrary to the winter when immobilization was the dominant process on the forest floor.

N and P mineralization rates, however, differed in the three regrowths; the former being faster in the 7-year old regrowth and the latter in the 16-year old regrowth. Causes and significance of such a differential pattern of N and P mineralization in young and old regrowth is not clearly understood, but this might have definitely contributed to the enhanced P availability in soils supporting the older regrowths.

CHAPTER 8

GENERAL DISCUSSION

* COMMUNITY DYNAMICS AND TREE REGENERATION
* FOREST MICROCLIMATE
* CHANGES IN SOIL CHARACTERISTICS
* ROLE OF LITTER IN SOIL ORGANIC MATTER AND N AND P DYNAMICS
* ROLE OF FINE ROOTS IN SOIL ORGANIC MATTER AND N AND P DYNAMICS
* RELATIVE IMPORTANCE OF LITTER AND FINE ROOTS

COMMUNITY DYNAMICS AND TREE REGENERATION

The study of floristic composition and other important community parameters in the three stands revealed that the early successional community that developed after partial tree cutting in a subtropical humid forest was characterized by the predominance of grasses and seedlings and saplings of shade intolerant *Pinus kesiya*. Shade tolerant species were uncommon in the community due to high light intensity and relatively low soil moisture. However, gradual closing of canopy due to growth of sprouts from the cut trees of *Q. dealbata*, *R. arboreum*, *Q. griffithii* and *S. khasiana* led to a marked alteration in the microclimate within the community favouring the growth of shade tolerant species in the ground vegetation.

The change in the community structure in terms of species composition was slow from 7- to 13-year old regrowth as is evident from higher dissimilarity index between the two stands. This difference was gradually narrowed down between 13- and 16-year old regrowths indicating greater similarity between the two with respect to species composition and physiognomy. The species richness index (Magurran 1988) also increased during vegetation recovery, approaching to a level comparable to an undisturbed oldgrowth humid subtropical forest of the area (Rao *et al.* 1990).

There was an overall straight-line negative relationship between density and diameter of the trees in all stands. However, a gradual increase in the frequency of larger DBH trees (25-30 cm)in the older stands indicated progressive stabilization in the tree population within the community.

All broadleaved tree species at the study site regenerated through sprouts. An assessment of the sprouting behaviour of different tree species in terms of average sprout number per stump indicated that *Q. dealbata* , *Rhododendron arboreum*, *Quercus griffithii* and *S. khasiana* were good sprouters (5-6 sprouts per stump) as compared to species like *Myrica esculenta*, *Litsea khasiana*, *Castonopsis kurzii* and *Schima wallichii* having 2-4 sprouts per stump. The sprouting potential of the stumps depended mostly on diameter, height and angle of the cut (Khan 1986). There was a marked increase in the number of sprouting stumps from 7- to 16-year old stand, clearly suggesting faster recovery in the older stands. However, after 13 years the pace of recovery declined as is evident from RSG values which registered only 12% increase from 13- to 16-year old regrowth.

FOREST MICROCLIMATE

Analysis of forest microclimate indicated that the light intensity and air temperature near the ground were reduced by 11%, while relative humidity increased by *ca.* 20% from 7- to 16-year old regrowth. Soil temperature in the surface layer (0-10 cm) was relatively higher than subsurface layers. High respiratory activity due to concentration of litter, microbes and fine roots in the surface layer might have contributed to relatively high temperature in this layer. Conversely, lower metabolic activity in the subsoil layers as shown by Kaspar and Bland (1992) might have resulted into a decline in temperature at lower depths.

Concentration of fine roots and organic matter in the surface soil layer (0-10 cm) influenced bulk density both along depth gradient in the soil and age gradient of the stand. A marked increase in soil moisture level during secondary succession could be attributed to a gradual closing of canopy, accumulation of litter on the forest floor, an increase in soil organic matter (SOM) and a marked difference in clay content between the stands.

CHANGES IN SOIL CHARACTERISTICS

A notable increase in organic matter content and nutrient elements in the soil from 7- to 16-year old regrowth was related to the dense growth of vegetation *vis-a-vis* greater inputs of litter and fine roots. According to Odum (1960) and Aweto (1981), the organic matter content in the top soil approaches to the level of mature forest by the end of 10th year of secondary succession. In the present study, WHC, SOM, TKN, available-P and CEC steadily increased until 16 years of regrowth. The values obtained from the 16-year old stand are comparable to those reported by Das *et al.* (unpublished data) for a mature broadleaved forest, located about 15 km away from the present study site. The changes in soil characteristics were more prominent in the top layer (0-10 cm) which received huge amount of detrital matter in the form of litter and fine roots.

