ROLE OF FINE ROOTS AND SOIL MICROBES IN C, N & P DYNAMICS IN A HUMID TROPICAL FOREST ECOSYSTEM OF NORTHEAST INDIA

BY
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THE NORTH EASTERN HILL UNIVERSITY

DECLARATION

I, Atiqur Rahman Barbhuiya, hereby declare that the subject matter of this thesis entitled "**Role of fine roots and soil microbes in C, N & P dynamics in a humid tropical forest ecosystem of northeast India**" is the record of work done by me, that the content of this thesis did not form basis of the award of any previous degree to me or to the best of my knowledge to anybody else, and the thesis has not been submitted by me for any research degree in any other University/Institute.

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

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Chapter 1

Introduction

The tropical rainforests are dense, evergreen vegetation characterized by high diversity of plant and animal species. They are one of the most fragile and complex terrestrial ecosystems on Earth, presently occupying less than 7% area of Earth's surface in America, Southeast Asia and Africa (Richards 1952; Whitmore 1998). Within continental Asia, patches of tropical rainforests are found in Indo-China, South China and northeast India (Whitmore 1998). The tropical wet evergreen forest patches also occur in the Western Ghats of India. In northeast India, tropical rainforests are restricted to the far eastern part of the region, particularly in Tirap and Changlang districts of Arunachal Pradesh and Tinsukia and Dibrugarh districts of Assam. Although a major portion of these forests has been brought under protected area management, they are still threatened by anthropogenic activities.

Tropical forests worldwide are exposed to a variety of disturbances ranging from frequent localized events to less frequent, landscape level or multiple disturbance events. Natural disturbances and concomitant recovery are integral aspects of normal ecosystem behaviour (White 1979). Human disturbances, on the other hand, differ in kind, scale, intensity and frequency and sometimes they may be more severe and extensive than the natural disturbances. Shifting cultivation and extraction of timber and NTFP's species are major causes of disturbance in the humid tropics (Reiners 1980), which have destroyed vast tracts of the humid tropical forest ecosystem. Logging and timber removal or

conversion of forest to other land uses has long-term consequences on secondary vegetation, nutrient cycles and water balance (Turner *et al.* 1997).

Several workers have reported that removal or loss of forest cover alters physico-chemical characteristics of soil (Joergensen and Raubuch 2002) and adversely affects the soil hydrological regime, microclimate, energy balance and enhances soil erodibility (Fenn *et al.* 1993). Input of organic matter and nutrients to soil through litter and root mass help improve nutrient availability by favourably altering the hydrology and physico-chemical and biological properties of the soil. The periodicity, extent and pattern of litter fall and litter decomposition are important in this respect (Ambasht 1985).

The fine root system of plants play crucial roles in the fluxes of energy and matter in the ecosystem and carry out essential functions of soil resource acquisition (Aerts *et al.* 1992; Fahey and Hughes 1994). The amount of carbon and nitrogen cycled through fine roots may be as much as or more than that cycled through the above ground litter (Arthur and Fahey 1992). The development of an extensive surface root mat is one of the major mechanisms that enhance nutrient conservation in tropical rain forest, growing particularly on leached and nutrient poor soils (Jordan and Herrera 1981; Cuevas and Medina 1988). The unsuberized roots in the mat are primarily responsible for the retention of nutrients (Edwards and Grubb 1982). In the tropical rainforest fine roots confined to the topsoil layer contribute significantly to soil organic matter and nutrient dynamics in soil by their fast turnover rate (Joslin and Henderson 1987).

The fine roots increase the surface area for growth and multiplication of soil microorganisms, which play an important role in the cycling of mineral nutrients necessary for plant growth (Anderson and Domsch 1980). The soil microbial biomass

constitutes a transformation matrix for organic materials in the soil and act as a labile reservoir of plant-available nutrients (Jenkinson and Ladd 1981; Singh *et al.* 1989). Changes in the microbial population in response to variations in soil conditions (moisture, carbon, nutrients, temperature, pH) have important bearing on nutrient cycling (Diaz-Ravina *et al.* 1995). Soil microbial biomass serves as an indicator of slower and less easily detectable soil organic matter changes (Johnson and Curl 1972), and plays an active role in nutrient conservation in the tropical soils (Maithani *et al.* 1998).

The pockets of the tropical rainforest in northeast India are found in the Jeypore Reserve Forest of Assam. These are exposed to varied types of anthropogenic disturbances. Logging and extraction of NTFP's are two major human activities which are disrupting the structure and functioning of ecosystem.

Objectives

The present study analyses the role of fine roots and microbial biomass in the nutrient enrichment of the topsoil in a humid tropical forest ecosystem and evaluates the effects of anthropogenic disturbances on their dynamics. The specific objectives of the research were:

(i) To study the seasonal and spatial changes in fine roots (<2 mm diameter) and soil microbial population,

(ii) to study the accumulation of C, N and P in fine roots and microbial biomass and their turnover, and

(iii) to study the N and P mineralization patterns in the undisturbed and disturbed stands.

Chapter 2

Review of literature

Forests around the world especially those in the tropics have undergone severe disturbances due to anthropogenic activities. Among these, human settlement in forest areas, clearance of forest and its conversion into agricultural land etc., have in many cases produced harmful long-term effects leading to soil degradation and associated nutrient loss. It is well known that forest clearance for agriculture, a typical situation in the tropics, decreases biodiversity, limits natural vegetation and simplifies the ecosystem structure. The most important consequence of tree felling in the forest ecosystem is degradation of land and soil, both in terms of its structure and quality.

Disturbances which compact the soil, remove the litter layer and top soil, and increase overflow, have significant effects on nutrient cycling processes and forest regrowth. Analysis of physico-chemical properties of soil along with the changes in fine roots biomass and productivity and microbial biomass following disturbance in forest ecosystem are important for evolving appropriate strategies for the reclamation of a degraded ecosystem.

Effects of disturbance on soil

The vegetational diversity of a region is influenced by topography, soil, climate and its geographical location (Tilman 2000). Tropical rain forests are among the most diverse vegetation in the world (Whitmore 1998; Richards 1952), and their species richness and diversity are influenced by a variety of factors including soil nutrient status (Hubbell 1979; Asthon and Hall 1992) and water availability (Walsh 1996). Some studies

suggest that forests on soils of high nutrient availability may also have lower species richness than forests on intermediate nutrient availability (Lee *et al.* 2002). Species diversity has also been correlated with rainfall (Hartshom 1980) and disturbance level (Rao *et al.* 1990).

Large changes in vegetation cover are taking place in the humid tropics as forests are being converted in to pastures and agricultural fields. An expected result of the removal of tree biomass and changes in land use is decline in soil organic matter, alteration in its physico-chemical characteristics (Boyle 1975; Spaans *et al.* 1989), soil hydrological regime, energy balance and soil erodibility (Lal 1989). Deterioration of soil quality through the loss of soil organic carbon, nitrogen and other nutrients due to deforestation has been reported by several authors (Srivastava and Singh 1989). Changes in soil microenvironment due to deforestation leads to disruption of decomposition process which ultimately results in to poor carbon and nutrient balance in the soil. Nutrient dynamics in forest soil is also influenced by stand age (Gholtz *et al.* 1985), tree species composition (Miller 1984) and site conditions.

Fine root dynamics

Fine roots play an important role in the development of soil as a substrate (Berg 1986; Joslin and Henderson 1987), though they represent only a small portion of total plant biomass (Kurz 1989; Vogt *et al.* 1991). However, the importance of fine roots in nutrient cycling and as a component of forest productivity is not proportional to their contribution to the total biomass.

The high concentration of fine roots in the top few centimeters of soil is an important feature of tropical rain forest (Klinge 1973; Jenik 1978). They are most likely

involved in the uptake of nutrients in woody plants (Bohm 1979). The greatest proportion of fine roots in many forests is located in the upper soil horizon (Vogt *et al.* 1983). They are abundant in the organic horizon accounting for 40-70% of total fine root biomass in the soil profile (Vogt *et al.* 1996). Dead roots make up 50-80% of the total biomass (Vogt *et al.* 1986) resulting from the rapid turnover of fine roots (Hendrick and Pregitzer 1993).

Studies have demonstrated large seasonal and yearly variation in fine root biomass (Santantonio and Hermonn 1985; Makkonen and Helmisaari 1998), which is influenced by vegetation and soil characteristics (Arunachalam *et al.* 1996c). Seasonal fluctuation in fine roots has been reported from tropical and subtropical forests (Silver and Vogt 1993; Singh and Singh 1993; Arunachalam *et al.* 1996c; Sundarapandian and Swamy 1996). The large structural roots (coarse roots) are more stable and do not exhibit significant seasonal or annual dynamics (Harris *et al.* 1980; Powell and Day 1991). Harris *et al.* (1980) suggested that the large roots may experience a cyclic renewal.

Fine root production is an important component of both dry matter production and nutrient cycling in forest ecosystem (Vogt *et al.* 1986; McClaugherty *et al.* 1982). Soil temperature, moisture and growth regulating substances, carbohydrate availability, respiration rate, symbiotic and competitive relationships determine root productivity (Persson 1980). The quantity and turnover of roots in forest soils have been determined by Nadelhoffer and Raich (1992) and Hendrick and Pregitzer (1993). Fine root input can be large in many forest ecosystems due to fast turnover and a high percent of total carbon allocated to the belowground compartment (Vogt *et al.* 1996). Findings of several studies suggest that the fine roots contribute significant amount of detritus to the decomposition system (McClaugherty *et al.* 1982; Vogt *et al.* 1982; Bloomfield *et al.* 1993;

Arunachalam *et al.* 1996b) through fast turnover rate. Root turnover is an important carbon pathway to the soil (Dilustro *et al.* 2002). Several methods have been employed for estimating fine root turnover in perennial ecosystem and the values obtained by different methods are quite variable (Gill and Jackson 2000). For example, in the northern hardwood forest, the minirhizotron method yielded values ranging from 50 to 90% turnover of fine root biomass annually (Hendrick and Pregitzer 1993; Burton *et al.* 2000; Tierney and Fahey 2002), while in sequential and ingrowth coring methods 30 to 100% turnover was obtained in an annual cycle (Aber *et al.* 1985; Fahey and Hughes 1994). N budget method yielded turnover estimates as low as 30% (Aber *et al.* 1985; Nadelhoffer *et al.* 1984). The soil core method calls for the sequential collection of replicated organic and mineral soil cores throughout the growing season (Ericsson and Persson 1980). Annual production and turnover rates are based on the observed temporal fluctuations in fine root biomass (Kurz and Kimmins 1987; McClaugherty *et al.* 1982). This most commonly used method has yielded tremendous amount of information on fine roots biomass in terrestrial ecosystems (Gower *et al.* 1992). The factors that control root life span are poorly understood. It is generally accepted that in forest systems, root growth and senescence occur simultaneously during the active growing season of the plant. Life span of fine roots in forest system is estimated to vary from several weeks to several years and is often shorter than leaf life span (Hendrick and Pregitzer 1993).

Across a range of ecosystems, net belowground primary production may be greater than the above ground production and nutrient concentrations in fine roots may be higher than those in the foliage (Meier *et al.* 1985). The amount of carbon and nutrients returned to the soil by fine root turnover may equal or exceed that from leaf litter (Joslin

and Henderson 1987; Raich and Nadelhoffer 1989). Minimal retranslocation of nutrients from roots upon senescence also contribute to the importance of fine roots in nutrient cycling (Aerts 1990; Nambiar and Fife 1991). Studies revealed higher nutrient concentrations in <2 mm diameter roots than in those of 2-5 mm diameter roots (Gordon and Jackson 2000).

Nutrient release from decomposing roots is an important pathway of nutrient flux in terrestrial ecosystems (Joslin and Henderson 1987; Fahey *et al.* 1988). Fogel and Cromack (1977); Persson (1982); Vogt *et al.* (1983); McClaugherty *et al.* (1982); Bloomfield *et al.* (1993); Arunachalam *et al.* (1996d); Comas *et al.* (2000); Dilustro *et al.* (2001) have studied root decomposition in different ecosystems. Temperature, moisture and plant tissue chemistry are considered to have the greatest influence on decomposition rates (Vitousek *et al.* 1994). Nitrogen, phosphorus and carbon content influence root decomposition (Gorisson *et al.* 1995). Larger diameter roots decompose at slower rates than smaller diameter roots (Persson 1982; Gholtz *et al.* 1985; Dilustro *et al.* 2001).

Microbial biomass C, N and P dynamics

Soil microbial biomass comprises the part of soil organic matter barring the live root fractions and soil organisms larger than 5×10^{-15} m^3 (Jenkinson and Ladd 1981). The microbial indices and their relationship with various factors in the temperate (Priha 1999; Leiros *et al.* 2000; Priha *et al.* 2001), tropical (Vance *et al.* 1987; Singh *et al.* 1989; Sarathchandra *et al.* 1989; Joergensen *et al.* 1995; Salamanca *et al.* 2002; Dinesh *et al.* 2003) and subtropical (Arunachalam *et al.* 1996a; 1997; Arunachalam and Arunachalam 2000; Arunachalam and Pandey 2003; Upadhyaya *et al.* 2004) forests have been extensively studied. Microbial biomass acts as an important ecological indicator and is

responsible for decomposition and mineralization of plant and animal residues in soil. The microbial biomass may be a main source of nutrients for the plant and may help in nutrient conservation (Singh *et al.* 1989). It constitutes a transformation matrix for all the natural organic material in soil and acts as a labile reservoir of plant available nutrients (Jenkinson and Ladd 1981). According to Powlson *et al.* (1987), soil microbial biomass responds much more rapidly than the total organic matter to any change in organic inputs. Thus microbial biomass can be considered as an ecological marker for analyzing and predicting the long term effects of perturbations in soil subsystem (Smith and Paul 1990).

Due to the rapid turnover rate of microbial biomass, plant available nutrients are released faster; this makes its contribution to nutrient cycling far greater than its size might suggest (Schnurer *et al.* 1985). Therefore, changes in the size of the microbial biomass affect the cycling of N and P and their availability to plants (Diaz-Ravina *et al.* 1995).

The role of microorganisms in the turnover of C, N and P compounds in soil has been a focus of several studies of soil productivity (Sikora *et al.* 1994). The information on variation in microbial biomass and activity in relation to vegetation type, soil factors, climates are limited (Zak *et al.* 1994). There is even less information available on relationships between microbial biomass and specific microbial activities (*eg.* N mineralization, soil respiration) in forests (Schimel 1995). These relationships have important implications for evaluation of plant-soil-microbial control on ecosystem processes (Aber *et al.* 1991). Soil with a relatively high organic matter inputs usually develop a larger microbial biomass (Srivastava 1992). Strong positive correlations between microbial biomass -C and inorganic -P and -N in soil have been reported in dry

tropical soils (Srivastava and Singh 1989) and in a range of United Kingdom soils (Brookes *et al.* 1985). In dry tropical soils of India, Srivastava and Singh (1988) reported that about 96% variability in microbial -P concentration could be explained by organic -P concentration in soil. Primary productivity of forest and grassland ecosystems are generally limited by N availability in soil, which is combined or closely associated with soil organic matter (Schnitzer 1991). Microbial biomass constitutes a significant part of the potentially mineralizable N that is available to plants (Bonde *et al.* 1988; Singh *et al.* 1991). In some studies, the amount of microbial biomass was found to be a good indicator of the rate of N mineralization (Paul and Voroney 1984; Azam *et al.* 1986). Though the soil microbial biomass contributes a relatively small fraction of the total biomass in the terrestrial ecosystems than in plant nutrient cycling. Their growth and activity are influenced by climate, soil moisture content, pH, quality and quantity of substrates and N, P, S concentrations in soil (Orchard and Cook 1983; Anderson and Domsch 1993; Anderson and Joergensen 1997).

Information on the seasonal fluctuation in microbial biomass within an annual cycle is available mostly for agricultural soils. Some workers have reported large annual fluctuations in the microbial biomass (Lynch and Panting 1980; Ross *et al.* 1981), while others observed only small annual changes (Schnurer *et al.* 1986; Patra *et al.* 1990). The tropical forest ecosystems differ from the temperate forests with respect to seasonal fluctuation in microbial biomass. In tropical forest soils, the peak microbial biomass has been recorded during winter (Luizao *et al.* 1992; Maithani *et al.* 1996; Arunachalam *et al.* 1996a; Arunachalam and Arunachalam 2000) when the temperature is low, while the values are low during rainy season when temperature and moisture conditions are

plentiful for the microbial activity. In temperate forest peak microbial biomass in soil was recorded during summer or spring by Diaz-Ravina *et al.* (1993), while von Lutzow *et al.* (1992) recorded highest biomass N in autumn and lowest during summer.

N and P mineralization

Nutrients returned to the soil through litter is released following its decomposition and mineralization. Rates of litter decomposition and mineralization are influenced by a large number of factors including temperature and soil moisture condition, and by the chemical and physical nature of the litter. An estimation of the release of nitrogen from soil organic matter may be regarded as a prime indicator of soil fertility (Antil *et al.* 2001). The proportion of total soil organic N that is released annually varies widely from <2% to more than 10% of total N, depending on the soil type and other conditions (Burtholomew and Kirkham 1960). Thus, the accumulation of organic N in the longer term may not be related directly to the ability of the soil to sustain the rate of N released. However, the net amount of N mineralized *i.e.*, the difference between gross mineralization and gross immobilization indicates the ability of the soil to satisfy the immediate requirements of plants.

Of the different fractions of soil organic matter, macro particles comprise a significant component of the 'light' fraction of organic matter. Macro-organic matter is generally thought to consist of dead fibrous materials in a state of partial decomposition, including that from roots, but not including living materials (Whitehead *et al.* 1990). Warren and Whitehead (1988) suggested that the macro-organic matter fractions in grassland soil might contribute substantially to the available N. This conclusion was derived from the observation that plant uptake of N was significantly decreased in soil

where macro-organic matter had been removed. The mineral constituents of the soil matrix show close associations with organic materials, which exert important control over the mineralization process (Hassink 1993). A close interaction between the decay products and microbial activity in clay soils has been reported by Gregorich *et al.* (1991).

The primary microbial processes involved in fresh residue and humus turnover in soils are mineralization and immobilization of soil N. The activities of microorganisms involved in N mineralization are affected by both biotic and abiotic factors (Clarhom and Rosswall 1980; Sarathchandra *et al.* 1989), and by management practices (Zaman *et al.* 2002).

Factors which influence the rate of N mineralization include soil texture (Hassink 1992), moisture, pH and temperature (Stanford *et al.* 1973). The effects of temperature and moisture content on soil N cycling have extensively been studied, often with conflicting results. However, little is known about the influence of understorey management and its interactions with soil temperature and moisture content on N mineralization and nitrification processes (Zaman and Chang 2004). Joergensen *et al.* (1995) reported that temperature, rather than moisture, appears to be the critical factor affecting microbial biomass and their activities in forest and agricultural soils.

Studies in forests and grasslands have shown that gross nitrogen mineralization is often greater than net nitrogen mineralization and does not differ due to differences in species composition (Stark and Hart 1997; Verchot *et al.* 2001). The rate of gross mineralization indicates that microbial nitrogen loop strongly dominates nitrogen cycling. This loop consists of decomposition of soil organic matter and return of nitrogen to the soil upon microbial death. Thus plant carbon drives the microbial nitrogen loop and

determines net nitrogen mineralization rates (Verchot *et al.* 2001). Plant available nitrogen is determined by what is left after microbial uptake (Knops *et al.* 2002). Mature forest stands show a linear relationship between productivity and nitrogen mineralization (Reich *et al.* 1997), and differences among stands and species are reflected in the soil organic matter pools (Finzi *et al.* 1998). Soil microbes are often limited by carbon (Jackson and Caldwell 1989). Root exudates and root turnover are important sources of carbon for soil microbes (Grayston *et al.* 2001). The quality and quantity of this carbon supplied by plants can determine the rate of net nitrogen mineralization (Schmidt *et al.* 1997), which, in turn, can influence the total amount of NO^-_3 produced as well as leached from the ecosystem.

Next to nitrogen, phosphorus is a major essential nutrient required by plants, which is absorbed largely as orthophosphate ions ($H_2PO^-_4$ and HPO_4), which are present in the soil solution. In soil, phosphorus exists both in organic and inorganic forms. These are important sources of P for plant and microbial uptake. The organic form exists mostly in humus and other organic materials, while the inorganic form occurs in combination with Al, Fe, Mg, Ca and other elements, most of which are not soluble and therefore not available to plants and microbes. P availability is also controlled by soil, moisture content, aeration and pH which influence microbial transformation of phosphorus.

Soil physico-chemical processes are more important than basal mineralization in releasing plant available inorganic P (Oehl *et al.* 2004). Duration and intensity of weathering affects forms of soil P. In highly weathered soils, the proportion of organic P is usually greater than in young soils, especially the labile inorganic P. This conceptul model developed by Walker and Syers (1976) from soil sequences in New Zealands has

been confirmed for a chronosequence in Hawaii (Crews *et al.* 1995) and by a literature review of soil P fractions in natural ecosystems (Cross and Schlesinger 1995). In general, P mineralization and immobilization are similar to those of N in that both processes occur simultaneously in soils.

Chapter 3

Study site: Location, geology and site characteristics

Location

The study was carried out in and around Jeypore Reserve Forest of Dibrugarh Forest Division of Assam (latitude 27° 05′ to 27° 28′N; longitude 95° 20′ to 95° 38′E; altitude 220 m asl) on the southern bank of the river Brahmaputra (Figure 3.1). Champion and Seth (1968) have classified this forest as Assam Valley Tropical Wet Evergreen Forests (I-IB/CI). The study area is a part of the Joy-Dihing Biosphere Reserve (90-480 m asl) covering an area of about 108 km^2. About two-third area in the northern side of Jeypore Reserve Forest is more or less flat and the southern side is hilly. The forest is bounded by Dilli river in the southwest, Namsang river in the east and Buri-Dihing river in the northwest. Apart from these rivers, innumerable seasonal streams and streamlets, mostly rain-fed, drench the reserve forest.

The present study was carried out in and around Jeypore Reserve Forest. Two disturbed and one undisturbed stands were selected for the detailed study. The disturbed stand was divided into two parts on the basis of disturbance index (Rao *et al.* 1990). Using the ratio of basal area of cut stumps to the total stand basal area as disturbance index, sites were categorized into moderately (MD, disturbance index 54%) and highly-disturbed (HD, disturbance index 88%) stands.

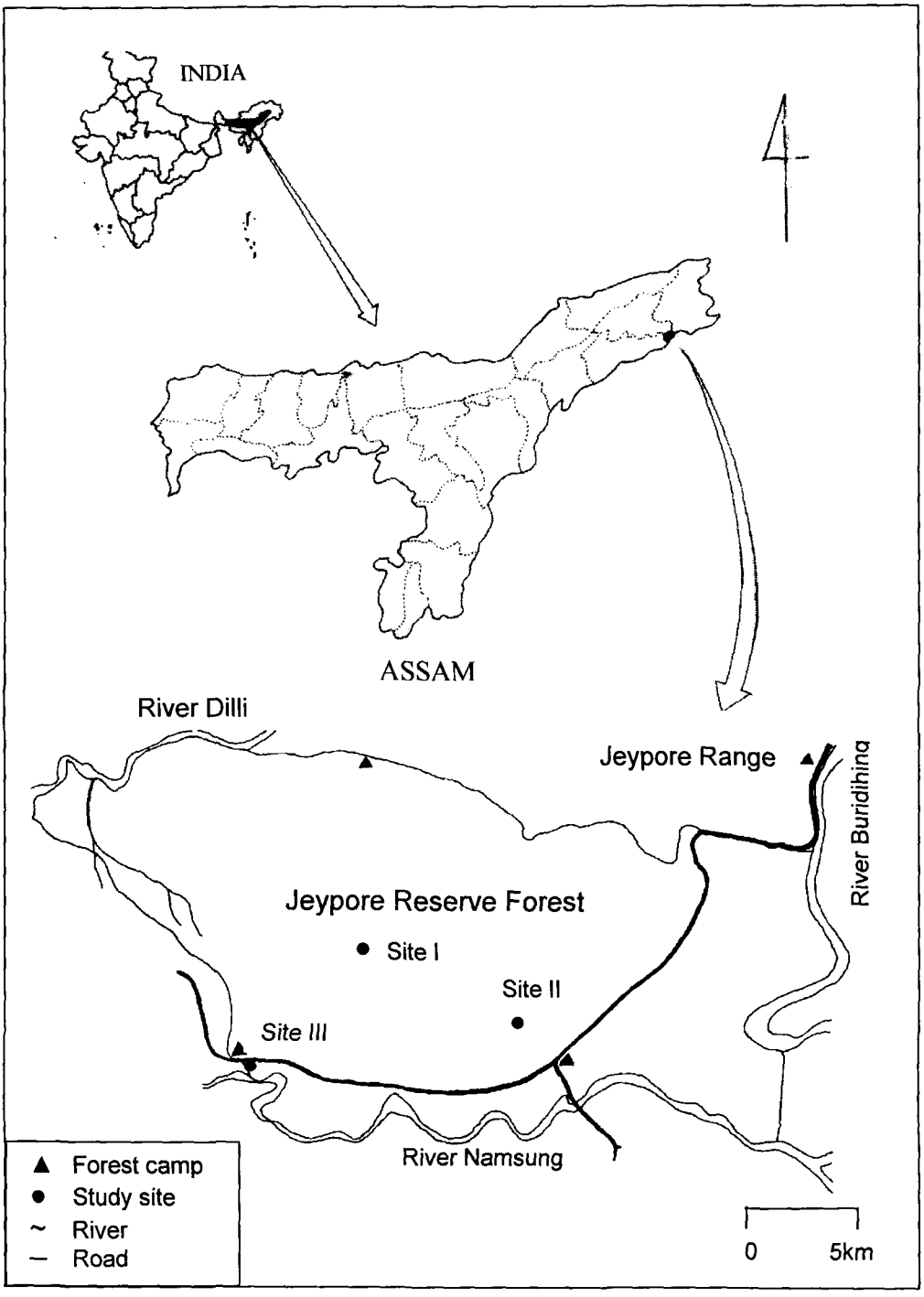

Figure 3. 1. Location of Jeypore Reserve Forest in Assam, northeast India.

The moderately-disturbed stand (Figure 3.2) was selectively logged (*ca.* 2 ha) and dominated by *Mesua ferrea, Terminalia myriocarpa, Alangium begonifolium, Tetrameles nudiflora, Duabanga grandiflora, Sapium baccatum,* etc. The highly disturbed stand (*ca.* 2.5 ha) was at a distance of about 1 km from the undisturbed stand (Figure 3.2). It was clear-felled 10 years ago for settled cultivation. Here rice, maize, mustard and chilies were grown occasionally. A few individuals of *Biscofia javanica, Dillenia indica, Duabanga grandiflora, Bombax ceiba* and *Albizzia* sp. were present at this stand. The undisturbed stand (*ca.* 2 ha) was in the core area of the Jeypore Reserve Forest. Mature large (>90 cm DBH) trees of *Dipterocarpus macrocarpus, Shorea assamica, Mesua ferrea, Tetrameles nudiflora, Castanopsis indica* and *Vatica lanceaefolia* were abundant in this stand.

Geology and soil

The rocks of this region belong to the tertiary and quaternary formation. The oldest tertiary formation consists of a group of gray and black splintery shells with interbeds sandstones and the youngest tertiary sequence consists of pebbles bed alternating with clays and soft sandstones. The quaternary sequence consists of clays, loose coarse sand, gravels and boulder and comprises of a group of old alluvium rocks containing lignified fossil wood. The metamorphic rocks are also found in the area which is composed of quartzes, slates and varieties of schistose rocks (Rahman 2002).

The soil can be classified into two classes, old alluvial and new alluvial. The old alluvial soil or the higher level soil occurring along the Buri-Dihing river is clay or sandy loam. The new alluvial soil or low level soil is of recent origin. It occurs along the banks

of Buri-Dihing, Namsang rivers and contains clay, silt, sand and shingles. The texture of the soil varies from sandy loam to clay loam with 1-5% stones.

Climate

The area falls within the humid tropical climate with well pronounced wet summer and winter seasons. Mean monthly temperature varies between 7 °C and 36 °C. The hottest months are July and August (35 °C) and the coldest months (8 °C) are December and January. Hail storms are common during March to June end. The annual rainfall ranges between 2500 and 5000 mm, about 85% of which is received during the wet season (Figure 3.3). Relative humidity remains very high through out the year (Figure 3.4).

Vegetation

The vegetation shows the general characteristics of the tropical evergreen forest. The heterogeneous forests found in the area can be broadly classified into the following types as per Champion and Seth's (1968) classification of forest types of India.

I. IB/CI- Northern Tropical Evergreen Forests- Assam valley tropical wet evergreen (Dipterocarps)
II. 3/ I S2 B- North Indian Tropical Moist Deciduous forests (Eastern Hollock Forests)
III. Miscellaneous Forests.

Type I (IB/ CI) Assam valley tropical wet evergreen forests are easily distinguished by the dominance of *Dipterocarpous macrocarpus* and *Shorea assamica* tree species in the canopy layer. Apart from these species, less frequent canopy trees with tall cylindrical boles and comparatively smaller and lighter crowns are also present in the forest. Notable among them are *Altingia excelsa*. *A. excelsa* is commonly found on small hill tops and

well drained higher sites. Other canopy trees are *Artocarpous chaplasha*, *Cinnamomum glaucesence*, *Terminalia myriocarpa*, *T. bellerica*, *Ailanthus grandis*, *Canarium strictum*, *Dysoxylum procerum*, *Tetrameles nudiflora*, etc.

The subcanopy of the forest has tree species like *Mesua ferrea*, *Castonopsis indica*, *Endospermum chinensis*, *Taluma hodgsonii*, *Syzygium cuminii*, *Duabanga grandiflora*, *Vatica lanceaefolia*, *Sapium baccatum*, *Garcinia paniculata* etc. Among these *M. ferrea* often grows gregariously.

The shade bearing species like *Baccaurea sapida*, *Vatica lanceaefolia*, *Mallotus roxburghii*, *Knema longifolia*, *Sterculia hamiltonii*, *Dysoxylum binactiferum* and *Pseudostachyum polymorphum* etc constitute an undercanopy layer. The shrubby forest undergrowth has gregarious species like *Blastus cocchinensis*, *Saprosma ternatum*, *Leea umdraculifera*, *Capparis multiflora*, *Saurauia sp.*, *Melastoma sp.*, *Laportea crenulate*, *Pinanga gracilis* etc. The herbaceous flora on the ground cover consists of ferns and *Phrynium pubinerve*, *Bochameria sp.*, *Impatiens sp.*, *Polygonum sp.*, and *Musa sp.* Orchids and ferns form the bulk of epiphytes. The common epiphytes are *Aexhenanthes sp.*, *Hoya sp.*, *Dischidia sp.* and the common lianas include *Derris ferruginea*, *Millettia cunoifolia*, *Hodgsonia macrocarpa*, *Entada purseatha*, *Rhaphidophora descuriva*, *Ventilage madraspatana*, etc. The moist shady forest floor has a thick layer of litter and humus.

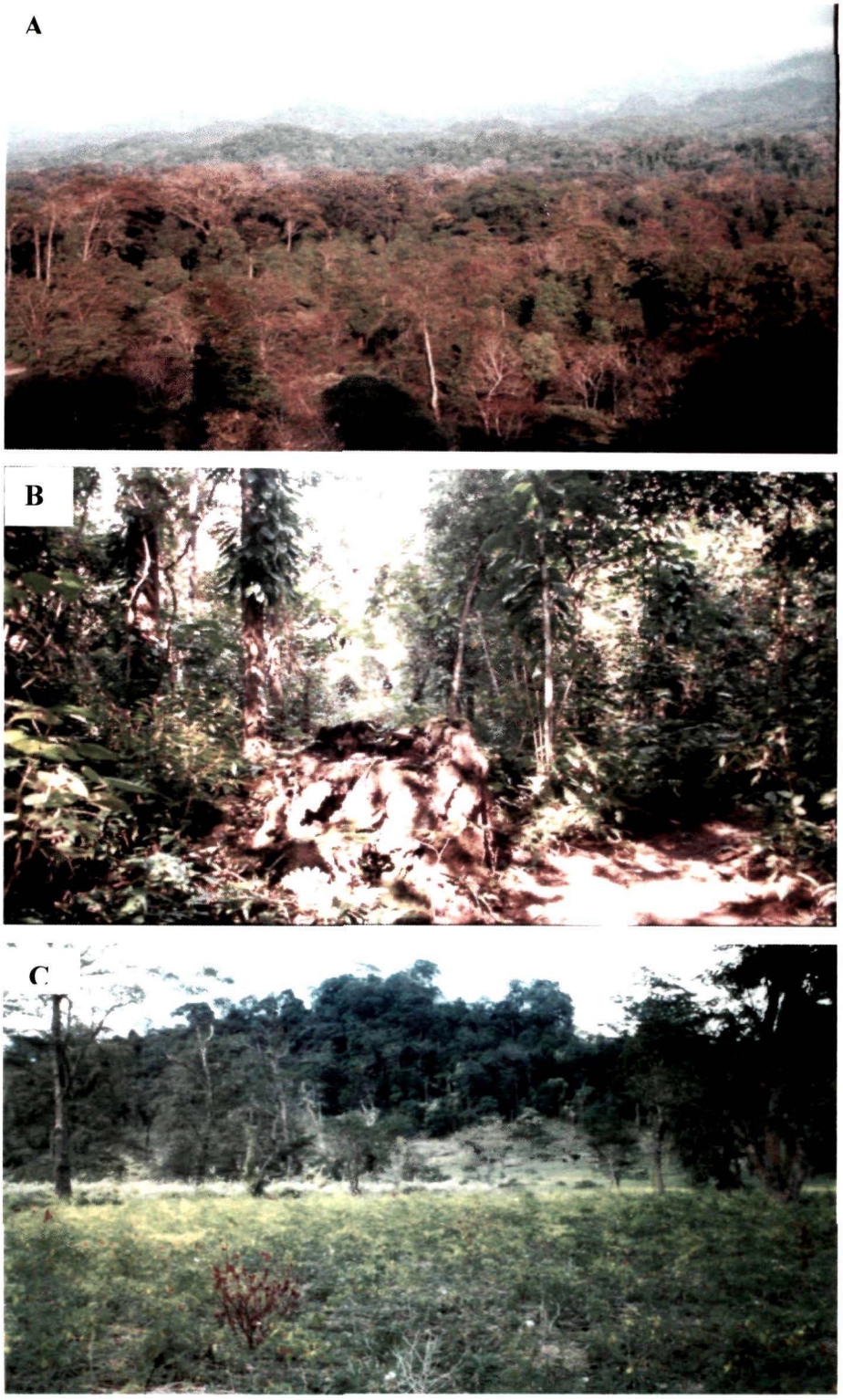

Figure 3.2. Overview of the three study stands: (A) undisturbed (B) moderately disturbed and (C) highly disturbed stands.

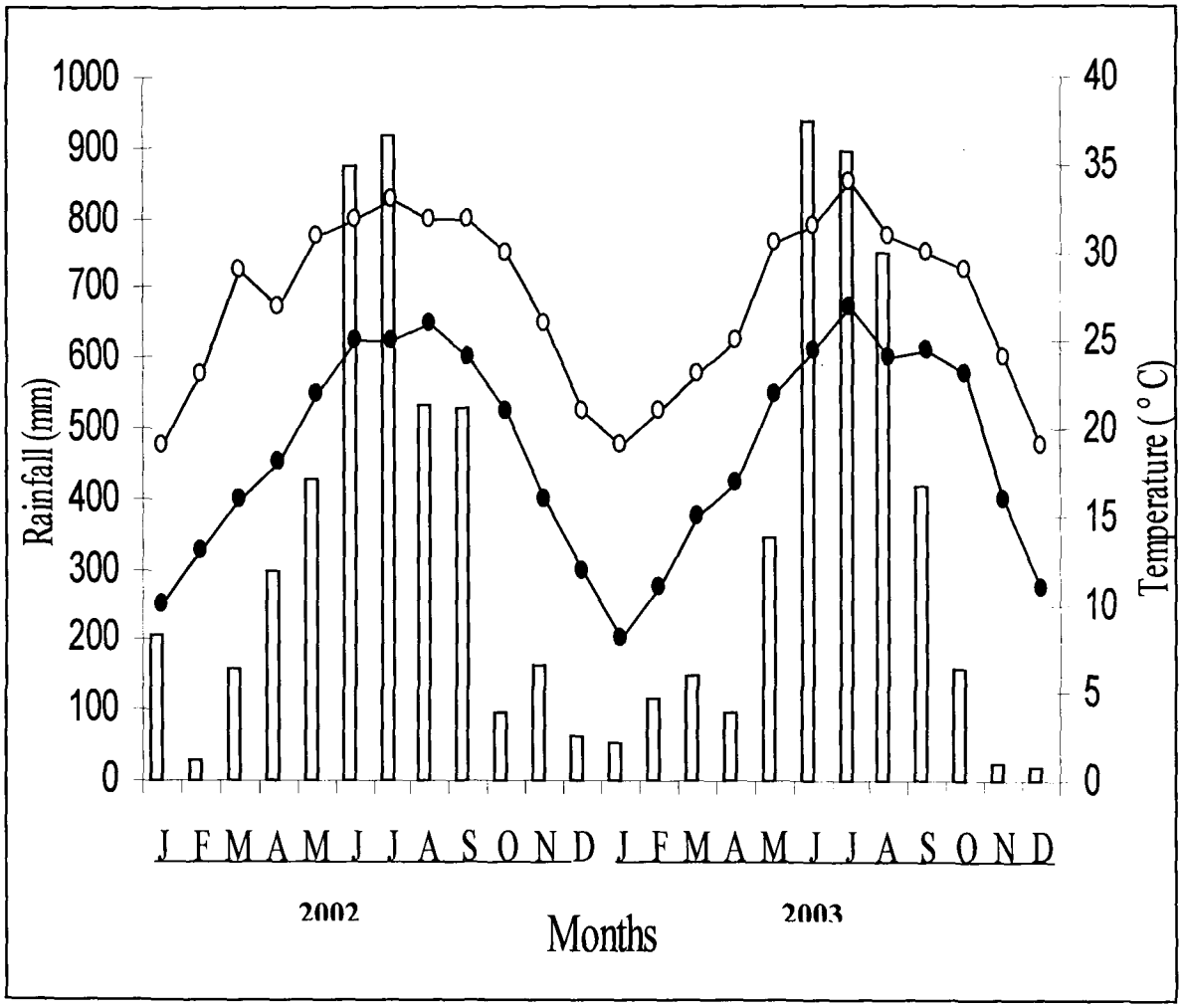

Figure 3.3. Rainfall, maximum and minimum air temperatures at the study area.
(□) total monthly rainfall, (○) mean monthly maximum and (●) minimum temperatures.

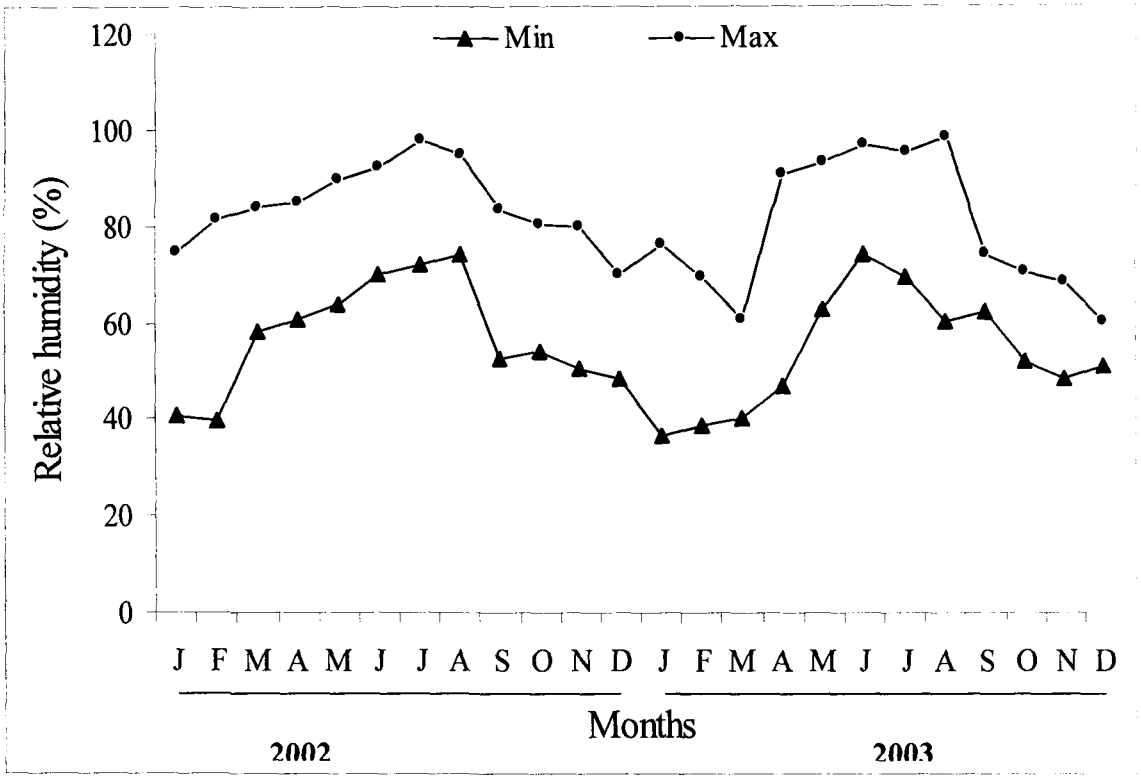

Figure 3.4. Monthly variation in maximum and minimum relative humidity at the study area.

Chapter 4

Vegetation and soil

Introduction

It is well known that forest clearance for agriculture in the tropics decreases biodiversity, limits natural vegetation and simplifies the ecosystem structure. Besides, it has a detrimental effect on soil properties, since forest clearance modifies the microclimatic conditions at the ground level, and changes the amount and quality of organic input to the soil (Dinesh *et al.* 2003). Disturbance in the forest also leads to the fragmentation of the community and alteration in tree dynamics. Factors of soil complex such as pH, organic matter and nutrient contents influence plant growth and succession on degraded sites (Pandey and Singh 1985).

Knowledge of the amount, forms and distribution of soil carbon (C), nitrogen (N) and phosphorus (P) are essential for understanding nutrient dynamics in soils, since mechanisms of nutrient dynamics in forest soils vary from one nutrient element to another, stand age (Gholtz *et al.* 1985), tree species (Miller 1984) and intrinsic properties of the environmental conditions of the sites.

Vegetation structure, microclimatic condition and soil properties of the undisturbed and disturbed forest stands were studied in order to assess the impact of disturbance on these characteristics of the ecosystems.

Methods

Vegetation

Vegetation of undisturbed, moderately-disturbed and highly-disturbed stands was studied during 2002-2003. In each stand, density, frequency and basal area of individual plant species were determined in randomly placed quadrats of different sizes. Twenty five quadrats (10m x 10m) for tree species, twenty quadrats (5m x 5m) for shrubs species and fifty quadrats (1m x 1m) were sampled for herbaceous species in each of the three stands. Nomenclature of plant species followed Hooker (1872-1897). Relative frequency, density and basal area were calculated (Philips 1959) for trees and shrubs, and the sum of these represented importance value index (IVI) for the woody species (Curtis 1959). For herbaceous species, IVI was calculated by summing up relative frequency, relative density and relative abundance values.

The Shannon's species diversity index was computed as, $H'=-\sum (n_i/N) \log (n_i/N)$, where H'=Shannon's index of general diversity (Shannon and Weiner 1963), n_i=importance value index of each species, N=total importance value index.

Forest microclimate

The microclimate in the three stands was studied by measuring light intensity, relative humidity and air temperature in January, April, July and October during 2002 and 2003 to represent winter, spring, rainy and autumn seasons respectively. All the three parameters were measured randomly at ten places close to the ground surface in each stand. The light intensity was measured using a digital lux meter (TES 1332). The air temperature and relative humidity were measured using a

thermo-hygrometer (EXTECH). Soil temperature was measured using a soil thermometer (SYMAX).

Soil

Soil sampling: Soil samples were collected in January, April, July and October during 2002 and 2003. In each stand, 20 samples were collected using a steel corer (5.5 cm inner diameter) from two soil depths (0-15 and 15-30 cm) after clearing the litter layer. The replicated samples of a particular depth was thoroughly mixed site-wise to obtain a composite sample. After removing stones, pebbles and large pieces of plant materials, the samples were sieved using 2 mm mesh size sieve. The screened samples were stored in polythene bags for analysis.

Soil analysis: Soil texture was determined by Bouyouncos hydrometer method (Bouyouncos 1962) and bulk density was determined by soil core method (Blake and Hartge 1986). Water holding capacity (WHC) was determined according to Keen's box method given by Piper (1944), while soil moisture content was measured gravimetrically by incubating 10 g of field moist soil sample in a hot-air oven at 105 °C for 24 h. Soil organic carbon (SOC) was determined by dichromate oxidation and titration with ferrous ammonium sulphate (Walkey 1947). Total Kjeldahl nitrogen (TKN) was estimated following semi-micro Kjeldahl procedure by acid-digestion, distillation and titration (Anderson and Ingram 1993). For total P concentration, soil sample was digested using a triacid mixture, followed by colorimetric reaction (molybdenum blue method) with ammonium molybdate and stannous chloride (Jackson 1958). Cation exchange capacity (CEC) was determined after extracting the exchangeable bases from the soil with 1M ammonium acetate (pH 7.0), followed by

the replacement of ammonium N with magnesium oxide (Allen *et al.* 1974). The pH of the soil sample was determined in a soil-water suspension (1:2.5 w/v H_2O) using a digital pH meter (Systronics M 335).

For available N and P contents, field moist soil samples (50 g) were shaken with 2M KCL (250 ml) for NH^+_4-N and NO^-_3-N and 0.5M $NaHCO_3$ was used for PO^-_4-P (100 ml, pH 8.5) in a rotatory shaker for 2 h and the suspension was filtered through Whatman filter paper No.1 and/or 44. Nitrate-N (NO^-_3-N) was measured by phenol disulphonic acid method (Jackson 1958) and ammonium-N (NH^+_4-N) by phenate method (Wetzel and Lickens 1979). Available phosphorus (PO^-_4-P) was measured by molybdenum blue method (Jackson 1958). All the analyses were done in triplicates and the final results were expressed on oven-dry weight basis.

Statistical analysis

Data were statistically analyzed using ANOVA (three-way) to study the effects of stand, season and soil depth on soil physico-chemical variables. Pearson correlation coefficients and regression were worked out according to Zar (1974), wherever necessary.

Results

Floristic composition, density, basal area and diversity index

In total, 201 plant species (88 tree species, 55 shrubs and 58 herbs) belonging to 164 genera and 77 families were recorded in this study. About 57 families were present in the undisturbed stand, 61 in the moderately-disturbed stand and 39 in the highly-disturbed stand. Fifty eight families had single representative species and 8 families had more than 5 species. Members of Euphorbiaceae,

Lauraceae, Rubiaceae, Meliaceae and Magnoliaceae were common in the undisturbed stand, while those of Euphorbiaceae, Lauraceae, Rubiaceae, Clusaceae and Meliaceae were common in the moderately-disturbed stand. In the highly-disturbed stand species of Euphorbiaceae, Poaceae and Moraceae families were abundant.

In the undisturbed stand tree species were distributed in four distinct strata. The emergent trees (height >25 m) included *Dipterocarpus macrocarpus, Shorea assamica, Tetrameles nudiflora, Ailanthus grandis, Sapium baccatum, Cinnamomum glanduliferum, Elaeocarpus ganitrus, Talauma phellocarpa,* etc. The canopy layer (height 10-25 m) was composed of *Mesua ferrea, Castanopsis indica, Canarium bengalense, Terminalia chebula, Talauma hodgsoni, Michelia* spp. *Litsea salicifolia,* and *Alstonia scholaris.* The subcanopy had *Baccaurea sapida, Vatica lanceaefolia, Dysoxylum reticulatum* and *Diospyros variegata etc.* Similar distribution pattern of plants species were also observed in the moderately disturbed stand with lower number of species; whereas in the highly disturbed stand no such stratification was observed. The highly disturbed stand was composed of a few sparsely distributed species like *Alangium chinese, Baccurea sapida, Vatica lancefolia* and *Mesua ferrea.*

Species richness varied according to disturbance gradient in different stands. The number of tree species increased from 13 in the highly disturbed stand to 53 and 82 in the moderately disturbed and undisturbed stands respectively (Table 4.2). Shrubs species also decreased with the increase in disturbance (Table 4.3). However, maximum (35) number of herb species was recorded in the moderately disturbed stand and minimum (20 species) in the undisturbed stand (Table 4.4).

Tree density and basal area were negatively related to the intensity of disturbance. In general, the Shannon's index of diversity for trees and shrub were greater in the moderately-disturbed stand, 1.52 and 1.34 respectively, and lowest (H'=1.04) for tree species in the highly-disturbed stand The diversity index for herbaceous species was lowest (H'=1.09) in the undisturbed stand among the three stands (Table 4.1). The overall species diversity was highest in the moderately disturbed stand, and lowest in the highly disturbed stand; it was at intermediate level in the undisturbed stand.

Table 4.1. Phyto-sociological analysis of the undisturbed and disturbed stands.

	UD	MD	HD
Number of species			
Trees	82	53	13
Shrubs	34	32	12
Herbs	20	35	28
Number of genera			
Trees	50	46	12
Shrubs	33	31	10
Herbs	19	30	25
Number of families			
Trees	29	32	12
Shrubs	20	14	11
Herbs	18	20	16
Total density (no. ha^{-1})			
Trees	658	369	41
Shrubs	7500	3740	1160
Herbs (no. $100m^{-2}$)	74	220	130
Basal area (m^2 ha^{-1})			
Trees	85.55	20.83	5.02
Shrubs	2.61	0.60	0.37
Herbs (m^2 m^{-1})	0.17	0.44	0.27
Diversity index			
Trees	1.39	1.52	1.04
Shrubs	1.06	1.34	0.95
Herbs	1.09	1.22	1.06

UD-Undisturbed, MD-moderately disturbed, HD-Highly disturbed stands.

Table 4.2. Importance value index (IVI >5), density (Den., trees ha^{-1}) and basal area (BA, m^2 ha^{-1}) of tree species (≥ 30 cm GBH) in the undisturbed and disturbed stands.

Stand/ Species	Family	IVI	Den.	BA
Undisturbed				
Actinodaphne obovata Bl.	Lauraceae	6.52	17.5	1.03
Canarium bengalense Roxb.	Burseraceae	6.66	15	1.03
Croton joufra Roxb.	Euphorbiaceae	6.36	17.5	0.54
Diospyros variegata Kurz.	Ebenaceae	5.68	15	0.31
Dipterocarpus macrocarpus Vesq.	Dipterocarpaceae	66.21	127.5	23.8
Dysoxylum grande Hiern.	Meliaceae	9.61	25	1.00
Dysoxylum reticulatum King	Meliaceae	15.43	45	1.61
Elaeocarpus ganitrus Roxb.	Elaeocarpaceae	5.01	12.5	0.83
Mesua ferrea L.	Clusaceae	31.00	80	6.60
Shorea assamica Dyer.	Dipterocarpaceae	52.41	90	20.37
Talauma phellocarpa King.	Magnoliaceae	6.78	12.5	1.75
Vatica lanceaefolia Bl.	Dipterocarpaceae	17.97	60	1.12
Unidentified (porbotia morhal*)		10.17	32.5	1.34
Moderately disturbed				
Canarium bengalense Roxb.	Burseraceae	7.04	20	0.84
Castanopsis indica A. DC.	Fagaceae	18.91	35	8.03
Diospyros variegata Kurz.	Ebenaceae	6.27	17.5	0.47
Dipterocarpus macrocarpus Vesq.	Dipterocarpaceae	53.76	147.5	17.16
Dysoxylum procerum Hiern.	Meliaceae	5.07	10	1.53
Dysoxylum reticulatum King	Meliaceae	6.31	20	0.64
Endospermum chinense Benth.	Euphorbiaceae	5.39	12.5	1.94
Mesua ferrea L.	Clusaceae	27.64	70	9.04
Sapium baccatum Roxb.	Euphorbiaceae	10.16	15	4.9
Shorea assamica Dyer.	Dipterocarpaceae	59.09	125	25.93
Tetrameles nudiflora R. Br.	Datiscaceae	6.77	10	2.98
Vatica lanceaefolia Bl.	Dipterocarpaceae	14.65	57.5	1.04
Unidentified (porbotia morhal*)		7.14	30	0.63
Highly disturbed				
Alangium chinense Lour.	Alangiaceae	11.88	42.5	0.65
Baccaurea sapida Muell and Arg.	Euphorbiaceae	13.52	42.5	0.78
Canarium bengalense Roxb.	Burseraceae	15.18	25	3.57
Croton joufra Roxb.	Euphorbiaceae	6.52	17.5	0.54
Diospyros variegata Kurz.	Ebenaceae	6.54	17.5	0.36
Dipterocarpus macrocarpus Vesq.	Dipterocarpaceae	24.20	47.5	5.11
Duabanga sonneratioides Buch.	Sonneratiaceae	6.54	7.5	1.85
Dysoxylum binectariferum Hk.f	Meliaceae	14.75	37.5	1.48
Endospermum chinense Benth.	Euphorbiaceae	7.29	17.5	0.68
Ficus elastica Roxb.	Moraceae	6.34	2.5	2.52
Mesua ferrea L.	Clusaceae	32.27	62.5	6.32
Shorea assamica Dyer.	Dipterocarpaceae	32.63	75	5.63
Talauma hodgsoni Hk. f. &Th.	Magnoliaceae	15.90	35	2.17
Terminalia bellerica Roxb.	Combretaceae	5.16	12.5	0.47
Terminalia chebula Retz.	Combretaceae	6.7	10	1.97
Vatica lanceaefolia Bl.	Dipterocarpaceae	13.89	47.5	0.81

* Local name

Table 4.3. Importance value index (IVI >10), density (Den. individuals ha^{-1}) and basal area (BA, m^2 ha^{-1}) of shrubs in the undisturbed and disturbed stands.

Stands/ Species	Family	IVI	Den.	BA
Undisturbed				
Bauhinia vahlii Wight & Arn.	Caesalpinaceae	10.72	200	0.081
Blastus cochinchinensis Lour.	Melastomaceae	70.57	3040	1.060
Myxopyrum smilacifolium Bl.	Oleaceae	12.38	260	0.006
Styrax serrulatum Roxb.	Styraceae	12.93	280	0.083
Saprosoma ternatum Hk.f.	Rubiaceae	48.33	1860	0.422
Moderately disturbed				
Blastus cochinchinensis Lour.	Melastomaceae	73.08	1600	0.036
Dalbergia tamarindifolia Roxb	Papilionaceae	15.48	180	0.010
Debregeasia sp.	Urticaceae	10.35	100	0.032
Lasianthus hookeri Clarke	Rubiaceae	10.11	100	0.003
Maesa indica Wall.	Myrsinaceae	13.70	160	0.011
Myronuron nutans Wall	Rubiaceae	12.97	140	0.020
Psychrotia silhetensis Hk.f.	Rubiaceae	11.42	120	0.005
Randia dumetorum Lamk.	Rubiaceae	17.05	200	0.036
Saprosoma ternatum Hk.f.	Rubiaceae	15.98	200	0.082
Highly disturbed				
Blastus cochinchinensis Lour.	Melastomaceae	29.34	540	0.024
Boehmeria pendulifolia Wedd.	Urticaceae	10.19	120	0.004
Camellia sinensis (L.) O. Ktze.	Theaceae	19.55	300	0.120
Clerodendron infortunatum (L.) Gaertn.	Verbenaceae	15.31	220	0.091
Combretum dasystachyum Kurz.	Combretaceae	12.41	160	0.009
Dalbergia tamarindifolia Roxb	Papilionaceae	19.20	300	0.012
Ixora acuminata Roxb.	Rubiaceae	12.41	160	0.018
Laportea crenulata Gaud.	Urticaceae	15.45	220	0.028
Maesa indica Wall.	Myrsinaceae	14.56	200	0.012
Myronuron nutans Wall	Rubiaceae	18.35	280	0.020
Pinanga gracilis (Roxb) Bl.	Arecaceae	21.72	360	0.006
Saprosoma ternatum Hk.f.	Rubiaceae	12.77	160	0.220

Table 4.4. Importance value index (IVI>10), density (individuals m^{-1}) and abundance of herbs in the undisturbed and disturbed stands.

Stands/ Species	Family	IVI	Density	Abundance
Undisturbed				
Achryanthes aspera L.	Amaranthaceae	17.22	0.45	3.00
Adiantum caudatum L.	Adiantaceae	34.86	1.17	2.61
Andropogon sp.	Poaceae	38.43	1.32	2.65
Diflugossa colorata (Nees.) Bremek.	Acanthaceae	33.02	1.07	2.39
Dryopteris sparsa (D.Don) O. Ktze.	Dryopteridaceae	13.65	3.00	1.33
Forrestia nudiflora L.	Commelinaceae	34.46	1.07	2.05
Piper sylvaticum Roxb.	Piperaceae	14.82	0.35	1.56
Pouzolzia sanguinea (Blume) Merr.	Urticaceae	13.72	0.12	5.00
Pteris pellucida Presl.	Pteridaceae	10.27	0.15	3.00
Setaria glauca Beauv	Poaceae	17.06	0.42	3.40
Unidentified - (*Hatikuhiar**)	Araliaceae	11.44	0.22	1.13
Moderately disturbed				
Buddleja asiatica Lour.	Buddlejaceae	10.11	0.32	1.44
Diplazium esculantum	Athyriaceae	24.58	0.97	1.77
Forrestia nudiflora L.	Commelinaceae	22.31	1.05	2.80
Panicum sp.	Poaceae	32.48	1.87	6.82
Pharulopsis dorsiflora (Retz) Sentapu.	Acanthaceae	12.40	0.42	1.55
Piper sylvaticum Roxb.	Piperaceae	15.31	0.57	1.77
Selaginella wallachii (Hk & Grev) Spr.	Selaginaceae	13.40	0.52	2.10
Highly disturbed				
Adiantum caudatum L.	Adiantaceae	22.30	1.27	2.55
Dryopteris sparsa (D.Don) O. Ktze.	Dryopteridaceae	26.36	1.75	4.12
Eriocholoa polystachya Hb.K.	Poaceae	17.23	0.95	2.71
Forrestia nudiflora L.	Commelinaceae	17.49	0.92	2.31
Lygodium japonicum (Thnb.) Sw.	Lygodiaceae	11.92	0.55	2.00
Polygonum chinense L.	Polygonaceae	13.15	0.67	3.00
Setaria glauca Beauv	Poaceae	46.13	3.55	5.07

* Local name

Microclimate

Microclimate exhibited marked seasonal fluctuation with peak temperature and relative humidity during July and trough in winter season. The peak light intensity was observed during spring and lowest during rainy and autumn seasons. The effect of disturbance was more prominent on light intensity, which was several fold higher in the highly disturbed stand than the undisturbed stand. Air temperature also showed an increasing trend with increase in the disturbance level but relative humidity decreased with the increase in disturbance intensity (Figure 4.1).

Physical properties of soil

Soil temperature was high (32.55 °C and 33.98 °C) during summer and rainy seasons and low (17.73 °C and 19.27 °C) in winter, and it increased significantly with the increasing degree of disturbance (Figure 4.2). While the proportion of sand particles increased with the disturbance intensity, the proportion of clay decreased significantly ($P<0.05$) from the undisturbed to highly disturbed stand (Table 4.5). The water holding capacity (WHC) of the soil ranged 38.18- 66.48%; the highest value being in the undisturbed stand (66.48%) and lowest (38.18%) in the highly disturbed stand. Bulk density also varied significantly ($P<0.05$) between the stands (0.67-1.01g cm^{-3}). Highest bulk density (1.01g cm^{-3}) was recorded in the highly disturbed stand and lowest (0.67 g cm^{-3}) in the undisturbed stand. Soil moisture content varied significantly between seasons and soil depths ($F=2.38$, $P<0.05$), though it was invariably higher in the undisturbed stand than the disturbed stands (Figure 4.3).

Table 4.5. Soil physical properties in the undisturbed and disturbed stands.

Parameters	Undisturbed		Moderately-disturbed		Highly-disturbed	
	0-15 cm	5-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm
Sand (%)	58.30	61.68	64.44	64.13	78.07	72.94
	±2.43	±3.12	±0.85	±3.67	±2.89	±5.20
Silt (%)	12.00	11.36	22.02	22.18	13.64	19.18
	±0.08	±0.31	±1.03	±0.62	±0.33	±1.00
Clay (%)	29.70	26.96	13.54	13.69	8.29	7.88
	±2.04	±1.10	±0.30	±0.07	±0.12	±0.08
Textural class	SCL	SCL	SL	SL	SL	SL
WHC (%)	66.48	64.52	52.03	51.16	38.40	38.18
	±2.60	±3.72	±1.44	±2.85	±2.82	±1.03
Bulk density ($g\ cm^{-3}$)	0.67 ±0.008	0.73 ±0.005	0.83 ±0.02	0.85 ±0.007	0.88 ±0.008	1.01 ±0.03

WHC- water holding capacity, SCL –sandy clay loam, SL- sandy loam.
± SE (n=12).

Chemical properties of soil

Soil was acidic in all the stands, but the maximum acidity (4.86) was recorded in the undisturbed stand. There was little seasonal variation in the soil pH (Figure 4.4) in all the three stands. The pH though not significantly different, was generally lower in the surface soil layer than the subsurface layer. Soil organic carbon (SOC), cation exchange capacity (CEC), total Kjeldahl nitrogen (TKN), total P and ammonium-N (NH^{+}_{4}-N), nitrate-N (NO^{-}_{3}-N) and available-P (PO^{-}_{4}-P) contents were low in the disturbed stands as compared to the undisturbed stand (Table 4.6). In all the stands the nutrients concentrations were greater in the surface soil layer (0-15 cm) than in the subsurface soil layer (15-30 cm) (Table 4.6). Cation exchange capacity

gradually decreased from the undisturbed to moderately disturbed and highly disturbed stands. This trend was observed both in the surface and subsurface layers.

Soil organic carbon (SOC) declined from 16.71 mg g^{-1} in the undisturbed stand to 5.20 mg g^{-1} in the highly disturbed stand. It was significantly ($F=12.51$, $P<0.05$) lower at 15-30 cm soil depth. In the undisturbed and moderately disturbed stands, maximum SOC was recorded during rainy season and minimum during winter. In the highly disturbed stand, however, the value was high (9.43 mg g^{-1}) during winter and low (4.50 mg g^{-1}) during autumn. Year-wise variation in SOC was significant ($P<0.05$) only in the undisturbed stand (Figure 4.5).

Total Kjeldahl N (TKN) varied significantly with season ($F=6.70$, $P<0.005$) and it decreased with the increase in disturbance intensity. Maximum concentration (6.61 mg g^{-1}) of TKN was recorded in the surface soil layer of the undisturbed stand and minimum (1.80 mg g^{-1}) in the subsurface soil layer of the highly disturbed stand (Table 4.6). Seasonal variation of TKN was also significant ($P<0.05$) with maximum value (7.50 mg g^{-1}) during rainy season and minimum (1.10 mg g^{-1}) during autumn in both the undisturbed and moderately disturbed stands. Whereas, in the highly disturbed stand it was low during rainy and high during winter season (Figure 4.6).

Total P concentration decreased with the increase in disturbance intensity. Maximum (0.90 mg g^{-1}) was recorded in the undisturbed stand and minimum (0.41 mg g^{-1}) in the highly disturbed stand. The total P concentration in soil was high during rainy season and low during winter in all the stands. It showed a declining trend with the soil depth in all the stands (Figure 4.7).

Mean annual NH^{+}_{4}-N, NO^{-}_{3}-N and PO^{-}_{4}-P concentrations showed a declining trend with the increase in disturbance intensity (Table 4.6). During the two annual cycles, NH^{+}_{4}-N, NO^{-}_{3}-N and PO^{-}_{4}-P showed wide variations. NH^{+}_{4}-N concentration was maximum during rainy period and minimum during winter season in the undisturbed and moderately disturbed stands, however, in the highly disturbed stand, the peak (3.98 $\mu g\ g^{-1}$) was recorded during winter and minimum (1.71$\mu g\ g^{-1}$) during rainy season at both soil depths (Figure 4.8). NO^{-}_{3}-N concentration varied significantly between seasons, soil depths and stands ($F=2.95$, $P<0.05$); its maximum peak was recorded during rainy season and trough during winter (Figure 4.9) in all the stands. Available PO^{-}_{4}-P concentration were maximum (15.30 $\mu g\ g^{-1}$) during rainy in the undisturbed and moderately disturbed stands, but in the highly disturbed stand, maximum (6.35 $\mu g\ g^{-1}$) was obtained during summer and minimum (2.22 $\mu g\ g^{-1}$) during rainy season. Seasonal variation in PO^{-}_{4}-P was significant ($P<0.05$) only in the undisturbed stand (Figure 4.10).

The percentage contribution of NO^{-}_{3}-N to total N was more than the NH^{+}_{4}-N and it increased with the increase in disturbance intensity. PO^{-}_{4}-P contribution to total P decreased significantly with the increase in disturbance level from the undisturbed stand (1.47%) to the highly disturbed stand (0.83%). The contribution of inorganic N and P to total N and P was significantly ($P<0.05$) higher during rainy season in all the three stands.

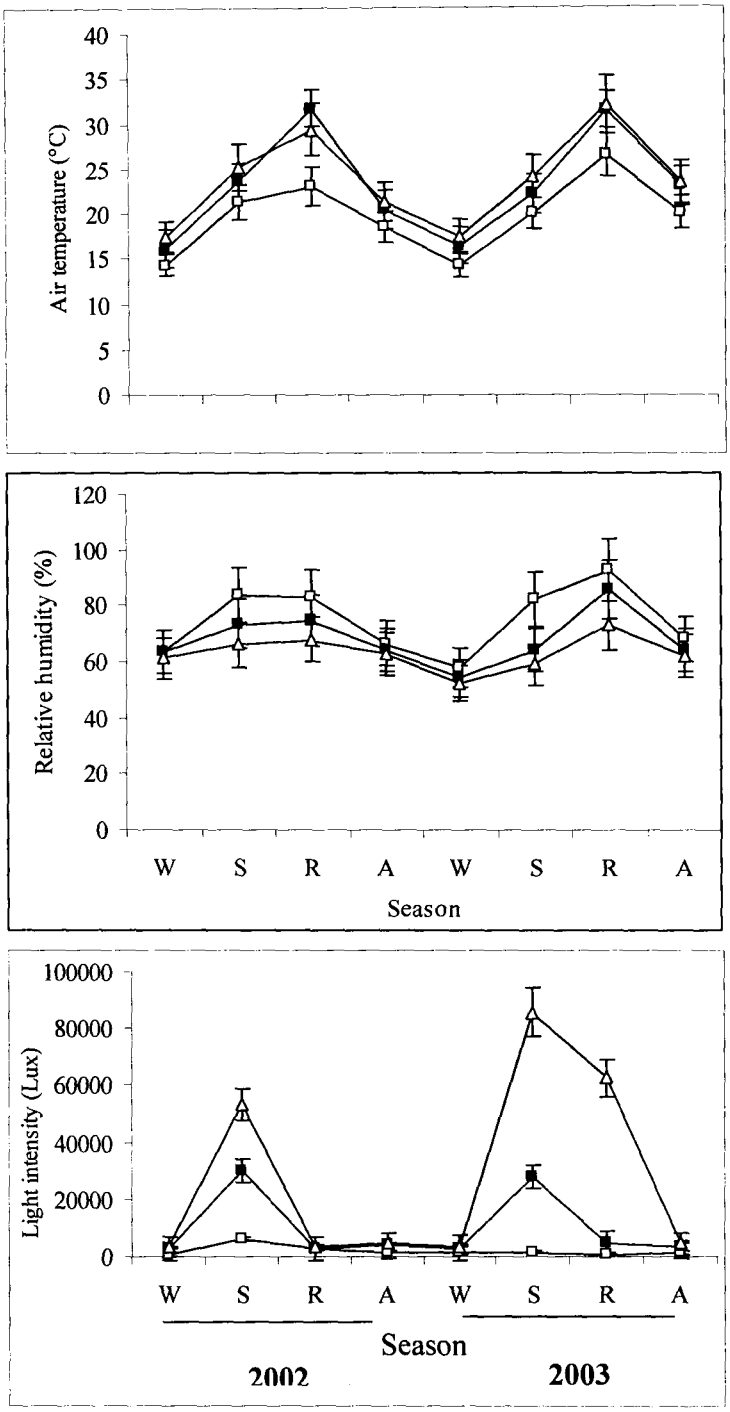

Figure 4.1. Seasonal variation in microclimatic variables in the undisturbed (□), moderately (■) and highly-disturbed (Δ) stands. Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

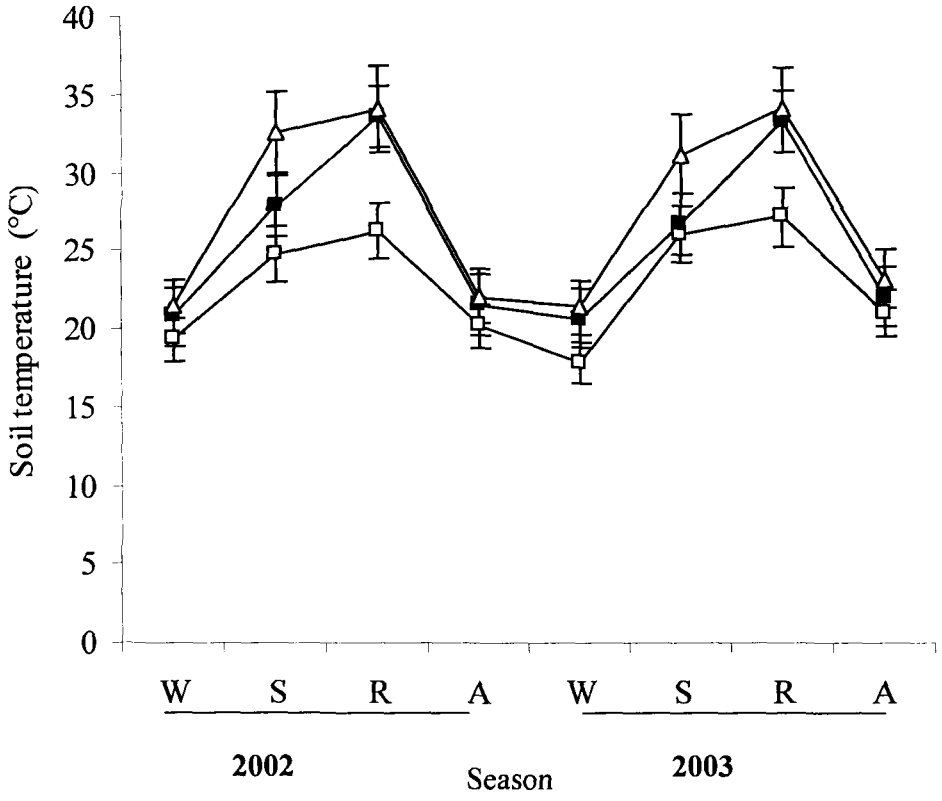

Figure 4.2. Seasonal variation in soil temperature of undisturbed (□), moderately (■) and highly-disturbed (Δ) stands. Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

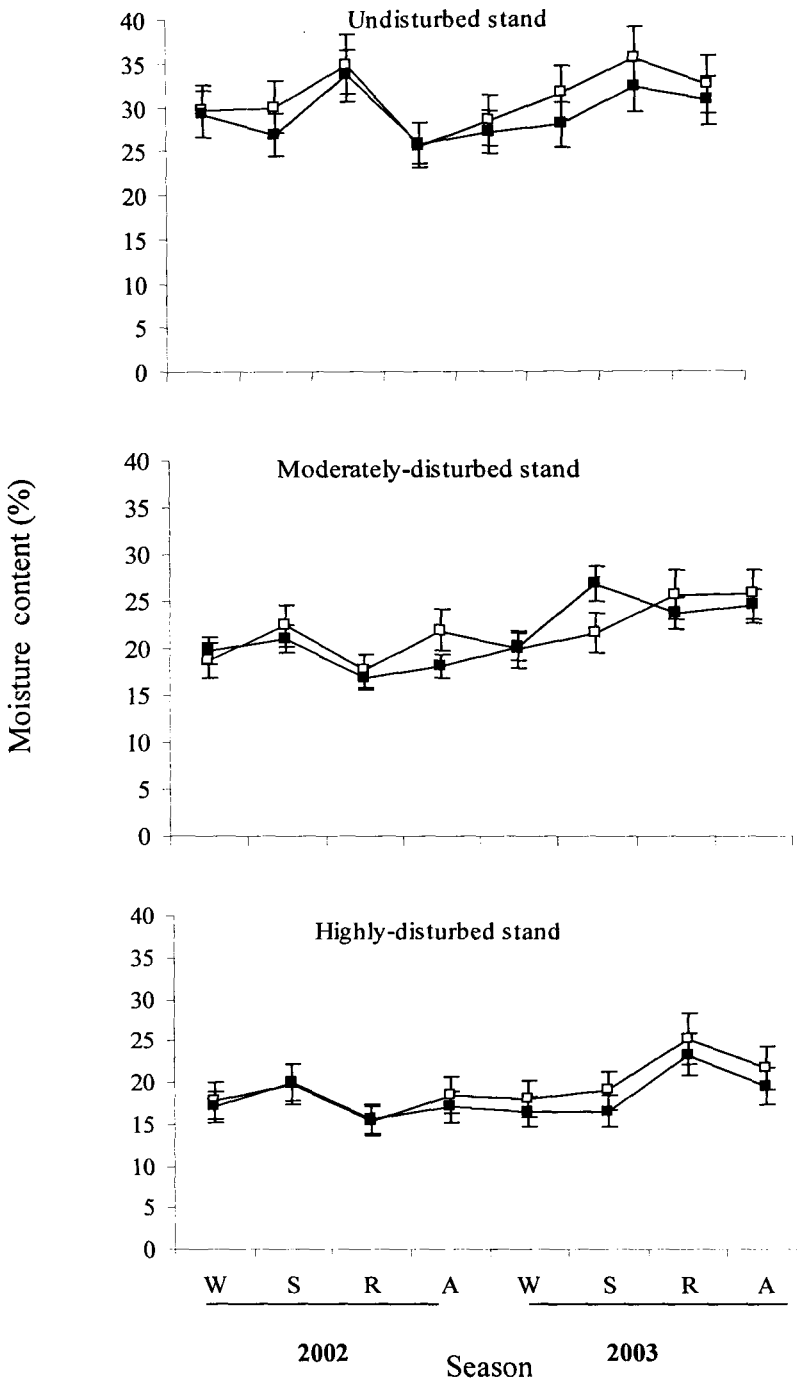

Figure 4.3. Seasonal variation in soil moisture content in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

Table 4.6. Soil chemical properties of the undisturbed, moderately- and highly-disturbed stands. Each value is mean of four seasons across the year.

Parameters/	2002						2003					
	UD		MD		HD		UD		MD		HD	
Soil depth (cm)	0-15	15-30	0-15	15-30	0-15	15-30	0-15	15-30	0-15	15-30	0-15	15-30
pH	4.86	4.94	5.68	5.77	6.00	6.24	5.05	5.23	5.81	5.94	6.27	6.48
	±0.23	±0.21	±0.15	±0.07	±0.14	±0.20	±0.23	±0.16	±0.14	±0.07	±0.14	±0.11
SOC (mg g^{-1})	16.71	13.90	9.50	7.72	7.71	6.01	16.20	14.12	9.51	8.21	6.01	5.20
	±0.41	±0.80	±0.20	±0.52	±0.81	±0.73	±1.44	±1.70	±0.46	±0.20	±0.31	±0.38
CEC (meg^{-1})	0.18	0.16	0.11	0.09	0.06	0.05	0.18	0.16	0.10	0.09	0.06	0.05
	±0.001	±0.001	±0.006	±0.005	±0.003	±0.002	±0.001	±0.001	±0.007	±0.006	±0.002	±0.001
TKN (mg g^{-1})	6.61	5.60	3.74	2.91	2.53	2.00	6.21	5.92	3.41	3.00	2.47	1.80
	±0.30	±0.21	±0.44	±0.33	±0.44	±0.40	±0.48	±0.36	±0.47	±0.40	±0.49	±0.24
P (mg g^{-1})	0.90	0.81	0.73	0.70	0.50	0.45	1.00	0.90	0.81	0.74	0.53	0.41
	±0.01	±0.02	±0.07	±0.03	±0.07	±0.02	±0.09	±0.08	±0.05	±0.07	±0.04	±0.05
NH^{+}_{4}-N (µg g^{-1})	9.69	6.89	3.37	2.97	2.64	2.20	10.31	7.74	4.97	4.23	3.09	2.50
	±0.76	±0.95	±0.36	±0.37	±0.31	±0.33	±1.01	±0.43	±0.44	±0.33	±0.29	±0.36
NO^{-}_{3}-N (µg g^{-1})	11.63	9.65	8.73	6.95	6.78	5.82	11.82	10.20	7.06	5.53	5.46	4.46
	±0.49	±0.52	±0.36	±0.83	±0.48	±0.70	±0.28	±0.46	±0.18	±0.30	±0.17	±0.12
PO^{-}_{4}-P (µg g^{-1})	13.31	10.91	8.11	6.76	6.16	5.62	12.90	10.79	7.41	5.85	5.21	4.40
	±0.78	±1.21	±0.38	±0.58	±0.50	±0.38	±0.78	±0.25	±0.37	±0.42	±0.85	±0.03
C/N	2.53	2.48	2.56	2.65	3.08	3.00	2.38	2.38	2.79	2.73	2.50	2.88
N/P	7.33	7.00	5.28	4.14	5.00	5.00	6.80	6.55	4.25	4.28	4.80	4.50
C/P	18.55	17.37	13.57	11.00	15.40	15.00	16.20	15.66	11.87	11.71	12.00	13.00

± S.E. (n=4); UD-Undisturbed, MD-moderately disturbed, HD-Highly disturbed stands.

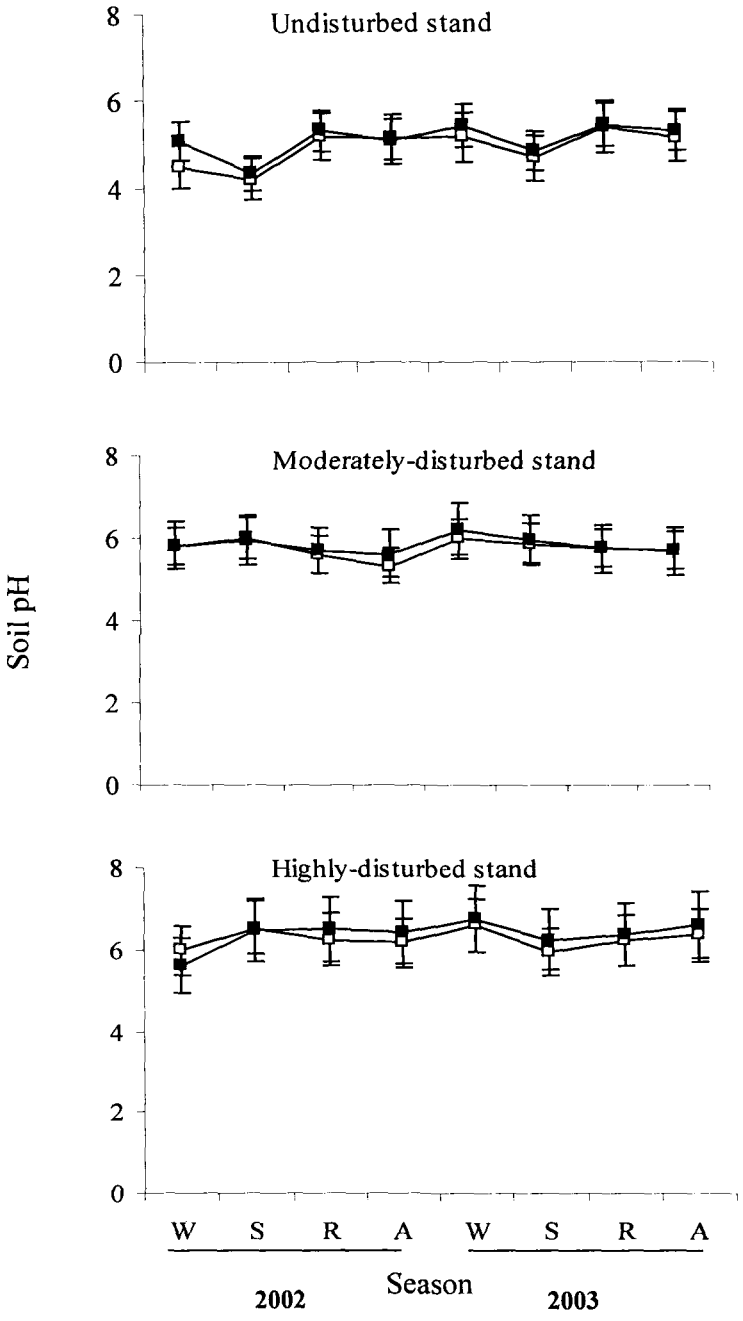

Figure 4.4. Seasonal and depth wise variation in soil pH in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represent standard error (n=12).
W-winter, S-spring, R-rainy and A-Autumn.

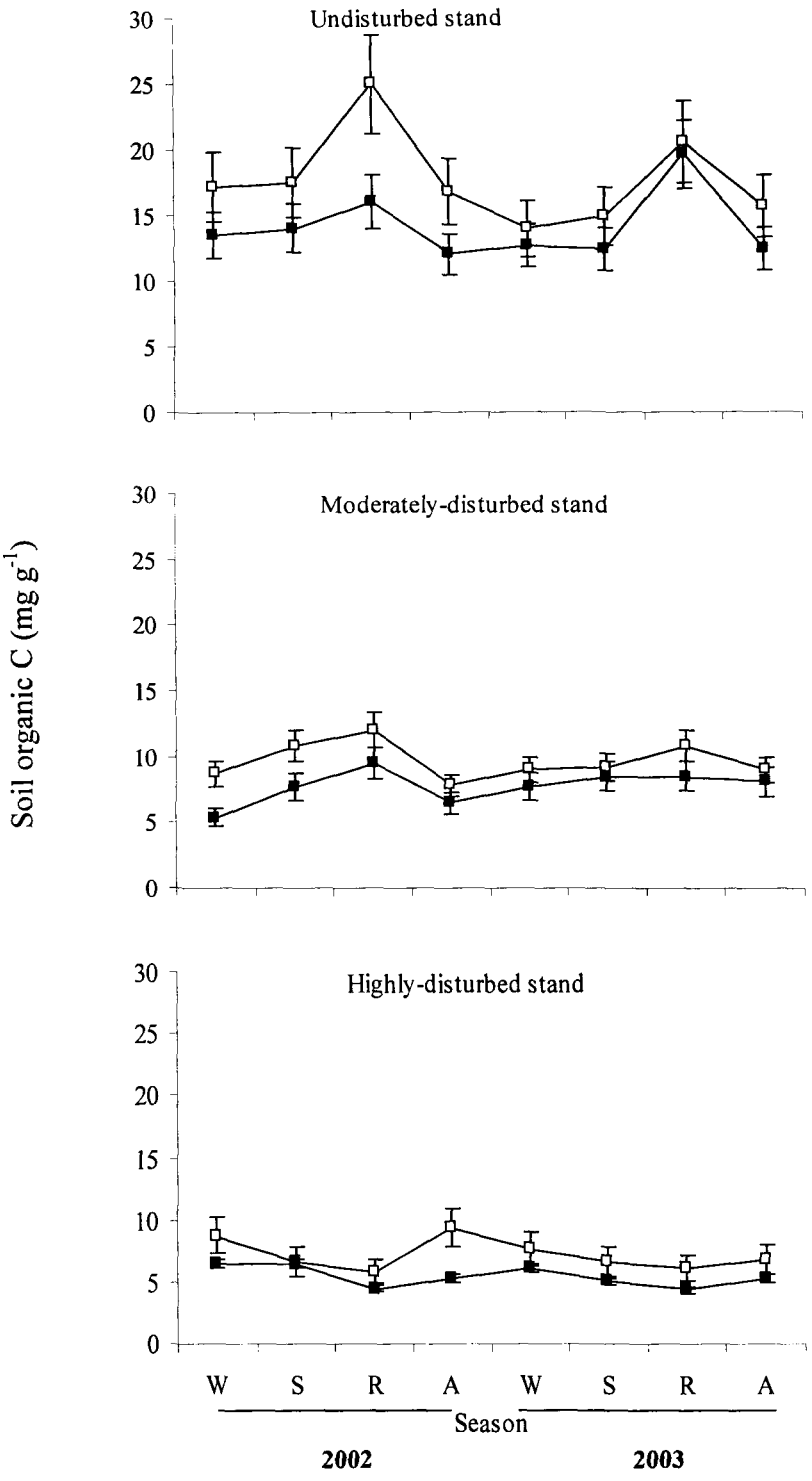

Figure 4.5. Seasonal changes in organic carbon in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represents standard error (n=12).
W-winter, S-spring, R-rainy and A-autumn.