ROLE OF LITTER IN ORGANIC MATTER AND N AND P DYNAMICS

Addition of detritus through annual litterfall and its accumulation increased during the course of vegetation recovery after disturbance and both were directly related to the density and basal area of woody species in the community. These results do not conform the findings of some other workers who could not establish the cause-effect relationship between basal area and litterfall in close-canopied temperate forest ecosystems (Bray and

Gorham 1964, Stohlgren 1988) and tropical moist deciduous forest ecosystem (Mohankumar and Deepu 1992). However, a significant positive correlation between litter production and age of the stand ($r=0.997$, $P<0.05$) was in agreement with the findings of Odum (1961), Das and Ramakrishnan (1987), O'Connell and Menage (1982), Toky and Ramakrishnan (1983) and Singh (1990) in succesional communities. The ratio of leaf litter to total litterfall is comparable to several other tropical rain forests (Bray and Gorham 1964).

Nutrients (N and P) input and their storage on the forest-floor litter was mainly dependent on litter production and accumulation, respectively. Significantly higher amount of N was channelized through litter than P in all regrowths. This agrees with the findings of Gosz *et al.* (1972) and Rai and Proctor (1986). Input and accumulation of N and P gradually increased upto 13 years of forest regrowth and then declined. This was related to higher N and P concentrations in the litter of the 13-year old regrowth compared to the other two stands.

The litter turnover and nutrient mineralization rates on the forest floor was influenced by the chemical composition of the decaying material. For example, leaf litter showed a faster turnover rate than the non-leaf litter since it usually had low lignin and high N concentrations than the non-leaf litter and was devoid of much of the sclerophyllous cells (Singh and Gupta 1977, Swift *et al.* 1981, Vogt *et al.* 1991, Couteaux *et al.* 1995). High lignin and low N concentrations resulted in a markedly slow rate of decomposition in the leaf litter of *R. arboreum*. On the contrary, needles of *P. kesiya* in the 7-year old regrowth, with high lignin and high nitrogen concentrations (Table 6.13) showed rapid weight loss in comparison to other broadleaved species, thereby indicating an overriding influence of N concentration in litter decay. Besides chemical composition, rainfall, soil moisture and mean air temperature strongly influenced the rate of leaf litter decomposition in all three stands. The faster decay of *Q. dealbata*

leaves in the 16-year old regrowth than in the 13-year old regrowth is attributed to the favourable changes in the forest microclimate that led to better growth and activity of soil microbial population.

N and P release during leaf litter decay was influenced by seasonal cycle in climatic variables. Warm-humid season being more favourable for mineralization was characterized by rapid rate of N and P release from the decomposing leaf litter contrary to the winter when immobilization was the dominant process on the forest floor. About 90% of the N and P returned through annual litterfall, was recycled every year, and their turnover rates did not vary between the stands.

ROLE OF FINE ROOTS IN ORGANIC MATTER AND N AND P DYNAMICS

The fine roots followed a unimodal growth pattern in the regenerating forest stands. In the 7-year old regrowth root mass peaked during autumn, while in the other two stands the peak values were obtained during winter/spring season. High root mass generally coincided with the period of shoot/leaf senescence and low spring biomass corresponded to the period of active shoot growth. The seasonal changes in fine root mass also reflected the variation in production and decomposition processes through seasons (Ford and Deans 1977, Srivastava *et al.* 1986, Visalakshi 1994). For instance, low fine root mass occurred in July (peak rainy month) when decomposition rate was at its peak due to high temperature and humid conditions. While, high standing crop during post-rainy season was synchronized with a decline in decomposition rate due to fall in soil moisture level and atmospheric temperature. This suggests that root growth and mineralization processes were not synchronized in the developing communities. However, such a synchronistic relationship between fine root growth and nutrient mineralization is expected in ecosystems which are in static equilibrium (Aber *et al.* 1983, Couteaux *et al.* 1995)

About 83% of the total roots were present in the top 0-20 cm soil layer. This value is very high compared to 60% concentration of fine roots in the top 15 cm layer in *Pinus taeda* (Harris *et al.* 1977) and 71% in *Abies amabilis* (Vogt *et al.* 1981) plantations. Relatively greater proportion of fine roots in the 7-year old regrowth compared to the 13- and 16-year old stands is attributed to the dominance of greases, tree seedlings and saplings in the early successional community. A gradual transformation of fine feeder roots of trees into large structural roots during vegetation recovery might have resulted into decline in the proportion of fine roots in the older regrowths.