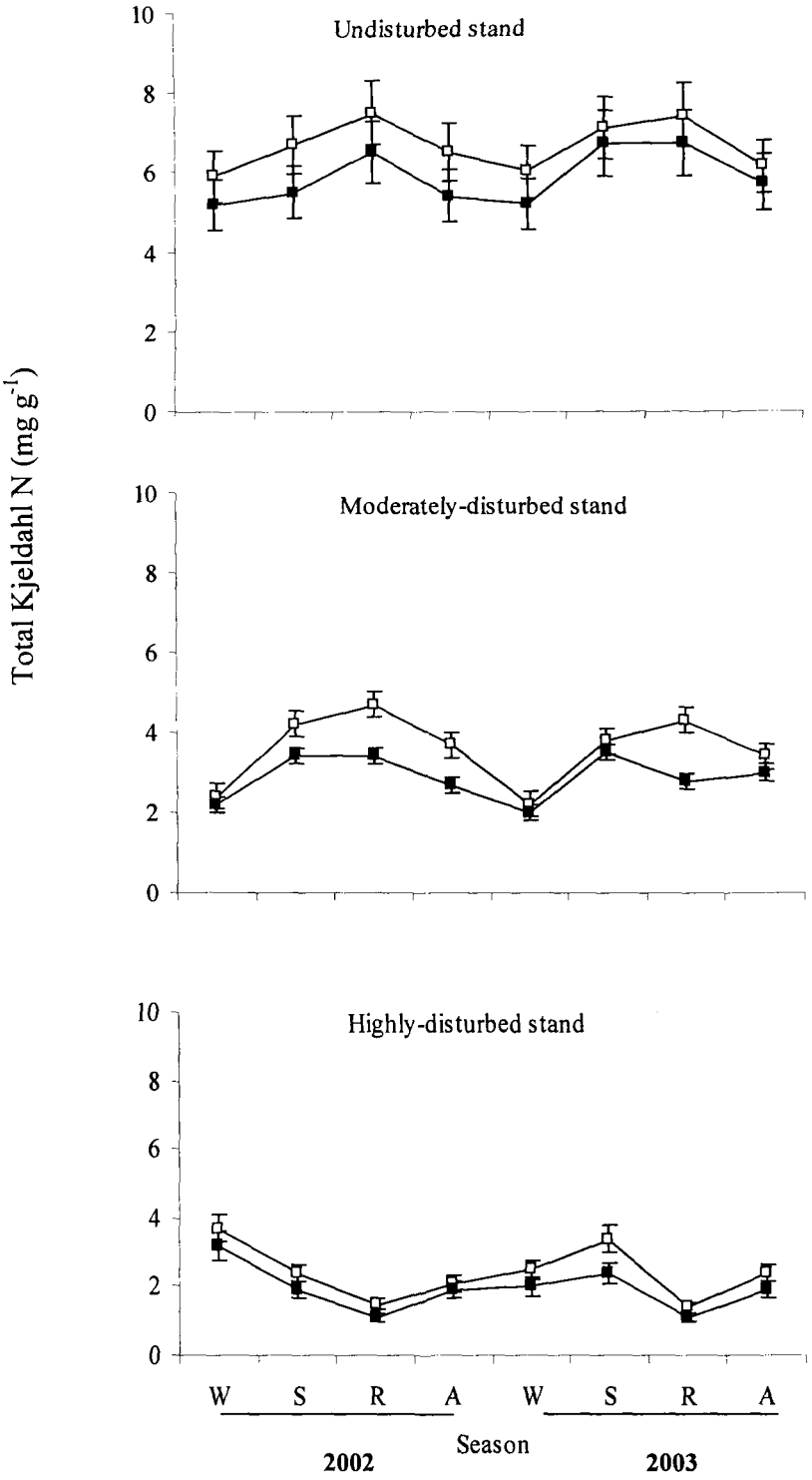

Figure 4.6. Seasonal variation in total Kjeldahl nitrogen in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

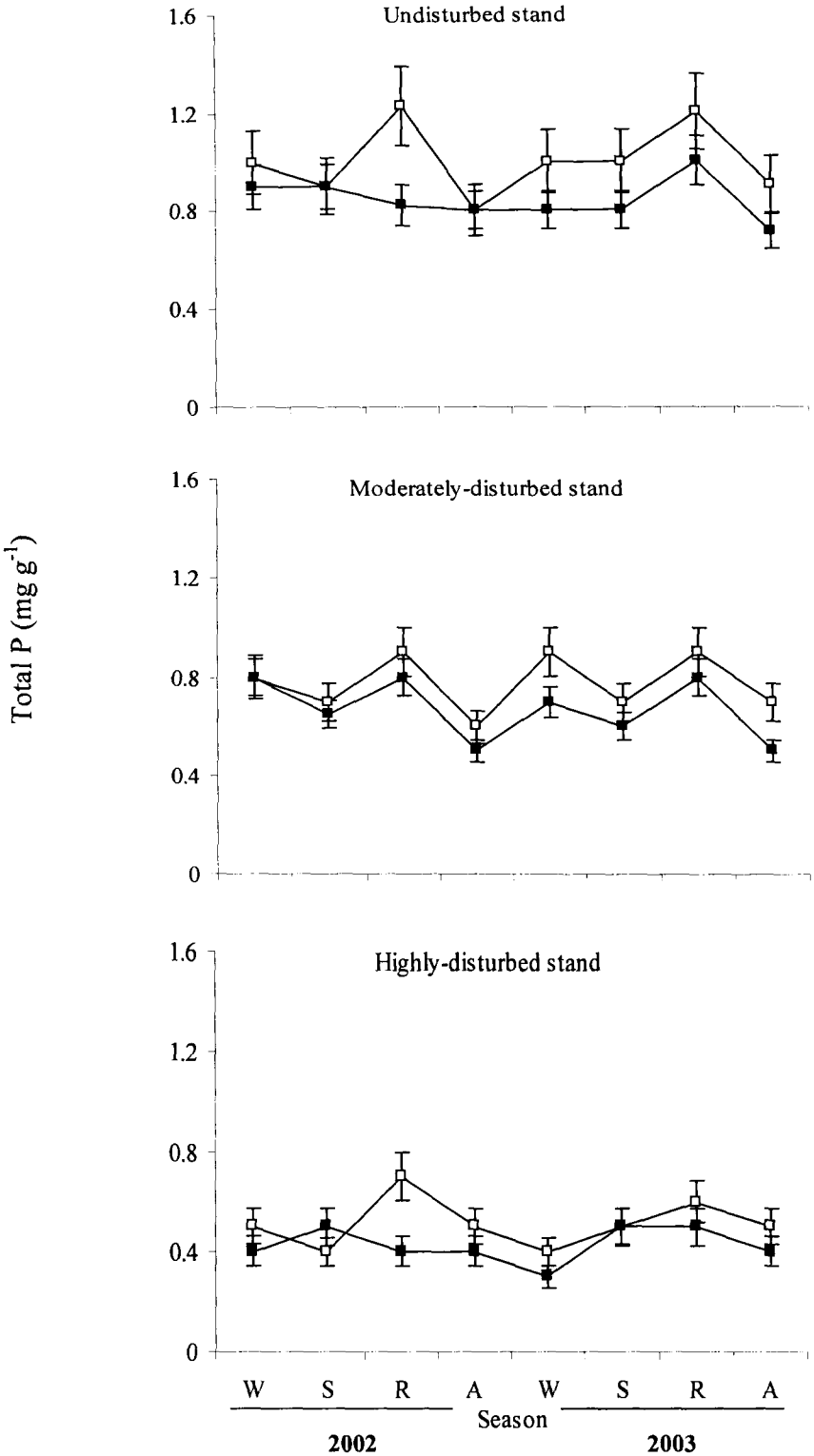

Figure 4.7. Seasonal changes in phosphorus concentration in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

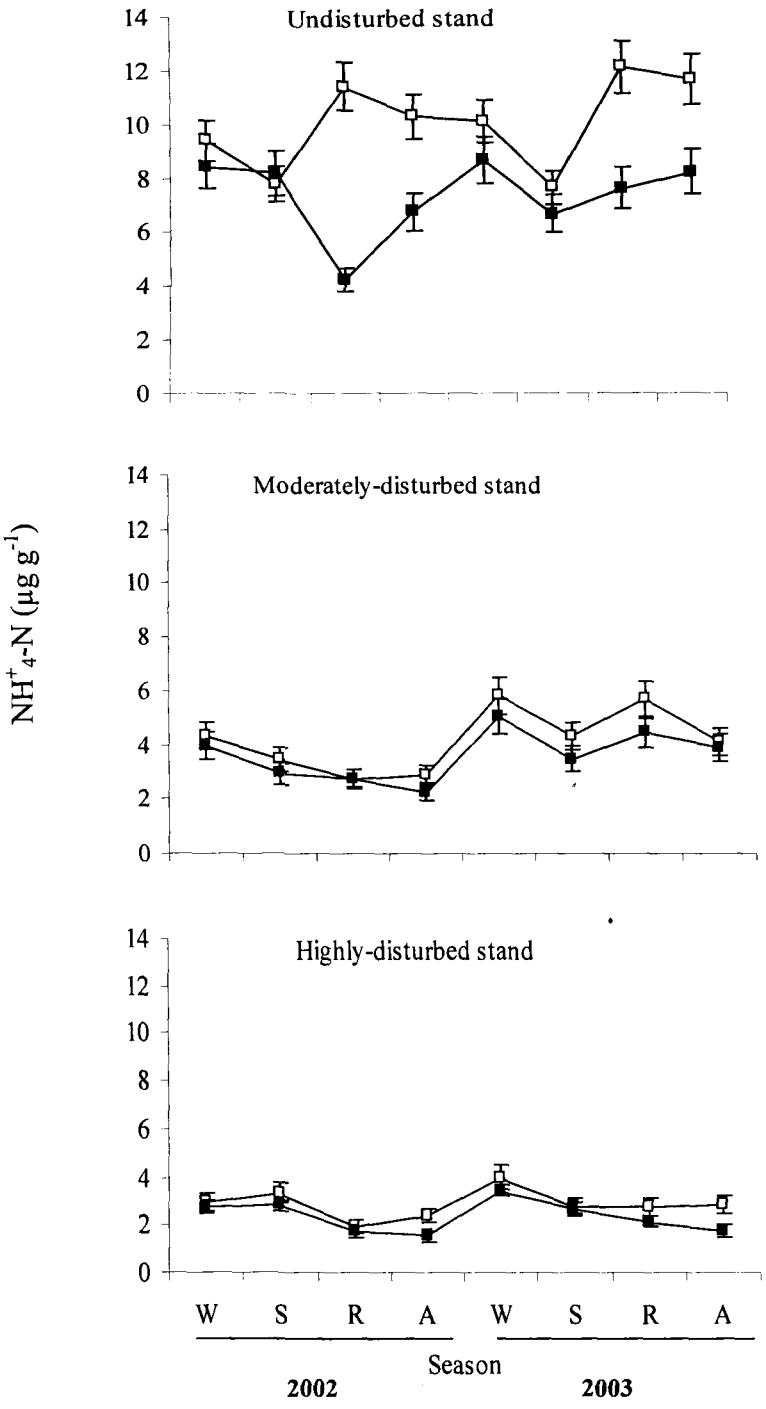

Figure 4.8. Seasonal changes in available NH^+_4-N (µg g^{-1}) in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

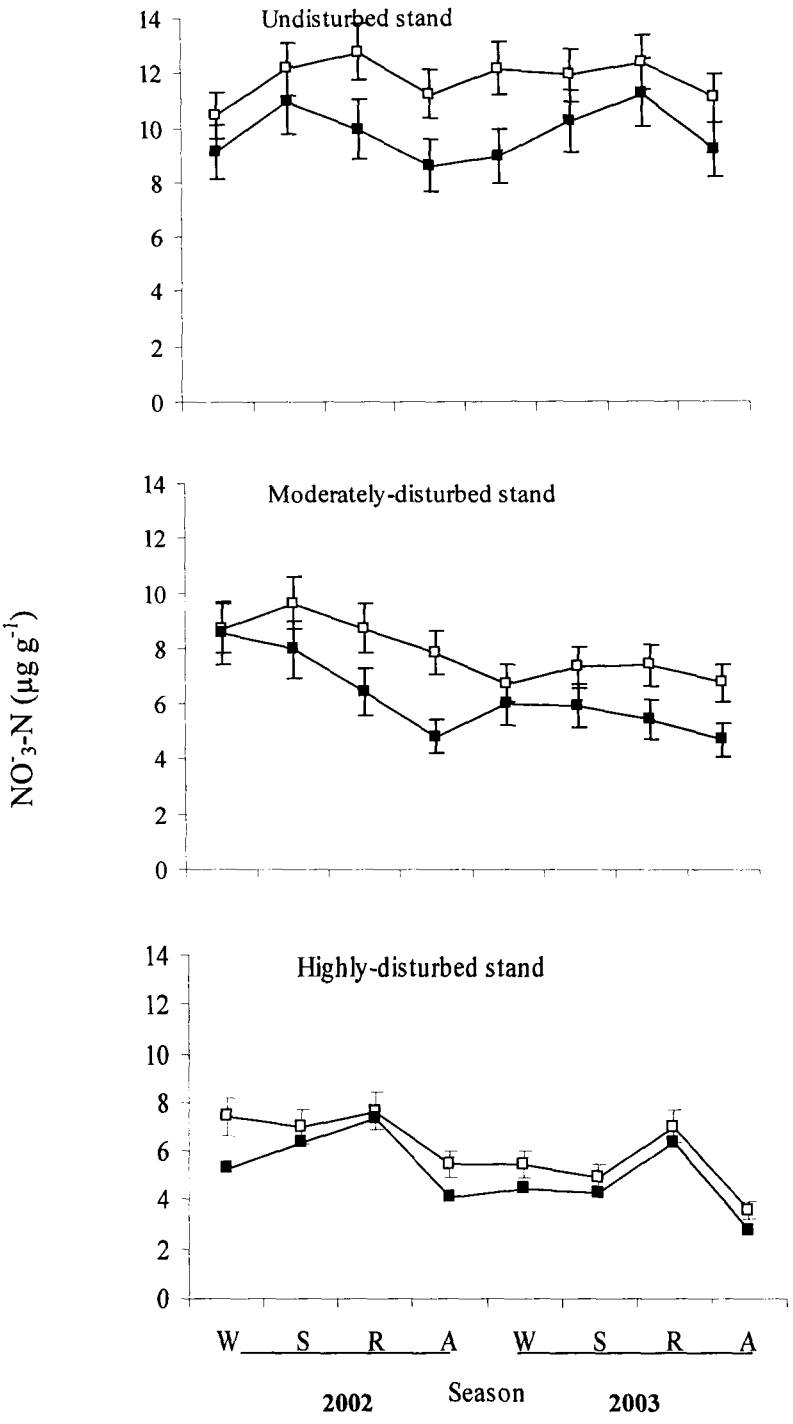

Figure 4.9. Seasonal variation in available NO^{-}_{3}-N (µg g^{-1}) in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

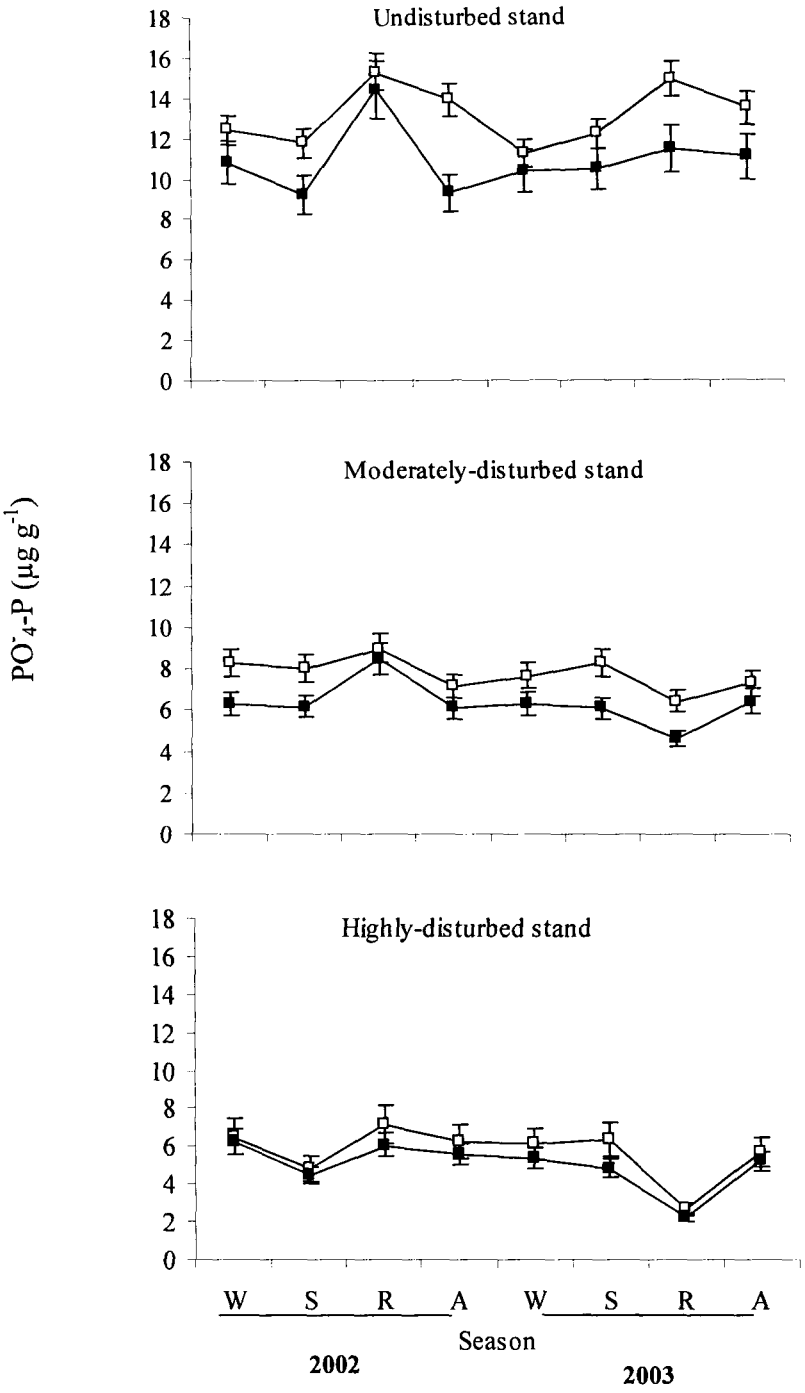

Figure 4.10. Seasonal changes in available PO_4^--P (µg g^{-1}) in the undisturbed and disturbed stands (□ 0-15 and ■ 15-30 cm soil depths). Vertical lines represent standard error (n=12). W-winter, S-spring, R-rainy and A-autumn.

Discussion

Vegetation

The community in all the stands were dominated by *Dipterocarpus macrocarpus, Shorea assamica, Mesua ferrea and Vatica lanceaefolia* with a few exceptions in the highly disturbed stand. The community characteristics like species composition, density, basal area and diversity index showed marked difference between the undisturbed and disturbed stands. The undisturbed stand had a high density of tree species than the other disturbed stands. This decline in tree density in the moderately and highly disturbed stands was mainly due to selective cutting of trees, clear felling and occasional cultivation of annual crop species that caused poor regeneration. Human induced disturbances such as cultivation, selective logging, clearfelling and NTFPs extraction and grazing were also responsible for changes in the species number, density and basal area (Rao *et al.* 1990).

Reduction in basal area was also related to the disturbance level. According to Smiet (1992), basal area values could be related to the stand disturbance index.

Decline in shrubs species with increasing disturbance could be due to increase in solar radiation on the forest floor and consequent increase in surface temperature and reduced competition from the canopy trees (Rao *et al.* 1990). Analysis of microclimatic data showed that light intensity and temperature were significantly higher in the disturbed stands than the undisturbed stand.

Microclimate

Thinning of canopy trees was responsible for increasing light intensities, soil and air temperatures on the forest floor on one hand and decreasing relative humidity

on the other. Similar seasonal fluctuations in microclimate, has also been reported by Lee (1978) in mixed Dipterocarp forest in Malaysia and Barik *et al.* (1992) in subtropical broad leaved forest of Meghalaya, Northeast India. 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 constituents plant species (Lal 1987; Chen *et al.* 1999). The environment in the undisturbed forest was characterized by low light intensity and temperature of air and soil and high soil moisture and relative humidity as compared to the disturbed stands.

Physico-chemical properties of soil

Forest clearance also reduces organic matter input and may change the amount and quality of litter (Hendrickson *et al.* 1989; Dinesh *et al.* 2003). Loss of canopy trees increased the erosion of top soil during extreme rainfall events (Scholes *et al.* 1994), increases the proportion of sand in the disturbed stands due to loss of finer soil particles (Eyre 1968). This could be one of the reasons for lower proportion of finer soil particles in the highly disturbed stand than the moderately and undisturbed stands. Higher soil moisture in the undisturbed stand as compared to the disturbed stands is related to low solar insolation and dense litter layer on the forest floor. Whereas greater proportion of sand particles, low soil organic matter and higher temperature could be the possible reasons for the lower soil moisture content in the disturbed stands. Maximum retention of moisture in the surface soil layer might be due to greater soil organic matter content in this layer. Decrease in moisture and water holding capacity of soil in the disturbed stands due to change in soil texture

from sandy clay loam in undisturbed stand to sandy loam in the disturbed stands. In all the three stands, water holding capacity was more in surface soil layer due mainly to relatively higher clay content and accumulation of organic matter in the top soil layer.

Disturbance significantly increased soil bulk density due to loss of soil organic matter, which has an adverse effect on root penetration, water infiltration and gas exchange (Sanchez *et al.* 1983). This may facilitate nutrient runoff from soil.

The low soil pH in the undisturbed stand as compared to the disturbed stands could be the result of lower rate of leaching leading to greater accumulation of partially decayed organic matter in the soil (Arunachalam and Arunachalam 1999). The increased acidity in the soil of the undisturbed stand, might have influenced leaching and re-adsorption of base cations through the soil profile. The decrease in pH during spring/ summer in the undisturbed stand could be due to greater accumulation of decayed organic matter in the soil surface. Besides seasonal variation, the soil pH showed an increasing trend with soil depth and disturbance. Similar temporal and spatial changes in soil pH have been reported by Mishra and Ramkrishnan (1983) and Arunachalam and Arunachalam (1999) in different terrestrial ecosystems of northeast India. In the disturbed stands comparatively higher pH was due to reduced organic matter accumulation. McGrath *et al.* (2001) also reported that conversion of tropical forests in to agricultural and other land use raises soil pH. Greater CEC in the undisturbed stand is related to greater inputs of organic matter and its fast turnover. Since organic matter content in the upper layer of soil was high, it had higher CEC than in the lower soil layer which had relatively low soil

organic matter. Significantly lower concentration of C, N and P in disturbed stands compared to undisturbed stand might be attributed faster rate of decomposition of organic matter due to increase soil temperature and higher rates of microbial decomposition (Alegre *et al.* 1988) as well as greater nutrient losses from the soil system. Reduction in forest floor organic matter following clear felling, logging has also been reported for other forest and soil types (Covington 1981).

NO^{-}_{3}-N, NH^{+}_{4}-N, PO^{-}_{4}-P concentrations were positively related to soil moisture content and soil temperature. Favourable rainfall and soil temperature helped in faster decay of organic matter therefore enhanced nutrient (NO^{-}_{3}-N, NH^{+}_{4}-N and PO^{-}_{4}-P) availability in the surface soil layer.

Disturbance that caused significant decrease in vegetal cover, had its deleterious effects on soil organic C, total Kjeldahl N and P. This is evident from positive correlation between community parameters and SOC, total Kjeldahl N and P contents of soil (Table 4.7).

Table 4.7. Relationship of woody vegetation characteristics with soil organic -C, total Kjeldahl N and P (n=3)

Parameter	Equation	r	P
Tree density (no. ha^{-1})			
SOC (mg g^{-1})	y=10.666+0.025x	0.878	0.05
TKN (mg g^{-1})	y=1.963+0.0065x	0.930	0.05
P (mg g^{-1})	y=0.478+0.0006x	0.998	0.001
Tree basal area (m^2 ha^{-1})			
SOC (mg g^{-1})	y=12.345+0.192x	0.995	0.001
TKN (mg g^{-1})	y=2.480+0.048x	0.998	0.001
P (mg g^{-1})	y=0.551+0.004x	0.881	0.05

Chapter 5

Biomass and nutrient dynamics of fine and coarse roots

Introduction

Roots, the connecting link between vegetation and soil, provide anchorage to plants and serve vital functions of absorption and translocation of water and nutrients. They exert a significant influence on soil profile development, and on dying, roots contribute to soil organic matter content (McClaugherty *et al.* 1982; Fahey *et al.* 1988). In tropical evergreen low land forests roots represent about 12% of the total plant biomass (Sanford 1990). The importance of fine root dynamics to forest biogeochemical cycling is widely recognized (Norby and Jackson 2000), yet understanding of factors controlling the distribution, production and mortality of fine roots remains poor (Vogt *et al.* 1996). The relative importance of fine roots in nutrient cycling and as a component of forest productivity is not proportional to their contribution to the total biomass (Arunachalam *et al.* 1996c). Small diameter roots (<2 mm diameter) are often assumed to be the most important size fraction for mineral uptake in woody plants (Bohm 1979).

Across a range of ecosystems, net primary production can be greater in below ground than in above ground plant parts (Caldwell 1987). Further, nutrient concentrations in the fine roots may be greater than those in the foliage (Meier *et al.* 1985) and they have faster turnover rate (Vogt *et al.* 1983). Nutrient release from the decomposing roots is a pathway of significant nutrient flux in any terrestrial ecosystem (Joslin and Henderson 1987; Fahey *et al.* 1988; Arunachalam *et al.* 1996d). In forest ecosystems, for example, the amount of carbon (C) and nutrients returned to the soil from fine root turnover may

equal or exceed that from the leaf litter (Joslin and Henderson 1987; Raich and Nadelhoffer 1989). Understanding the relationship between fine roots (<2 mm diameter) and coarse roots (>2 -≤5 mm diameter) and nutrient release patterns during their decomposition is also important in nutrient cycling studies (Meentemeyer 1978; Vogt *et al.* 1991). The factors that regulate the rate of decomposition and nutrient mineralization include soil moisture, temperature, microbial activity and resource quality of decomposing materials (Bloomfield *et al.* 1993). Recent studies have related root decomposition to root chemistry (Silver and Miya 2001), nitrogen availability (Hendricks *et al.* 2000), hydrologic fluctuations (Baker III *et al.* 2001) and temperature and precipitation (Gill and Jackson 2000).

Many tropical rain forests have extensive root mats developed over the nutrient deficient mineral soils. Such dense superficial root systems (Ramakrishnan and Singh 1983; Sanford 1990) aid to nutrients conservation through their direct transfer from decomposing litter to roots (Stark and Jordan 1977). Knowledge of changes in root biomass and its distribution in the soil profile as a result of land-use cover change would improve our understanding of the consequences of deforestation on vegetation (Jackson *et al.* 2000). Tropical forests are exposed to a variety of disturbances ranging from frequent, localized events to less frequent, landscape or multiple disturbance events (Lugo and Scatena 1995). Fewer studies have addressed the effects of disturbance on fine roots dynamics in tropical wet evergreen forests of northeast India. This chapter presents data on fine and coarse root biomass, production, turnover and decomposition in disturbed and undisturbed stands of a tropical wet evergreen forest in northeast India.

Method

Root sampling

In undisturbed, moderately and highly disturbed stands, roots sampling was undertaken in the four seasons (January, April, July and October) during 2002-2004, following soil-core method (Bohm 1979). Ten randomly located soil samples were collected from two successive depths (0-15 and 15-30 cm) in each stand using a long tubiform steel corer (5.5 cm diameter x 50 cm height). The core samples were taken to the laboratory in sealed polybags and stored in a deep freeze at -20 °C for analysis.

Fine (<2 mm diameter) and coarse (>2 mm diameter) roots in each sample were separated in the laboratory by wet-sieving method (Bohm 1979), *i.e.*, soil samples were soaked for 1 h and then washed through different sieve sizes (0.50-5.00 mm pore size) with a gentle spray of tap water until most of the mineral soil and friable organic particles were washed out. Remaining root materials were placed on ordinary filter paper and sorted to remove small stones and litter fragments. Live and dead roots were hand sorted on the basis of colour and texture, dead roots were dark and spongy while live roots were brown and firm (Persson 1982). In case of doubt, roots were cut with a sharp razor and examined under magnification for colour and cohesion between cortex and periderm. The diameter of roots was measured by using a Vernier caliper. The roots were categorized into four different diameter classes (*viz.* <1 mm, 1-2 mm, 2-5 mm and ≥5-10 mm) for further analysis.

Dry matter and production of roots

Cleaned live and dead root samples were oven-dried at 80 °C ±5 °C for 48 h and weighed. Annual fine and coarse roots production by diameter class and depth was

estimated by summing positive increments in biomass (increments significant at $P<0.05$) between sampling dates (Fairley and Alexander 1985).

Root turnover

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

Statistical analysis

Three-way ANOVA was used to test the difference between stand, season and soil depth. Pearson correlation coefficients were worked out to show the relationships of fine and coarse roots mass with soil physico-chemical properties.

Root decomposition

Chemical analysis of root samples

The oven-dried fine and coarse root materials were powdered in a laboratory Wiley mill to pass through 1 mm pore size stainless steel mesh and analysed for their chemical composition. The ash content was determined by igniting 1g of ground litter sample at 550 °C for 6 h in a muffle furnace. Carbon (C) content was calculated as 50% of the ash-free mass. Nitrogen (N) was estimated following semi-micro Kjeldahl procedure by acid digestion, distillation and titration according to Anderson and Ingram (1993). Total phosphorus (P) was determined by triacid digestion, followed by colorimetric reaction with ammonium and stannous chloride (molybdenum blue method;

Jackson 1958). The C, N and P accumulation in biomass of fine and coarse roots were calculated by multiplying dry mass with respective element concentration.

For decomposition study, roots from top 0-15 cm soil layer were collected in bulk from all the three stands during April 2002. They were carefully washed under a gentle flow of tap water to remove adhering soil and accompanying organic debris and separated into fine (<2 mm) and coarse (>2-5 mm) roots using Vernier caliper. Only live fine and coarse roots were air-dried in the laboratory and sub-samples were kept at 80 °C for 48 h in a hot-air oven for determining the dry mass. The oven-dried materials were powdered in a laboratory Wiley mill to pass through 1 mm pore size stainless steel mesh and analysed for their initial chemical composition. Lignin, cellulose and hemicellulose contents were determined gravimetrically according to Anderson and Ingram (1993).

Decomposition of root litter was studied using the nylon bag technique (Gilbert and Bocock 1960). Five gram air-dried root material was placed in each nylon (1 mm x 1 mm mesh size) litter bag (15 cm x 15 cm). Sub-samples of air-dried materials were taken in triplicate from each stand for dry weight determination. Seventy five bags were buried in the top 0-15 cm soil layer during May 2002 in each stand. From each stand, five bags of fine and coarse roots were separately retrieved at 30, 60, 90, 120, 150, 180, 210, 240, 270, 300, 330, 360, 390 and 420 days after incubation and brought to the laboratory carefully avoiding loss of materials from the litter bags. These were washed in a bucket full of tap water by swirling briefly and carefully decanting through a 2 mm mesh size sieve to remove extraneous matter and oven-dried at 105 °C after 24 h. The samples were powdered and analyzed for total N and P concentration.

Computation

Annual decay constant (k) was calculated following the negative exponential decay model (Olson 1963): $k= \ln (X/X_o)/t$, 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 period. The N and P mineralization constants (k_N and k_P) were calculated by substituting dry weight with the total amount of N and P present in the root samples (Singh and Shekar 1989). The time required for 50% (t_{50}) and 99% (t_{99}) decay was calculated as $t_{50}=0.693/k$ and $t_{99}=5/k$ (Olson 1963).

Two-way ANOVA was used to study the effects of site and times on nutrient release. The relationships between weight loss and soil physico-chemical variables were analysed by computing simple linear regressions (Zar 1974). Regression analysis was also used to assess the effect of chemical composition of root on decomposition. Composite polynomial regression model, $Y=a+bX_1+cX_2$ and $Y=a+bX_1+cX_2+dX_3$ was constructed using dummy factors as the indicator variables (Zar 1974) to distinguish different phases of decomposition. By using this equation an expected decay curve was fitted to the root mass data obtained at different time intervals in the decomposition study. In these equations, Y is the mass remaining, 'a' is the Y intercept (constant), 'b' is the rate of change in Y with respect to time, and 'c' and'd' are shifts parameters for adjustment of the Y intercept in Phase-II and Phase-III respectively. The shift parameters were the dummy factors equivalent to zero, if the decay was slow, and/or 1 if the decay was fast (Arunachalam *et al.* 1996d).

Results

Seasonal variation in root mass

On an over all basis, maximum live root biomass in all diameter classes was recorded during rainy season, while the minimum occurred during winter in the undisturbed and moderately disturbed stands. An opposite trend was observed in the highly disturbed stand, where peak biomass was recorded during winter and minimum during rainy season (Table 5.1). The very fine roots (<1 mm diameter) was significantly ($P<0.01$) higher in the highly disturbed stand, while the amount of fine root biomass (1-2 mm diameter) was higher in the undisturbed and moderately disturbed stands (Figure 5.1).

Maximum fine root mass (8060.95 kg ha^{-1}) was recorded in the undisturbed stand and minimum (2286.36 kg ha^{-1}) in the highly disturbed stand. Coarse root biomass did not varied significantly between undisturbed and moderately disturbed stands but varied significantly ($P<0.001$) between undisturbed and highly disturbed stands. It ranged between 585.31 kg ha^{-1} in highly disturbed stand and 4285.39 kg ha^{-1} in the undisturbed stand. Fine and coarse dead root mass varied significantly ($P<0.05$) between stands, varying from 1553.58-3160.35 kg ha^{-1} in the undisturbed stand to 268.80-724.31 kg ha^{-1} in the highly disturbed stand (Tables 5.4). In the highly disturbed stand, fine roots represented about 92% of total roots, while in the moderately and highly disturbed stands their proportion declined to about 74%. In general, the contribution of fine roots mass was significantly ($P<0.05$) greater than the coarse root mass in all the three stands.

Table 5.4. Mean annual total root mass (kg ha^{-1}) in the undisturbed and disturbed stands. Each value is the mean of eight seasons across the two years.

Study Site	Soil depth (cm)	Fine roots (kg ha^{-1}) Live	Fine roots (kg ha^{-1}) Dead	Coarse roots (kg ha^{-1}) Live	Coarse roots (kg ha^{-1}) Dead
UD	0-15	5462.12	1957.27	1438.93	617.67
		±271.91	±225.23	±78.62	±24.18
	15-30	2598.83	1203.08	2801.46	935.91
		±74.70	±86.01	±157.19	±37.12
	Total	**8060.95**	**3160.35**	**4285.39**	**1553.58**
MD	0-15	3467.99	1370.64	1135.57	377.18
		±112.38	±79.96	±88.34	±12.02
	15-30	1687.67	570.11	2674.08	810.69
		±106.19	±26.78	±92.56	±66.15
	Total	**5155.66**	**1940.75**	**3809.65**	**1187.87**
HD	0-15	2183.48	683.64	366.89	179.63
		±177.96	±24.29	±16.71	±8.87
	15-30	102.88	40.67	218.42	89.17
		±3.56	±1.09	±6.79	±2.13
	Total	**2286.36**	**724.31**	**585.31**	**268.80**

± SE (n=24)

UD-Undisturbed, MD-Moderately-disturbed, HD-Highly-disturbed stand.

The total fine root mass showed wide seasonal variations in all the stands with peak values during rainy season. The minimum value (1651.10 kg ha^{-1}) was recorded during rainy season in the highly disturbed stand. Dead fine root mass contributed 25-49% to the total fine root mass. The contribution was high during winter season and low during spring or rainy season (Figure 5.4). Total coarse root biomass varied significantly ($P<0.001$) between seasons and stands. In the undisturbed and moderately disturbed stands the values were high during rainy season and low during winter season. On the contrary, in the highly disturbed stand, it was maximum during winter and minimum during spring. The seasonality in dead coarse root mass was similar to that of dead fine root mass with greater contribution in the highly disturbed stand (Figure 5.5).

Vertical distribution of root mass

Both in the undisturbed and disturbed stands major portion (66-98%) of fine roots was present in the surface soil layer (0-15 cm) (Figure 5.2). The proportion of fine roots to the total root mass in this layer was 67% in the highly disturbed stand and 38% in the moderately disturbed stand. The subsurface soil layer (15-30 cm) had about 4-34% of total fine root mass (Figure 5.3). The decrease in fine root biomass at lower depth was significant ($F=27.09$, $P<0.01$) in all the three stands. In the surface layer the highest value (5462.12 kg ha^{-1}) was recorded in the undisturbed stand and the lowest (2183.48 kg ha^{-1}) in the highly disturbed stand. Amount of fine roots in the surface layer increased significantly ($P<0.001$) from highly disturbed to undisturbed stand. Amount of live fine root mass in undisturbed and moderately disturbed stands was significantly ($P<0.01$) higher in rainy season both in the surface and subsurface soil layers (Table 5.2).

The coarse root mass ranged between 218.42-2801.46 kg ha^{-1} with greater values at the lower soil depth. However, in the highly disturbed stand the maximum mass (366.89 kg ha^{-1}) was recorded in the upper soil layer. Dead fine root mass ranged between 360.33-1514.00 kg ha^{-1} in the upper and 869.07-1628.16 kg ha^{-1} in lower soil depths in the highly disturbed and undisturbed stands respectively. Maximum (1127.02 kg ha^{-1}) dead coarse root mass was recorded in the lower soil layer of the undisturbed stand and the minimum (50.78 kg ha^{-1}) was obtained in the lower soil layer of the highly disturbed stand (Table 5.3). The difference in the amount of dead root mass at the two soil depths was not significant.

Table 5.1. Seasonal variation in root biomass (kg ha^{-1}) of different diameter classes in the undisturbed and disturbed stands.

Diameter class (mm)	2002 W	2002 S	2002 R	2002 A	2003 W	2003 S	2003 R	2003 A
Undisturbed stand								
<1	3217.54	3437.50	4610.00	3484.00	3165.00	3263.00	4686.00	3810.10
	±128.65	±220.03	±348.00	±211.36	±187.12	±88.63	±109.63	±328.23
1-2	3784.34	3947.77	5269.52	3915.60	5189.30	4189.00	5319.61	4198.98
	±223.15	±125.23	±426.32	±89.75	±180.32	±110.26	±358.12	±172.65
2-5	2011.00	2407.00	3354.00	2252.67	2573.00	2780.00	3128.55	2402.24
	±214.56	±274.56	±126.56	±176.89	±326.65	±214.85	±140.36	±99.32
>5	1203.00	1819.23	2214.84	1476.04	1276.00	1468.00	2308.00	1651.60
	±108.32	±220.36	±310.23	±92.48	±159.20	±180.32	±148.00	±139.97
Moderately-disturbed stand								
<1	1998.00	2022.05	3140.00	2208.32	2108.047	2260.50	3128.07	2242.54
	±203.36	±132.36	±97.56	±98.23	±112.63	±220.33	±142.56	±362.06
1-2	2558.72	2804.58	3248.56	2769.00	2399.60	2309.20	3455.10	2596.84
	±165.23	±284.23	±138.36	±154.23	±80.36	±129.68	±110.67	±106.58
2-5	2261.02	2493.31	2823.05	2430.05	2299.50	2369.04	2841.67	2448.17
	220.06	±352.36	±180.85	±231.56	±114.97	±121.30	±307.89	±206.35
>5	1208.54	1134.54	1513.90	1227.54	1309.44	1828.00	1634.08	918.42
	±132.55	±170.89	±210.56	±220.36	±112.88	±204.85	±185.69	±104.88
Highly-disturbed stand								
<1	1886.50	1659.70	1191.00	1245.55	1948.56	1428.97	1250.60	1141.68
	±155.48	±155.63	±210.36	±83.63	±195.94	±154.32	±80.00	±148.96
1-2	971.75	720.10	591.54	668.54	1091.04	1139.55	590.40	734.25
	±108.56	±39.00	±28.32	±48.21	±49.62	±110.04	±31.02	±110.02
2-5	356.09	226.02	356.40	284.93	450.48	517.94	382.69	385.84
	±26.94	±10.05	±29.63	±14.00	±42.03	±11.64	±25.96	±73.02
>5	258.00	218.00	162.60	190.00	281.00	244.00	166.50	202.00
	±60.36	±73.83	±53.26	±55.48	±24.36	±23.00	±21.68	±37.40

± SE (n=5), W-winter, S-spring, R-rainy, A-autumn.

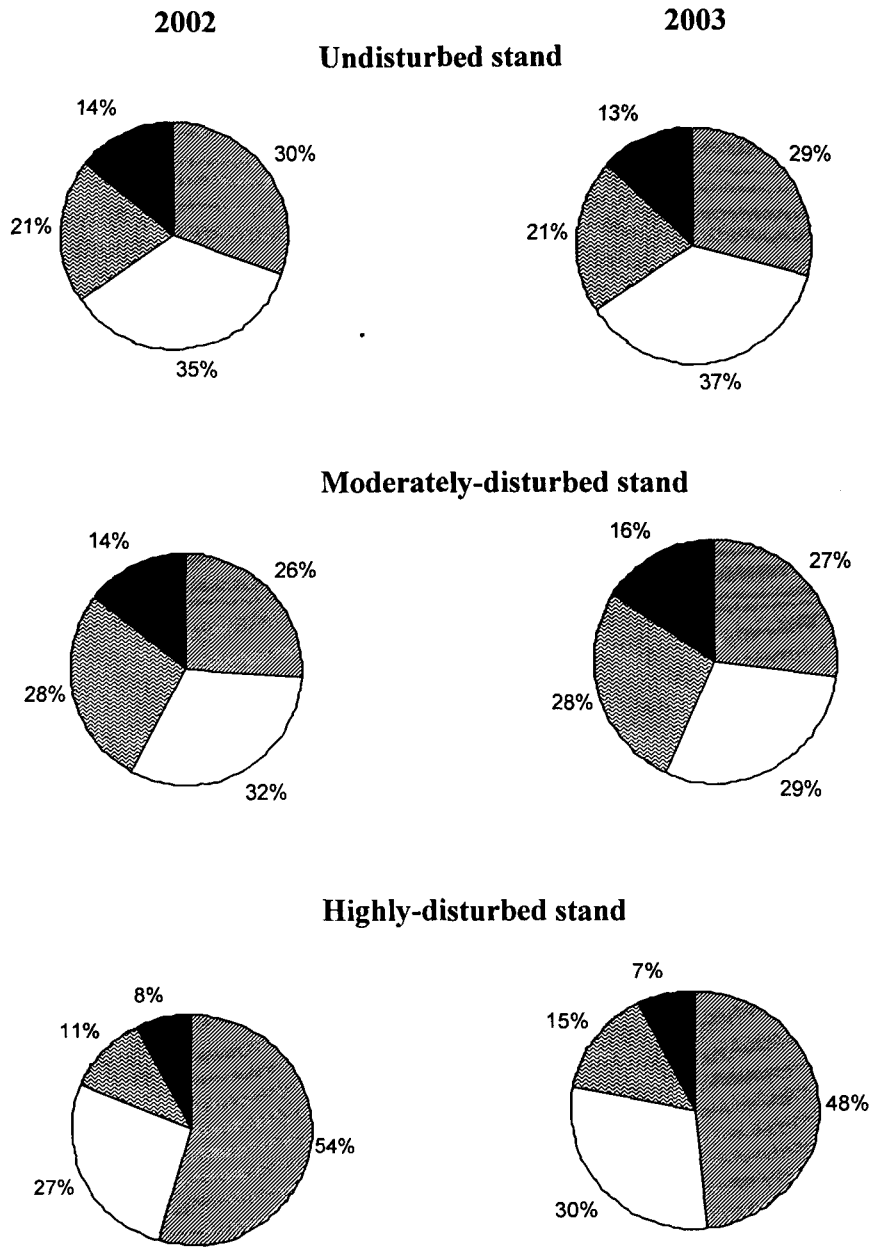

Figure 5.1. Relative proportion of biomass of different diameter classes of roots in the undisturbed and disturbed stands.

Table 5.2. Seasonal and depth wise variation in live and dead mass (kg ha^{-1}) of fine roots (≤ 2 mm diameter) in the undisturbed and disturbed stands.

Study site	Season	2002				2003			
		Live		Dead		Live		Dead	
		0-15	15-30	0-15	15-30	0-15	15-30	0-15	15-30
UD	Winter	4657.10	2344.78	1718.00	1455.00	5164.70	2190.00	2210.03	1628.16
		±315.86	±302.00	±156.36	±78.56	±315.23	±325.26	±245.26	±178.56
	Spring	4878.55	2506.72	1220.70	1386.00	5132.00	2320.00	1918.00	970.00
		±506.38	±158.65	±100.32	±136.58	±389.57	±236.00	±127.23	±78.67
	Rainy	6749.52	3130.00	1687.00	1129.08	7000.56	3005.05	1408.57	869.07
		±467.23	±148.23	±110.23	±147.36	±500.07	±247.35	±110.36	±89.66
	Autumn	4896.60	2503.00	1174.50	1106.55	5217.98	2791.10	1182.66	1080.82
		±368.75	±248.36	±186.36	±100.36	±458.63	±220.02	±168.05	±95.63
MD	Winter	3241.22	1315.50	1565.10	527.50	2741.07	1767.00	1650.00	323.86
		±158.36	±136.25	±100.03	±48.63	±268.41	±148.69	±236.08	±33.60
	Spring	3324.55	1502.08	1309.00	326.00	2737.00	1832.70	1372.00	279.55
		±550.13	±120.36	±129.85	±31.72	±128.56	±104.23	±173.00	±21.37
	Rainy	4332.56	2056.00	1142.00	636.40	4333.03	2250.14	1188.16	649.04
		±607.23	±256.85	±124.23	±57.56	±486.07	±243.23	±106.25	±87.63
	Autumn	3500.92	1477.00	1224.90	273.98	3537.70	1301.68	1100.54	218.40
		±371.55	±76.67	±201.33	±12.58	±169.86	±117.93	±78.96	±22.08
HD	Winter	2812.00	46.25	1431.90	7.00	2967.12	62.48	1514.00	14.75
		±245.03	±2.85	±108.63	±0.20	±268.63	±7.44	±153.52	±1.01
	Spring	2281.25	98.55	334.67	46.85	2441.52	127.00	460.05	21.18
		±178.63	±10.51	±22.30	±4.55	±176.34	±20.36	±14.63	±1.06
	Rainy	1651.10	131.54	489.12	72.50	1720.60	120.40	491.05	75.67
		±115.88	±24.63	±31.36	±3.78	±108.76	±10.52	±33.25	±3.84
	Autumn	1817.06	97.03	388.00	50.50	1771.16	107.77	360.33	36.87
		±200.43	±14.30	±27.26	±1.56	±118.60	±14.00	±42.17	±2.10

± SE (n=5).

UD-Undisturbed, MD-Moderately-disturbed and HD-Highly-disturbed stands.

Table 5.3. Seasonal and depth wise variation in live and dead mass (kg ha^{-1}) of coarse roots (2 - ≥5 mm diameter) in the undisturbed and disturbed stands.

Study site	Season	2002				2003			
		Live		Dead		Live		Dead	
		0-15	15-30	0-15	15-30	0-15	15-30	0-15	15-30
UD	Winter	748.50	2429.50	581.00	991.54	1331.00	2512.00	1039.35	1127.02
		±66.13	±145.63	±28.63	±63.23	±140.36	±263.25	±113.00	±148.03
	Spring	1329.33	2896.90	478.56	671.50	1430.00	2818.00	657.00	932.00
		±117.06	±248.75	±56.85	±39.68	±110.03	±188.76	±78.69	±100.86
	Rainy	2290.84	3278.00	749.56	1109.08	2296.00	3140.55	680.00	1049.56
		±278.08	±314.55	±58.56	±110.05	±117.36	±401.78	±48.79	±178.63
	Autumn	1139.54	2589.17	438.33	840.76	1306.24	2747.60	317.56	765.79
		±123.25	±221.23	±68.56	±89.63	±112.36	±210.30	±33.88	±88.61
MD	Winter	933.00	2526.56	387.50	1140.90	893.50	2714.44	333.70	1527.28
		±142.36	±315.56	±57.36	±118.66	±96.40	±214.56	±31.45	±117.60
	Spring	1169.54	2458.27	361.00	886.00	1117.10	3079.94	264.00	1120.00
		±108.96	±318.22	±45.87	±55.76	±114.25	±288.65	±14.67	±163.78
	Rainy	1480.40	2856.55	420.09	1009.00	1601.15	2874.60	388.50	991.60
		±109.63	±348.63	±57.63	±88.63	±110.10	±247.58	±24.36	±68.35
	Autumn	1092.00	2565.59	458.04	858.54	797.87	2316.72	404.66	652.26
		±166.48	±315.23	±76.36	±46.87	±67.56	±189.50	±61.07	±27.63
HD	Winter	383.54	230.55	230.00	101.07	476.00	255.48	307.70	189.72
		±78.56	±37.36	±31.85	±9.86	±32.56	±22.36	±23.10	±18.63
	Spring	265.32	178.70	168.00	80.90	486.00	275.94	241.00	202.00
		±29.63	±33.14	±12.56	±3.45	±10.96	±28.36	±41.03	±32.44
	Rainy	278.92	240.08	99.67	135.54	320.52	228.67	137.00	75.00
		±16.96	±28.60	±13.57	±15.06	±23.15	±23.68	±17.86	±13.60
	Autumn	320.55	154.38	137.00	50.78	404.32	183.52	116.67	58.34
		±42.58	±10.76	±16.34	±2.50	±28.96	±17.96	±23.54	±2.87

± SE (n=5)

UD-Undisturbed, MD-Moderately-disturbed and HD-Highly-disturbed stands.

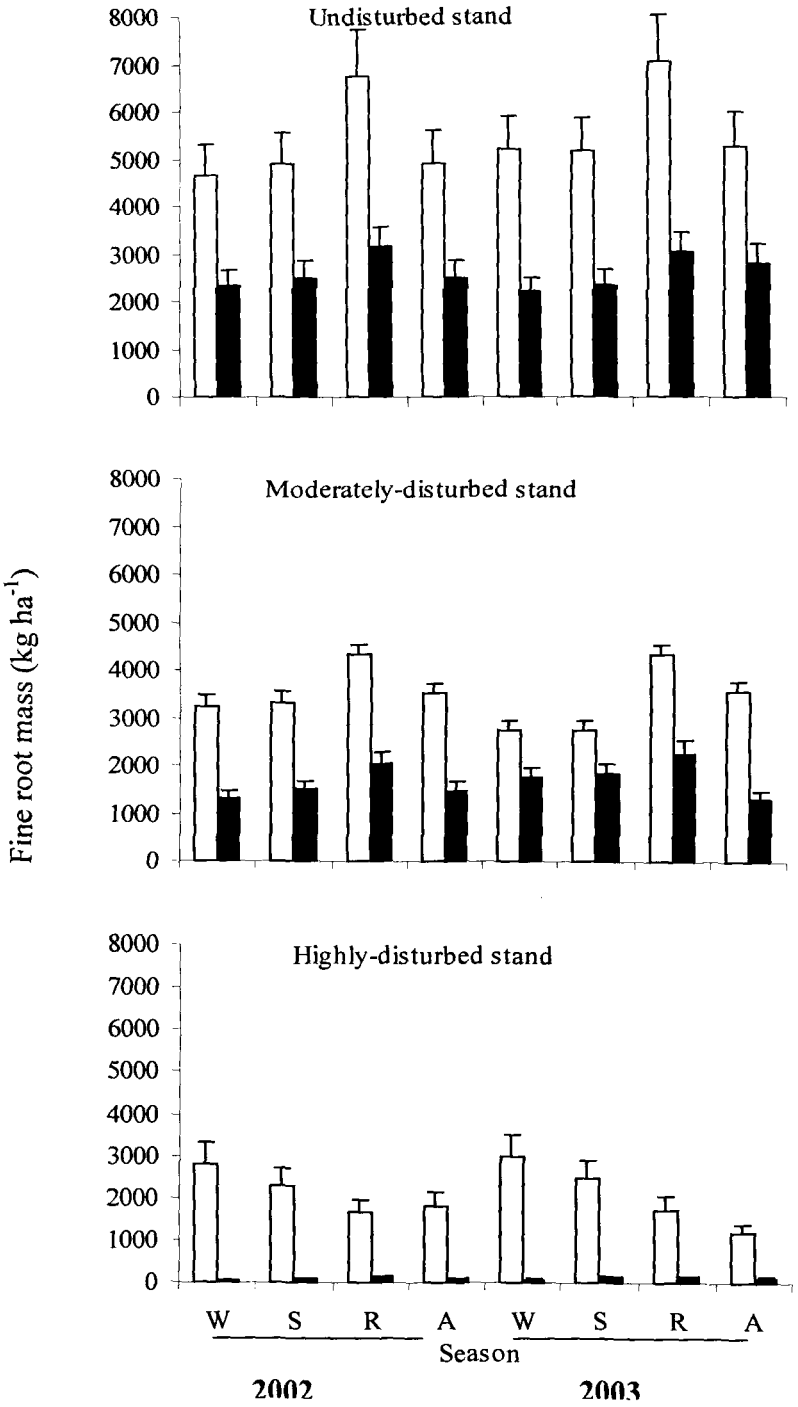

Figure 5.2. Distribution of fine root mass (kg ha^{-1}) in upper (□ 0-15 cm depth) and lower (■ 15-30 cm depth) soil layers of the undisturbed and disturbed stands. Vertical lines represent standard error (n=5).
W-winter, S-spring, R-rainy, A-autumn.

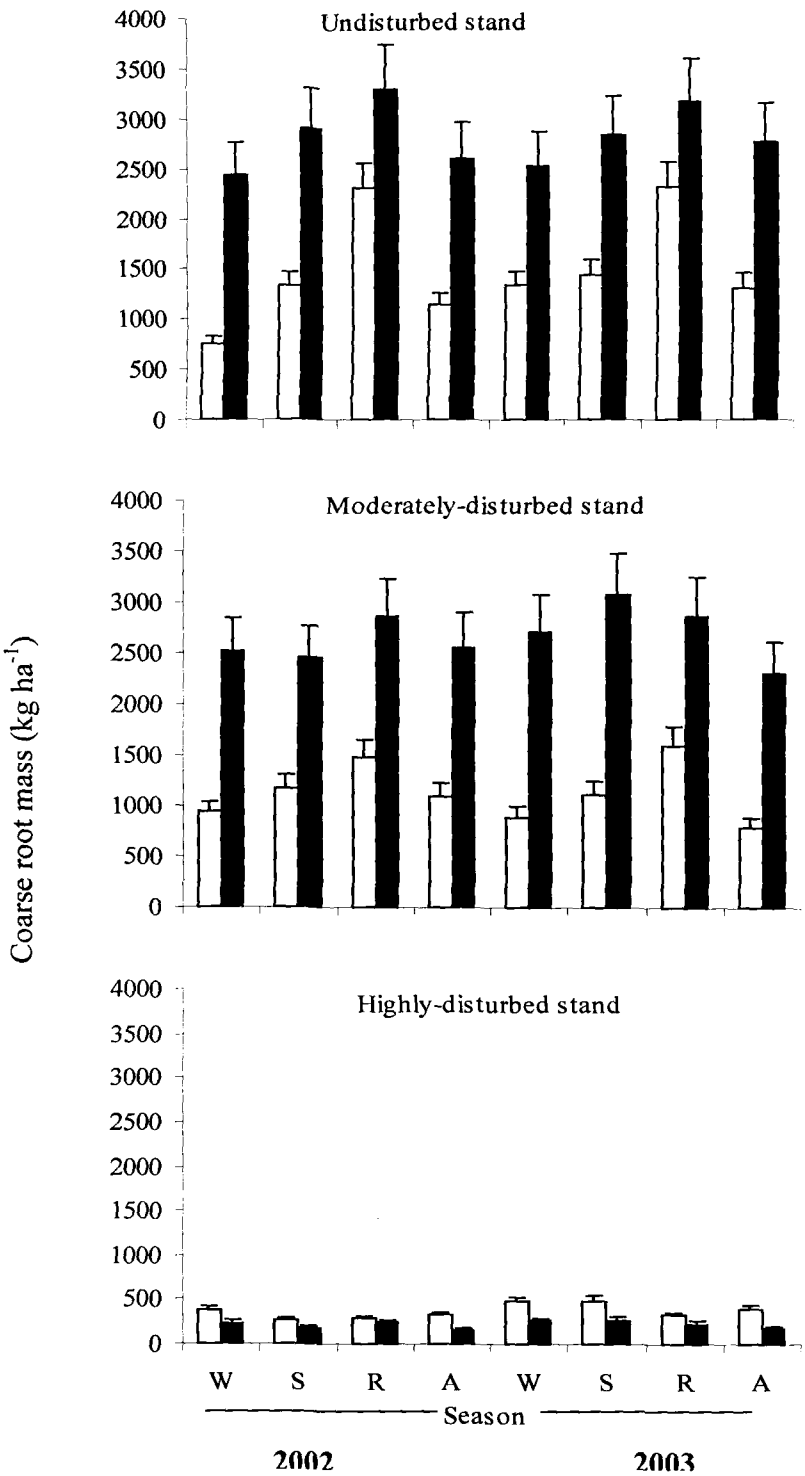

Figure 5.3. Distribution of coarse root mass (kg ha^{-1}) in upper (□ 0-15 cm depth) and lower (■ 15-30 cm depth) soil layers of the undisturbed and disturbed stands. Vertical lines represent standard error (n=5).
W-winter, S-spring, R-rainy, A-autumn.

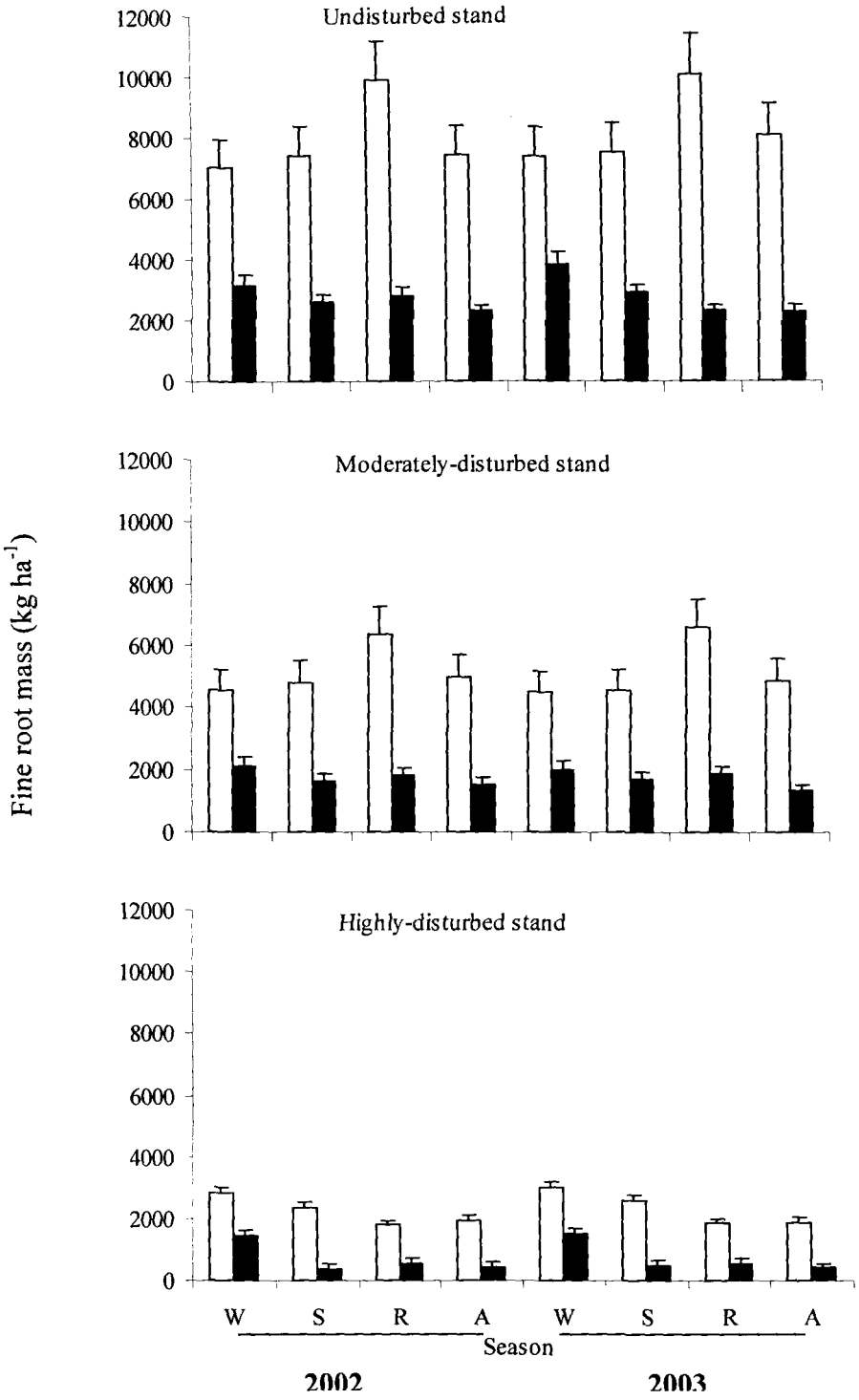

Figure 5.4. Seasonal variation in live (□) and dead (■) fine root mass in the undisturbed and disturbed stands. Vertical lines represents standard error (n=5). W-winter, S-spring, R-rainy, A-autumn.

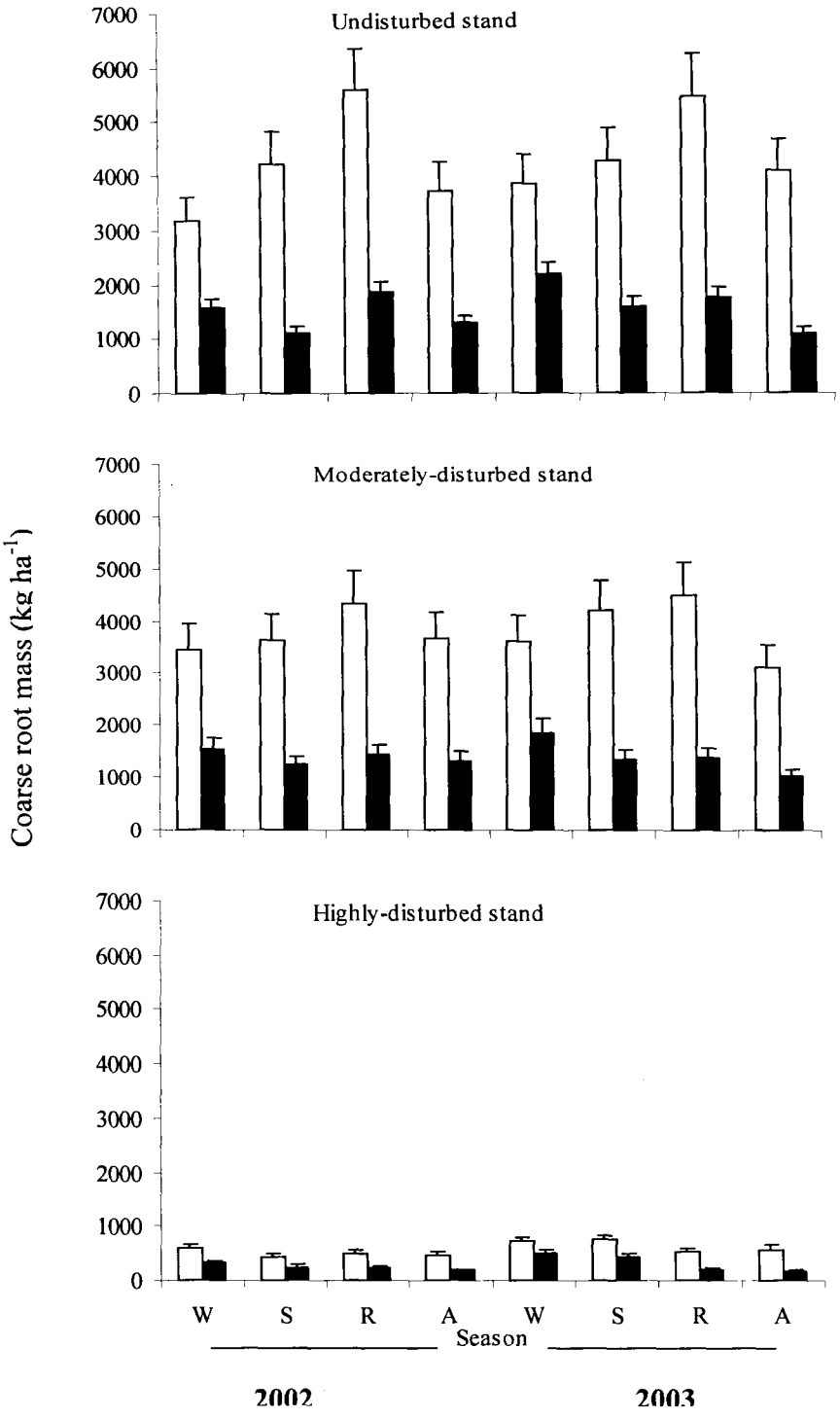

Figure 5.5. Seasonal variation in live (□) and dead (■) coarse root mass in the undisturbed and disturbed stands. Vertical lines represents standard error (n=5). W-winter, S-spring, R-rainy, A-autumn.

Root production and turnover

Annual fine roots (<2 mm diameter) production was 2684-3145 kg ha^{-1} yr^{-1} in the undisturbed stand, 1832-2446 kg ha^{-1} yr^{-1} in the moderately disturbed stand 1101-1401 kg ha^{-1} yr^{-1} in the highly disturbed stand. Production and turnover of different size classes of roots varied significantly ($P<0.001$) between the two years of study; it was greater in 2002 than 2003 (Table 5.5). In general, fine and coarse roots production was significantly ($P<0.05$) higher in the undisturbed stand than the disturbed stands (Table 5.6).

Fine root production was greater during rainy season in the moderately and undisturbed stands whereas in the highly disturbed stand higher production was recorded during dry season. The production of fine roots decreased significantly ($P<0.05$) with the increase in soil depth. In the surface soil layer fine root production ranged from 1316 kg ha^{-1} yr^{-1} in the highly disturbed stand to 2361 kg ha^{-1} yr^{-1} in the undisturbed stand. Similarly, the coarse root production also decreased with the depth except in the moderately disturbed stand, where it did not varied significantly during 2002. Coarse root production ranged from 197 to 1150 kg ha^{-1} yr^{-1} in the upper soil layer, while in the lower layer it varied from 94 to 849 kg ha^{-1} yr^{-1}. The contribution of fine roots to total root production in the upper soil layer was 93, 72 and 66% in the highly disturbed, undisturbed and moderately disturbed stands respectively. In the lower layer their maximum (28%) contribution was in the undisturbed stand and minimum (7%) in the highly disturbed stand. The coarse roots contribution to total root production ranged between 34-55% in the upper layer and 41-45% in lower layer (Table 5.6).

The turnover rate of fine and coarse roots was significantly higher in the upper soil layer of the undisturbed stand. Fine roots turnover was significantly ($P<0.001$) lower

in the subsurface soil layer in the undisturbed and disturbed stands. Coarse roots turnover varied significantly ($P<0.05$) between the undisturbed, moderately disturbed and highly disturbed stands with low values in the highly disturbed stand. In general, the faster turnover rate was recorded in the surface soil layer of undisturbed stand and it decreased with the increase in the intensity of disturbance and depth (Table 5.6). Fine roots biomass was strongly ($r=0.704$-0.834, $P<0.001$) correlated with soil physico-chemical properties (Table 5.12). Analysis of variance showed significant seasonal and depth wise differences in biomass and production of fine and coarse roots (Table 5.13).

C, N and P accumulation and turnover

N and P concentration in roots was inversely related to its diameter. However, there was a significant increase in C concentration with the increase in diameter. Carbon, N and P concentrations in roots also differed significantly with stands and seasons. Comparison between stands indicated that N and P concentration was significantly ($P<0.05$) higher in the undisturbed stand than the disturbed stands (Tables 5.8 and 5.9). The C concentration did not varied significantly between the stands (Table 5.7).

Two-way ANOVA revealed significant ($F=3.41$, $P<0.05$) difference in N and P concentration in fine roots due to season, with higher values during rainy season and lower values during winter in all the stands. Similar seasonal trend was also observed in the coarse roots ($F=5.12$, $P<0.01$) (Table 5.14). Year to year variation in N and P concentration was also significant.

Mean annual C accumulation and its turnover varied significantly ($P<0.05$) between stands and fine and coarse roots. C accumulation in fine roots and its turnover decreased with the increase in the degree of disturbance (Table 5.7). C accumulation in

the coarse roots was greater in the undisturbed and moderately disturbed stands. The turnover rate of both fine and coarse roots decreased from the undisturbed to highly disturbed stand (Table 5.6). Similar trends were also recorded for N and P (Tables 5.8 and 5.9).

Table 5.5. Annual production and turnover of roots of four different diameter classes in the undisturbed and disturbed stands.

Diameter class (mm)	Annual production ($kg\ ha^{-1}\ yr^{-1}$)		Turnover rate		Turnover time (yr)	
	2002	2003	2002	2003	2002	2003
Undisturbed stand						
<1	1711.46	1521.00	0.39	0.37	2.56	2.70
1-2	2758.88	1306.17	0.39	0.35	2.56	2.85
2-5	1663.33	677.87	0.33	0.24	3.03	4.16
>5	1011.84	670.00	0.23	0.24	4.35	4.16
Moderately-disturbed stand						
<1	1142.00	1020.02	0.33	0.30	3.03	3.33
1-2	689.26	1145.90	0.26	0.25	3.85	4.00
2-5	562.03	512.00	0.20	0.23	5.00	4.35
>5	461.26	506.56	0.18	0.18	5.56	5.56
Highly-disturbed stand						
<1	703.01	1023.06	0.30	0.31	3.33	3.23
1-2	499.50	392.36	0.30	0.31	3.33	3.23
2-5	295.93	99.12	0.26	0.28	3.85	3.57
>5	91.00	56.85	0.24	0.20	4.17	5.00

Table 5.6. Annual production and turnover of fine and coarse roots in the undisturbed and disturbed stands.

Study site	Soil depth (cm)	Production ($kg\ ha^{-1}\ yr^{-1}$)				Turnover rate				Turnover time (yr)			
		Fine roots		Coarse roots		Fine roots		Coarse roots		Fine roots		Coarse roots	
		2002	2003	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003
UD	0-15	2360.52	1868.56	1033.80	1149.94	0.47	0.45	0.27	0.28	2.12	2.22	3.70	3.57
	15-30	785.22	815.05	848.50	728.55	0.33	0.34	0.28	0.26	3.03	2.94	3.57	3.85
MD	0-15	1091.34	1596.03	547.40	707.65	0.34	0.36	0.22	0.20	2.94	2.78	4.54	5.00
	15-30	740.58	850.11	547.13	465.50	0.31	0.32	0.17	0.15	3.23	3.13	5.88	6.67
HD	0-15	1316.02	1023.27	197.08	103.80	0.26	0.21	0.16	0.14	3.85	4.76	6.25	7.14
	15-30	85.29	85.40	102.48	93.48	0.13	0.19	0.12	0.11	7.69	5.26	8.33	9.04

UD-Undisturbed, MD-Moderately-disturbed and HD-Highly-disturbed stands.

Table 5.7. C accumulation (kg ha^{-1}) and turnover rate (year) in fine and coarse roots

Soil depth (cm)	Fine roots		Coarse roots	
	Accumulation	Turnover rate	Accumulation	Turnover rate
Undisturbed stand				
0-15	613.94 ±18.95	5.17 ±0.03	256.27 ±6.54	4.98 ±0.01
15-30	292.11 ±10.50	3.70 ±0.08	498.94 ±21.33	4.80 ±0.05
Moderately-disturbed stand				
0-15	423.09 ±8.95	4.27 ±0.04	230.18 ±7.86	4.25 ±0.10
15-30	205.89 ±12.03	3.90 ±0.08	542.04 ±5.68	3.22 ±0.06
Highly-disturbed stand				
0-15	282.33 ±7.63	3.10 ±0.05	72.49 ±2.34	2.96 ±0.008
15-30	13.30 ±1.07	2.07 ±0.03	43.15 ±3.41	2.37 ±0.08

± SE (n=24)
Each value is the mean of four seasons and two years

Table 5.8. N accumulation (kg ha^{-1}) and turnover rate (year) in fine and coarse roots

Soil depth (cm)	Fine roots		Coarse roots	
	Accumulation	Turnover rate	Accumulation	Turnover rate
Undisturbed stand				
0-15	123.44 ±8.63	1.03 ±0.005	19.28 ±1.25	0.38 ±0.02
15-30	58.73 ±53.09	0.74 ±0.04	37.54 ±3.61	0.36 ±0.01
Moderately-disturbed stand				
0-15	68.67 ±7.33	0.69 ±0.02	16.92 ±0.85	0.31 ±0.004
15-30	33.42 ±2.85	0.61 ±0.03	39.84 ±2.67	0.23 ±0.004
Highly-disturbed stand				
0-15	20.08 ±1.03	0.22 ±0.004	2.45 ±0.16	0.10 ±0.001
15-30	1.95 ±0.06	0.15 ±0.003	1.46 ±0.09	0.08 ±0.001

± SE (n=24)
Each value is the mean of four seasons and two years

Table 5.9. P accumulation (kg ha^{-1}) and turnover rate (year) in fine and coarse roots

Soil depth (cm)	Fine roots		Coarse roots	
	Accumulation	Turnover rate	Accumulation	Turnover rate
Undisturbed stand				
0-15	26.76 ±3.01	0.23 ±0.005	4.89 ±0.05	0.10 ±0.002
15-30	12.73 ±0.63	0.16 ±0.002	9.52 ±0.08	0.09 ±0.001
Moderately-disturbed stand				
0-15	13.87 ±1.11	0.14 ±0.004	3.41 ±0.02	0.06 ±0.001
15-30	6.75 ±0.34	0.13 ±0.007	8.02 ±0.16	0.05 ±0.003
Highly-disturbed stand				
0-15	8.08 ±0.14	0.09 ±0.007	0.66 ±0.03	0.03 ±0.001
15-30	0.38 ±0.07	0.06 ±0.001	0.39 ±0.04	0.02 ±0.0006

± SE (n=24)
Each value is the mean of four seasons and two years

Root decomposition

Initial root chemistry

N concentration varied from 13.7-25.9 mg g^{-1} in fine roots and 10.8-20.2 mg g^{-1} in coarse roots. P concentration ranged from 0.40-1.4 mg g^{-1} in fine roots and 0.20-0.90 mg g^{-1} in coarse roots. Concentration of both the nutrient elements in fine and coarse roots were significantly ($F=3.35$, $P<0.05$) different between the stands. In general, N and P concentration decreased with the increase in disturbance intensity and root diameter. C and lignin concentration increased from the undisturbed stand to highly disturbed stand. Over all, the nutrient concentration was significantly ($P<0.05$) higher in the fine roots than in the coarse roots. Highest lignin content (230.7 mg g^{-1}) was recorded in coarse roots in the highly disturbed stand and lowest (177.9 mg g^{-1}) in fine roots of the undisturbed stand. C/N and lignin/N ratios also increased with the increase in disturbance intensity. Cellulose and hemicellulose concentration was low in the fine roots of the undisturbed forest stand and high in the coarse roots of the highly disturbed stand (Table 5.10).

Weight loss during root decomposition

The weight loss pattern of decomposing roots was similar in the three stands (Figures 5.6 and 5.7). Fine roots showed two distinct phases, while in the coarse roots three phases were observed. The first phase that lasted for about 60 days in fine roots (Figure 5.6) and 120 days in coarse roots was characterized by a slow rate of decomposition (0.11% weight loss day^{-1}) (Figure 5.7). This was followed by a period of rapid weight loss (0.52% weight loss day^{-1}) lasting for the next 60 days in fine roots and 90 days in coarse roots. During the third phase *i.e.*, between 180 to 420 days the coarse

roots decomposed at an average rate of 0.09% weight loss day^{-1} in the disturbed and undisturbed stands.

The annual decay constant (k) for fine roots varied from 2.96 in the highly disturbed stand to 4.70 in the undisturbed stand. The corresponding values for the coarse roots were 1.32 and 3.14 respectively. The differences in decay rates between fine and coarse roots ($F=8.41$, $P<0.05$) and between stands ($F=11.21$, $P<0.01$) were statistically significant

Table 5.11. Decay (k) and mineralization constants (k_N and k_P) of fine and coarse roots in the undisturbed and disturbed stands

	Fine roots			Coarse roots		
Parameters	UD	MD	HD	UD	MD	HD
Dry matter						
k	4.70	4.04	2.96	3.14	1.57	1.32
t_{50}	0.15	0.17	0.23	0.22	0.44	0.52
t_{99}	1.06	1.24	2.55	1.59	3.18	3.78
N-mineralization						
k	1.16	0.97	0.76	0.61	0.64	0.93
t_{50}	0.59	0.71	0.91	1.14	1.08	0.75
t_{99}	4.31	5.15	6.56	8.19	7.81	5.37
P-mineralization						
k	2.62	1.77	1.25	1.82	1.44	1.12
t_{50}	0.26	0.39	0.55	0.38	0.48	0.62
t_{99}	1.91	2.82	4.00	2.75	3.47	4.46

UD-Undisturbed, MD-Moderately-disturbed and HD-Highly-disturbed stands.
t_{50} - the time required to achieve 50% decay, t_{99}- the time required to achieve 99% decay.

Nutrient concentration and release during root decomposition

N and P concentration in fine roots recorded 36-42% release during the initial 90 days of incubation and then increased upto 180 days and again declined until 300 days (Figures 5.8 and 5.9). On the contrary, the initial drop in nutrient concentration in the

coarse roots occurred after 90 days, followed by an increase upto 240 days and a decline until 420 days (Figures 5.8 and 5.9).

The drop in concentration of nutrients indicated the release while increase in concentration after initial decline suggests immobilization. The release of nutrients was directly proportional to weight loss both in fine and coarse roots. Overall, the rate of N and P release from decaying fine and coarse roots decreased from undisturbed to highly disturbed stand (Figures 5.10 and 5.11). As a result N and P mineralization constants (k_N and k_P) also decreased in the disturbed stands (Table 5.11).

Table 5.10. Initial chemical composition of fine (FR; <2 mm diameter) and coarse (CR; >2 mm diameter) roots in the undisturbed and disturbed stands.

Study site	Root category	C ($mg\ g^{-1}$)	N ($mg\ g^{-1}$)	P ($mg\ g^{-1}$)	Lignin ($mg\ g^{-1}$)	Cellulose ($mg\ g^{-1}$)	Hemi-cellulose ($mg\ g^{-1}$)	C/N	N/P	Lignin /N
UD	FR	135.8	25.9	1.4	177.9	208.2	114.8	5.2	18.5	6.9
		±5.6	±0.4	±0.01	±23.6	±30.7	±10.4	±0.1	±0.8	±0.1
	CR	210.5	20.2	0.9	193.7	214.7	106.8	10.4	22.4	9.6
		±17.6	±1.1	±0.04	±23.1	±20.7	±10.1	±0.8	±16.7	±0.7
MD	FR	150.0	23.1	0.8	207.5	206.8	60.2	6.5	28.9	8.9
		±7.6	±0.1	±0.01	±23.1	±42.1	±0.2	±0.1	±0.4	±0.1
	CR	287.2	21.0	0.3	218.2	295.8	50.3	13.7	70.0	10.4
		±24.1	±0.8	±0.01	±19.6	±26.3	±2.5	±1.3	±2.1	±0.9
HD	FR	200.4	13.7	0.4	226.3	287.7	51.7	14.6	34.3	16.5
		±12.3	±0.4	±0.01	±19.6	±30.6	±2.0	±2.1	±0.8	±2.3
	CR	336.8	10.8	0.2	230.7	301.6	51.0	31.18	54.0	21.4
		±26.0	±1.0	±0.01	±21.4	±23.1	±1.7	±2.0	±1.1	±2.5

± S.E. (n=5)
UD-Undisturbed, MD-Moderately-disturbed and HD-Highly-disturbed stands.

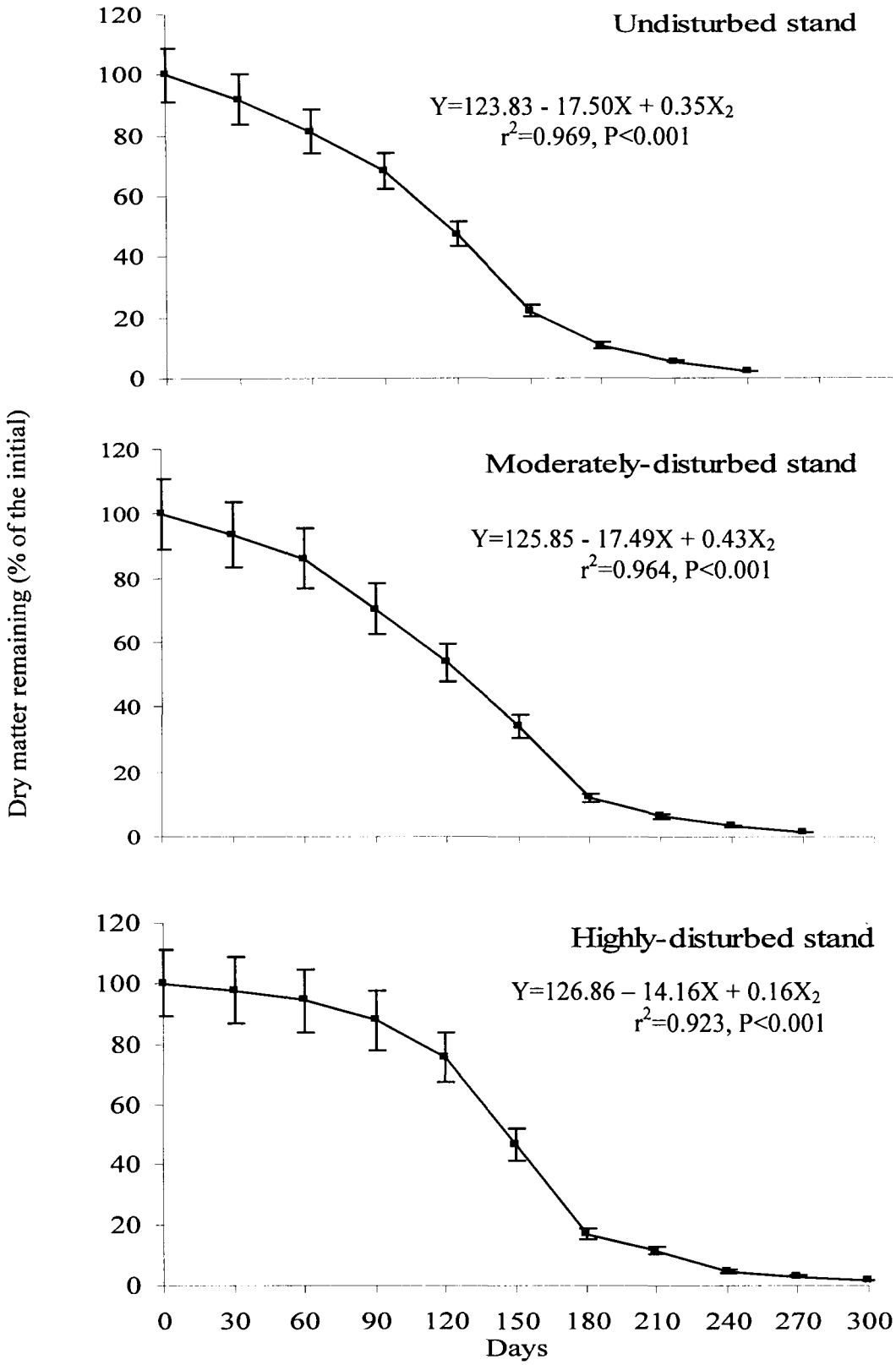

Figure 5.6. Decay pattern of fine roots in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5).

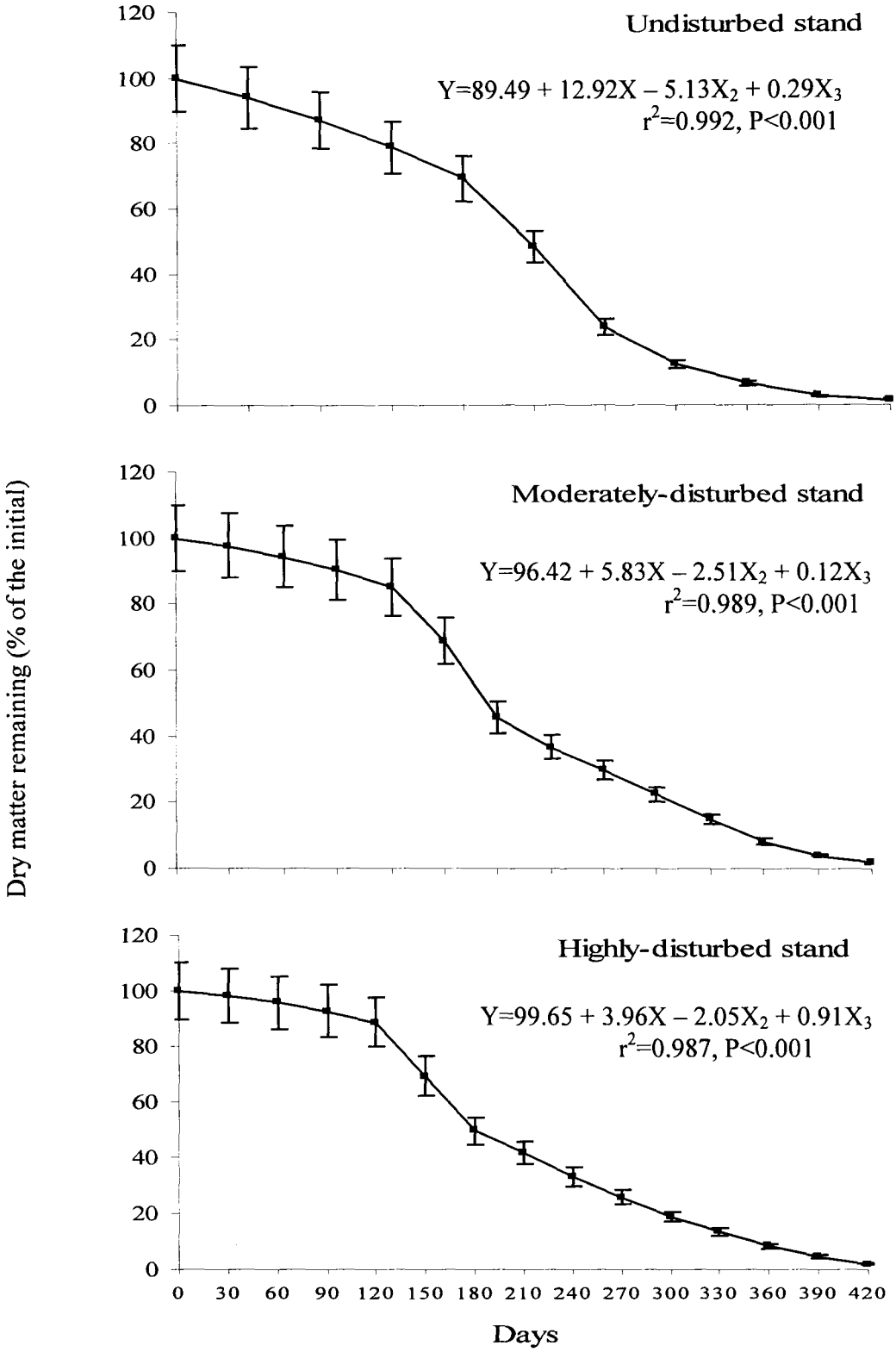

Figure 5.7. Decay pattern of coarse roots in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5).