Results obtained in the present study fully corroborates the findings of Ford and Deans (1977) who opined that production and accumulation of fine roots in the surface soil layers were related to high nutrient concentration and greater moisture retention in the soil surface. However, the results do not agree with the findings of several other workers (cf. Vogt *et al.* 1991).

Since litter and organic matter on the forest floor provide space for root growth (Vogt *et al.* 1981), a gradual increase in the root biomass from 7- to 16-year old stand could be related to litter accumulation during the course of vegetation recovery.

During the initial phase of decomposition, the fine root turnover was faster in the 7-year old regrowth which could be attributed to higher initial N and lower C/N ratio. Pandey and Singh (1981) have also reported that initial nitrogen concentration plays an important role in organic matter decomposition in an oak-conifer forest. An overall increase in decay rate during revegetation of the disturbed stand could be related to a variety of factors such as rainfall, soil moisture, soil pH, SOM content, and microbial population and its activity.

Table 8.1 Annual balance sheet of litter and fine roots and net gain of organic matter (OM), N and P in soil during 1993-1994 in the three forest regrowths.

Variable	7-year old regrowth			13-year old regrowth			16-year old regrowth		
	OM	N	P	OM	N	P	OM	N	P
Initial stock (A) (January 1993)									
Soil	188679.7	11853	8.42	271881.0	15781	28.57	420150.0	21433	34.52
Litter									
Leaf	1518.6	14.73	0.76	1580.6	22.60	0.95	2204.4	21.16	1.32
Total	1959.4	16.92	0.99	3241.9	37.97	1.79	2840.7	25.72	1.58
Roots									
Fine	4934.7	43.86	3.46	11319.8	98.19	6.56	12301.6	51.86	8.10
Total	5232.7	45.49	3.62	12285.6	103.77	7.02	22295.9	57.42	8.76
Annual input (B)									
Litter									
Leaf	10357.7	98.10	4.80	12949.2	141.30	7.40	14825.8	111.40	7.30
Total	11902.4	106.10	5.20	16059.1	153.40	8.60	17492.1	128.50	8.70
Roots									
Fine	18648.3	157.86	10.90	22283.3	189.08	11.96	18619.5	160.22	8.81
Total	23028.8	181.60	13.25	39060.3	275.09	19.61	30885.9	234.82	15.13
Total input (A+B)									
Litter									
Leaf	11876.3	112.83	5.56	14529.8	163.90	8.35	17030.2	132.56	8.62
Total	13861.8	123.02	6.19	19301.0	191.37	10.39	20332.8	154.22	10.28
Roots									
Fine	23583.0	201.70	14.36	33603.1	287.27	18.52	30921.1	212.10	16.91
Total	28261.5	227.10	16.87	51355.9	381.86	26.63	53181.8	292.24	23.89
Final stock (C) (October 1994)									
Soil	210459.0	12350	34.80	303129.2	17208	51.36	432068.9	22008	56.52
Litter									
Leaf	875.3	7.69	0.47	1204.8	13.67	0.76	1491.4	15.54	0.82
Total	1003.2	8.49	0.60	1386.2	15.14	0.84	1622.1	18.22	0.90

Table 8.1 continued

Variable	7-year old regrowth			13-year old regrowth			16-year old regrowth		
	OM	N	P	OM	N	P	OM	N	P
Roots									
Fine	6081.5	50.75	3.71	8627.7	105.78	5.94	9431.8	52.10	6.28
Total	7492.9	58.50	4.38	13367.0	188.33	8.10	12035.8	71.31	7.57
Release during decomposition									
Litter									
Leaf	11001.0	105.14	5.09	13325.0	150.23	7.59	15538.8	117.02	7.81
Total	12858.6	114.53	5.59	17914.8	176.23	9.55	18710.7	136.00	9.38
Roots									
Fine	17501.5	150.95	10.65	27975.4	181.49	12.60	21489.30	160.00	10.63
Total	20768.6	168.60	12.49	37988.9	193.53	18.53	41146.2	221.03	16.32
Net Gain in soil (C - A)	21779.3	497.00	26.38	31468.2	1427.00	22.79	11918.9	573.00	22.00

All the values are expressed in kg ha^{-1}

The annual decay constants for fine roots in the 7-, 13- and 16-year old regrowths (k=1.62-1.74) were well within the reported range for forests and croplands in the tropic (0.3-3.0). But the values are very high as compared to those (0.02-0.71) reported for the temperate ecosystems.