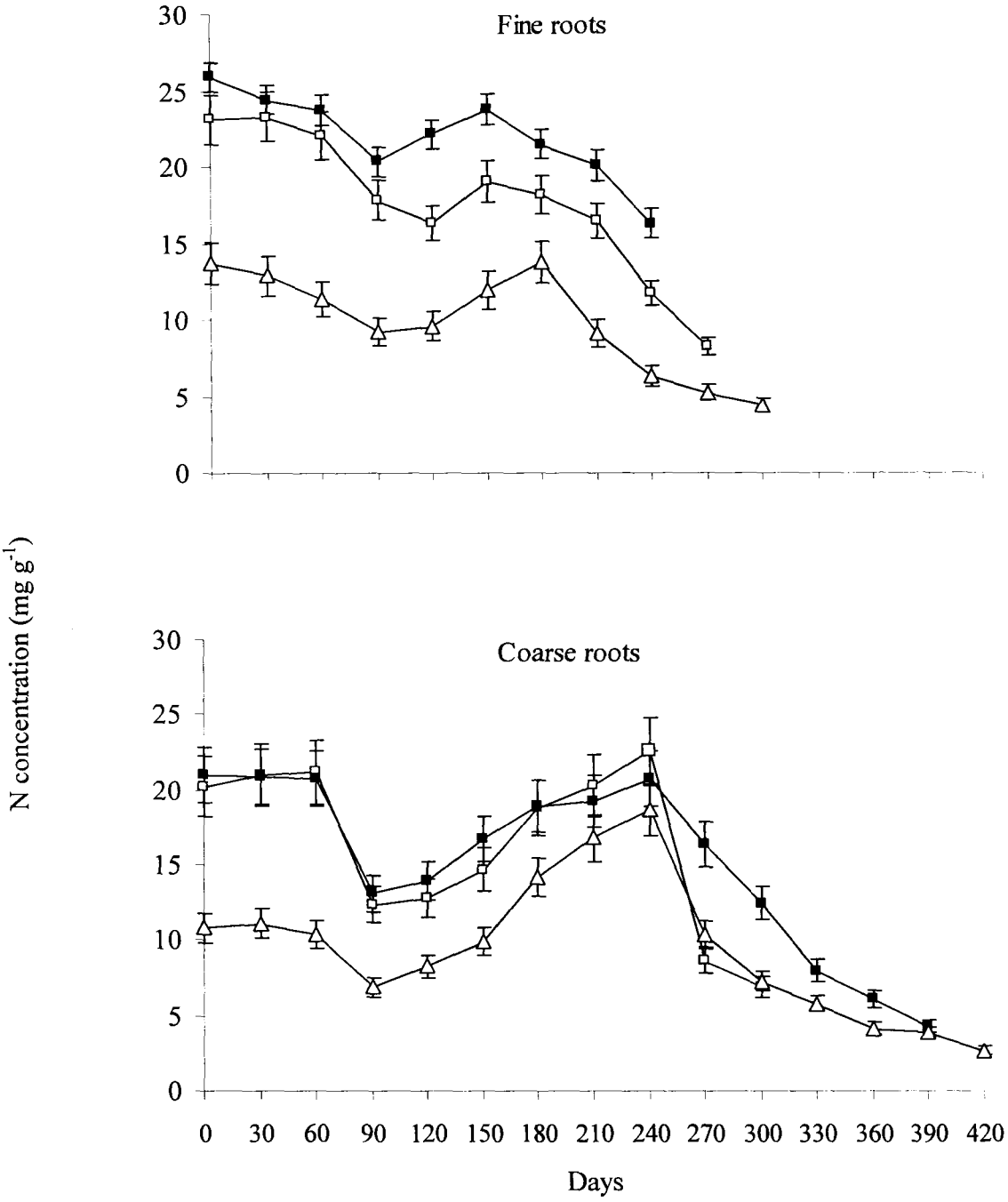

Figure 5.8. Changes in N concentration (mg g^{-1}) in decaying fine and coarse roots of undisturbed (■), moderately-disturbed (□) and highly-disturbed (Δ) stands. Vertical lines represent standard error (n=3).

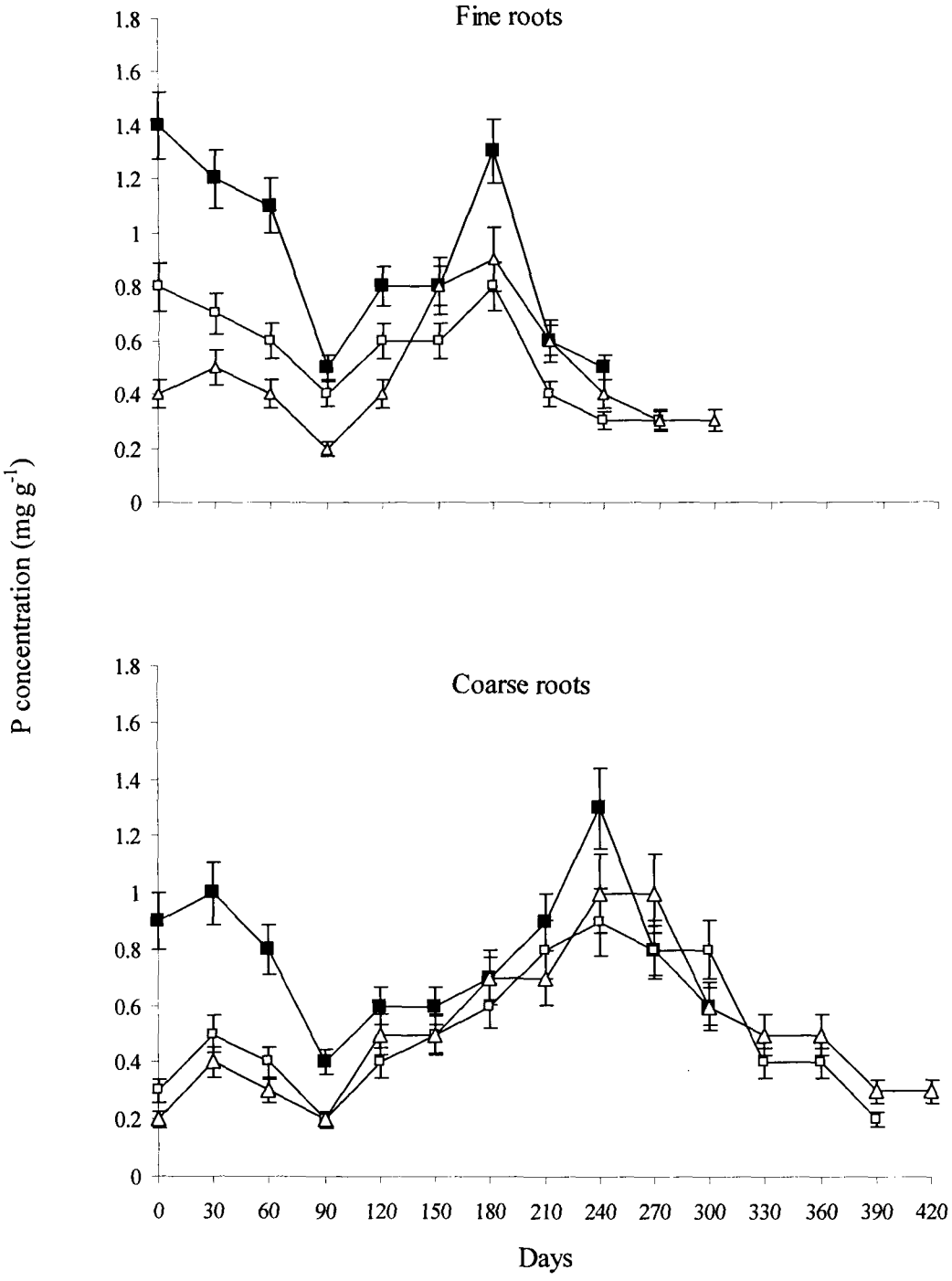

Figure 5.9. Changes in P concentration (mg g^{-1}) in decaying (a) fine and (b) coarse roots of undisturbed (■), moderately-disturbed (□) and highly-disturbed (Δ) stands. Vertical lines represent standard error (n=3).

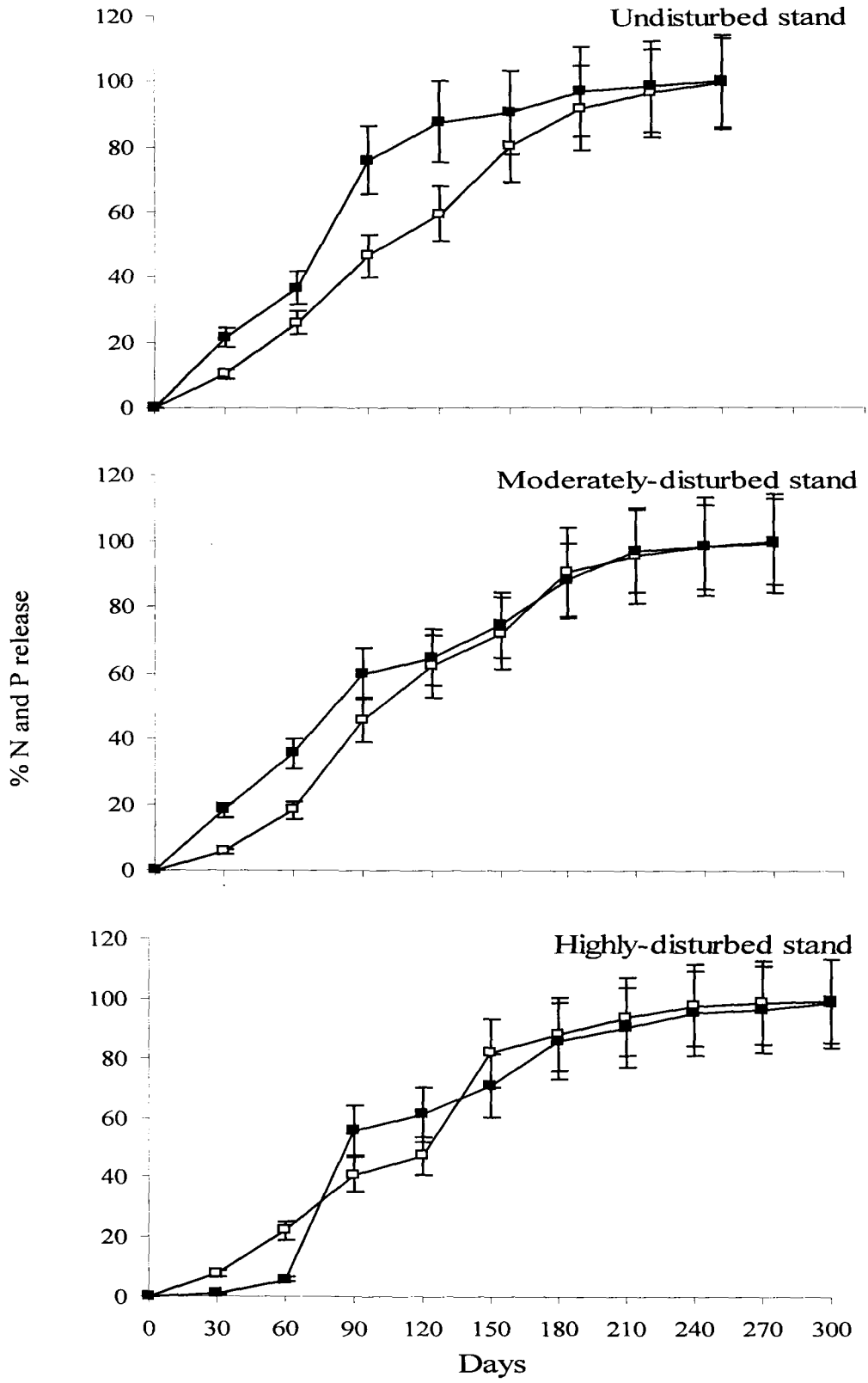

Figure 5.10. N (□) and P (■) release (%) during decomposition of fine roots in the undisturbed and disturbed stands. Vertical lines represent standard error (n=3).

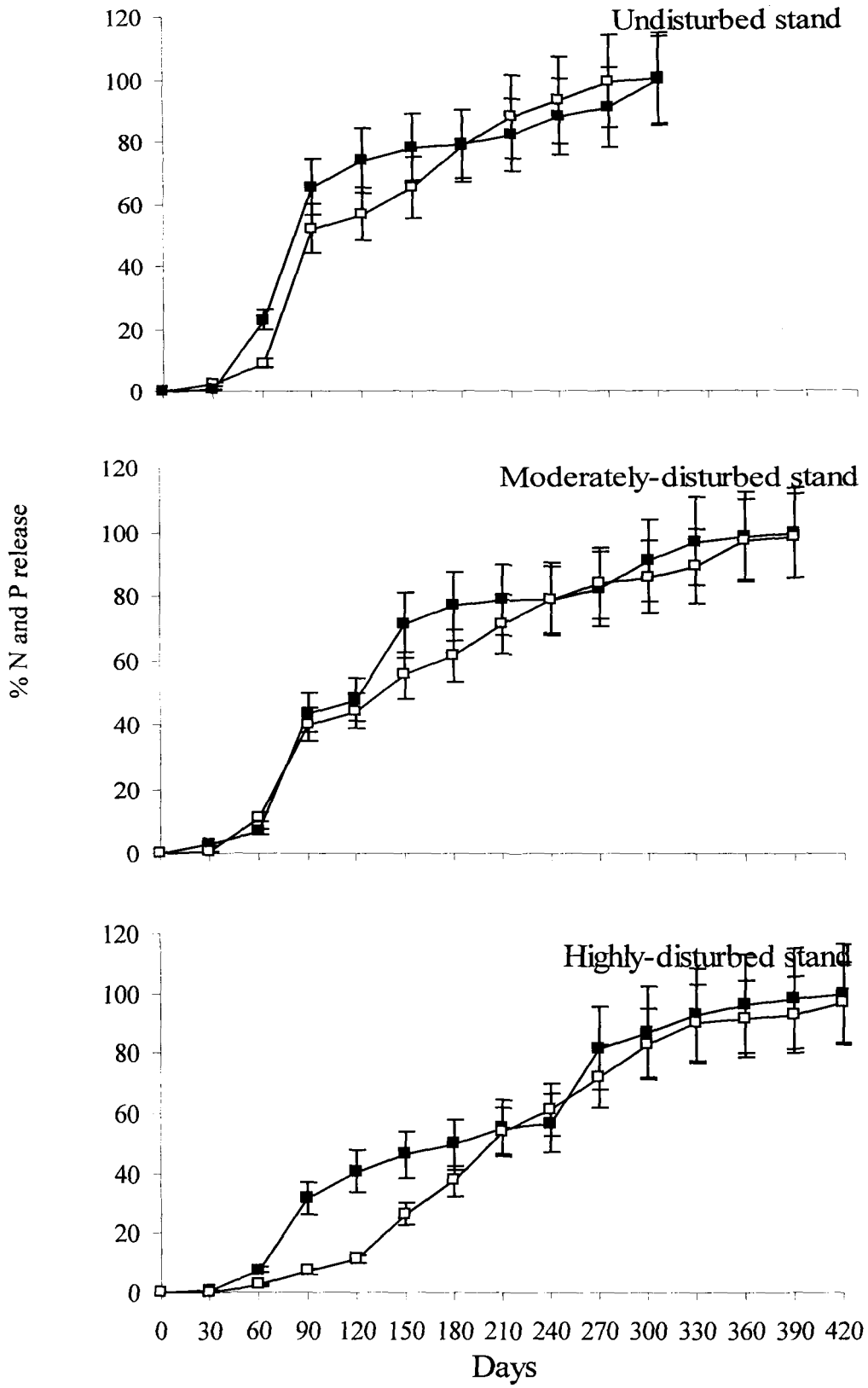

Figure 5.11. N (□) and P (■) release (%) during decomposition of coarse roots in the undisturbed and disturbed stands. Vertical lines represent standard error (n=3).

Discussion

Biomass, production and turnover

High density of fine roots in the top a few centimeters of soil help in uptake and conservation of nutrients within tropical rain forest ecosystem (Klinge 1973; Jenik 1978). These have access to the greater concentration of nutrients in the topsoil layer where nutrients are returned through litterfall and throughfall (Maycock and Congdon 2000). Accumulation of litter on the surface soil promotes nutrient concentration and fine root accumulation in the upper layer of the soil (Bowen and Nambiar 1984; Cuevas 1995). The vertical distribution of roots observed in the present study is consistent with general pattern of root biomass concentration in tropical forests (Sanford 1989; Jackson *et al.* 1996; Sundarpandian and Swamy 1996). Differences in the relative distribution of root biomass at different soil depths were evident when undisturbed stand was compared with the disturbed stands. In particular, the highly disturbed stand had more than 90% of their fine root biomass within the first 15 cm soil layer compared with 67% in undisturbed and moderately disturbed stands. Greenland and Kowal (1960) reported that 86% of the root biomass in a 40 years old secondary forest in Ghana was present in the top soil (30 cm depth), while de Castro and Kauffmann (1998) found that 71% of the root biomass in 'Cerrado denso' communities of the Brazilian cerrado occurred in the upper soil (30 cm depth), and 64-72% of the root biomass was present in undisturbed tropical floodplain forests of the Chamela region in western Mexico (Renteria-Rodriguez 1997).

Seasonal response of fine roots is well documented in tropical and subtropical forests (Silver and Vogt 1993; Arunachalam *et al.* 1996c; Sundarpandian and Swamy 1996). The increased root biomass during the rainy season correspond to the period of

rapid nutrient release from decaying litter during this period (Khiewtam and Ramakrishnan 1993). The wide variation in fine roots biomass during rainy season than during dry months as observed in this study may be due to spatial heterogeneity in the availability of nutrients. Roy and Singh (1994) have reported that the accumulation of litter and soil organic matter on level microsites and topographic depressions, standing dead trees or their remains and the channels created by the decaying thick roots, create nutrient patches where fine root proliferate. Fine root proliferation in fertile patches has been reported from different ecosystems (Cuevas and Medina 1988; Jackson and Caldwell 1989; Caldwell 1994). Despites the large spatial variations, statistically significant temporal changes (Persson 1980; Makkonen and Helmisaari 1998) suggest that fine roots grow and senesce rapidly, probably due to change in soil temperature and moisture.

Measurement of fine root production in natural ecosystem is extremely difficult (Cuevas and Medina 1988), and studies so far available show a wide range of variation (1.1 to 30.2 x 10^3 kg ha^{-1} yr^{-1}) (*c.f.* Sundarpandian and Swamy 1996). The fine root production estimated (1589.44-7145.51 kg ha^{-1} yr^{-1}) by using the sequential core method are comparable with those of tropical forest of Western Ghats, South India (Sundarpandian and Swamy 1996), humid subtropical forest of Meghalaya, Northeast India (Arunachalam *et al.* 1996), Amazonian forests of Brazil (Klinge 1973), and Red oak and maple forest of North America (McClaugherty *et al.* 1982). Many workers have argued that estimates of total production from biomass data can be a serious underestimation due to unaccountable losses by root respiration, decomposition and exudation (Hendricks *et al.* 1993). Singh *et al.* (1984); Hendricks *et al.* (1993) have,

however, suggested that variations in root mass can lead to extremely large estimation of root production if all the positive increments of roots mass during successive samplings are summed up. According to Sims and Singh (1978), the summing up of significant positive increments in root mass during successive samplings appears to give reliable results.

About 60-75% of fine root production occured in the surface soil layer, this finding is within the reported range 57–81% from the humid tropical forest (Arunachalam *et al.* 1996c) and much higher than that reported (35%) from dry tropical forest of Mexico (Castellanos *et al.* 2001). Ford and Deans (1977) suggested that high concentration of fine roots in the surface soil layer of the forest is related to higher nutrient concentration and greater moisture retention due to sufficient detrital materials on the surface soil. These conditions on the forest floor may reduce root production at the lower soil depth (Campo *et al.* 1998). In the undisturbed forest stand thick litter layer and favourable temperature and moisture conditions throughout the year were responsible for the higher fine root biomass and production in the upper soil layer. The fine root system developed in the surface layer of the soil undergoes a rapid change due to disturbance (Hendrick and Pregitzer 1993; Sundarapandian and Swamy 1998). A marked reduction in fine and coarse root production from undisturbed to highly disturbed stands observed in the present study has also been reported by Castellanos *et al.* (2001). They found that conversion of tropical dry forest to pasture resulted in a 56% decrease in fine root production in the uppermost 5 cm of soil.

Root turnover decreased with the increasing soil-depth and diameter. Results clearly demonstrate that root turnover rate decreased with the increase in disturbance,

which suggest that shorter roots lifespan are associated with high nutrient soil condition (Pregitzer *et al.* 1993). The longevity of a root may be inversely related to the resource availability, *i.e.*, root mortality may coincide with vegetal cover depletion. Jackson and Caldwell (1989) considered that plants might be able to regulate the degree of root proliferation in accordance with their demand for nutrients, and the present data suggest that root longevity and turnover may also be variable in response to changes in resource availability in the relatively disturbed stands.

C, N and P accumulation and turnover in roots

In the present study, nutrient concentration in roots was influenced by the species composition of the stand. Other factors which influenced nutrient concentration in roots were the relative proportion of dead tissues and larger roots which had invariably lower concentration than small roots. The N and P concentration was significantly higher during rainy season, may be due to rapid uptake of nutrients. In the disturbed stands lower nutrient could be related to low soil nutrient status. Rose (1988) and Gleeson and Tilman (1990) found higher nutrient concentration in old communities than in younger communities.

Concentration along with root mass influenced C, N and P accumulation in fine and coarse roots. Thus, higher C, N and P accumulation occurred in the undisturbed stand than the disturbed stands. These results suggest that increase in root biomass resulted in increased nutrient accumulation. C, N and P turnover rate in fine and coarse root was low in disturbed stands and lower depth, due to limited input of organic matter. A decrease trend in nutrient turnover rates of fine and coarse roots in the disturbed stands suggests a

gradual development of organic matter and nutrient conservation mechanism during secondary succession (Aerts 1990).

The present study reveals that fine and coarse roots biomass varied greatly with season, species composition, tree density and basal area. Fine root biomass and production were significantly altered by disturbances like selective logging and clear-felling of trees. This study also suggest that root turnover was high when nutrient availability and soil organic matter content in soil was high due to addition of more organic materials and better moisture condition. Greater fine root concentration in the top soil helps in nutrient conservation from further leaching. Thus, it is concluded that fine root dynamics play a key role in nutrient conservation and are therefore important for the maintenance of these degraded ecosystems.

Root decomposition

Large chemical differences were found in the initial chemical composition of fine and coarse roots. The variations in the substrate quality of fine and coarse roots between stands were correlated with vegetation structure and nutrient availability (Arunachalam *et al.* 1997). Further, nutrient concentration in roots was strongly influenced by their diameter (Arunachalam *et al.* 1996d). The significant inverse relationships between root diameter and nutrient concentration have also been reported by Gordon and Jackson (2000) based on the data from a range of ecosystems from temperate, tropical and tundra systems. In the present study too, N and P concentration decreased from fine to coarse roots (Table 5.10). N and P concentration in fine and coarse roots was significantly ($P<0.001$) higher in the undisturbed stand, due to greater availability of soil nutrients (refer to Table 4.6, Chapter 4).

The initial slow rate of root decay (upto 60 days) could be attributed to the time lag in the colonization and establishment of microbes on the litter (Alexander 1977). This was followed by a rapid rate of weight loss due to the net effect of a large number of processes such as utilization of readily available energy sources by microbes, leaching of water soluble organic compounds, inorganic salts and non-structural carbohydrates from the decomposing root litter (Bloomfield *et al.* 1993; Arunachalam *et al.* 1996d). A marked reduction (after 180 days) in the decay rate might be related to the relatively higher percentage of recalcitrant fractions like cellulose, lignin and tannin in the decaying root tissue (Fogel and Cromack 1977). Within the different phases of weight loss, seasonal fluctuations were also observed in all the stands. The warm-humid period was characterized by a faster rate of decay (0.52% weight loss day^{-1}), while the dry cold period was marked by a slow decay rate (0.11% weight loss day^{-1}). A seasonal change in the rate of litter decomposition has been observed by many workers in the tropical forest ecosystems. This has been attributed to soil moisture condition (Rochow 1974; Bhatt *et al.* 1985), ambient temperature (Swift *et al.* 1979) and microbial activity (Singh and Gupta 1977). The faster rate of weight loss of fine roots in the undisturbed stand could also be due to higher initial N concentration and lower lignin content (Table 5.10). Coarse roots with high lignin and C/N ratio decomposed slowly than the fine roots with low lignin and low C/N ratio.

A marked decline in nutrient concentration during the initial phase (3 months) of decomposition may be ascribed to leaching losses caused by rainfall during that period. Subsequent increase in nutrient concentrations could be the result of microbial immobilization (Anderson 1973). A similar trend has been reported by Prescott *et al.*

(1993) for leaf litter and by Arunachalam *et al.* (1996d) for fine roots. Differences in root decomposition rate constant and nutrient (N and P) mineralization rate might be explained by the differences between the tissue chemistry and site characteristics. Higher decay constant in the undisturbed stand was probably because of favourable soil temperature and moisture and larger decomposer population. The lower 'k' values in disturbed stands suggest that disturbance reduce decomposition rate and input of available nutrients for plant growth.

During decomposition, mineralization of the organic N into inorganic form mainly depends on the C/N ratio of the material. So, fine roots with higher nutrient concentration and low C/N ratio mineralized rapidly than coarse roots with lower nutrient concentration and greater C/N ratio. Phosphorus (P) mineralization during decomposition was quite similar to that of N release, the rate of release was slightly slower than N. Both N and P mineralization constants (k_N and k_P) for fine and coarse roots were low in the disturbed stands might be due to lower soil microbial activities in these stands.

Thus, besides substrate quality, decomposition rate was also influenced by natural fertility, site-specific factors such as soil moisture regime, microbial activity and nutrient availability (Table 5.15). Human disturbance that changed above ground vegetation has an adverse impact on decomposition process.

Table 5.12. Correlations coefficients (r) showing relationships of fine and coarse roots biomass and necromass (kg ha^{-1}) with soil physico-chemical properties (n=24).

Variable	Soil depth (cm)	Fine root mass		Coarse root mass	
		Live	Dead	Live	Dead
Moisture (%)	0-15	0.782***	0.286 ^{ns}	0.271 ^{ns}	0.190 ^{ns}
	15-30	0.654**	0.269 ^{ns}	0.258 ^{ns}	0.285 ^{ns}
WHC (%)	0-15	0.796***	0.456*	0.661**	0.505*
	15-30	0.604**	0.287 ^{ns}	0.445*	0.555**
BD (gm cm^{-3})	0-15	0.768***	0.502*	0.648**	0.371 ^{ns}
	15-30	0.647***	0.401*	0.678**	0.307 ^{ns}
SOC (mg g^{-1})	0-15	0.794***	0.374 ^{ns}	0.609**	0.130 ^{ns}
	15-30	0.737***	0.316 ^{ns}	0.304 ^{ns}	0.145 ^{ns}
TKN (mg g^{-1})	0-15	0.838***	0.837***	0.550*	0.462*
	15-30	0.604**	0.465*	0.495*	0.435*
P (mg g^{-1})	0-15	0.728***	0.437*	0.382 ^{ns}	0.213 ^{ns}
	15-30	0.608**	0.613**	0.532*	0.257 ^{ns}

***P< 0.001, **P<0.01, *P<0.05, ns-not significant.
WHC-water holding capacity; BD-bulk density

Table 5.13. Three way ANOVA showing effects of season, soil depth and stand on total root mass (kg ha^{-1}) and production (kg ha^{-1} yr^{-1}).

Interaction	Root mass			Root production		
	df	F	P	df	F	P
Fine roots						
Season	3	78.87	0.001	-	-	-
Depth	1	4098.75	0.001	1	135.57	0.001
Stand	2	2232.28	0.001	2	147.90	0.001
Season x depth	3	8.56	0.001	-	-	-
Season x stand	6	57.92	0.001	-	-	-
Depth x stand	2	43.51	0.001	2	24.61	0.001
Season x depth x stand	6	28.32	0.001	-	-	-
Coarse roots						
Season	3	49.76	0.001	-	-	-
Depth	1	11.65	0.05	1	19.86	0.05
Stand	2	177.92	0.01	2	72.58	0.001
Season x depth	3	0.64	0.59	-	-	-
Season x stand	6	21.50	0.001	-	-	-
Depth x stand	2	2.38	0.103	2	5.36	0.02
Season x depth x stand	6	4.93	0.01	-	-	-

Table 5.14. Three way ANOVA showing effects of season, root size and stands on N and P concentration (mg g^{-1}) in roots.

Variables	N concentration			P concentration		
	df	F	P	df	F	P
Fine roots						
Stand	2	220.72	0.001	2	98.02	0.001
Season	3	11.62	0.001	3	94.01	0.001
Diameter	1	21.18	0.001	1	61.09	0.001
Stand x season	6	3.41	0.007	6	8.04	0.001
Diameter x season	3	0.25	0.86	3	3.04	0.04
Diameter x stand	2	1.45	0.24	2	3.01	0.06
Season x diameter x stand	6	1.25	0.29	6	2.63	0.03
Coarse roots						
Stand	2	243.54	0.001	2	1.53	0.23
Season	3	57.41	0.001	3	7.42	0.001
Diameter	1	111.73	0.001	1	105.64	0.001
Stand x season	6	5.12	0.001	6	3.95	0.003
Diameter x season	3	6.35	0.001	3	0.58	0.62
Season x diameter x stand	6	1.43	0.223	6	0.72	0.64

Table 5.15. Root decomposition (% weight loss day^{-1}) as influenced by soil characteristics and initial root chemistry.

		Fine roots			Coarse roots		
Variable	df	Regression equation	r	P	Regression equation	r	P
Weight loss vs. soil characteristics							
Soil temperature (° C)	23	Y=21.55+0.25x	0.684	0.001	Y=21.62+0.58x	0.207	ns
Soil moisture (%)	23	Y=26.53+0.12x	0.784	0.001	Y=18.79+0.32x	0.543	0.01
Organic C (mg g^{-1})	23	Y=16.99-0.07x	-0.355	ns	Y=17.70-0.27x	-0.402	0.05
Total N (mg g^{-1})	23	Y=7.12-0.033x	-0.493	0.05	Y=6.34-0.07x	-0.312	ns
Total P (mg g^{-1})	23	Y=1.01-0.002x	-0.198	ns	Y=0.98-0.006x	-0.301	ns
Weight loss vs. initial chemistry							
Lignin (mg g^{-1})	7	Y=181.46-0.87x	-0.851	0.005	Y=167.54-4.64x	-0.848	0.005
Cellulose (mg g^{-1})	7	Y=194.37-1.87x	-0.701	0.05	Y=175.49-8.39x	-0.719	0.05
Hemicellulose (mg g^{-1})	7	Y=100.98-0.923x	-0.673	0.05	Y=118.12-5.27x	-0.713	0.05
C (mg g^{-1})	7	Y=132.78-1.34x	-0.844	0.001	Y=117.57-6.27x	-0.818	0.05
N (mg g^{-1})	7	Y=26.50+0.29x	0.909	0.001	Y=29.90+1.36x	0.907	0.001
P (mg g^{-1})	7	Y=1.45+0.02x	0.712	0.05	Y=1.79+0.14x	0.669	0.05
Lignin/N	7	Y=6.14-0.23x	-0.943	0.001	Y=3.52-1.06x	-0.883	0.005
C/N	7	Y=4.23-0.24x	-0.947	0.001	Y=1.78-1.04x	-0.846	0.005

r= correlation coefficient, P-significance level and ns= not significant.

Chapter 6

Dynamics of soil microbial population and biomass -C, -N and -P

Introduction

Microorganisms play important roles in regulating ecosystem processes such as nutrient mineralization, soil carbon storage, trace gas fluxes, transformation of aqueous solutes, and processing of water pollutants (Mooney *et al.* 1987; Schlesinger 1997; Groffman and Bohlen 1998). Interactions among plants, soil, hydrology and microorganisms regulate nutrient cycling in ecosystems. These interactions vary in time and space, greatly complicating ecosystem-level assessment of nutrient loss following disturbances and changes in species composition (Vitousek *et al.* 1994). Changes in the microbial population in response to variations in soil conditions such as moisture, C, nutrients, temperature, pH etc have important implications for nutrient cycling (Diaz-Ravina *et al.* 1995). In many ecosystems soil microbial biomass is closely linked to aboveground plant productivity (Zak *et al.* 1994), suggesting their dependence on inputs of reduced carbon to the soil through litter (Allen and Schlesinger 2004).

Understanding of the dynamics of microbial biomass following forest disturbances is important to develop synchronized strategies for reclamation and management of degraded lands (Mroz *et al.* 1986). This is particularly critical in the humid tropics where soils are leached and generally nutrient poor. Soil microbial biomass serves as a sensitive indicator of slower, less easily detectable soil organic matter changes (Mroz *et al.* 1986) and plays an active role in nutrient conservation in the tropical soils (Sarathchandra *et al.* 1984) by preventing leaching of nutrients (Theng *et al.* 1989). Soil

microbial biomass responds much more rapidly than the total organic matter to any change in organic inputs (Powlson *et al.* 1987), and its measurement is a valuable tool for understanding and predicting the long-term effects of changes in soil conditions.

The present chapter examines the seasonal fluctuation in microbial population (bacteria and fungi) and biomass (C, N and P) and quantifies their contribution to soil nutrient pool in the undisturbed and disturbed stands of a tropical wet evergreen forest of northeast India.

Method

Soil sampling

Soil samples were collected from both undisturbed and disturbed forest stands during January, April, July and October during 2002 and 2003 that represents winter, spring, rainy and autumn seasons, respectively. From each stand, ten soil cores (5.5 cm inner diameter) were collected randomly from 0-15 and 15-30 cm soil depths. After removing the litter layer, these were mixed depth wise to obtain composite samples. After removing stones, pebbles and large pieces of plant material, the samples were sieved by 2 mm mesh size and used for microbial biomass -C, -N and -P analysis.

Soil microbial population

For the estimation of bacterial and fungal population, soil samples were collected separately from the two soil depths using a sterilized corer. The samples were brought to the laboratory in sealed containers and bacterial and fungal populations were estimated within 24 h of sampling. Bacterial population was estimated by Waksman's (1952) method using nutrient agar medium at 10^5 dilution and fungal population was studied by

dilution plate method (Johnson and Curl 1972) using rose Bengal agar medium at 10^4 dilution in water. The inoculated Petri dishes were incubated for 24 h (30±1 °C) for bacteria, and for five days (25±1 °C) for fungi. The colonies were counted using the digital colony counter.

Microbial biomass -C, -N and -P

Chloroform fumigation-extraction (CFE) method was used to estimate microbial-C (MBC), -N (MBN) and -P (MBP). MBC and MBN were determined in fresh soil by chloroform-fumigation extraction method (Brookes *et al.* 1985; Vance *et al.* 1987). In the CFE method, 50 ml beaker containing 15 g fresh soil samples and a 100 ml beaker with 25 ml alcohol-free chloroform were placed in a vacuum desiccator. Another desiccator was maintained without chloroform and both the desiccator was kept under darkened conditions for 72 h at room temperature. Then, the fumigated desiccator was evacuated using a vacuum pump. The soil samples were transferred to 250 ml conical flask and the fumigated and unfumigated soils were extracted with 200 ml 0.5M K_2SO_4 and it was kept for shaking for 20 minutes in a rotatory shaker at 110 rpm. The extracts were filtered through a Whatman No. 42 filter paper and the filtrates (10 ml) were digested using H_2SO_4 in a block digestor at 145-155 °C for 30 minutes. The digest was titrated against ferrous ammonium sulphate (0.2N) using 1, 10 phenanthroline monohydrate as indicator. For MBN, the digested filtrate was distilled by steam using semi-micro Kjeldahl distillation unit and titrated against hydrochloric acid (0.05N). MBP was determined by chloroform fumigation-extraction method (Brookes *et al.* 1982) using 0.5M, $NaHCO_3$ as extracting solution. The MBC, MBN and MBP were calculated as follows: Microbial C = (E_C of fumigated soil - E_C of unfumigated soil) x 2.64 (Vance *et al.* 1987); Microbial N=

(E_N in fumigated soil - E_N in unfumigated soil)/ 0.54 (Brookes *et al.* 1985) and Microbial P = (E_P of fumigated soil - E_P of unfumigated soil)/ 0.40 (Brookes *et al.* 1982), where E_C, E_N and E_P are extractable C, N and P respectively.

Statistical analysis

Three-way ANOVA was used to test the effect of season and soil depth on microbial population and biomass. Correlation and regression tests were applied to study the relationship between microbial biomass -C, -N and -P and soil characteristics following Zar (1974).

Results

Microbial population

Bacterial and fungal population was significantly ($P<0.01$) greater in the undisturbed stand than the disturbed stands (Table 6.1). All the values were greater in the top soil layer (0-15 cm). In all the three stands, peak bacterial and fungal population was observed during rainy season and the minimum during winter (Figures 6.1 and 6.2). Both bacterial and fungal population varied significantly between stands, seasons and soil depths (Table 6.7). The bacterial population was higher than fungal population in all the three stands. Year-wise variation in microbial population was not significant.

Among the physical and chemical properties of soil, moisture content, water holding capacity, soil organic carbon, total Kjeldahl N and P showed significant positive correlations with both bacterial and fungal population. The relationship with bulk density was negative. Bacterial and fungal population did not show any relationship with soil pH.

Table 6.1. Bacterial and fungal population in soils of the undisturbed and disturbed stands.

	Soil depth (cm)	2002			2003		
		UD	MD	HD	UD	MD	HD
Bacteria*							
	0-15	98.59	67.64	51.66	93.98	63.86	47.26
		±7.83	±4.91	±4.63	±6.62	±5.43	±3.18
	15-30	91.08	56.48	42.01	80.98	55.16	40.18
		±7.99	±4.28	±2.58	±8.12	±5.86	±3.43
Fungi**	0-15	28.82	16.36	13.32	29.35	20.45	15.88
		±0.87	±1.26	±1.70	±1.69	±1.07	±0.92
	15-30	22.53	14.06	11.46	23.36	17.00	13.03
		±1.76	±0.63	±1.36	±1.94	±1.41	±0.99

± SE (n=12)
* Number of colonies x 10^5 g^{-1} dry weight of soil
** Number of colonies x 10^4 g^{-1} dry weight of soil.
UD-Undisturbed, MD-Moderately-disturbed and HD-Highly-disturbed stands.

Table 6.7. Three way ANOVA showing effects of season, stand and soil depth on bacterial and fungal population.

Variable	Bacteria			Fungi		
	df	F	P	df	F	P
Season	3	5.27	0.003	3	6.99	0.001
Stand	2	71.35	0.001	2	153.03	0.001
Depth	1	8.01	0.007	1	35.12	0.001
Season x depth	3	2.19	0.093	3	2.01	0.039
Season x stand	6	1.91	0.092	6	2.96	0.015
Depth x stand	2	3.12	0.089	2	4.15	0.022
Season x depth x stand	6	2.56	0.095	6	1.96	0.024

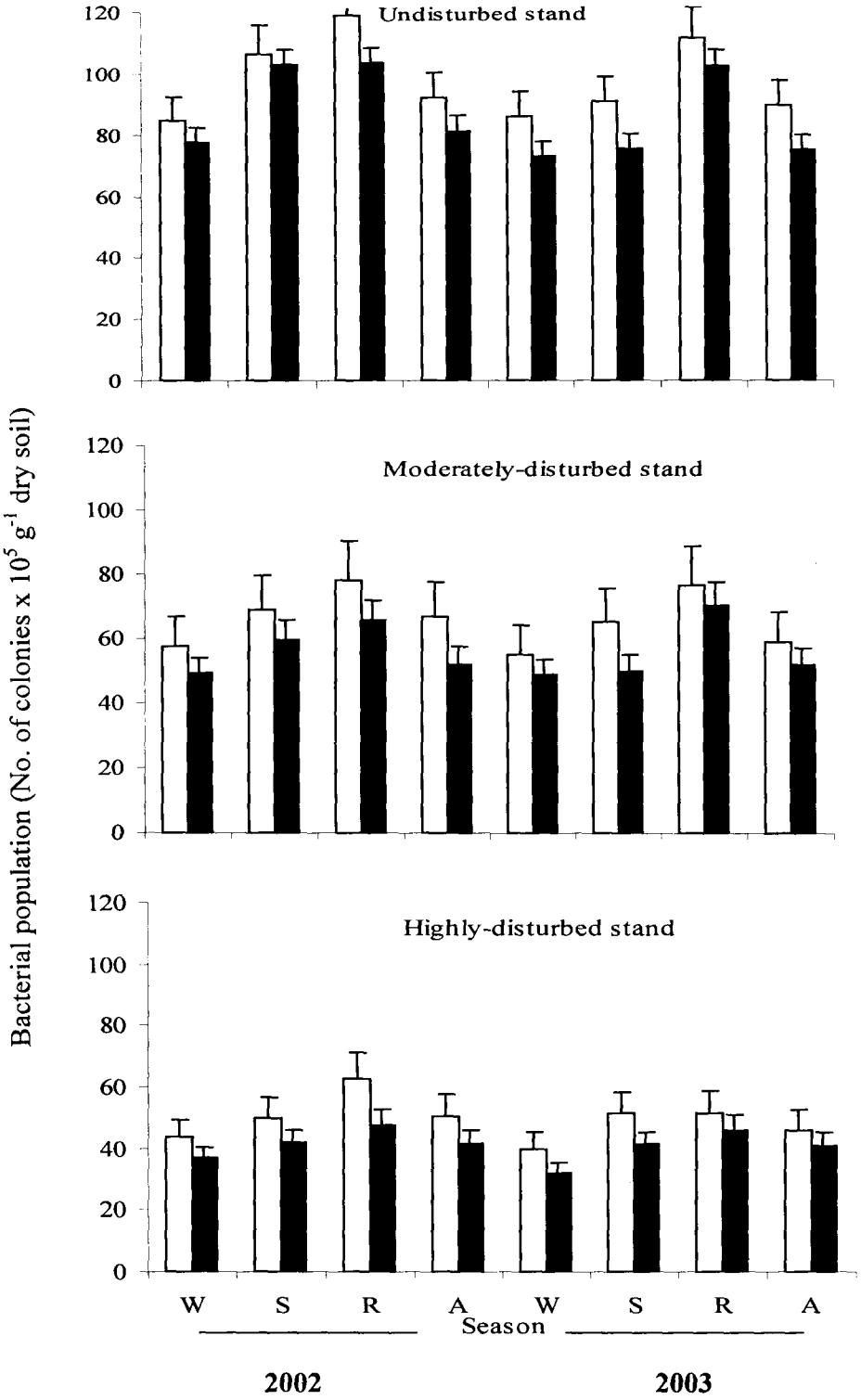

Figure 6.1.Seasonal variation in bacterial population (□-0-15; ■-15-30 cm soil depths) in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5). W-winter, S-spring, R-rainy, A-autumn.

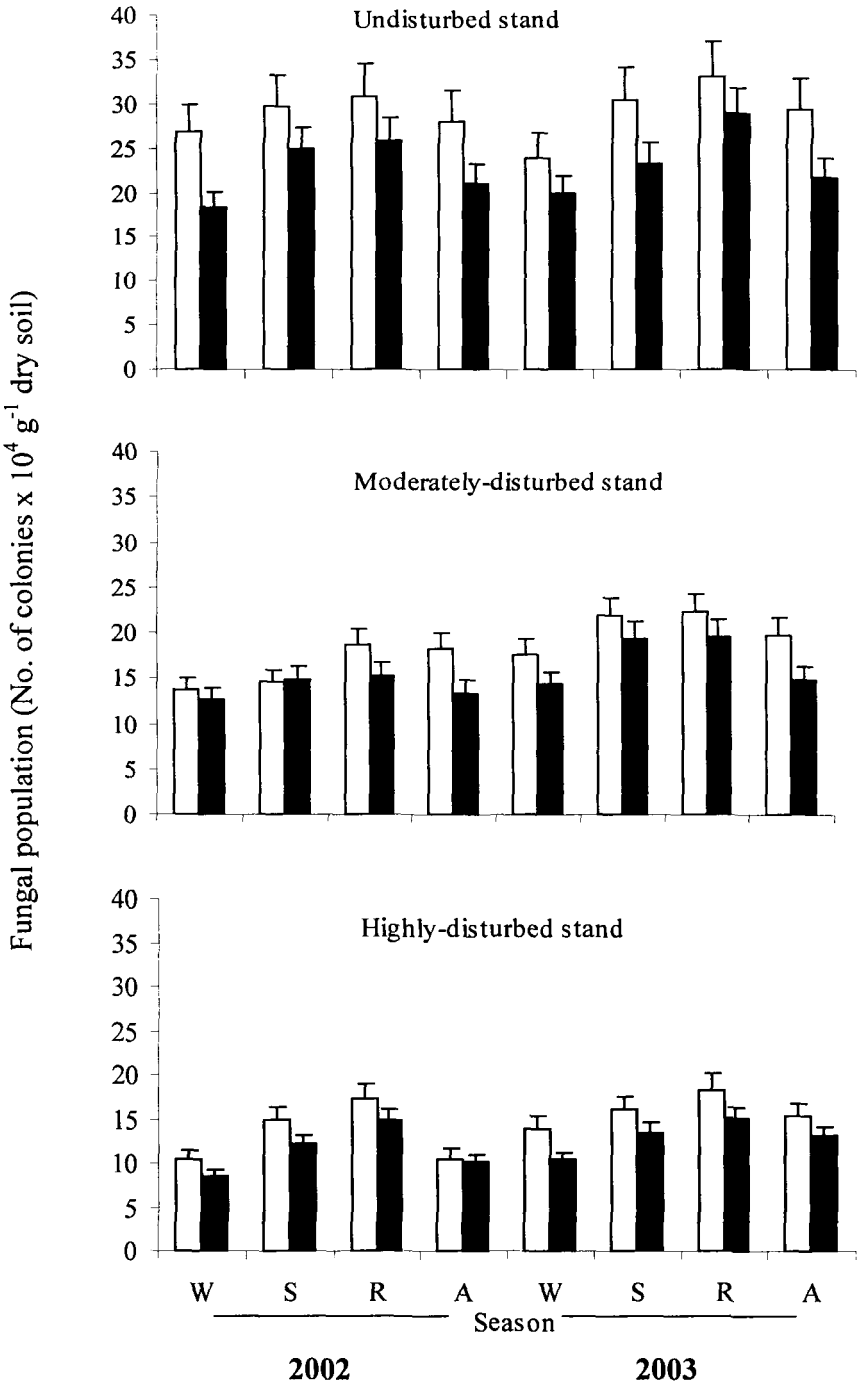

Figure 6.2. Seasonal variation in fungal population (□-0-15; ■-15-30 cm soil depths) in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5). W-winter, S-spring, R-rainy, A-autumn.

Microbial biomass -C, -N and -P

Microbial biomass -C, -N and -P decreased with the increase in disturbance intensity from the undisturbed to highly disturbed stand and soil depth (Tables 6.2). The variations in microbial biomass between seasons, soil depths and stands were significant (Table 6.6). The range of variation in microbial biomass -C was 246-361, 322-712 and 548-1146 μg g^{-1} in the highly disturbed, moderately disturbed and undisturbed stands respectively. The values were minimum during rainy season and maximum during winter in all the three stands (Figure 6.3).

Table 6.6. Three way ANOVA showing effects of season, stand and soil depth on microbial biomass -C, -N and -P (μg g^{-1}).

Variable	MBC			MBN			MBP		
	df	F	P	df	F	P	df	F	P
Season	3	64.01	0.001	3	29.67	0.001	3	41.65	0.001
Stand	2	291.38	0.001	2	241.84	0.001	2	159.51	0.001
Depth	1	34.52	0.001	1	19.98	0.001	1	20.49	0.001
Season x depth	3	0.85	0.472	3	2.30	0.088	3	1.10	0.057
Season x stand	6	20.67	0.001	6	7.94	0.001	6	14.65	0.001
Depth x stand	2	6.99	0.002	2	8.34	0.001	2	1.56	0.077
Season x depth x stand	6	2.68	0.052	6	3.02	0.014	6	2.65	0.053

The microbial biomass -N values were 27.05-48.16, 30.96-57.39 and 45.29-92.72 μg g^{-1} in the highly disturbed, moderately disturbed and undisturbed stands. The surface soil layer had higher microbial biomass -N concentration than the lower soil layer in all

the stands. Marked seasonality in microbial biomass N was recorded in all the stands, it was low during rainy season and high during winter in all the three stands (Figure 6.4).

The peak values for microbial biomass -P were 52.22, 39.47 and 28.75 $\mu g\ g^{-1}$ in undisturbed, moderately disturbed and highly disturbed stands, respectively. It varied significantly ($P<0.05$) between seasons and depths in all the stands. Its seasonal trend in both the soil layers was similar to that of microbial biomass -N, it was maximum during winter and minimum during rainy season (Figure 6.5). The upper soil layer had higher concentration than the lower layer.

Contribution of microbial biomass -C, -N and -P to total soil nutrient pool

The percentage contribution of microbial biomass -C to total soil organic -C ranged between 3.61-6.16 in the upper and 4.52-6.15 in the lower soil layer. The maximum (6.16%) percentage contribution was in the moderately disturbed stand and minimum (3.61%) in the highly disturbed stand. The depth wise variation was also significant ($P<0.05$); the values were greater in the lower soil depth. The proportion of microbial biomass-C in soil organic -C was maximum during rainy and minimum in winter season (Table 6.3).

The percentage contribution of microbial biomass -N to total Kjeldahl nitrogen decreased significantly ($P<0.05$) with the increase in soil depth. In the upper layer it ranged between 0.53 and 1.93% and in the lower soil layer 0.52 and 1.46%. The moderately disturbed stand had the highest proportion of microbial biomass-N in soil, while its proportion was minimum in the highly disturbed stand. Seasonal difference was insignificant. In the highly disturbed stand, maximum contribution was recorded during rainy and minimum during winter season (Table 6.4).

The contribution of microbial biomass -P to total -P did not vary significantly between seasons and soil depths. The maximum contribution (5.22%) of microbial biomass -P to total -P was recorded in the undisturbed stand during rainy season and minimum (2.02%) during rainy season in the highly disturbed stand (Table 6.5).

Microbial C/N, C/P and N/P ratios

The C/N ratio in microbial biomass (7.55-20.28) was higher in the lower soil layer than the upper soil layer (7.55-15.32). Moderately disturbed stand had higher value than the undisturbed and highly disturbed stands; the latter had the lowest value. The seasonality in microbial C/N was inconsistent and the seasonal variation was insignificant.

The microbial C/P ratio ranged between 13.22-25.99 in the upper and 12.08-25.93 in the lower soil layer. In general, it was greater in the lower soil layer than the upper soil layer. The ratio was significantly ($P<0.05$) lower in the highly disturbed stand and higher in the moderately disturbed stand. The seasonal variation though insignificant, the values were higher in the rainy season in the undisturbed stand. The moderately and highly disturbed stands showed greater values during winter and lower during rainy season.

The N/P ratio varied between 1.28-2.22 in the upper and 1.25–2.62 in the lower soil depths. In general, the ratio was higher in the surface soil layer than the subsurface soil layer. In the undisturbed and moderately disturbed stands the ratio was greater during spring season and lower during winter. In the highly disturbed stand it was minimum during rainy and maximum during winter season.

Table 6.2. Mean microbial biomass -C, -N and -P (μg g^{-1}) and their contribution (%) to total soil nutrient (C, N and P) pool in the undisturbed and disturbed stands.

Parameter	Soil depth (cm)	Year/ stand 2002 UD	2002 MD	2002 HD	2003 UD	2003 MD	2003 HD
MBC	0-15	770.31	505.26	355.64	936.45	586.13	361.59
		±87.40	±71.94	±24.48	±120.00	±69.96	±33.27
	15-30	629.21	435.21	297.97	783.49	504.46	314.02
		±75.26	±57.91	±30.40	±102.21	±66.98	±29.41
MBN	0-15	73.21	36.63	34.16	69.84	47.59	38.90
		±9.25	±4.64	±2.94	±7.94	±6.58	±5.22
	15-30	58.60	30.96	28.87	63.46	42.22	35.30
		±6.58	±3.57	±0.75	±6.37	±6.36	±4.59
MBP	0-15	38.73	22.23	22.46	46.23	31.62	25.15
		±5.64	±1.79	±1.48	±6.75	±4.67	±2.23
	15-30	31.80	23.01	18.86	43.76	29.78	22.72
		±6.33	±2.35	±1.34	±6.80	±4.66	±2.27
Percent contribution							
MBC to SOC	0-15	4.61	5.31	4.62	5.78	6.16	3.61
	15-30	4.52	5.65	4.96	5.52	6.15	6.03
MBN to TKN	0-15	1.10	0.99	1.36	1.03	1.39	1.62
	15-30	1.05	1.07	1.44	1.08	1.40	1.96
MBP to P	0-15	4.30	3.17	4.49	4.62	3.95	5.03
	15-30	3.97	3.28	4.71	4.86	4.25	5.68

± SE (n=12)
UD-Undisturbed, MD-Moderately-disturbed and HD-Highly-disturbed stands
MBC-microbial biomass carbon, MBN-microbial biomass nitrogen, MBP-microbial biomass phosphorus, SOC-soil organic carbon.

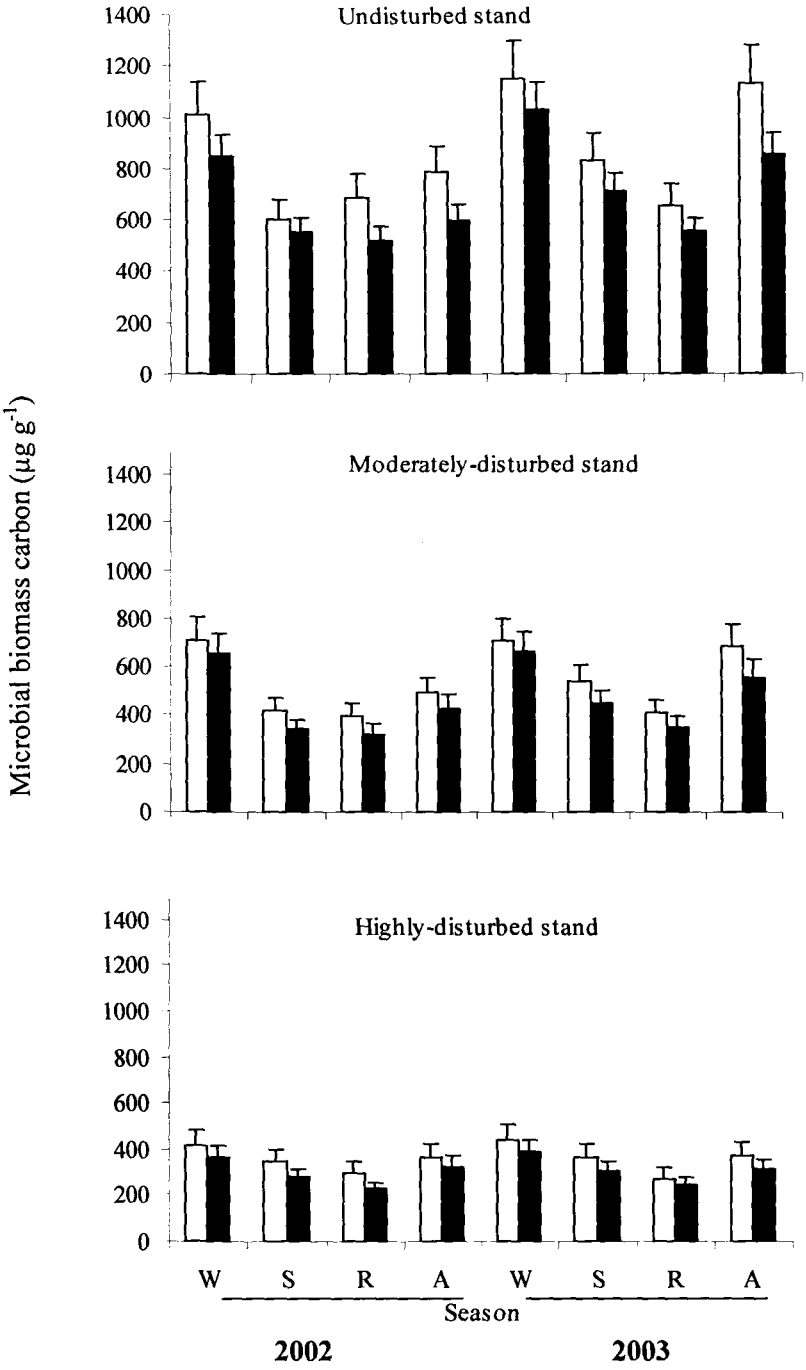

Figure 6.3. Seasonal variation in microbial biomass carbon (□-0-15; ■-15-30 cm soil depths) in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5). W-winter, S-spring, R-rainy, A-autumn.

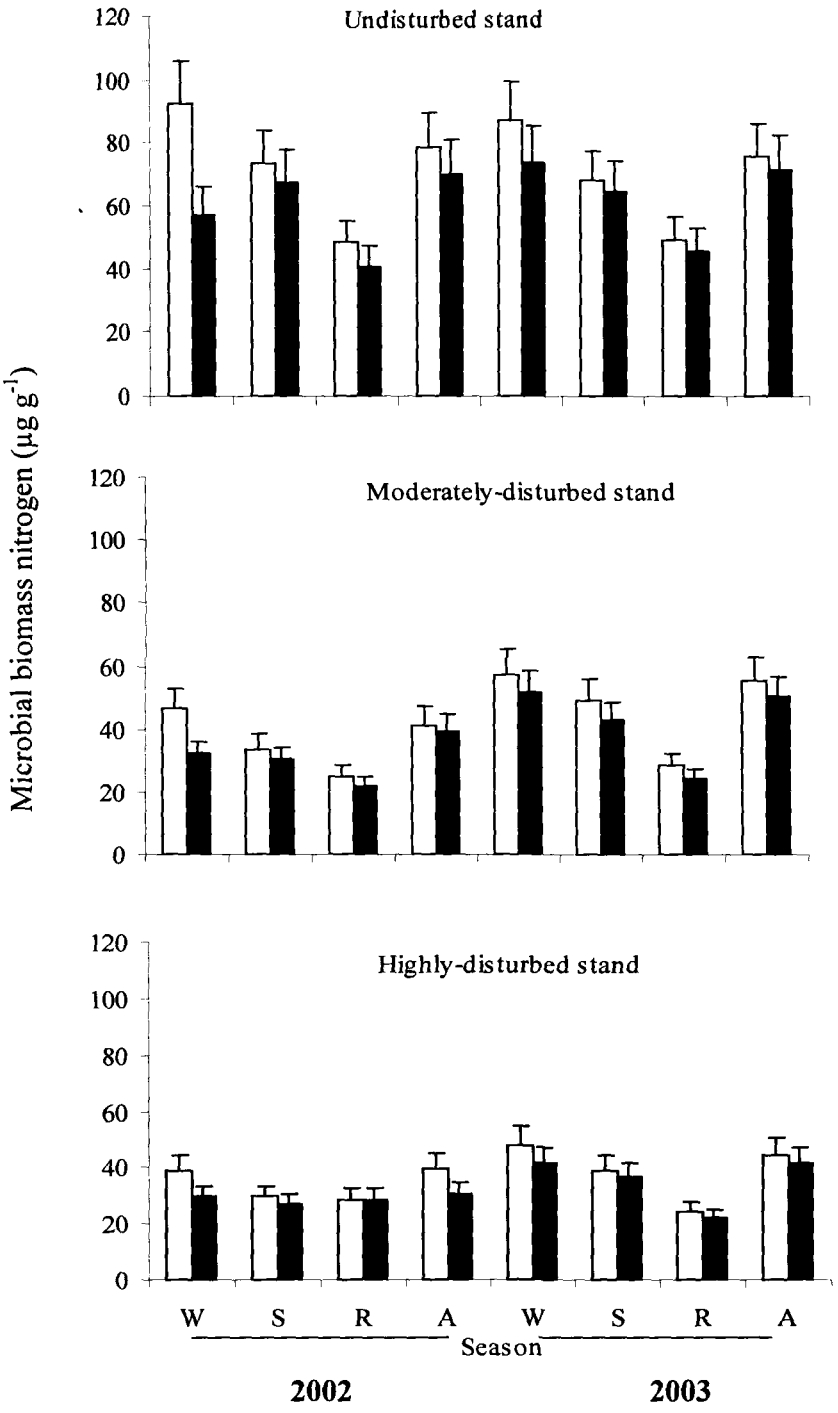

Figure 6.4. Seasonal variation in microbial biomass nitrogen (□-0-15; ■-15-30 cm soil depths) in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5). W-winter, S-spring, R-rainy, A-autumn.

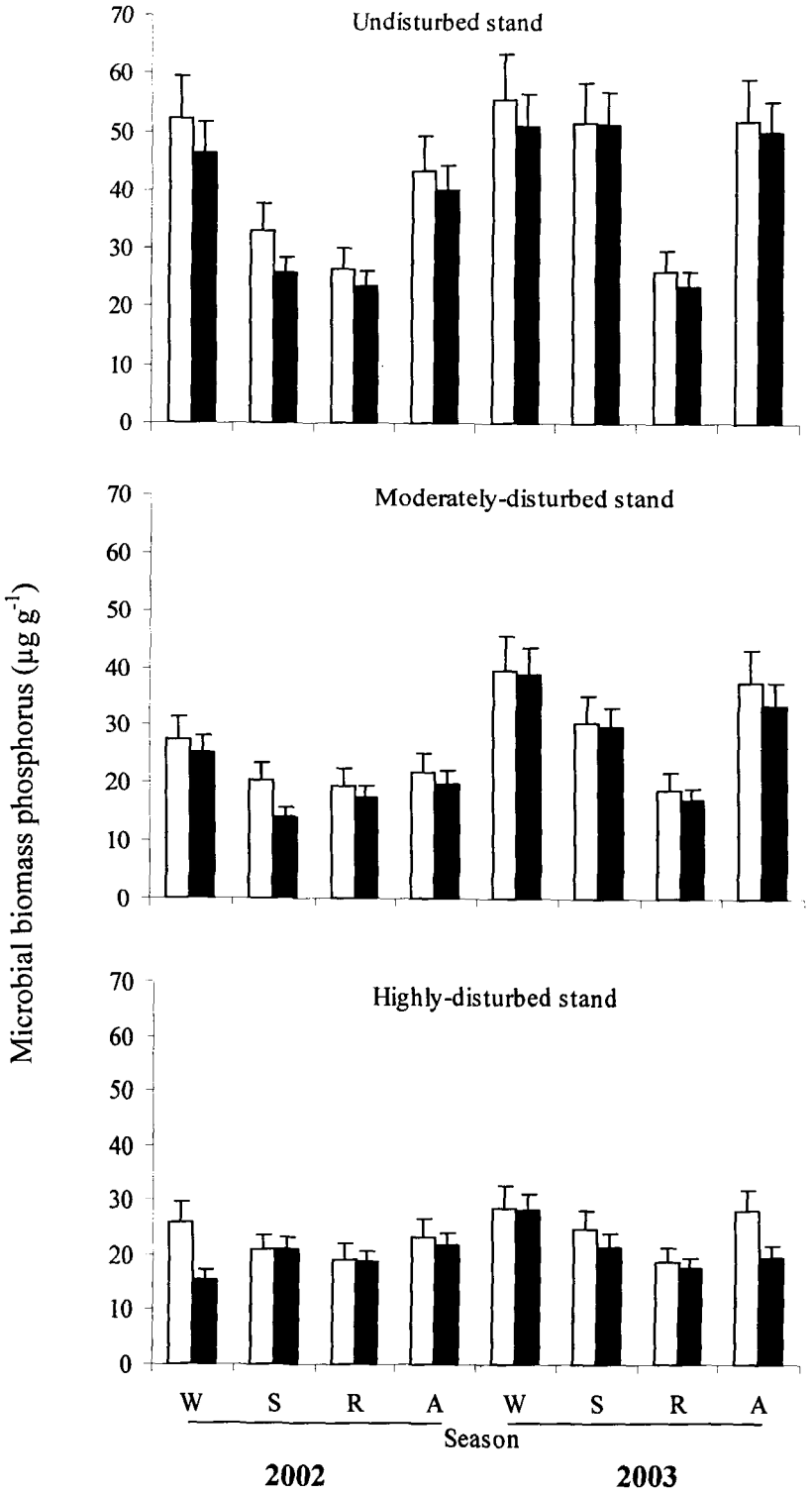

Figure 6.5. Seasonal variation in microbial biomass phosphorus (□-0-15; ■-15-30 cm soil depths) in undisturbed and disturbed stands. Vertical lines represent standard error (n=5). W-winter, S-spring, R-rainy, A-autumn.

Table 6.3. Seasonal changes in percent contribution of MBC to total soil organic carbon concentration in the undisturbed and disturbed stands.

Study site	Soil depth (cm)	Year/ season 2002 W	2002 S	2002 R	2002 A	2003 W	2003 S	2003 R	2003 A
Undisturbed stand									
	0-15	5.86 ±0.08	3.44 ±0.01	2.74 ±0.09	4.68 ±0.11	8.24 ±0.30	5.59 ±0.07	3.16 ±0.12	7.20 ±0.06
	15-30	6.29 ±0.18	3.95 ±0.02	3.21 ±0.01	4.87 ±0.07	8.15 ±0.40	5.74 ±0.07	2.81 ±0.01	6.91 ±0.38
Moderately-disturbed stand									
	0-15	8.18 ±0.06	3.85 ±0.01	3.32 ±0.08	6.33 ±0.03	7.89 ±0.12	5.83 ±0.05	3.80 ±0.08	7.54 ±0.14
	15-30	12.07 ±2.13	4.40 ±0.02	3.38 ±0.04	6.59 ±0.03	8.57 ±0.05	5.24 ±0.20	4.14 ±0.06	6.90 ±0.11
Highly-disturbed stand									
	0-15	4.71 ±0.02	5.13 ±0.03	5.03 ±0.05	3.89 ±0.01	5.59 ±0.06	5.43 ±0.01	4.50 ±0.06	5.37 ±0.05
	15-30	5.62 ±0.12	4.24 ±0.36	5.00 ±0.10	6.13 ±0.05	6.38 ±0.09	6.02 ±0.09	5.59 ±0.08	5.89 ±0.05

± SE (n=5)
W-winter, S-spring, R-rainy, A-autumn.

Table 6.4. Seasonal changes in percent contribution of MBN to soil total Kjeldahl nitrogen concentration in the undisturbed and disturbed stands.

Study site	Soil depth (cm)	Year/ season 2002 W	2002 S	2002 R	2002 A	2003 W	2003 S	2003 R	2003 A
Undisturbed stand									
	0-15	1.57 ±0.03	1.10 ±0.01	0.64 ±0.002	1.20 ±0.03	1.45 ±0.01	0.95 ±0.003	0.66 ±0.006	1.23 ±0.08
	15-30	1.09 ±0.10	1.02 ±0.08	0.62 ±0.02	1.08 ±0.05	1.41 ±0.04	0.95 ±0.03	0.60 ±0.05	1.04 ±0.03
Moderately-disturbed stand									
	0-15	1.93 ±0.05	0.81 ±0.01	0.53 ±0.03	1.11 ±0.06	2.60 ±0.10	1.29 ±0.03	0.66 ±0.02	1.62 ±0.08
	15-30	1.46 ±0.03	0.80 ±0.02	0.64 ±0.01	1.06 ±0.03	1.58 ±0.02	1.11 ±0.06	0.63 ±0.001	1.60 ±0.02
Highly-disturbed stand									
	0-15	1.05 ±0.03	1.22 ±0.05	1.91 ±0.07	1.88 ±0.03	1.02 ±0.20	1.14 ±0.03	1.93 ±0.01	1.84 ±0.06
	15-30	0.92 ±0.03	0.62 ±0.06	0.57 ±0.10	0.61 ±0.01	0.66 ±0.08	0.52 ±0.03	0.99 ±0.06	0.57 ±0.07

± SE (n=5)
W-winter, S-spring, R-rainy, A-autumn.

Table 6.5. Seasonal changes in percent contribution of MBP to soil phosphorus concentration in the undisturbed and disturbed stands.

Study site	Soil depth (cm)	Year/ season 2002 W	2002 S	2002 R	2002 A	2003 W	2003 S	2003 R	2003 A
Undisturbed stand									
	0-15	5.22 ±0.30	3.67 ±0.12	2.40 ±0.06	5.39 ±0.09	5.54 ±0.01	5.13 ±0.11	2.17 0.03	6.49 ±0.33
	15-30	5.15 ±0.11	2.85 ±0.06	2.39 ±0.03	4.98 ±0.06	5.35 ±0.20	5.08 ±0.10	2.12 ±0.01	6.21 ±0.03
Moderately-disturbed stand									
	0-15	3.42 ±0.08	2.90 ±0.05	2.18 ±0.01	3.64 ±0.30	4.38 ±0.33	4.36 ±0.04	2.09 ±0.08	5.38 ±0.73
	15-30	3.14 ±0.13	2.33 ±0.05	2.16 ±0.001	3.52 ±0.06	3.56 ±0.15	4.35 ±0.50	2.12 ±0.07	4.69 ±0.06
Highly-disturbed stand									
	0-15	5.22 ±0.55	5.24 ±0.23	2.76 ±0.03	4.68 ±0.08	7.18 ±0.34	4.96 ±0.06	3.15 ±0.04	5.61 ±0.20
	15-30	3.88 ±0.05	4.18 ±0.32	2.65 ±0.11	4.43 ±0.16	7.06 ±0.18	4.32 ±0.08	2.02 ±0.12	4.88 ±0.03

± SE (n=5)
W-winter, S-spring, R-rainy, A-autumn.

Discussion

Soil microbial population

Soil microbial population varied seasonally in all stands. Their population was greater in the undisturbed stand where soil was rich in organic matter than in the disturbed stands. Low microbial population during winter season is attributed to low temperature and water stress. Conversely the peak in rainy season, was due to high ambient temperature and higher soil moisture level in soil. The surface soil usually contains high organic matter which in presence of adequate moisture supply is acted upon by the microorganisms to decompose the complex organic residues into simpler forms; hence the number of microorganisms was higher in the upper soil layer of the soil profile (Maithani *et al.* 1996). Vegetation characteristics also increased soil microbial population as it is evident from a positive correlation ($P<0.05$) between plant density and bacterial ($r=0.937$) and fungal ($r=0.931$) population in the soil. Positive correlations ($r=0.804$ to 0.946) of soil organic carbon, TKN and total P concentration with microbial population explain the importance of soil nutrients in influencing the bacterial and fungal populations in the forest stands.

Microbial biomass -C, -N and -P

With the increase in disturbance, the microbial biomass -C, -N and -P decreased significantly because of lower inputs of organic matter in the soil. In general, microbial biomass -C, -N and -P were low during the rainy season when microbial population was large due to favourable temperature and soil moisture condition. Sarathchandra *et al.* (1984) reported that relatively greater demand for nutrients by plants during the rainy season when the majority of them are at their peak vegetation growth further limited the availability of nutrients to soil microbes, thereby reducing their immobilization in microbial biomass. Nonetheless, greater

accumulation of litter and fine roots favoured the growth of microbial population and also accumulation of microbial biomass -C, -N and -P in the undisturbed stand. However, a decline in the disturbed stands can be attributed to lower inputs of organic matter in the soil. In the highly disturbed stand much reduction of microbial biomass -C, -N and -P occurred due to occasional cultivation practices. The decline in the microbial biomass has been reported when natural ecosystems were converted into cultivable lands (Dalal and Mayer 1987; Gupta and Germida 1988 and Srivastava and Singh 1989).

The microbial biomass -N values (27-93 $\mu g\ g^{-1}$) were lower as compared to the findings reported from coniferous forest (52-125 $\mu g\ g^{-1}$) (Martikainen and Palojarvi 1990), broadleaved deciduous forest (132-240 $\mu g\ g^{-1}$) and evergreen forest (42-242 $\mu g\ g^{-1}$) (Das *et al.* 1997).

Microbial biomass -P values (16-56 $\mu g\ g^{-1}$) were, however, well within the reported range (5-67 $\mu g\ g^{-1}$) for woodland soils (Brookes *et al.* 1984). Seasonal changes in microbial biomass -P was similar to microbial biomass-N. Similar seasonal changes have been reported by Sarathchandra *et al.* (1989) from grassland soils of New Zealand. Significant positive correlations between microbial -P with organic -C (0.778; $P<0.01$), TKN (0.794; $P<0.01$) and total P (0.606; $P<0.01$) showed the importance of soil organic matter as well as TKN and P contents on microbial biomass-P. In dry tropical soils of India, Srivastava and Singh (1988) reported that about 96% of the variability in microbial P could be explained by the variability in soil organic -P.

A high microbial C: N ratio indicates greater proportion of fungi, whereas a low ratio indicates a higher proportion of bacteria in the soil metabolism (Anderson and Domsch 1980; Bremer and van Kessel 1992). In disturbed stands, both bacterial

and fungal populations were lower than the undisturbed stand, but the difference in the microbial C/N ratio was not significant. The mean C/N ratio (11-14) in microbial biomass of the three sites was higher than the values (6-9) reported by Martikainen and Palojarvi (1990) for various coniferous forest soils, but was similar to disturbed chaparral soils (7-13) reported by Fenn *et al.* (1993). The differences in the form and availability of N may also affect the microbial C: N ratio. The C: N ratio in the microbial biomass is not always comparable for different soils (Dalal and Mayer 1987) because E_N (fraction of biomass N released after chloroform fumigation) varies from 0.20-0.30 (Voroney and Paul 1984) to 0.68 (Shen *et al.* 1984). In the present study a E_N value of 0.54 was used. The higher C/N ratio in the lower soil layer than in the upper layer was mainly due to the lower microbial biomass -N in the former. The microbial C/P ratios at the three sites were, however, well within the range (14.37-20.72) reported by Brookes *et al.* (1984) from grassland and cultivated fields in the United Kingdom. A wide variation in C/P ratio indicates that the relationship between the two parameters is quite complex (Joergensen *et al.* 1995).

The contribution (4-6%) of microbial biomass -C to soil organic -C was more at the present study sites than the several other tropical forests (1.5-5.3%) (Theng *et al.* 1989; Luizao *et al.* 1992). Maithani *et al.* (1996) have reported 0.7-1.7% contribution by microbial biomass-C to soil organic-C in selectively felled subtropical humid forests of northeast India. Arunachalam and Pandey (2003) have reported 2-4.3% contribution in shifting agricultural fields in the humid tropics of Arunachal Pradesh, India. However, contribution of microbial -N to total soil Kjeldahl nitrogen was much lower (1.3-1.7%) compared to a range of forest soils (3.4-5.9%) and forest regrowth (7.3-8.3%) (Martikainen and Palojarvi 1990; Maithani *et al.* 1996). This might be due to low total Kjeldahl nitrogen in the soil. The low percentage (1.50-

1.89%) contribution of microbial biomass -P to total soil -P as compared to the values reported by Brookes *et al.* (1984) from deciduous woodland (4.7%), grassland (2-4.3%), arable land (1.4-3.5%) and Arunachalam *et al.* (1996a) from humid subtropical forest (1.4-4.7%), could perhaps be due to low availability of -P in the soil for microbial immobilization (Srivastava and Singh 1988). Nevertheless, significant positive correlations between microbial biomass -C, -N and -P indicate that the dynamics of these three elements are closely interlinked in the tropical soils (Arunachalam 2003).

In conclusion, felling of trees altered the vegetation and soil characteristics as well as microbial biomass -C, -N and -P, which decreased from low to high disturbance regime. The biomass values were generally low during rainy season when vegetative growth of plants was at its peak and high during post-rainy periods due to enhanced microbial immobilization. Further, the microbial biomass -C, -N and -P declined with decreased water holding capacity and concentration of organic C, total Kjeldahl nitrogen and P in the soil.

Chapter 7

In situ N and P mineralization

Introduction

Release of nutrients by biological mineralization is crucial for maintaining the cycling of essential nutrients immobilized in dead plant material and also for continued productivity of terrestrial ecosystem (Bremer 1965). The availability of nutrients in forest ecosystem depends on efficient cycling of nutrients within the ecosystem. Through this cycle, nutrients are returned to the soil following the death of plant tissues, released from litter through decomposition and mineralization and taken up by vegetation (Prescott 2002). Available forms of essential nutrients such as ammonium-N, nitrate-N and phosphate-P vary in different ecosystems due to differences in soil temperature, moisture, soil organic matter stock, microbial activity *etc.* (Arunachalam 2002). Nitrogen mineralization is of crucial importance in natural tropical forest ecosystem where it has been reported to be limiting nutrient for plant growth. N cycling in tropical and temperate forests has been studied by several workers (Nadelhoffer *et al.* 1984; Adams *et al.* 1989; Singh *et al.* 1991). Recent nutrient cycling models focus primarily on the role of N dynamics on long-term forest growth and sustainability (Schoenholtz *et al.* 2000).

Phosphorus in soil exists in a variety of complex organic and inorganic molecules. Its availability in nature can control forest ecosystem growth and productivity (Schlesinger 1997). Phosphorus limitation is common in relatively old and highly weathered soils found in the tropics, where adsorbed and recalcitrant forms of P dominate and less so in temperate ecosystems with relatively young soils

(Vitousek and Farrington 1997). Within the forest ecosystem, P is tightly cycled and conserved in the upper soil organic horizons; its loss to lower soil horizons is minimal (Fiorentino *et al.* 2003). Research investigating changes in available N and P resulting from forest conversion to other land use is important to understand the impacts of deforestation on regional biogeochemical cycles, and to improve management practices to minimize environmental degradation (Sanchez *et al.* 1983; Szott and Palm 1996).

This chapter discusses the impact of disturbance on *in situ* N and P mineralization pattern in soils of humid tropical forest stands.

Methods

N and P mineralization was studied seasonally *in situ* by buried polythene bag technique (Eno 1960). Sampling was done during April, July, October and November representing spring, rainy, autumn and winter seasons respectively. During each sampling date, ten randomly located paired soil cores samples were collected from 0-15 and 15-30 cm soil depths in undisturbed and disturbed stands using a steel corer (5.5 cm inner diameter). Samples of one core of each pair was sealed in polythene bag after removing roots and organic debris and placed at its respective depth. The samples of other core were brought to the laboratory and composite sample was made for each soil depth stand-wise. These were sieved through 2 mm mesh and moisture content, ammonium-N, nitrate-N and available-P were determined within 24 h. Ammonium-N, nitrate-N and available-P were extracted from fresh soil samples using KCl (0.2N), deionized water and alkaline $NaHCO_3$ (0.5 M). These were determined colorimetrically using indophenol blue, phenol disulphonic acid and molybdenum blue methods respectively (Jackson 1958). After 3 months, the buried bags were retrieved from each stand, the soil samples were pooled according to depth and analyzed for final ammonium-N, nitrate-N and available-P contents. The changes in

nitrate-N and available-P were obtained by subtracting the initial concentrations from the corresponding final concentrations. The resultant values were referred to as nitrification and P mineralization rates respectively. Net N mineralization was calculated as the sum of the changes in extractable ammonium and nitrate nitrogen over the three months. All analysis was carried out in triplicate and results were expressed on oven-dry (24 h at 105 °C) mass basis.

Statistical analysis

The data were analyzed using ANOVA (Three-way) to find out whether or not the variations due to soil depths, seasons and stands were statistically significant. Linear regression and correlation coefficients were worked out following Zar (1974) to study the relationships between mineralization and variables of climatic and edaphic environment.

Results

Nitrification, N and P mineralization rates were higher in the undisturbed stand, and the rate decreased with the increase in disturbance intensity. Maximum nitrification rate (4.18 $\mu g\ g^{-1}\ mo^{-1}$) was recorded in the undisturbed stand and minimum (2.27 $\mu g\ g^{-1}\ mo^{-1}$) in the highly disturbed stand. In all the three stands higher nitrification rate was recorded in the upper (0-15 cm) soil layer than the lower (15-30 cm) soil layer.

The N mineralization rate ranged between 3.24 and 8.14 $\mu g\ g^{-1}\ mo^{-1}$ and P 1.60 and 2.90 $\mu g\ g^{-1}\ mo^{-1}$ in the highly disturbed and undisturbed stands respectively. In general, net N and P mineralization rates were greater in the undisturbed stand and lower in the highly disturbed stand. Nitrification, N and P mineralization rates decreased with the increase in disturbance intensity.

Seasonal variations in N and P mineralization and nitrification rates were similar in all the three stands. In both the years, nitrification rate was maximum during rainy season and minimum during winter in the undisturbed and disturbed stands (Figure 7.1). In general, N and P mineralization peaked during rainy season and low during winter in all the three stands (Figures 7.2-7.3).

Analysis of variance indicated that the differences in the N and P mineralization rates due to seasons, stands and soil depths were significant at different levels (Table 7.2). N and P mineralization were positively correlated with soil physico-chemical properties and microbial population. Vegetation characteristics such as density and basal area of the woody vegetation also influenced N and P mineralization rates (Table 7.3).

Table 7.1. Nitrification and N and P mineralization ($\mu g\ g^{-1}\ mo^{-1}$) rate in the undisturbed and disturbed stands.

	Undisturbed		Moderately-disturbed		Highly-disturbed	
Soil depth (cm)	0-15	15-30	0-15	15-30	0-15	15-30
Nitrification	4.46	3.19	3.88	2.91	2.70	1.83
	±0.02	±0.05	±0.001	±0.06	±0.05	±0.08
N-mineralization	8.14	6.56	6.00	4.49	4.75	3.24
	±0.13	±0.08	±0.10	±0.05	±0.02	±0.01
P-mineralization	2.90	2.48	2.65	1.74	2.31	1.60
	±0.09	±0.01	±0.06	±0.01	±0.006	±0.01

± SE (n=12).

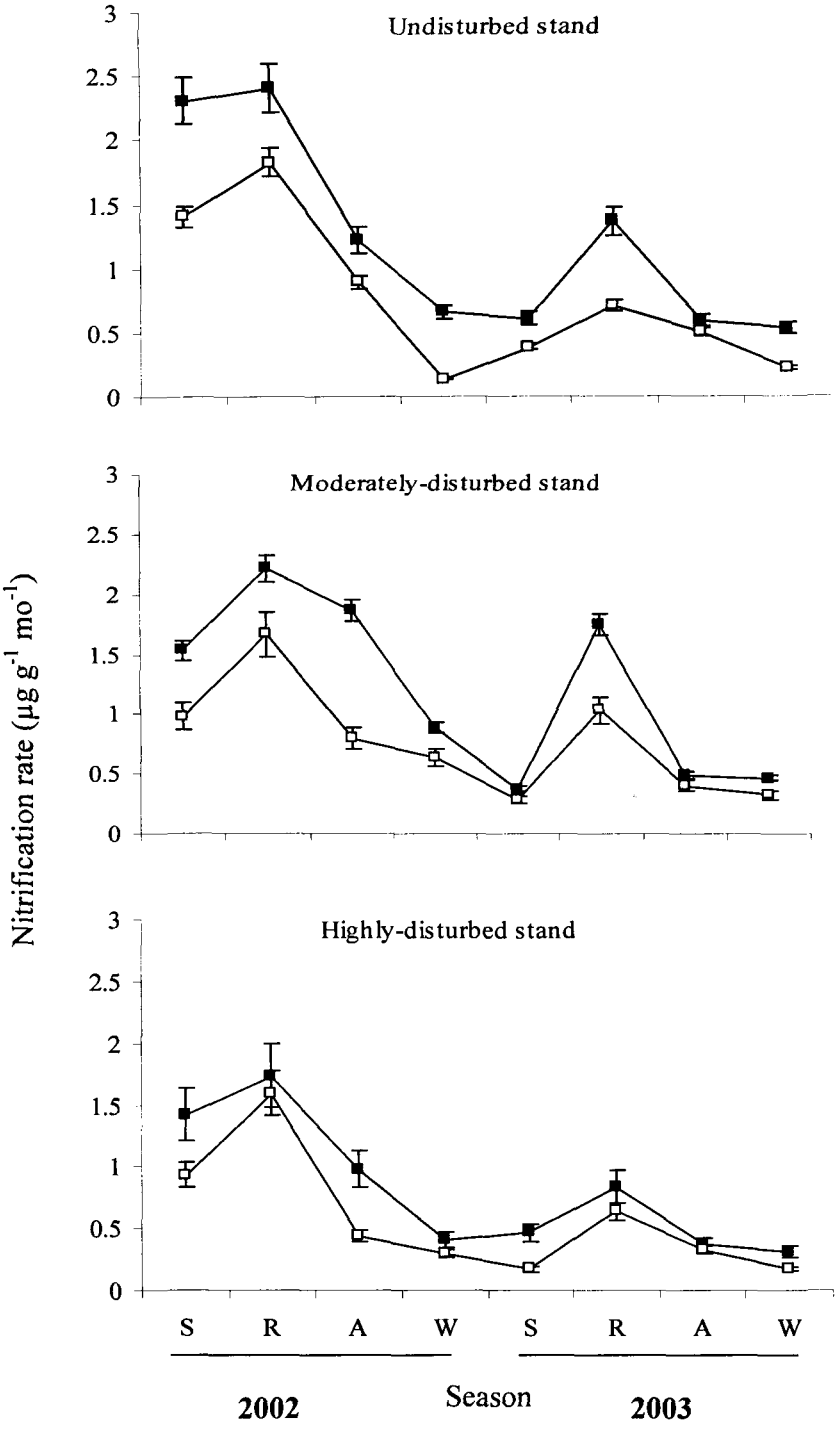

Figure 7.1.Seasonal variation in nitrification rate (■- 0-15 and □-15-30 cm soil depths) in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5). S-spring, R-rainy, A-autumn and W-winter.