N and P mineralization pattern was similar in all regrowths, but their rates varied in the three stands; the former being faster in the young stand and the latter in the old stand. Causes and significance of such a differential rate of N and P mineralization in young and old regrowths is not clearly understood, but this might have definitely contributed to the P availability in soils supporting the older regrowths.

RELATIVE IMPORTANCE OF LITTER AND FINE ROOTS

Annual input of organic matter on the forest floor and mineralization of N and P during decay of both litter and fine roots increased for about 13 years of secondary succession following disturbance, after which they were leveled off. Annual balance sheet of organic matter, N and P inputs, their accumulation and release are given in Table 8.1. Fine roots added more to organic matter, and N and P dynamics in the soil than the litter. Litter contributed *ca.* 12-23% N and 24-44% P to the net annual gain in soil. While, the corresponding values for the fine roots were 13-30% and 42-57%, respectively.

In case of fine roots, mineralization rate of N was higher than P during early stages of vegetation recovery. This trend was reversed after 15 years of regrowth. Conversely, P turnover rate in the litter was faster in 16-year old regrowth, while N turnover was maximum in the 7-year old regrowth. Such an alteration in mineralization and turnover rates of N and P during the course of vegetation recovery could be a reflection of the change in nutrient requirements of vegetation during the course of time.

The input:output ratio for litter-N (1.07-1.13) and -P (1.09-1.11) did not vary significantly between regrowths. Whereas the, ratios for both fine root-N (1.32-1.59) and P (1.35-1.57) increased from 7- to 16-year old regrowth. In general, the input-output ratios for litter mass and nutrients increased with the progression of vegetation recovery, while those for the fine roots increased significantly from 7- to 13-year old regrowth only. Further, greater input of organic matter and nutrients through fine roots coupled with faster release of nutrients than the litter indicated that fine roots played a more important role in the organic matter and nutrient accumulation in soil during revegetation of the disturbed humid subtropical forest ecosystem.

CHAPTER 9

SUMMARY

* VEGETATIONAL CHANGES
* MICROENVIRONMENTAL AND EDAPHIC CHANGES
* ROLE OF LITTER
* ROLE OF FINE ROOTS
* CONCLUSION

The humid subtropical broadleaved forests of Meghalaya are exposed to various kinds of anthropogenic disturbances of varying magnitude caused by shifting agriculture and massive tree felling for developmental and fuelwood purposes. The disturbed forests are often left for natural recovery of vegetation and soil fertility. The main objective of the present study was to study the relative importance of litter and fine roots in organic matter and N and P dynamics in soil during recovery of degraded humid subtropical forest ecosystem in Meghalaya. Besides emphasising the role of litter and fine roots, changes in soil and vegetation characteristics and microclimatic conditions were also investigated. The study was conducted during 1993-94 in 7-, 13- and 16-year old stands, regrowing after selective tree cutting in a subtropical humid forest ecosystem located near Shillong (latitude 25°34'N, longitude 91°56'E, altitude 1900 m asl), the capital of Meghalaya, India.

VEGETATIONAL CHANGES

The 7-year old regrowth was dominated by early successional species like *Eupatorium adenophorum*, *Litsea elongata*, *Pinus kesiya* and sprouting stumps of *Quercus dealbata*, *Corylopsis himlalayana* and *Schima khasiana*. The 13-year old regrowth having thin ground vegetation was dominated by *Q.*

dealbata and *C. kurzii*. *Rhododendron arboreum* and *Q. dealbata* were dominant in the 16-year old regrowth. In this stand the forest floor had a dense growth of shade-tolerant herbs, pteridophytes and mosses.

The number of species in the community sharply declined from 41 in the 7-year old stand to 25 in the 16-year old regrowth. But the number of tree species as well as its species richness index markedly increased during the same period. The species richness index of shrub and herb species, however gradually declined with the regrowth of the forest.

Density and basal area of trees increased significantly from 180 plants ha^{-1} and 3.1 m^2 ha^{-1} in the 7-year old regrowth to 1140 plants ha^{-1} and 44.2 m^2 ha^{-1}, respectively in the 16-year old regrowth. The shrub density was lowest in the 16-year old regrowth and highest in the 13-year old regrowth. Density and basal area of herbaceous species were maximum in the 7-year old stand and minimum in the 13-year old stand. Dominance in the 16-year old community was more evenly distributed than in the 7- and 13-year old regrowths. In all regrowths, tree density and diameter showed an overall straight-line negative relationship.