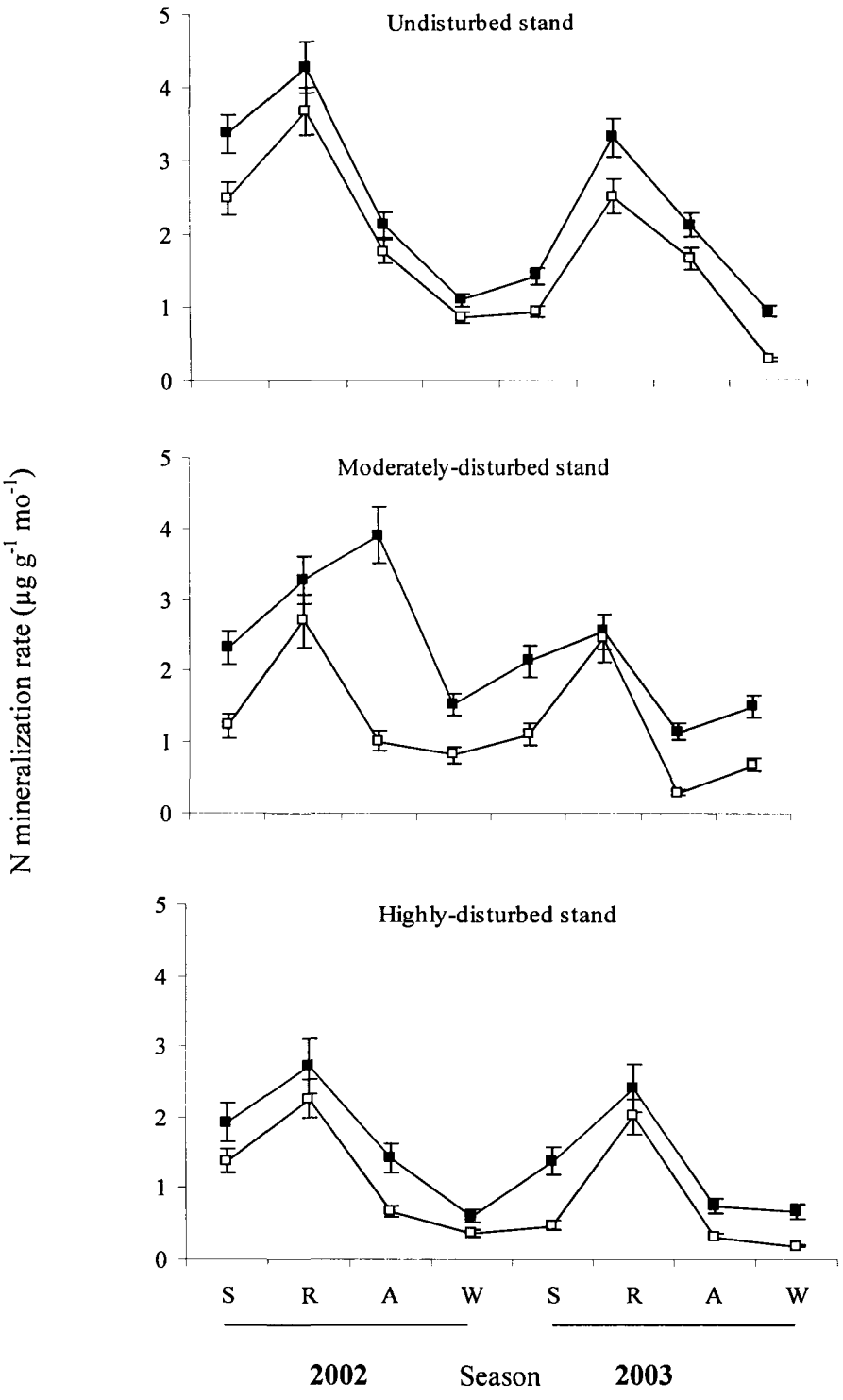

Figure 7.2. Seasonal variation in N mineralization rate (■- -15 and □-15-30 cm soil depths) in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5). S-spring, R-rainy, A-autumn and W-winter.

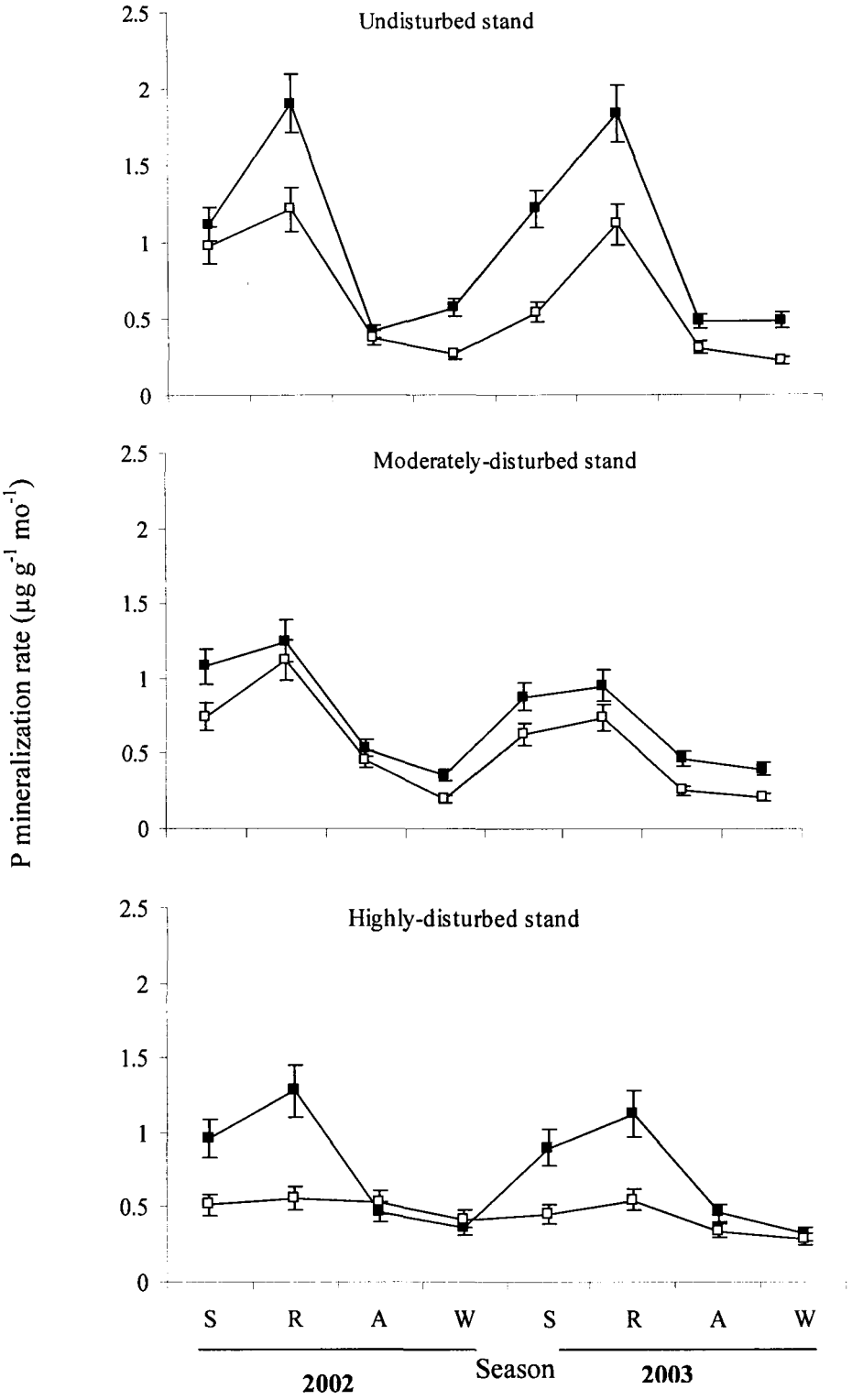

Figure 7.3. Seasonal variation in P mineralization rate (■-0-15 and □-15-30 cm soil depths) in the undisturbed and disturbed stands. Vertical lines represent standard error (n=5). S-spring, R-rainy, A-autumn and W-winter.

Discussion

The above results show that removal of vegetation substantially altered the N and P mineralization processes. Wells and Joergensen (1979) opined that the removal of relatively N rich materials during whole tree harvest may decrease N mineralization and pool size of available N. Vitousek (1981) reported that the removal of slash during whole tree harvesting decreases microbial immobilization of N and its pool size.

Differences in nitrification in the undisturbed and disturbed stands could be due to the differences in organic matter in the soil surface. More soil organic matter in the undisturbed stand might have supplied more readily available C sources to the soil microbes resulting in increased nitrification rate in the undisturbed stand and lower rates in the disturbed stands due to less availability of soil organic matter. Nitrification was consistently near about 50% of the total N mineralization (Table 7.1) indicating that nitrifying microorganisms are very active in all the three stands. Similar results were also reported by Perez *et al.* (1998) in the montane forest of south Chile.

Variation in soil type and soil texture led to differences in soil moisture content, inorganic N and P concentrations, nitrification and N and P mineralization rates. Moisture content, inorganic -N and -P concentrations and N and P mineralization rates were higher in the undisturbed stand than the disturbed stands, where proportion of clay content was high in soil. Clayey soil can hold more water that led to greater availability of soil organic matter and ultimately greater microbial activities and nutrient mineralization. Net N and P mineralization and nitrification rates were higher in soils with higher clay content. Lower rates in the disturbed stands could be explained by reduction in soil

organic carbon, total Kjeldahl nitrogen and P concentration. Changes in a small fraction of soil organic matter could have larger effects on ecosystem N dynamics (Wedin and Tilman 1990). Over all, N mineralization rate (3.2-8.1 $\mu g\ g^{-1}\ mo^{-1}$) recorded in this study was substantially lower than the values reported from different tropical ecosystems (8-68 $\mu g\ g^{-1}\ 10\ days^{-1}$) (Vitousek and Matson 1985). One possible reason for the low rate of mineralization could be the long incubation period.

There was an increase in the rate of N and P mineralization and nitrification during rainy season in the undisturbed and disturbed stands which resulted in increased availability of nutrients in the soil during this period. Similar results have been reported by Burke (1989) in a sagebrush steppe landscape and by Theodore and Bowen (1983) from soils of *Pinus radiata* forest in Australia. Increased rates of N and P mineralization and nitrification during rainy/ summer season were also due to the increase in above and below ground biomass and soil nutrient pool in the undisturbed and moderately disturbed stands. Hence, nutrient mineralization at these two stands acted as an important source of available N and P for plant uptake and growth during the peak vegetative growth period. Although in the highly disturbed stand above and below ground biomass did not increased during summer season still N and P mineralization rate was higher because of greater microbial activity and favourable temperature and moisture condition in soil. In general, in the highly disturbed stand, cultivation apparently changed the pattern of mineralization with lower rates of nitrification and N and P mineralization. This was probably due to runoff of nutrients from the soil surface because of heavy rainfall in the area.

P mineralization also decreased from undisturbed to disturbed stands. Greater P mineralization rate in the undisturbed stand may be due to greater availability of organic matter and moist-warm condition (Biederbeck 1978) which favour microbial activity. Reductions in P mineralization rate in the disturbed stands were due to the low soil organic matter content, total Kjeldahl nitrogen and P concentration and lower microbial activity. Mordelet *et al.* (1996) reported that enhanced biological activity prevailing under tree canopies due to large root biomass and microbial activities favours greater nutrient mineralization.

Table 7.2. Three-way ANOVA showing effect of season, stand and soil depth on N and P mineralization rates ($\mu g\ g^{-1}\ mo^{-1}$).

Variables	N mineralization			P mineralization		
	df	F	P	df	F	P
Season	3	166.75	0.001	3	416.77	0.001
Depth	1	74.79	0.001	1	197.35	0.001
Stand	2	137.12	0.001	2	62.71	0.001
Season x depth	3	3.64	0.019	3	26.32	0.001
Depth x stand	2	2.89	0.065	2	9.47	0.001
Season x depth x stand	6	1.77	0.024	6	10.16	0.001

Table 7.3. Correlation coefficients (r) showing relationships between N and P mineralization rates (μg g^{-1} mo^{-1}) with soil physico-chemical and microbial characteristics (n=20) and density and basal area of woody vegetation (n=3) in the undisturbed and disturbed stands

Variables	N mineralization	P mineralization
Soil properties		
Temperature (° C)	0.633**	0.786**
Moisture content (%)	0.436*	0.589*
SOC (mg g^{-1})	0.453*	0.629**
TKN (mg g^{-1})	0.723**	0.508*
P-conc. (mg g^{-1})	0.433*	0.460*
Microbial properties		
Bacterial population†	0.592**	0.522*
Fungal population ‡	0.611**	0.451*
Vegetation		
Density (plants ha^{-1})	0.793*	0.850*
Basal area (m^2 ha^{-1})	0.862**	0.986***

***P< 0.001, **P<0.01, *P<0.05
SOC-soil organic carbon
† Number of colonies x 10^5 g^{-1} dry weight of soil
‡ Number of colonies x 10^4 g^{-1} dry weight of soil.

Chapter 8

General discussion

The undisturbed stand of humid tropical forest was characterized by well defined vegetation stratification where plants were distributed in four distinct strata. Similar stratification was observed in the moderately disturbed stand with lower number of tree species. However, in the highly disturbed stand the stratification was completely disrupted, and only a few tree species were sparsely distributed in the stand. Selective logging and clear felling caused a significant reduction in species richness, density and basal area of trees and shrubs in the disturbed stands. But the number of herbaceous species increased in the moderately disturbed stand due to reduced competition of the canopy trees and better light intensity and temperature regimes on the forest floor. Overall, species diversity (Shannon diversity index) was greater in the moderately disturbed stand. Disturbance is widely believed to be one of the factors in increasing species diversity (Connell 1978; Huston 1994). Disturbance of mild intensity leads to the creation of treefall gap with varied microenvironmental condition that favours many light demanding species to germinate (Pickett and White 1985, White *et al.* 1985).

Disturbance of strong intensity as noticed at the study site was responsible for increasing light intensity and temperature of soil and air in the disturbed stands on one hand, and decreasing relative humidity on the other. Contrary to this the microclimate in the undisturbed forest was characterized by low light intensity and temperature of air and soil and high soil moisture as compared to the disturbed stands.

Table 8.1. Vegetation, microclimate and soil characteristics of the undisturbed and disturbed stand.

Parameter / Soil depth (cm)		Undisturbed	Moderately disturbed	Highly disturbed
Vegetation				
Number of tree species		82	53	13
Tree density (No. ha^{-1})		658	369	41
Tree basal area (m^2 ha^{-1})		85.55	20.83	5.02
Microclimate				
Light intensity (Lux)		2717±85.03	9879±106.50	14250±387.06
Air temperature (°C)		18.07±1.23	20.43±0.86	32.95±3.14
Relative humidity (%)		78.21±3.50	69.03±3.88	61.51±2.37
Soil				
Texture		Sandy clay loam	Sandy loam	Sandy loam
WHC (%)	0-15	66.48±2.60	52.03±1.44	38.40±2.82
	15-30	64.52±3.72	51.16±2.85	38.18±1.03
Bulk density	0-15	0.67±0.008	0.83±0.02	0.88±0.008
(g cm^{-3})	15-30	0.73±0.005	0.85±0.007	1.01±0.03
Moisture	0-15	29.86±1.91	20.18±1.17	17.96±0.96
content (%)	15-30	28.94±1.73	18.77±0.92	17.43±0.93
pH	0-15	4.95±0.23	5.74±0.15	6.13±0.14
	15-30	5.08±0.19	5.85±0.09	6.36±0.16
SOC (kg ha^{-1})	0-15	11024.85±513.67	7889.15±248.60	6865.00±348.03
	15-30	10227.30±398.00	6770.25±177.67	6519.55±480.64
TKN (kg ha^{-1})	0-15	4294.70±148.08	2967.25±133.35	2200.00±78.65
	15-30	4204.80±107.63	2511.75±168.42	1919.00±101.63
P (kg ha^{-1})	0-15	636.50±22.01	619.10±33.59	453.20±17.68
	15-30	624.15±10.41	612.00±21.64	434.30±18.97

SOC-soil organic carbon, WHC-water holding capacity.
Each value is the mean of eight seasons across the two years (± SE; n=24).

Loss of canopy trees increased the loss of fine particles from top soil layer during extreme rainfall events. This was responsible for increase in the proportion of sand in the soil of the disturbed stands as compared to the undisturbed stand. Moisture and water holding capacity of soil got reduced in the disturbed stands due to change in soil texture from sandy clay loam in the undisturbed stand to sandy loam in the disturbed stands.

The chemical characteristics of soil also differed markedly between the undisturbed and disturbed stands. Low soil pH in the undisturbed stand could be the result of greater accumulation of partially decomposed organic matter on the forest floor while higher soil pH in the disturbed stands was due to low accumulation of decomposed organic matter. Significantly greater soil organic C, cation exchange capacity, total Kjeldahl nitrogen, ammonium-N, nitrate-N, P and available-P concentration in the undisturbed stand might be due to greater inputs of organic matter through above ground and below ground litter.

Fine and coarse roots biomass and production in the humid tropical forest ecosystem, besides being influenced by vegetation characteristics and seasonality of the climate, was adversely affected by disturbance. The undisturbed stand with greater tree density and basal area had greater root mass compared to the disturbed stands. A significant ($P<0.001$) reduction in root mass and production in the disturbed stands is attributed to the change in the tree species composition and decrease in stand basal cover ($r=0.903$, $P>0.01$) and density ($r=0.999$, $P>0.001$). The humid tropical forest with thick above ground vegetation, is characterized by a dense network of fine roots on the forest floor. They play an important role in the conservation of nutrients in tropical rainforests (Klinge 1973; Jenik 1978). Lower fine roots mass and production in disturbed stands

may, therefore be attributed to tree thinning, causing lower input of organic matter accumulation and nutrients on the forest floor. About 76% of the fine roots (>2 mm diameter) were found in the top organic matter and nutrient rich soil layer (0-15 cm). Vertical distribution of fine roots in the soil obtained in the present study is in confirmity with the pattern reported by several workers (*e.g.* Sanford 1989; Arunachalam *et al.* 1996c; Sundarapandian and Swamy 1996) from the wet subtropical and tropical semi evergreen forests. The root biomass and production of various tropical and temperate forests are compared in Table 8.5. Root biomass and production values obtained in the present study are comparable with those of tropical forest of Western Ghats, South India (Sundarpandian and Swamy 1996), humid subtropical forest of Meghalaya, Northeast India (Arunachalam *et al.* 1996c), Amazonian forests of Brazil (Klinge 1973), and Red oak and maple forest of North America (McClaugherty *et al.* 1982).

The fine and coarse roots responded strongly to seasonality of rainfall and temperature. This is evident from greater root biomass during warm-rainy season and lower biomass during dry-winter season. The decline in fine root biomass during winter season may be related to their poor or no growth and mortality due to low temperature and moisture stress. However, in the highly disturbed stand greater root mass recorded during winter season could be attributed to higher density of grass species in the stand. Occasional disturbance of soil in the rainy season for cultivation purposes in the highly disturbed stand could be another possible reason for lower fine root biomass. Such a seasonal response of fine roots is well documented in tropical and subtropical forests (Silver and Vogt 1993; Arunachalam *et al.* 1996c; Sundarpandian and Swamy 1996). The root production decreased with the increase in diameter and disturbance intensity. About

60-70% of fine root production in the surface soil layer is attributed to accumulation of sufficient detrital materials on the forest floor that increase the surface root production owing to conducive microclimate for the development of new roots.

Root turnover rate was also influenced by soil depth, root size and disturbance intensity. Faster root turnover in the undisturbed stand may be viewed as a mechanism of rapid nutrient release that help in meeting the demand of plant species. Plants growing in nutrient-poor environment might increase root life span to avoid nutrient loss (Gill and Jackson 2000). A slower turnover rate of fine and coarse roots in the disturbed stands might be helpful in retention of organic matter and nutrients in soil following disturbance (Aerts 1990). Larger diameter roots (coarse roots) showed slow turnover rate, as the larger diameter roots serve as a transport conduits and initiates new laterals as well as absorbs soil resources and may be preferentially preserved by the plant (Wells and Eissenstat 2001). However, slow turnover rate of fine and coarse roots in the subsoil (15-30 cm depth) layer might be due to depletion of soil moisture and nutrients availability. The nutrient concentration in roots of the undisturbed stand was high and low in the disturbed stands. Rose (1988) and Gleeson and Tilman (1990) have reported greater concentration of nutrients in the older communities than in the younger ones. Soil nutrient level might have also played a role in influencing nutrient concentration in roots.

Nutrient accumulation in fine roots was greater than the coarse roots in the undisturbed and disturbed stands. Fine roots contributed 11-91 kg ha^{-1} N and 4-20 kg ha^{-1} P to the soil nutrient pool, whereas coarse roots contributed 2-28 kg ha^{-1} N and 0.53-7 kg ha^{-1} P in the highly disturbed and undisturbed stands respectively. These results suggest that increase in root biomass also enhanced nutrient accumulation.

Root decomposition differed markedly between the undisturbed and disturbed stands. Differences in root decomposition and N and P mineralization rate might be explained on the basis of differences in tissue chemistry and site characteristics. During decomposition, fine roots with greater N and P concentration and low lignin and C/N ratio decomposed rapidly than coarse roots with low N and P concentration and greater lignin and C/N ratio. Decay and N and P mineralization rates of fine and coarse roots were low in the disturbed stands. This might be the result of lower soil microbial population in these stands. Prescott *et al.* (1993) reported that increasing soil nutrient availability could modulate the production of extracellular enzymes by the microbial community and the rate of decomposition.

Table 8.2. Biomass and production of fine and coarse roots in the undisturbed and disturbed stands.

Parameter / Soil depths (cm)	Undisturbed	Moderately disturbed	Highly disturbed
Fine root mass (<2 mm diameter) (kg ha^{-1})			
0-15	7419.39±301.42	4838.63±124.68	2867.12±116.64
15-30	3801.91±74.70	2257.78±237.12	143.67±8.67
Coarse root mass (2-5 mm diameter) (kg ha^{-1})			
0-15	2056.60±211.62	1512.75±214.09	546.52±13.48
15-30	3737.37±167.38	3457.77±108.56	307.59±6.48
Fine root production (kg ha^{-1} yr^{-1})			
0-15	2114.54±128.67	1315.18±86.32	1169.65±31.42
15-30	800.14±23.86	795.35±33.67	85.35±0.92
Coarse root production (kg ha^{-1} yr^{-1})			
0-15	1091.72±39.64	627.53±65.67	150.29±7.84
15-30	788.52±21.05	506.32±13.52	97.98±3.22

Each value is the mean of eight seasons across the two years (± SE; n=24).

In all the stands, peak bacterial and fungal population was recorded during rainy season when soil moisture and temperature conditions were favourable for their growth. Lower population during winter could be due to low temperature and water stress in soil (Maithani *et al.* 1996). Bacterial and fungal population was high (Bacteria=91 x 10^5 and Fungi=26 x 10^4 g^{-1} of soil) in the undisturbed stand where soil was rich in organic matter and nutrients and low (Bacteria= 45 x 10^5 and Fungi= 13 x 10^4 g^{-1} of soil) in the highly disturbed stand a low organic matter content and nutrients in soil.

The microbial biomass -C, -N and -P obtained in the present study are comparable with other forest ecosystems of the world (Table 8.6). Vegetation had the greatest effect on microbial biomass -C, -N and -P dynamics. In the disturbed stands low microbial

biomass were mainly due to loss of vegetation. Litter and root exudates are primary source of nutrients for microbes and roots are especially important for colonization of microorganisms. A significant positive correlation between total root biomass and microbial biomass indicates that roots contributed significantly in increasing microbial biomass in soil (Figure 8.1). Low root biomass in the disturbed stands might have caused reduction in microbial biomass. Microbial biomass -C, -N and -P was related to the size of microbial population. Relatively greater amount of -C, -N and -P in microbial biomass during winter when their population size was small (Bacteria= 38 x 10^5 and Fungi= 11 x 10^4 g^{-1} of soil) than the rainy season (Bacteria= 62 x 10^5 and Fungi= 19 x 10^4 g^{-1} of soil) when their population was large requires further investigation to explain this situation. A significant positive correlation ($r=0.899$, $P<0.001$) between soil total Kjeldahl N and microbial -N and positive correlation between organic C, TKN and P concentration in soil and microbial -P, show the importance of soil organic matter and nutrients in determining accumulation of nutrients by the soil microbes (Coleman *et al.* 1983).

Over all, the percentage contribution of microbial biomass N and P to soil nutrient pool was low as compared to the earlier reports (Martikainen and Palojarvi 1990), but their rapid turnover rate might be contributing to greater nutrient availability in the undisturbed stand.

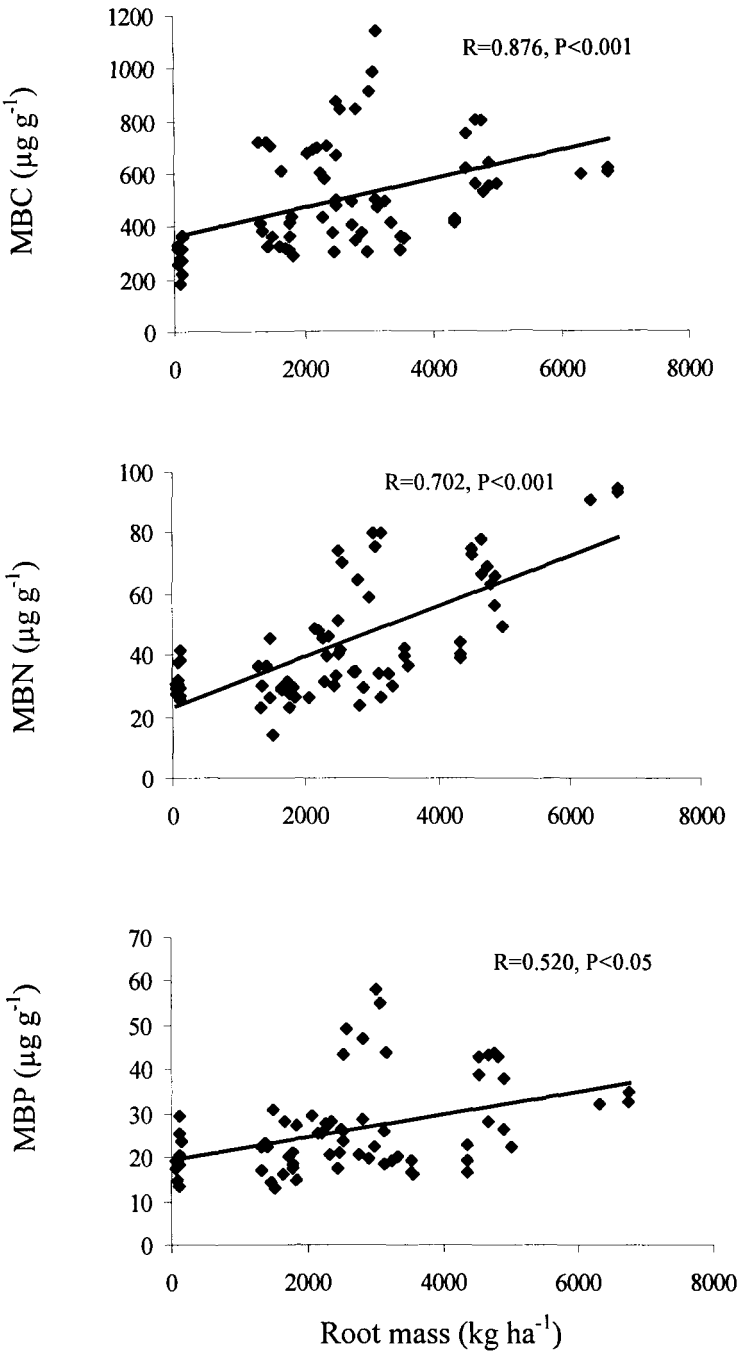

Figure 8.1. Relationship between microbial biomass -C, -N and -P with total root mass.

Removal of vegetation altered the N and P mineralization processes by reducing organic matter, microbial population and pool size of available nutrients in the soil. N and P mineralization rate was dependent on availability of organic matter, microbial activity and favourable moist-warm condition on the forest floor. A positive relation between root mass and N and P mineralization rate (Table 8.4) observed in the present study indicates the positive role of root mass on N and P mineralization in soil. Paterson (2003) studied the effects of roots on mineralization, and concluded that the flow of C from roots was quantitatively significant in affecting mineralization in soil.

From the foregoing discussion, it is evident that destruction of above ground vegetation adversely affected the fine roots and microbial dynamics in soil as well as its physico-chemical characteristics (Tables 8.1-8.3). Greater accumulation of fine roots in the undisturbed stand helped in microbial colonization and immobilization of nutrients.

Table 8.3. Microbial population and biomass -C, -N and -P in the undisturbed and disturbed stands.

Parameter / Soil depths (cm)		Undisturbed	Moderately disturbed	Highly disturbed
Microbial population				
Bacteria*	0-15	96.29±4.82	65.75±3.59	49.46±1.12
	15-30	86.03±1.18	55.82±6.86	41.09±1.67
Fungi**	0-15	29.09±1.06	18.41±0.32	14.60±0.76
	15-30	22.94±0.88	15.53±0.14	12.25±0.32
Microbial biomass (kg ha^{-1})				
C	0-15	571.76±51.01	452.93±13.52	315.59±12.68
	15-30	515.63±18.96	399.96±28.70	309.05±12.06
N	0-15	47.93±0.87	34.95±1.03	32.15±1.00
	15-30	44.55±0.90	30.98±0.88	31.40±1.03
P	0-15	28.46±1.48	22.55±1.02	20.94±0.68
	15-30	27.57±0.89	22.43±0.67	20.09±1.01

Each value is the mean of eight seasons across the two years (± SE; n=24).
* Number of colonies x 10^5 g^{-1} dry weight of soil
** Number of colonies x 10^4 g^{-1} dry weight of soil.

Table 8.4. Correlations coefficients showing relationship of total root biomass (kg ha^{-1}) with certain community parameter, microbial biomass, population and mineralization rate

Variable	r	P
Vegetation		
Tree density (plants ha^{-1})	0.996	0.001
Tree basal area (m^2 ha^{-1})	0.903	0.01
Microbial properties		
Bacterial population*	0.826	0.001
Fungal population**	0.604	0.005
Microbial biomass -C (μg g^{-1})	0.876	0.001
Microbial biomass -N (μg g^{-1})	0.702	0.001
Microbial biomass -P (μg g^{-1})	0.520	0.05
N mineralization rate (μg g^{-1} mo^{-1})	0.718	0.001
P mineralization rate (μg g^{-1} mo^{-1})	0.706	0.001

r= correlation coefficient, P-significant level
* Number of colonies x 10^5 g^{-1} dry weight of soil
** Number of colonies x 10^4 g^{-1} dry weight of soil.

Table 8. 5. Total root biomass and production in forest ecosystems of the world

Forest type	Location	Sampling depth (cm)	Diameter class (mm)	Root biomass (x 10^3 kg ha^{-1})	Root production (x 10^3 kg $ha^{-1}yr^{-1}$)	Source
Humid tropical evergreen forest	Assam	30	≤5	2.8 – 12.4	1.6 – 7.2	Present study
Wet subtropical forest	Meghalaya	30	<15	0.7 – 9.4	5.9 – 14.7	Arunachalam *et al.* 1996c
Wet subtropical forest	Meghalaya	30	<1	1.9 – 3.4	1.1	Khiewtam and Ramkrishnan 1993
Tropical semi evergreen forest	Kodayar	25	<1	1.4 – 5.1	4.7 – 6.1	Sundarpandian and Swamy 1996
Tropical dry evergreen forest	Coromondel	10	≤2	1.3 – 2.3	1.0 – 1.2	Visalakshi 1994
Tropical dry deciduous forest	Varanasi	50	<6	4.0 – 5.5	2.4 – 2.8	Singh and Singh 1981
Temperate forest	North America	30	<3	5.1	9.9	McClaugherty *et al.* 1982
Central Amazonian rain forest	Brazil	18	≤2	8.43	-	Klinge 1973
Northern Hardwood forest	HBEF New Hemisphere	32	2	4.3 – 4.7	2.4 – 2.6	Fahey and Hughes 1994
Temperate forest	Missouri	100	≤5	14.6	1.18	Joslin and Henderson 1987

HBEF-Hubbard Brook Experimental Forest
All the production values were calculated on the basis of sequential core method

Table 8. 6. Microbial biomass carbon, nitrogen and phosphorus in forest ecosystems of the world

Forest type	Location	MBC ($\mu g\ g^{-1}$)	MBN ($\mu g\ g^{-1}$)	MBP ($\mu g\ g^{-1}$)	Source
Humid tropical evergreen forest	Assam	246 – 1146	27 – 92	18 – 52	Present study
Wet subtropical sacred forest	Meghalaya	1272 – 1649	215 – 285	14 – 46	Arunachalam and Arunachalam 2000
Wet subtropical pine forest	Meghalaya	58 – 294	36 – 118	5 – 20	Arunachalam *et al.*1996a
Wet subtropical broad leaved forest	Meghalaya	123 – 814	52 – 125	5 – 67	Maithani *et al.* 1996
Tropical evergreen forest	Arunachal Pradesh	801 – 1431	32 – 98	–	Arunachalam and Pandey 2003
Subtropical evergreen forest	Arunachal Pradesh	651 – 1629	61 – 87	–	Arunachalam and Pandey 2003
Tropical dry deciduous forest	Vindhyan Hill, U.P.	262 – 744	31 – 88	11– 31	Singh *et al.* 1989
Tropical dry deciduous forest	Vindhyan Hill, U.P.	332 – 609	27 – 65	12 – 26	Srivastava and Singh 1991
Wet tropical forest	Andaman	143 – 674	10 – 54	–	Dinesh *et al.* 2003
Humid temperate forest	Atlanta	282 – 1275	42 – 191	33 – 148	Diaz-Ravina *et al.* 1995
Northern Hardwood forest	HBEF New Hemisphere	400 – 1054	80 – 194	–	Bohlen *et al.* 2001
Temperate forest	Central Germany	317 – 2116	30 – 347	18 – 174	Joergensen *et al.* 1995

HBEF-Hubbard Brook Experimental Forest

The values of microbial biomass -C, -N and -P given above were determined by chloroform-fumigation extraction method.

Summary

The effect of human induced disturbance on fine roots and soil microbial biomass -C, -N and -P dynamics in humid tropical forest ecosystem of northeast India was studied in undisturbed, selectively logged and clear-felled stands. These stands are located in Jeypore Reserve Forest of Dibrugarh Forest Division of Assam (latitude 27° 05′ to 27° 28′N; longitude 95° 20′ to 95° 38′E; altitude 220 m asl) on the southern bank of the river Brahmaputra. The study was conducted during 2002-2004. Data on fine roots, microbial biomass, vegetation, soil and microclimatic characteristics were collected from the three stands on seasonal basis. Decomposition of roots and nitrogen and phosphorus mineralization studies were also undertaken in the undisturbed and disturbed forest communities.

The major findings of the study are summarized as under:

1. The undisturbed stand of the humid tropical forest was characterized by a well defined vegetation stratification, which was absent in the disturbed communities. Plants were distributed in four distinct strata in the undisturbed forest, similar stratification was observed in the moderately disturbed stand with lower number of tree species (53 species), however, in the highly disturbed stand no such stratification was recognized. Tree species richness in community was drastically reduced in the community due to disturbance from 82 species in the undisturbed stand to 13 species in the highly disturbed stand. But the number of herbaceous species increased in the moderately disturbed stand due to reduced competition from over story species and better light and temperature regimes on the forest

floor. This resulted in to greater species diversity in the moderately disturbed stand. However, disturbance caused a significant reduction in tree density and basal area.

2. There was a marked increase in light intensity (80%) and air temperature (45%) in the highly disturbed stand as compared to the undisturbed stand. In all the three stands, air temperature, light intensity and relative humidity were minimum during winter and maximum during rainy season.
3. Moisture and water holding capacity of soil got reduced due to disturbance due to the change in soil texture from sandy clay loam in undisturbed stand to sandy loam in the disturbed stands.
4. Soil was acidic in all the stands, but the maximum acidity (pH=4.86) was recorded in the undisturbed stand. Soil organic C, cation exchange capacity, total Kjeldahl N, ammonium-N, nitrate-N, P and available -P concentration was low in the disturbed stands as compared to the undisturbed stand. The seasonal variation in soil characteristics was also influenced by the disturbance, for instance, in the undisturbed and moderately disturbed stands soil organic C was high during rainy season and low during winter, but in the highly disturbed stand higher value was obtained during winter and lower during autumn.
5. Mean accumulation of fine (<2 mm diameter) roots was maximum (8061 kg ha^{-1}) in the undisturbed stand and minimum (2286 kg ha^{-1}) in the highly disturbed stand. Coarse roots (>2 mm diameter) mass did not vary significantly between the undisturbed and moderately disturbed stands, but it was significantly ($P<0.001$) lower in the highly disturbed stand than the undisturbed stand. It ranged between

585.31 kg ha^{-1} in the highly disturbed stand and 4285.39 kg ha^{-1} in the undisturbed stand. In general, the contribution of fine roots mass was significantly ($P<0.05$) greater than the coarse root mass in all the three stands.

6. Total root mass (fine and coarse roots) decreased drastically from 12346 kg ha^{-1} in the undisturbed stand to 2871 kg ha^{-1} in the highly disturbed stand.
7. In both undisturbed and disturbed stands major portion of fine roots was present in the surface (0-15 cm) soil layer. The highly disturbed stand had more than 90% of their fine root biomass within the upper 15 cm soil layer compared with 67% in the undisturbed and moderately disturbed stands.
8. Dead fine root mass contributed 25-49% to the total fine root mass and its maximum (49%) contribution was in the highly disturbed stand during winter season and minimum (25%) during rainy season in the undisturbed stand. The seasonality in dead coarse root mass was similar to that of fine root mass with maximum (55%) contribution in the highly disturbed stand.
9. Total root mass was maximum during rainy season and minimum during winter in the undisturbed and moderately disturbed stands. However, in the highly disturbed stand, maximum value was recorded during winter and minimum during rainy season.
10. Annual fine and coarse root production was 2914 and 1880 kg ha^{-1} respectively in the undisturbed stand. The corresponding values in the highly disturbed stand were 1255 and 248 kg ha^{-1}. The contribution of fine roots to total root production was 93, 72 and 66% in the highly disturbed, undisturbed and moderately disturbed stands respectively. Annual turnover rate was high in the undisturbed stand where

forest floor was covered by thick layer of litter and moisture content in the surface soil layer was high compared to the disturbed stands. In the disturbed stands where litter layer was sparse and thin and moisture content was low and annual root turnover rate was low.

11. C, N and P accumulation (C= 453 and 377, N= 91 and 28, P= 20 and 7 kg ha^{-1}) in fine and coarse roots was significantly higher in the undisturbed stand than in the moderately (C= 314 and 286, N= 51 and 28, P= 10 and 6 kg ha^{-1}) and highly disturbed (C= 148 and 58, N= 11 and 2, P= 4 and 0.53 kg ha^{-1}) stands.
12. The fine and coarse roots decomposition rate varied in the undisturbed and disturbed stands. This was related to the difference between tissue chemistry and site characteristics. Fine roots with greater N and P concentration and low lignin and C/N ratio decomposed rapidly than the coarse roots with low N and P concentration and greater lignin and C/N ratio. Therefore, the rate of N and P release from decaying roots decreased from the undisturbed to highly disturbed stand. Favourable soil temperature, moisture and greater microbial activity and nutrient availability in the soil increased the decay and mineralization rate of fine and coarse roots in the undisturbed stand as compared to the disturbed stands.
13. Fungal and bacterial population was greater in the undisturbed stand where soil was rich in organic matter, and fine roots were present in large numbers increasing the surface area for the colonization and growth of microbes. Reduced microbial population in the disturbed stands was related to lower inputs of organic matter and fine roots. In all the three stands, greater bacterial and fungal population was recorded during rainy season when high ambient temperature and

soil moisture was prevailing in the forest. Low microbial population was recorded during winter season when low soil temperature and water stress conditions prevailed both in the undisturbed and disturbed stands.

14. Input of C, N and P through the soil microbes was less in the disturbed stands than the undisturbed stand. Microbial biomass -C, -N and -P contributed 544, 46 and 28 kg ha^{-1} in the undisturbed stand, 426, 33 and 22 kg ha^{-1} in the moderately disturbed stand and 312, 31 and 20 kg ha^{-1} respectively in the soil of highly disturbed stand. The seasonal pattern of microbial biomass -C, -N and -P was influenced by the variation of soil moisture and temperature, with maximum values during cold-dry winter and minimum during warm-humid rainy season.
15. Destruction of vegetation reduced N and P mineralization rate. N and P mineralization and nitrification rates were higher in the undisturbed stand than the moderately and highly disturbed stands (refer to Table 7.1, Chapter 7). N and P mineralization rate was greater during rainy season in all the three stands when the temperature and soil moisture conditions were optimum for microbial growth and lower during dry-winter season.

It is concluded that destruction of above ground vegetation by selective logging and clear-felling caused a significant reduction in soil nutrient pool as well as fine roots and microbial biomass in the disturbed stands. Input of C, N and P through fine roots and soil microbes also decreased significantly in the highly disturbed stand.

References

Aber, J. D., Melillo, J.M, Nadelhoffer, K.J., McClaugherty,C. A., Pastor, J. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparision of two methods. Oecologia, 66:317-321.

Aber, J.D., McDowell, W., Nadelhoffer, K., Magil, A., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., Fernandez, I. 1998. Nitrogen saturation in temperate forest ecosystems. Bioscience, 48:921-934.

Aber, J.D., Mellilo, J.M, Nadelhoffer, K.J., Pastor, J., Boone, R.D. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. Ecological Applications, 1:303-315.

Adams, M.A., Polglase,P.J., Attwill, P.M., Weston, C.J., 1989. *In situ* studies of nitrogen mineralization and uptake in forest soil: some comments on methodology. Soil Biology and Biochemistry, 21:423-429.

Aerts, R. 1990. Nutrient use efficiency in evergreen and deciduous species from heath lands. Oecologia, 84:391-397.

Aerts, R., Bakker, C., Caluwe, H. De. 1992. Root turnover as determinant of the cycling of C, N and P in a dry heath land ecosystem. Biochemistry, 15:175-190.

Alegre, J.C., Cassel, D.K., Bundy, D.E.1988. Effects of land clearing method on chemical properties of an Ultisol in the Amazon. Soil Science Society of America Journal, 52:1283-1288.

Alexander, M. 1977. Introduction to Soil Microbiology, 2nd edition, John Wiley, New York.

Allen, A. and Schlesinger, W. 2004. Nutrient limitations to microbial biomass and activity in loblolly pine forests. Soil Biology and Biochemistry, 36:581-589.

Allen, S.E., Grimshaw, H.M., Parkinson, J.A., Quarmby, C. 1974. Chemical Analysis in Ecological Materials, Blackwell Scientific Publications, Oxford.

Ambasht, R.S., 1985. Primary productivity and soil and nutrient stability of an Indian Hilly Savanna Lands. In: J.C. Tothill and J.J. Mott (Editors), Ecology and Management of World's Savannas. Australian Academic Science, Canberra, pp.217-219.

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

Anderson, J. P. E. and Domsch K. H., 1980. Quantity of plant nutrients in the microbial biomass of selected soils. Soil Science, 130:211- 216.

Anderson, J.M. 1973. The breakdown and decomposition of sweet chestnut (*Castena sativa* Mill.) and beach (*Fagus salvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in carbon, hydrogen, nitrogen and polyphenol content. Oecologia, 12:275-288.

Anderson, T.H. and Domsch, K.H. 1993. The metabolic quotient for CO_2 (q CO_2) as a specific activity parameter to assess the effects of environmental conditions, such as pH, on the microbial biomass of forest soils. Soil Biology and Biochemistry, 25:393-395.

Anderson, T.H. and Joergensen, R.G. 1997. Relationships between SIR and FE estimates of microbial biomass C in deciduous forest soils at different pH. Soil Biology and Biochemistry, 29:1033-1042.

Antil, R.S., Lovell, R.D., Hatch, D. J., Jarvis, S.C. 2001. Mineralization of nitrogen in permanent pastures amended with fertilizer or dung. Biology and Fertility of Soils, 33:132-138.

Arthur, M.A. and Fahey, T.J., 1992. Biomass and nutrients in an Engelmann spruce sub alpine fir forest in north central Colorado: Pools, annual production and internal cycling. Canadian Journal of Forest Research, 22: 315-325.

Arunachalam, A. 2002. Dynamics of soil nutrients and microbial biomass during first year cropping in an 8-year jhum cycle. Nutrient Cycling in Agroecosystem, 64:283-291.

Arunachalam, A. 2003. Role of microbial biomass in soil nutrient dynamics along a jhum Cycle gradient. Journal of Tropical Forest Science, 15:279-288.

Arunachalam, A. and Arunachalam, K. 2000. Influence of gap size and soil properties on microbial biomass in a subtropical humid forest of north-east India. Plant and Soil, 223:185-193.

Arunachalam, A. and Pandey, H.N. 2003. Ecosystem restoration of jhum fallows in northeast India: microbial C and N along altitudinal and successional gradients. Restoration Ecology, 11:168-173.

Arunachalam, A., John, B., Maithani, K., Pandey, H.N., Tripathi, R.S. 1997. Vegetational and edaphic changes during secondary succession in subtropical pine and broadleaved forests in north east India. Ecology/Bratislava, 16:253-264.

Arunachalam, A., Maithani, K., Pandey, H. N., Tripathi, R. S. 1996a. The impact of disturbance on detrital dynamics and soil microbial biomass of a *Pinus kesiya* forest in northeast India.Forest Ecology and Management, 88: 273-282.

Arunachalam, A., Pandey, H.N., Maithani, K., Tripathi, R.S. 1996b. Organic matter and nutrient dynamics of fine and coarse roots during recovery of a felled subtropical humid forest. Russian Journal of Ecology, 28:380-385.

Arunachalam, A., Pandey, H.N., Tripathi, R.S., Maithani, K. 1996c. Biomass and production of fine and coarse roots during regrowth of a disturbed subtropical humid forest of north east India. Vegetatio, 123:73-80.

Arunachalam, A., Pandey, H.N., Tripathi, R.S., Maithani, K. 1996d. Fine root decomposition and nutrient mineralization patterns in a subtropical humid forest following tree cutting. Forest Ecology and Management, 86:141-150.

Arunachalam, K. and Arunachalam, A. 1999. Recovery of a felled subtropical humid forest: microclimate and soil properties. Ekologia, 18: 287-300.

Ashton, P.S. and Hall, P. 1992. Comparisions of structure among mixed Dipterocarp forests of northwestern Borneo. Journal of Ecology, 80:459-481.

Azam, F., Malik, K.A., Sajjad, M.I. 1986. Uptake by wheat and turnover in soil fractions of residual N from leguminous plant material and inorganic fertilizer. Plant and Soil, 95:97-108.

Baker, T.T. III., Conner, W.H., Lockaby, G., Stantorf, J.A., Burke, M.K. 2001. Fine root productivity and dynamics on a forested food plain in South Carolina. Soil Science Society of the American Journal, 65:545-556.

Barik, S.K., Pandey, H.N, Tripathi, R.S., Rao, P. 1992. Micro-environmental variability and species diversity in a subtropical broad leaved forest. Vegetatio, 103:31-40.

Berg, B. 1986. Nutrient release from litter and humus in coniferous forest soils: a mini review. Scand. Journal of Forest Research, 1:359-369.

Bhatt, S.C., Sarat, G.V., Pandey, S.C. 1985. Leaf litter decomposition in arid to semiarid climate conditions. Proceedings of Indian Academy of Sciences (Plant Sciences), 95:409-415.

Bierderbeck, V.O. 1978. Soil organic sulphur and fertility. In: Schnitzer and Khan S.V. (Eds.). Soil Organic Matter. Elsevier, Amsterdam, pp. 274-310.

Blake, G. R. and K. H. Hartge. 1986. Bulk density. In: Klute, A. (Eds.) Methods of Soil Analysis,Part-I, 2nd edition, Agron Monograph, ASA and SSSA, Madison, WI. pp.363-375.

Bloomfield, J., Vogt, K.A., Vogt, D.J. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. Plant and Soil, 150:233-245.

Bohlen, P.J., Groffman, P.M., Fahey, T.J., Driscoll C.T., Siccama, T.G. 2001. Plant-soil-microbial interactions in a northern hardwood forest. Ecology, 82:965-978.

Bohm, W. 1979. Methods of studying root systems. Springer-Verlag, New York, pp. 188.

Bouyouncos, G. J. 1962. Hydrometer method improved for making particle size analysis of soil. Agron Journal, 54:464-465.

Bonde, T.A., Schnurer, J., Rosswal, T. 1988. Microbial biomass as a fraction of potentially mineralizable nitrogen in soil from long-term field experiments. Soil Biology and Biochemistry, 20:447-452.

Bowen, G.E. and Nambiar, E.K. S. 1984. Nutrition of Plantation Forests. Academic Press, New York.

Boyle, J. R. 1975. Whole tree harvesting impact on site quality. Paper presented at the Tappi Annual Meeting 24-26 February, New York.

Bremer, J.M. 1965. Inorganic forms of nitrogen. In: Black, C.A., Evans, D.D., White, J.L., Ensminger, L.E., Clark, F.E. (Eds.). Methods of soil analysis, part II. Chemical and Microbiological Properties. American Society of Agronomy, Madison, Wis. pp.1179-1237.

Bremer, S. M. and van Kessel, C. 1992. Seasonal and microbial biomass dynamics after addition of lentil and wheat residues. Soil Science Society of America Journal, 56:1141-1146.

Brookes, P. C., Landman, A., Pruden G., Jenkinson, D. S. 1985. Chloroform fumigation and release of soil N: a rapid direct extraction method to measure microbial biomass N in soil. Soil Biology and Biochemistry, 17:837-842.

Brookes, P. C., Powlson, D. S., Jenkinson, D. S. 1984. Phosphorus in the soil microbial biomass. Soil Biology and Biochemistry, 16:169-175.

Brookes, P.C. Powlson, D.S., Jenkinson, D.S. 1982. Measurement of microbial biomass phosphorus in soil. Soil Biology and Biochemistry, 14:319-329.

Burke, I.C. 1989. Control of N mineralization in a sagebrush steppe landscape. Ecology, 17:1115-1126.

Burtholomew, W.V. and Kirkham, D. 1960. Mathematical descriptions and interpretations of culture induced soil nitrogen changes. 7th International Congress on Soil Science, Madison, Wisconsin, 2:471-477.

Burton, A.J., Pregtizer, K.S., Hendrick, R.L. 2000. Relationships between fine root dynamics and N availability in Michigan northern hardwood forests. Oecologia, 128:389-399.

Caldwell, M.M. 1987. Plant architecture and resource competition. In: Schulze, E.D., Zwolfer, H., (Eds.). Potentials and limitations of ecosystem analysis Ecological Studies, Vol. 61. Springer, Berlin Heidelberg, New York. pp. 164-179.

Caldwell, M.M. 1994. Exploiting nutrients in fertile soil microsites. In: Caldwell, M.M. and Pearcy, R.W. (Eds.). Ecophysiological processes: Above-and below ground. Academic Press, London. pp. 325-247.

Campo, J., Jaramillo, V.J., Maass, J.M. 1998. Pulses of soil phosphorus availability in a Mexican tropical dry forest: effect on seasonality and level of wetting. Oecologia, 115:167-172.

Castellanos, J., Jaramillo, V.J., Sanford, Jr. R.L., Kauffman, J.B. 2001. Slash-and- burn effects on fine root biomass and productivity in a tropical dry forest ecosystem in Mexico. Forrest Ecology and Management, 148:41-50.

Champion, H.G. and Seth, S.K., 1968. A Revised Survey of the Forest Types of India, Government of India Publication, Delhi.

Chen, J., Sari, C. S., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz., G.D., Brookshire, B.L., Franklin, J.F. 1999. Microclimate in forest ecosystem and landscape ecology. Bioscience, 49:288-297.

Clarholm, M. and Rosswal, T. 1980. Biomass and turnover of bacteria in a forest soil and a peat. Soil Biology and Biochemistry, 12:49-57.

Coleman, C.D., Reid, C.P.P., Cole, C.V. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research, 13:1-55.

Comas, L.H., Eissenstat, D.M., Lasko, A.N. 2000. Assessing root death and root system dynamics in a study of grape canopy pruning. New Phytologist, 147:171-178.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science, 199:1302-1310.

Covington, W.W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. Ecology, 62:41.48.

Crews, T.E., Kitayama, K., Fownes, J.H., Riley, R.H., Herbert, D.A., Mueller-Dombois, D., Vitousek, P.M. 1995. Changes in soil P fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology, 76:1407-1424.

Cross, A.F. and Schlesinger, W.H. 1995. A literature review and evaluation of the Hedley fractionation: applications to the bio geochemical cycles of soil P inn natural ecosystems. Geoderma, 64:197-214.

Cuevas, E. 1995. Biology of the belowground system of tropical dry forest. In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.) Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, pp. 362-383.

Cuevas, E. and Medina, E. 1988. Nutrient dynamics within Amazonian forests. II. Fine root growth nutrient availability and leaf litter decomposition. Oecologia, 76:222-235.

Curtis, J.T. 1959. The Vegetation of Wisconsin: An Ordination of Plant Communities. University of Wisconsin Press, Madison, Wisconsin.

Dalal, R.C. and Mayer, R. J. 1987. Long term trend in fertility of soils under continuous cultivation and cereal cropping in southern Queensland. VII. Dynamics of nitrogen mineralization potentials and microbial biomass. Australian Journal of Soil Research, 25: 461-472.

Das, A. K., Boral, L., Tripathi, R. S., Pandey, H. N. 1997. Nitrogen mineralization and microbial biomass-N in soil of a subtropical forest of Meghalaya, India. Soil Biology and Biochemistry, 29:1609-1612.

de Castro, E. A., and Kauffman, J. B. 1998. Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. Journal of Tropical Ecology, 14:263-283.

Diaz-Ravina, M., Acea, M.J. Carballas, T. 1995. Seasonal changes in microbial biomass and nutrient flush in forest soils. Biology and Fertility of Soils, 19:220-226.

Diaz-Ravina, M., Acea, M.J., Carballas, T. 1993. Seasonal fluctuations in microbial populations and available nutrients in forest soils. Biology and Fertility of Soils, 16:205-210.

Dilustro, J.J., Day, F.P., Drake, B.G. 2001. Effects of elevated atmospheric CO_2 on root decomposition in an oak scrub ecosystem. Global Change Biology, 7:581-589.

Dilustro, J.J., Day, F.P., Drake, B.G., Hinkle, C.R. 2002. Abundance, production and mortality of fine roots under elevated atmospheric CO_2 in an oak scrub ecosystem. Environmental and Experimental Botany, 48:149-159.

Dinesh, R., Ghosal Chaudhuri, S., Ganeshamurthy, A.N., Dey, C. 2003. Changes in soil microbial indices and their relationships following deforestation and cultivation in wet tropical forests. Applied Soil Ecology, 24:17-26.

Edwards, P.J. and Grubb, P.J. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. II. Soil characteristics and division of mineral elements between the vegetation and soil. Journal of Ecology, 70:649-666.

Eno, C.F. 1960. Nitrate production in the field by incubating the soil in polythene bags. Soil Science Society of America Proceeding, 24:277-279.

Ericsson, A and Persson, H. 1980. Seasonal changes in starch reserves and growth of fine roots of 20 years old Scot pine. An Ecosystem Study. Ecological Bulletin, 32:239-250.

Eyre, S.R. 1968. Vegetation and Soil: A World Picture, Edwards Arnold Publishers Ltd. UK.

Fahey, T.J. and Hughes, J.W. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest. NH. Journal of Ecology, 82:533-545.

Fahey, T.J., Hughes, J.W., Mou, P., Arthur, M.A.1988. Root decomposition and nutrient flux following whole tree harvest of northern hardwood forest. Forest Science, 34:744-768.

Fairley, R.I. and Alexandar, I.J. 1985. Methods of calculating fine root production in forests. In: Fitter, H. (Eds.). Ecological interactions in soils: plants, microbes and animals. Special Bulletin No.4, Blackwell Scientific, Oxford, U.K. pp. 37-42.

Fenn, M. E., Poth, M. A., Dunn, P. H., Barro, S. C. 1993. Microbial N and biomass, respiration and N mineralization in soil beneath two chaparral species along a fire- induced age gradient. Soil Biology and Biochemistry, 25: 457-466.

Finzi, A.C., van Breeman., N., Canham, C.D. 1998. Canopy tree-soil interactions with temperate forests species: effects on soil carbon and nitrogen. Ecological Applications, 8:440-446.

Fiorentino, I., Fahey, T.J., Groffman, P.M., Driscoll, C.E., Eagar, C., Siccama, T.G. 2003. Initial responses of phosphorus biogeochemistry to calcium addition in a northern hardwood forest ecosystem. Canadian Journal for Forest Research, 33:1864-1873.

Fogel, R. and Cromack, Jr. K. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology, 58:431-437.

Ford, E.D. and Deans, J.D. 1977. Growth of sitka spruce plantations: spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. Plant and Soil 47:463-485.

Gholtz, H.L, Perry, C.S., Cropper, Jr. W.P., Hendry, L. C. 1985. Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations. Forest Science, 31:463-478.

Gilbert, O. and Bocock, K.L. 1960. Changes in the leaf litter when placed on the surface of soils with contrasting humus types. II. Changes in the nitrogen content of oak and ash litter. Journal of Soil Sciences, 11:10-19.

Gill, R.A. and Jackson, R.B. 2000. Global pattern of root turnover for terrestrial ecosystem. New Phytologist, 147:13-31.

Gleeson, S.K. and Tilman, D. 1990. Allocation and transient dynamics of succession on poor soil. Ecology, 71:1144-1155.

Gordon, W.S. and Jackson, R.B. 2000. Nutrient concentration in fine roots. Ecology 81:275-280.

Gorissen, A., Van Ginkel, J.H., Keurentjes, J.J. B., Van Veen, J.A. 1995. Grass root decomposition is retarded when grass has been grown under elevated CO_2. Soil Biology and Biochemistry, 27:117-120.

Gower, S. T., Vogt, K.A., Grier, C.C. 1992. Carbon dynamics of rocky mountain Douglas-fir: influence of water and nutrient availability. Ecological Monographs, 62:43-65.

Grayston, S. J., Griffith, G. S., Mawdsley, J. L, Campbell, C. D, Bardgett, R.D. 2001. Accounting forvariability in soil microbial communities of temperate upland grassland ecosystems. Soil Biology and Biochemistry 33:533–551.

Greenland, J.D. and Kowal, J.M. L.1960. Nutrient content of moist tropical forest of Ghana. Plant and Soil, 12:154-174.

Gregorich, E.G., Voroney, R.P., Kachanoski, R.G. 1991. Turnover of carbon through the microbial biomass in soils with different texture. Soil Biology and Biochemistry, 23:799-805.

Groffman, P.M. and Bohlen, P.J. 1998. Soil and sediment biodiversity: cross-system comparisons and large-scale effects. Bioscience, 49:139-148.

Gupta V. V. S.R. and Germida, J.J. 1988. Distribution of microbial biomass and its activity in different soil aggregate size classes as affected by cultivation. Soil Biology and Biochemistry, 20:777-786.

Harris, W.F., Kinerson, R.S., McGinty, D. 1980. The dynamic belowground ecosystem. In: Waring, R.H. (Eds.). Forest: Fresh Perspective from Ecosystems Analysis. Oregon State University, Corvallis, OR, pp. 119-129.

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

Hassink, J. 1992. Effects of grassland management on N mineralization potential, microbial biomass and microbial biomass and nitrogen yield in the flowing year. Netherlands Journal of Agricultural Science, 40:173-185.

Hassink, J. 1993. Relationships between the amount and the activity of the microbial biomass in Dutch grassland soils: comparison of the fumigation-incubation method and the substrate-induced respiration method. Soil Biology and Biochemistry, 25:533-538.

Hendricks, J. J., Aber J. D., Nadelhoffer, K. J., Hallet, R.D. Nitogen control on fine roots substrate quality in temperate forest ecosystems. Ecosystems, 3:57-69.

Hendrick, R.L. and Pregitzer, K.S. 1993. The dynamics of fine root length, biomass and nitrogen content in two northern hardwood ecosystem. Canadian Journal of Forest Research, 23:2507-2520.

Hendricks, J. J., Nadelhoffer, K. J., Aber J. D. 1993. Assessing the role of fine roots in carbon and nutrient cycling. Trends in Ecology and Evolution 8:174–178.

Hendrickson, O.Q., Chatrapaul, L., Burgess, D. 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. Canadian Journal of Forests Research, 19:725-735.

Hooker, J.D. 1872-1897. The Flora of British India. 7 Vols. London.

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

Huston, M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, U.K.

Jackson, M. L. 1958. Soil Chemical Analysis, Prentice Hall, Englewood Cliffs, New Jersey.

Jackson, R.B. and Caldwell, M.M. 1989. The timing and degree of root proliferation in fertile soils microsites for three cold desert perennials. Oecologia, 81:149-153.

Jackson, R.B., Canadell, J., Ehlringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia, 108:389-411.

Jackson, R.B., Schenk, H.J., Jobbagy, E.G., Canadell, J., Colello, G. D., Dickinson, R. E., Field, C.B. Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D.W., Kleidon, A., Neilson, R.P., Parton, W.J., Sala, O.E., Sykes, M.T. 2000. Belowground consequences of vegetation change and their treatment in models. Ecological Applications, 10:470-483.

Jenik, J. 1978. Roots and root systems of tropical trees: morphologic and ecologic aspects. In: Zimmermann, M.H. and Tomlinson, P.B. (Eds.). Tropical trees as living systems. Cambridge University Press, Cambridge, England. pp. 323-349.

Jenkinson, D. S. and Ladd, J. N. 1981. Microbial biomass in soils: Measurement and turnover, In: Paul, E. A. and Ladd J. N. (Eds.). Soil Biochemistry Mercel Dekker, New York, pp. 415-471.

Joergensen, R. G. and M. Raubuch. 2002. Adenylate energy charge of a glucose-treated soil without adding a nitrogen source. Soil Biology and Biochemistry, 34: 1317-1324.

Joergensen, R. G., Anderson, T.H., Wolters, T. 1995. Carbon and nitrogen relationships in the microbial biomass of soils in beech (*Fagus sylvatica*) forests. Biology and Fertility of Soils, 19: 141-147.

Johnson, L. F. and Curl, E. A. 1972. Methods for the Research on Ecology of Soil Borne Plant Pathogens, Burgess Publishing Co., Minneapolis, Minnesota, USA.

Jordan, C.F. and Herrera, R. 1981. Tropical rain forests: are nutrients are really critical. Nature, 117:167-180.

Joslin, J.D. and Henderson, G.S. 1987. Organic matter and nutrients associated with fine root turnover in a white oak stand. Forest Science, 33:330-346.

Khiewtam, R.S. and Ramakrishnan, P.S. 1993. Litter and fine root dynamics of a relict sacred groove forest at Cherrapunji in northeast India. Forest Ecology and Management, 60:327-344.

Klinge, H. 1973. Root mass estimation in lowland tropical rainforests of Central Amazonia, Barzil. I. Fine root masses of pale yellow Lastosol and a giant Podzol. Tropical Ecology, 14:29-38.

Knops, J..M..H., Bradley, K. L., Wedin, D. A. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. Ecological Letters, 5:454–466.

Kurz, W.A. 1989. Net primary production, production allocation, and foliage efficiency in second growth Douglas-fir stands with differing site quality. Ph. D Thesis, University of British Columbia, Faculty of Forestry, Vancouver, BC, 224pp.

Kurz, W.A. and Kimmins, J.P. 1987. Analysis of error in methods used to determine fine root production in forests ecosystems: a simulation approach. Canadian Journal of Forest Research, 17:909-912.

Lal, R 1989. Soil degradation and conservation of tropical rain forest. In: Botkin, B.D., Caswell, M.F., Estes, J.E., Orio, A. A. (Eds.). Changing the Global Environment, Academic Press. pp. 135-153.

Lal, R. 1987. Tropical Ecology and Physical Edaphology, Wiley, New York.

Lee, H.S., Davies, S.J., LaFrankia, J.V., Tan, S., Yamakura, K., Itoh, A., Ohkubo, T., Ashton, P.S. 2002. Floristic and structural diversity of mixed Diptreocarp forest in Lambiar Hills National Park, Sarawak, Malaysia, Journal of Tropical Forest Science, 14:379-400.

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

Leiros, M.C., Trasar-Cepeda, C., Seoane, S., Gil-Sotres, F. 2000. Biochemical properties of acid soils under climax vegetation (Atlantic Oakwood) in an area of the European temperate-humid zone (Galicia, NW Spain): general parameters. Soil Biology and Biochemistry, 32:733-745.

Lugo, A.E. and Scatena, F.M. 1995. Ecosystem level properties of the Luquillo Experimental Forests with emphasis on the tabonuco forest. In: Lugo, A.E. and Lowe, C. (Eds.). Tropical forests, management and ecology. Springer-Verlag, New York, pp. 59-108.

Luizao, R. C., Bonde, C. T. A., Rosswall, T. 1992. Seasonal variation of soil microbial biomass–the effect of clear felling in a tropical rain forest and establishment of pasture in the Central Amazon. Soil Biology and Biochemistry, 24:805-813.

Lynch, J.M. and Panting, L.M. 1980. Cultivation and soil biomass. Soil Biology and Biochemistry, 12:29-33.

Maithani, K., Arunachalam, A., Tripathi, R. S., Pandey, H. N. 1998. Nitrogen mineralization as Influenced by climate, soil and vegetation in a subtropical humid forest in northeast India. Forest Ecology and Management, 109:91-101.

Maithani, K., Tripathi, R. S., Arunachalam,A., Pandey,H. N. 1996. Seasonal dynamics of microbial biomass C, N and P during regrowth of a disturbed subtropical humid forest in northeast India. Applied Soil Ecology, 4:31-37.

Makkonen, K. and Helmisaari, H.S. 1998. Seasonal and yearly variations of fine root biomass and necromass in a scot pine (*Pinus sylvestris* L.) stand. Forest Ecology and Management, 102:283-290.

Martikainen, P. J. and Palojarvi, A. 1990. Evaluation of the fumigation-extraction method for determination of microbial C and N in a range of forest soils. Soil Biology and Biochemistry, 27:797-802.

Maycock, C.R. and Congdon, R.A. 2000. Fine root biomass and soil N and P in North Queesland rainforests. Biotropica, 32:185-190.

McClaugherty, C.A., Aber, J.D., Melillo, J.M. 1982. The roles of fine roots in organic matter and nitrogen budgets of forest ecosystem. Ecology, 63:1481-1490.

McGrath, D.A., Duryea, M.L., Cropper, W.P. 2001. Soil phosphorus availability and fine root proliferation in Amazonian agro-forests 6 years following forest conversion. Agriculture, Ecosystems and Environment, 83:271-284.

Meentemeyer, V. 1978. Macro-climate and lignin control of decomposition rates. Ecology, 59: 465-472.

Meier, C.E., Grier, C.C., Cole, D.W. 1985. Below and above ground N and P use by *Abies amabilis* stands. Ecology, 66:1928-1942.

Miller, H.G. 1984. Dynamics of nutrients cycling in plantations ecosystems. In: Bowen, G.D and Nambiar, E.K.S. (Eds.). Nutrition of Plantation Forestry. Academic Press, Toronto.

Mishra, B.K. and Ramakrishnan, P.S. 1983. Slush and burn agriculture at higher elevations in north eastern India. I. Sediment, water and nutrient losses. Agriculture Ecosystem and Environment, 9: 69-82.

Mooney, H.A., Vitousek, P.M., Matson, P.A. 1987. Exchange of materials between terrestrial ecosystems and atmosphere. Science, 238:926-932.

Mordelet, P. Cook, G., Abbadie, L. Grably, M., Mariotti, A. 1996. Natural N-15 abundance of vegetation and soil in the Kapalga savanna, Australia. Australian Journal of Ecology, 21:336-340.

Mroz, G.D., Jurgensen, M.F., Fredrick, D.J. 1986. Soil nutrient changes following whole tree harvesting on tree northern hardwood sites. Soil Science Society of America Journal 49:1552-1557.

Nadelhoffer, K.J., Aber, J.D., Melillo, J.M. 1984. Seasonal pattern of ammonium and nitrate uptake in nine temperate forest ecosystems. Plant and Soil, 80:321-335.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Laundre, J.A. 1992. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology, 72:242-253.

Nadelhoffer, K.J. and Raich, J.W. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology, 73:1139-1147.

Nambiar, E.K.S. and Fife, D.F. 1991. Nutrient retranslocation in temperate conifers. Tree Physiology, 9:913-918.

Norby, R.J. and Jackson, R.B. 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytologist, 147:3-12.

Oehl, F., Frossard, E., Fliessbach, A., Dubois, D., Oberson, A. 2004. Basal organic phosphorus mineralization in soil under different farming systems. Soil Biology and Biochemistry, 36:667-675.

Olson, J.A. 1963. Energy storage and the balance of producers and decomposer in ecological system. Ecology, 44:322-331.

Orchard, V. and Cook, F.J. 1983. Relationships between soil respiration and soil moisture. Soil Biology and Biochemistry, 15:447-453.

Pandey, A.N. and Singh, J.S. 1985. Mechanisms of ecosystem recovery: a case study from Kumaun Himalaya. Journal of Reclamation and Revegetation Research, 3:271-292.

Patra, D.D., Brookes, P.C., Coleman, K., Jenkinson, D.S. 1990. Seasonal changes of soil microbial biomass in an arable and grassland soil which have been under uniform management for many years. Soil Biology and Biochemistry, 22:739-742.

Paul, E.A. and Voroney, R.P. 1984. Nutrient and energy flows through soil microbial biomass. In: Ellwood, D.C. *et.*al (Eds.). Contemporary Microbial Ecology, Academic Press, London, pp. 216-237.

Paterson, E. 2003. Importance of rhizodeposition in the coupling of plant and microbial productivity. European Journal of soil Science 54: 741-750.

Perez, C.A., Hedin, L.O., Armesto, J.J. 1998. Nitrogen mineralization in two unpolluted old growth forests of contrasting biodiversity and dynamics. Ecosystem, 1:361-373.

Persson, H. 1980. Spatial distribution of fine root growth, mortality and decomposition in a young Scots pine stand in central Sweden. Oikos, 34:77-87.

Persson, H. 1982. Changes in the tree and dwarf shrubs fine roots after clear cutting in a mature Scots pine stand. Swedish Coniferous Forest Project. Technical Report, 31.

Phillips E.A. 1959. Methods of Vegetation Study. Henry Holt & Company, New York.

Pickett, S.T and White, P.S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, London.

Piper, C. S. 1944. Soil and Plant Analysis, John Wiley and Sons, New York, USA.

Powell, S.W. and Day, Jr. F.P. 1991. Root production in four communities in the Great Dismal Swamp. American Journal of Botany, 78:288-297.

Powlson, D. S., Brookes, P. C., Christensen, B. T. 1987. Measurement of microbial biomass provides an early indication of changes in total soil organic matter due to straw incorporation. Soil Biology and Biochemistry, 19:159-164.

Powlson, D.S. and Jenkinson, D.S. 1981. A comparison of the organic matter biomass, adenosine triphosphate and minerazable nitrogen contents of ploughed and direct drilled soils. Journal of Agricultural Science, 97:713-721.

Pregitzer, K.S., Hendrick, R.L., Fogel, R. 1993. The demography of fine roots in response to patches of water and nitrogen. New Phytologist, 125:575-580.

Prescott, C., Taylor, B.R., Parsons, W.F.J., Dural, D.M., Parkinson, D. 1993. Nutrient release from decomposing litter in Rocky Mountain coniferous forest: influence of nutrient availability. Canadian Journal of Forest Research, 23:1576-1586.

Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. Tree Physiology, 22:1193-1200.

Priha, O. 1999. Microbial activities in soils under Scots pine, Norway spruce and silver birch. Finnish Forest Research Institute, Research Papers, 731, pp.50.

Priha, O., Grayston, S.J., Hiukka, R., Pennanen, T., Smolander, A. 2001. Microbial community structure and characteristics of the organic matter in soil sunder *Pinus sylvestris*, *Picea abies* and *Betulapendula* at two forest sites. Biology and Fertility of Soils, 33:17-24.

Rahman, F. 2002. Working Plan for Dibrugarh Forest Division, Assam.

Raich, J.W. and Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70, 1346-1354.

Ramakrishnan, P.S. and Singh, J.S. 1983. Distribution of fine roots in a subtropical humid forest of northeast India. Tropical Plant Science Research, 1:163-165.

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

Reich, P.B., Grigal, D.F., Aber, J.D., Gower, S.T. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology, 78:335-347.

Reiners, W.A. and Reiners , N.M. 1970. Energy and nutrient dynamics of forest floor of three Minnesota forest. Journal of Ecology, 58:497-519.

Reiners, W.A.1980. Nitrogen cycling in relation to ecosystem succession. In: Clarke, F.E. and Rosswal, T. (Eds.). Terrestrial Nitrogen Cycles: Processes Ecosystem Strategies and Management Impacts. Ecological Bulletin, Stockholm, 33:507-528.

Renteria-Rodriguez, L. 1997. Biomasa y alamacenes de carbono redcal en tres comunidades vegetales en la Costa de Jalisco. B.Sc. Thesis, Facultad de Ciencias,Universitdad Nacional Autonoma de Mexico. Mexico, D.F.

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

Rochow, J.J. 1974. Litterfall relations in a Missouri Forest. Oikos, 25:80-85.

Rose, S.L. 1988. Above and belowground community development in a marine sand dune ecosystem. Plant and Soil, 109:215-226.

Ross, D.J., Tate, K.R., Cairna, A., Meyrick, K.F. 1981. Fluctuations in microbial biomass indices at different sampling times in soils from tussock grasslands. Soil Biology and Biochemistry, 13:109-114.

Roy, S. and Singh, J.S. 1994. Consequences of habitat heterogeneity for availability of nutrients in a dry tropical forest. Journal of Ecology, 82:503-509.

Salamanca, E. F., Raubuch, M., Joergensen, R.G. 2002. Relationships between soil microbial indices in secondary tropical forest soils. Applied Soil Ecology, 21:211-219.

Sanchez, P.A., Villachica, J.H., Bandy, D.E. 1983. Soil fertility dynamics after clearing of a tropical rainforest in Peru. Soil Science Society of America Journal, 47:1171-1178.

Sanford, Jr. R.L. 1990. Fine root biomass under light gap openings in an Amazon rainforest. Oecologia, 83:541-545.

Santantonio, D. and Hermonn, R.K. 1985. Standing crop, production and turnover of fine roots on dry, moderate and wet sites of mature Douglas-fir in western Oregon. Annual Science Forest, 42:113-142.

Sarathchandra, S. U., Perrott, K. W., Upsdell, M. P. 1984. Microbiological and biochemical characteristics of a range of New Zealand soils under established pastures. Soil Biology and Biochemistry 16:177-183.

Sarathchandra, S.U., Perrott, K.W., Littler, R.A. 1989. Soil microbial biomass: influence of simulated temperature changes on size, activity and nutrient content. Soil Biology and Biochemistry, 21:987-993.

Schimel, J. 1995. Ecosystem consequences of microbial diversity and community structure. Ecological Studies. Springer-Verlag, Berlin.

Schlesinger, W.H. 1997. An analysis of global change. Biogeochemistry, Academic Press, San Diego, US.

Schmidt, I. K., Michelsen, A., Jonasson, S. 1997. Effects of labile soil carbon on nutrient partitioning between an arctic graminoid and microbes. Oecologia, 112: 557-565.

Schnitzer, M. 1991. Soil organic matter-the next 75 years. Soil Science, 151:41-58.

Schnurer, J., Clarholm, M., Rosswall, T. 1985. Microbial biomass and activity in an agricultural soil with different organic matter contents. Soil Biology and Biochemistry, 17:611-618.

Schnurer, J., Clarholm, M., Rosswall, T. 1986. Fungi, bacteria and protozoa in soil from four arable cropping systems. Biology and Fertility of Soils, 2:119-126.

Schoenholtz, S.H., VanMiegroet, H., Burger, J.A. 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. Forest Ecology and Management, 138:335-356.

Scholes, R.J., Dalal, R., Singer, S. 1994. Soil physics and fertility: The effects of water, temperature and texture. In: Woomer, P.L and Swift, M.J. (Eds). The Biological Management of Tropical soil Fertility.

Shannon, C.E. and Wiener, W. 1963. The Mathematical Theory of Communication. University of Illinois press, Urbana, III, USA pp. 177.

Shen, S.M., Pruden, G. Jenkinson, D.S. 1984. Mineralization and immobilization of nitrogen in fumigated soil and the measurement of microbial biomass N. Soil Biology and Biochemistry, 16:437-444.

Sikora, L.J., Yarkovchenko, V., Kaufman, D.D. 1994. Comparison of the rehydration method for biomass determination to fumigation-incubation and substrate induced respiration method. Soil Biology and Biochemistry, 26:1443-1445.

Silver, W.L. and Miya, R.K. 2001. Global pattern in root decomposition: comparisons of climate and litter quality effects. Oecologia, 129:407-419.

Silver, W.L. and Vogt, K.A. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. Journal of Ecology, 81:729-738.

Singh, K P. and Singh, R P. 1981 Seasonal variation and biomass and energy of small roots in tropical dry deciduous forest. Varanasi. India. Oikos, 37: 88-92.

Sims, P.L. and Singh, J.S. 1978. The structure and function of ten Western American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. Journal of Ecology, 66:573-597.

Singh, J. S., Ragubanshi, A. S., Singh, R. S., Srivastava, S. C. 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. Nature, London, 338:499-500.

Singh, J.S. and Gupta, S.R. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. The Botanical Review, 43:449-528.

Singh, J.S., Lauenroth, W.K., Hunt, H.W., Swift, D.M. 1984. Bias and random errors in estimators of net root production: a simulation approach. Ecology, 65:1760-1764.

Singh, K.P. and Shekar, C. 1989. Weight loss in relation to environmental factors during decomposition of maize and wheat roots in a seasonal dry tropical region. Soil Biology and Biochemistry, 21:73-80.

Singh, L. and Singh, J.S. 1993. Importance of short leaved components of a dry tropical forest for biomass production and nutrient cycling. Journal of Vegetational Science, 4:681-686.

Singh, R. S., Srivastava, S. C., Ragubanshi, A. S., Singh, J. S., Singh, S. P. 1991. Microbial C, N and P in dry tropical savanna: Effects of burning and grazing. Journal of Applied Ecology, 28:869-878.

Smiet, A.C., 1992. Forest ecology on Java: human impact and vegetation of montane forest. Journal of Tropical Ecology, 8:129–152.

Smith, J.L and Paul, E.A. 1990. The significance of soil microbial biomass estimations. In: Bollag, J.M., Stotzky, G. (Ed.). Soil Biochemistry, Marcel Dekker, New York. pp. 357-376.

Spaans, E.J.A., Baltissen, G.A.M., Bouma, M.R., Lansu, A. L. E., Schoonderbeek, D., Wielemaker, W.G. 1989. Changes in physical properties of young and old volcanic surface soils in Costa Rica after clearing of tropical rainforest. Hydrological Process, 3:383-392.

Srivastava, S. C. 1992. Influence of soil properties on microbial C, N and P in dry tropical ecosystems. . Biology and Fertility of Soil, 13:176-180.

Srivastava, S. C. and Singh, J. S. 1988. Carbon and phosphorus in the soil biomass of some tropical soils of India. Soil Biology and Biochemistry, 20:743-747.

Srivastava, S.C. and Singh, J.S. 1989. Effect on cultivation of microbial biomass C and N of dry tropical forest soil. Biology and Fertility of Soils, 8:343-348.

Srivastava, S.C. and Singh, J.S. 1991. Microbial C, N and P in dry tropical forest soils: effects of alternate land-uses and nutrient flux. Soil Biology and Biochemistry, 23:117-124.

Standford, G and Smith, S.J. 1972. Nitrogen mineralization potentials of soils. Soil Science Society of America Proceedings, 36:465-472.

Standford, G., Frere, M.H., Schwaninger, D.H. 1973. Temperature coefficient of soil nitrogen mineralization. Soil Science, 115:321-323.

Stark, J.M and Hart, S.C. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. Nature, 385:61-64.

Stark, N. and Jordan, C.F. 1977. Nutrient retention by the root mat of an Amazonian rainforest. Ecology, 58:434-437.

Sundarapandian, S.M. and Swamy, P.S. 1996. Influence of herbaceous species composition on fine roots biomass production in disturbed and undisturbed deciduous forests of Western Ghats in India. Acta Oecologica, 17:163-176.

Sundarpandian, S. and Swamy, P. S. 1998. Variations in fine root biomass and net primary productivity due to conversion of tropical forests into plantation crops and agroecosystems. In: James E. Box, Jr (Eds.). Root Demographics and Their Efficiencies in Sustainable Agriculture, Grassland and Forest Ecosystems. pp. 369-382.

Swift, M.J., Heal, O.W., Anderson, J.M. 1979. Decomposition in terrestrial ecosystems, Vol. 5. University of California Press, England.

Szott, L.T. and Palm, C.A. 1996. Nutrient stocks in managed and natural humid tropical fallows. Plant and Soil, 186:293-309.

Theng, B. K., Tate, G. K., Sollins, R. P. 1989. Constituents of organic matter in temperate and tropical soils. In: Coleman, D.C., Oades J.M., Uehara, G. (Eds.). Dynamics of Soil Organic Matter in Tropical Ecosystem. University of Hawaii Press, Honolulu. pp. 5-32.

Theodore, C. and Bowen, G.D. 1983. Effect of temperature, moisture and litter on nitrogen mineralization in *Pinus radiata* forest soil. Australian Journal of Forest Research, 13:113-119.

Tierney, G.L. and Fahey, T.J. 2002. Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron method. Canadian Journal for Forest Research, 32:1692-1697.

Tilman, D. 2000. Causes, consequences and ethics of biodiversity. Nature, 405:208-211.

Turner, C.L., Blair, J.M., Schattz, R..J., Neel, J.C. 1997. Soil N and plant responses to fire, topography and supplemental N in tall grass prairie. Ecology, 78:1832-1843.

Upadhyaya, K., Arunachalam, A., Arunachalam, K. 2004. Effect of bamboo foliage on soil respiration, microbial biomass and N mineralization. Journal of Bamboo and Rattan, 3:169-183.

Vance, E. D., Brookes, P. C., Jenkinson, D. S. 1987. An extraction method for measuring soil microbial biomass C. Soil Biology and Biochemistry, 19:703-707.

Verchott, L.V., Hlomes, Z., Mulon, L., Groffman, P.M., Lovett, G.M. 2001. Gross vs. net rates of N mineralization and nitrification as indicators of functional differences between forest types. Soil Biology and Biochemistry, 33:1889-1901.

Vishalakshi, N. 1994. Fine root dynamics in two tropical dry evergreen forests in southern India. Journal of Bioscience, 19:103-116.

Vitousek, P.M. 1981. Clear cutting and nitrogen cycling. In: Clark, F.E. and Rosswal, T.H. (Eds.). Nitrogen Cycling In Terrestrial Ecosystem: Processes, Ecosystem Strategies and Management Implications. Ecological Bulletin 33. Swedish Natural Science Research Council. Stockholm, Sweden.

Vitousek, P.M. and Farrington, H. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry, 37:63-75.

Vitousek, P.M. and Matson, P.A. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology, 66:1360-1376.

Vitousek, P.M., Turner, D.R., Parton, W.J., Sanford, R.L. 1994. Litter decomposition on the Muna Loa environment matrix. Hawaii: Patterns, mechanisms and models. Ecology, 75:418-429.

Vogt, K.A., Grier, C. C, Gower, S. T., Sprugel, D.G., Vogt, D.J. 1986.Overestimation of net root production: a real or imaginary problem? Ecology, 67:577-579.

Vogt, K.A., Grier, C.C., Meier, C.E., Edmonds, R.L. 1982. Mycorrhaizal role in a primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. Ecology, 63:370-380.

Vogt, K.A., Grier, G.C., Meier, C., Keyes, M.R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root input. Ecological Monographs, 53:139-157.

Vogt, K.A., Vogt, D.J., Bloomfield, J. 1991. Input of organic matter to the soil by tree roots. In: McMichael, B.L., Persson, H., (Eds.). Plant Roots and Their Environment Proceeding ISSR Symposium on Development in Agricultural and Managed Forest Ecology, Uppasala, Swden, Elsevier-Amsterdam. pp. 171-190.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J. Asbjoransen, H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil, 187:159-219.

von Lutzow, M., Zelles, L. Scheunert, I., Ottow, J.C.G. 1992. Seasonal effect of liming, irrigation and acid precipitation on microbial biomass N in a spruce (*Picea abies* L.) forest soil. Biology and Fertility of Soils, 13:130-134.

Voroney, R.P. and Paul, E.A. 1984. Determination of k_C and k_N in situ for calibration of chloroform fumigation method. Soil Biology and Biochemistry, 16:9-14.

Waksman, S. A. 1952. Soil Microbiology, John Wiley and Sons, New York, USA.

Walker, T.W. and Syers, J.K. 1976. The faith of phosphorus during pedogenesis. Geoderma, 15:1-19.

Walkey, A. 1947. A critical examination of a rapid method for determining organic carbon in soil-effects of variations in digestion conditions and inorganic soil constituents. Soil Science, 63:251-264.

Walsh, R.P.D. 1996. Drought frequency changes in Sabah and adjacent parts of Borneo since the late nineteenth century and possible implications for rainforest dynamics. Journal of Tropical Ecology, 12:385-407.

Warren, G.P. and Whitehead, D.C. 1988. Available soil N in relation to fractions of soil nitrogen and other soil properties. Plant and Soil, 112:155-165.

Wedin, D.A. and Tilman, D. 1990. Species effect on nitrogen cycling: a test with perennial grasses. Oecologia 84: 433-441.

Wells, C.E. and Eissenstat, D.M. 2001. Marked differences in survivorships among apple roots of different diameters. Ecology, 82:882-892.

Wells, C.G. and Joergensen, J. 1979. Effects of intensive harvesting on nutrient supply and sustain productivity. In: Leaf, A.L (Eds.). Impact of intensive harvesting on forest nutrients cycling. Syracuse University, Syracuse, New York, USA. pp. 212-230.

Wetzel, R.G. and Likens, G.E. 1979. Limnological Analysis. Saunders, Philadelphia.

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

Whitehead, D.C., Bristow, A.W., Lockyer, D.R. 1990. Organic matter and nitrogen in the unharvested fractions of grass swards in relation to the potential for nitrate leaching after ploughing. Plant and Soil, 123:39-49.

Whitmore, T.C. 1998. An Introduction to Tropical Rainforests, Claredon Press, Oxford.

Zak, D.R., Tilaman, D., Parmenter, R., Rice, C.W., Fisher, F.M., Vose, J., Milchunas, D., Martin, W. 1994. Plant production and soil microorganisms in late-successional ecosystems: a conditional-scale study. Ecology, 75:2333-2347.

Zaman, M. and Chang, S.X. 2004. Substrate type, temperature, and moisture content affects gross and net N mineralization and nitrification rates in agroforestry systems. Biology and Fertility of Soils, 39:269-279.

Zaman, M., Sakamoto, K., Goto, S., Hayashi, H., Inubushi, K. 2002. Effects of sewage sludge compost and chemical fertilizer application on microbial biomass and N mineralization. Soil Science and Plant Nutrition, 48:195-201

Zar, J. H. 1974. Biostatistical Analysis, 2nd Edition, Prentice Hall, Englewood Cliffs, New Jersey.