Broadleaved tree species regenerated mainly through sprouts, while the needleleaved *P. kesiya* reproduced through seeds. Sprouting stumps constituted 43, 75 and 87% of the total stump density in 7-, 13- and 16-year old regrowths, respectively. As a result, density increased from 220 ha^{-1} in the 7-year old regrowth to 1350 ha^{-1} in the 16-year old regrowth. The sprout growth in terms of number and basal area was relatively faster between 7- and 13-year old regrowth than between 13- and 16-year old stands.

MICROENVIRONMENTAL AND EDAPHIC CHANGES

Light intensity and air temperature near the ground showed a significant decline from 7- to 16-year old stand. Relative humidity,

however, showed a reverse trend. Soil moisture content increased with increasing stand age, while soil temperature showed a reverse trend. Generally, the temperature and moisture content in the surface soil layer (0-10 cm) were higher during rainy and autumn seasons, but subsurface layers (10-20 and 20-30 cm) had greater soil moisture content during winter and spring seasons. Both WHC and CEC declined with soil depth, but increased with stand age.

Soil texture varied from sandy loam in the 7-year old regrowth to sandy clay loam in the 13-year old regrowth and clay loam in the 16-year old regrowth. Soil pH fluctuated within a narrow range of 4.9-5.6 without showing significant seasonal and depthwise variations. SOC and SOM were significantly lower during rainy season and higher during autumn in all three forest regrowths. Both of them decreased with the increase in soil depth. Seasonal trends of TKN and available-P were similar to SOC. In general, SOC, SOM, TKN, available-P increased with the progressive development of vegetation.

ROLE OF LITTER

Litter accumulation on the forest floor increased significantly from 1231 kg ha^{-1} in the 7-year old regrowth to 2007 kg ha^{-1} in the 13-year old regrowth, and then it became levelled-off. Leaf litter mass on the forest floor increased with the progression of vegetation recovery. Accumulation of woody litter (<20 mm diameter) was more in the 13-year old regrowth compared to the 7- and 16-year old regrowths. In all stands, litter accumulation was maximum during winter or spring and minimum during autumn.

Litterfall increased significantly from 11902 kg ha^{-1} in the 7-year old regrowth to 17402 kg ha^{-1} in the 16-year old regrowth. The contribution of leaf litter to the total litter production in the three stands ranged between 78 and 88%. Production and accumulation of litter were positively

correlated with density and basal area of woody species, and OM, TKN and available-P in soil. In all regrowths, turnover rate of the leaf litter was faster than the woody and miscellaneous litter.

N concentration in the forest-floor litter was maximum either during autumn or winter, and minimum during spring in all three regrowths. While its concentration in the fresh litter was higher during autumn and lower during rainy season. Seasonal variation in P concentration both in forest-floor litter and fresh litter was not significant. Leaf and miscellaneous litter had higher N and P concentrations than the woody litter.

Mean standing state of N and P in the forest-floor litter was maximum in the 13-year old regrowth and minimum in the 7-year old regrowth. Generally, leaf litter accumulated more N and P than the woody and miscellaneous litter fractions. Seasonal variation was significant only for N. Addition of N and P to the forest floor through litter in the three regrowths exhibited a marked seasonality with highest inputs during February-April and lowest during June-September. Leaf litter contributed to about 80-99% N and 70-80% P annual nutrients input thorugh litter. N input through litter was maximum in 13- and 16-year old regrowths, and minimum in the 7-year old regrowth, while P input increased from young to old stand.

Decay pattern of leaf litter varied significantly between species and stands. Needles of *P. kesiya* decomposed in a three-phased manner, whereas, all broadleaved tree species except, *R. arboreum* showed only two phases. Leaves of *R. arboreum* decomposed at a constant rate throughout the study period. A composite linear decay model ($Y=a+bX_1+cX_2+dX_3$), fitted well for the decay pattern of *P. kesiya*, while a simple linear regression function, $Y=a+bX$ explained the weight loss pattern of *R. arboreum* leaf litter during decomposition. For other species, a multiple regression equation, $Y=a+bX_1+cX_2$ was more appropriate.

Decompositon of leaf litter (weight loss, mg day-1) was significantly correlated with initial lignin and N concentrations and lignin/N ratio of the litter, soil moisture, pH and TKN, and mean daily rainfall and mean monthly air temperature. N and P mineralization patterns during decomposition of leaf litter were similar in all five tree species studied. All of them were characterized by a phase of active N mineralization during rainy season followed by a period of microbial immobilization during winter.

ROLE OF FINE ROOTS

Fine root mass (FRM, <2 mm diameter) increased significantly from 6751 kg ha^{-1} in the 7-year old regrowth to 9088 kg ha^{-1} in the 16-year old regrowth. Coarse root mass (CRM, 2-15 mm diameter) as well as total root mass (TRM=FRM+CRM) increased significantly from the 7-year old regrowth to the 13-year old regrowth, beyond this age the increase was not significant.

The proportion of FRM decreased from 87% in the 7-year old regrowth to 77% in the 16-year old regrowth. The contribution of coarse roots followed a reverse trend. As a result, FRM/CRM ratio was significantly higher in the 7-year old regrowth than the 13- and 16-year old regrowths. In all three forest regrowths, the ratio was generally higher during winter and lower during rainy season.

Fine roots were concentrated (upto 65% of the TRM) mainly in the top soil layer (0-10 cm) in all three stands, and their proportion declined upto 19% in the 10-20 cm layer and further down (20-30 cm depth) to 15%. The amount of fine roots in the top soil layer increased with the increase in the age of the stand, but their proportion declined from 63% in the 7-year old regrowth to 57% in the 16-year old regrowth.

Annual fine root production increased upto 13 years of forest regrowth, after this age, the production declined by *ca.* 10% during next 3

years of regrowth. The contribution of fine roots to total root production decreased significantly from 88% in the 7-year old regrowth to 50% in the 16-year old regrowth.

Fine root productivity (kg m^2 day^{-1}) was positively correlated with mean monthly rainfall and maximum and minimum temperatures, SOM, TKN and available-P. Apart from these edapho-climatic factors, density and basal area of the woody species in the community also influenced the production and accumulation of fine roots. Turnover rate of fine roots did not vary significantly between regrowths and soil depths.

Fine roots had greater N and P concentrations than the coarse roots. Similarly live fraction of the fine roots had greater nutrients concentration than the necromass.

In all three regrowths, N accumulation in fine roots was maximum either during autumn or winter, and minimum during rainy season. On the other hand, maximum N stock in coarse roots was obtained during rainy or post-rainy seasons, and minimum during spring. N stock in fine roots was significantly ($P<0.05$) higher in the surface soil layer than the subsurface layers. Seasonal trend of P accumulation in fine and coarse roots was similar to N, but its stock was inversely related to soil depth.

Maximum amount of N (189 kg ha^{-1} yr^{-1}) was returned to the soil through fine roots in the 13-year old regrowth and the input was minimum (158 kg ha^{-1} yr^{-1}) in the 7-year old regrowth. P input through fine roots was also maximum (12 kg ha^{-1} yr^{-1}) in the 13-year old regrowth, but its minimum value (9 kg ha^{-1} yr^{-1}) was recorded in the 16-year old regrowth.

Fine roots decomposed in a three-phased manner. The decay rate was positively correlated with mean daily rainfall, soil moisture and pH, and negatively correlated with initial lignin concentration. The decay constant (k=1.62-1.74) increased with the age of the regrowth.

Release of nutrients from decaying fine roots was also influenced by seasonal cycle of mineralization and immobilization processes. Winter represented the period of N and P immobilization, while rainy season was the period of rapid mineralization when N and P contents in the decomposing fine roots recorded 46-58% decrease from the preceding spring season. The net annual N mineralization showed a marginal decrease from about 51% in the 7-year old regrowth to 46% in the 16-year old regrowth, while P showed a reverse trend by registering an increase from 37 to 51%, thereby contributing to its greater availability in the soil supporting the older regrowth.

CONCLUSION

The three forest regrowths differed markedly in community structure, soil physico-chemical properties and detritus (litter and fine roots) input, accumulation and turnover, despite the fact that all of them are located on a similar toposequence and have developed under similar climatic conditions. Recovery in soil fertility in the disturbed stands was closely related to the regrowth of woody vegetation, since production and accumulation of litter and fine roots were significantly correlated to the density of woody elements in the community. Litter production increased during vegetation regrowth until 16 years, but the fine root production showed a steady increase upto 13 years of forest regrowth, beyond this it levelled-off. Similar trend was observed in case of litter and fine root accumulation also. Accumulation of litter and fine roots were related to each other, but the latter added more organic matter, N and P to the soil thereby playing a more important role than the former in nutrient restoration in soil during the recovery of disturbed subtropical forest ecosystem.

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