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Fine root dynamics in undisturbed and disturbed stands of a tropical wet evergreen forest in northeast India

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Abstract: Biomass, production and turnover of fine roots were estimated in undisturbed and disturbed stands of a tropical wet evergreen forest and were shown to differ significantly ($P < 0.001$) between the stands. In the highly disturbed stand, more than 90 % of the fine root biomass was recorded in the surface soil layer, whereas in the moderately disturbed and undisturbed stands the proportion averaged 67 %. In the undisturbed stand, higher concentrations of fine roots in the surface soil layer were associated with higher nutrient concentrations and moisture retention in the undisturbed stand. Root turnover also decreased with increasing soil depth, root size and intensity of stand disturbance. In the undisturbed, moderately disturbed and highly disturbed stands the annual fine-root turnover was 3181, 1701 and 822 kg ha^{-1} yr^{-1}, respectively. The study revealed that growth and accumulation of fine roots varied with species composition, tree density and basal area. In this region, the contribution of fine roots in the build-up of soil organic matter and nutrient enrichment may be important for the reclamation of these degraded tropical wet evergreen forests.

Resumen: Se hicieron estimaciones de la biomasa, la producción y el recambio de raíces finas en rodales con y sin disturbio en un bosque tropical húmedo perennifolio y estas variables difirieron significativamente ($P < 0.001$) entre los rodales. En el rodal fuertemente perturbado más de 90 % de la biomasa de raíces finas fue registrada en la capa superficial de suelo, mientras que en los rodales con disturbio moderado o sin disturbio la proporción promedio fue de 67 %. En el rodal no perturbado, las concentraciones más altas de raíces de finas en la capa superficial del suelo estuvieron asociadas con concentraciones de nutrientes más altas y una mayor retención de nutrientes en el rodal no perturbado. El recambio de raíces también disminuyó conforme aumentaron la profundidad del suelo, el tamaño de las raíces y la intensidad de perturbación del rodal. En los rodales sin disturbio y con disturbio moderado y alto, el recambio anual de raíces finas fue de 3181, 1701 y 822 kg ha^{-1} año^{-1}, respectivamente. Este estudio reveló que el crecimiento y la acumulación de raíces finas varió con la composición de especies, la densidad de árboles y el área basal. En esta región, la contribución de las raíces finas a la acumulación de materia orgánica del suelo y al enriquecimiento de nutrientes puede ser importante para la recuperación de estos bosques tropicales húmedos perennifolios degradados.

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Resumo: A biomassa, a produção e o volume das raízes finas foram estimadas em povoamentos não disturbados e disturbados numa floresta tropical sempreverdehúmida emostraram-se significativamente diferentes ($P < 0,001$) entre as parcelas. Naparcela maisfortemente perturbada, mais de 90 % da biomassa das raízes finas foi registada na camada superficial do solo, enquantonaquelas moderadamente disturbadas e não perturbadas a proporção média foi de 67 %. Naparcela não disturbada, as maiores concentrações de raízes finas na camada superficial do solo foram associadas com a maior concentração de nutrientes e à retenção de humidade. O volume de raízes também diminuiu com o aumento da profundidade do solo, com o comprimento da raiz e da intensidade de perturbação da parcela. Nas parcelas não disturbadas, moderadamente perturbadas e fortemente perturbadas,a renovaçãoanual de raízes finas foi de 3181, 1701 e 822 kg ha ano^{-1}, respectivamente. O estudo revelou que o crescimento ea acumulação de raízes finas variaram com a composição das espécies, densidade de árvores e a área basal. Nesta região, a contribuição das raízes finas na acumulação de matéria orgânica do solo e enriquecimento de nutrientes pode ser importante para a recuperação destas florestas tropicais húmidas sempreverdes.

Key words: Biomass, fine roots, disturbance, production, tropical wet evergreen forest, turnover.

Introduction

Roots represent about 12 % of the total plant biomass in tropical evergreen lowland forests (McClaugherty *et al.* 1982). Though the importance of fine-root dynamics in forest biogeochemical cycling is widely recognized (Norby & Jackson 2000), understanding of factors controlling the distribution, production and mortality of fine roots still remains poor (Vogt *et al.* 1996). Many tropical rainforests develop extensive root mats in the nutrient-deficient mineral soil in which they typically occur. Such dense superficial root systems aid in nutrient conservation through the direct transfer of nutrients from decomposing litter to roots (Ramakrishnan & Singh 1983; Stark & Jordan 1977). Knowledge of changes in root biomass and its distribution in the soil profile as a result of changes in land-use cover would improve 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 & Scatena 1995). Few studies have addressed the effects of disturbance on fine-root dynamics in tropical wet evergreen forests of northeast India. The objective of the present study was to evaluate and understand the biomass and production of fine roots in these forests. We tested the hypothesis of Wilczynski & Pickett (1993) that increasing canopy gaps after disturbance would be associated with gaps in the root system, leading to reduced total fine-root biomass in the disturbed forests.

Study sites

The study was carried in and just outside the Jeypore Reserve Forest of the Dibrugarh Forest Division of Assam (latitude 27° 05´ to 27° 28´ N; longitude 95° 20´ to 95° 38´ E; altitude 220 m a.s.l.) on the southern bank of the river Brahmaputra. An undisturbed stand within the Jeypore Reserve Forest, and a disturbed area just outside it, were selected for detailed study. The two areas were about 1 km apart. The disturbed area was divided into two stands on the basis of the disturbance index. This was defined (Rao *et al.* 1990) as the ratio of the basal area of cut stumps to the total stand basal area, including the cut stumps. The two disturbed stands for study were categorized as moderately disturbed (MD: disturbance index 54 %) and highly disturbed (HD: disturbance index 88 %). The moderately-disturbed stand (*ca* 2 ha) had been selectively logged, and was dominated by *Mesua ferrea* L., *Terminalia myriocarpa* Van Heurek & Muell., *Alangium begonifolium* Baillon, *Tetrameles nudiflora* R. Br., *Duabanga grandiflora* (Roxb. ex DC.) Walp. and *Sapium baccatum* Roxb.[1]. The

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[1] Here, and in other similar lists, the species are in decreasing order of dominance. Nomenclature follows Hooker (1872-1897) and Kanjilal *et al.* (1934-1940).

highly disturbed stand (*ca.* 2.5 ha) had been clear-felled 10 - 15 years ago for settled cultivation practices. Rice, maize, mustard and chillies were grown occasionally. A few individuals of *Biscofia javanica* Blume*., Dillenia indica* L.*, Duabanga grandiflora* (Roxb. ex DC.) Walp.*, Bombax ceiba* L. and *Albizzia* sp. were present in this stand. The undisturbed stand (*ca.* 2 ha) was in the core area of the Jeypore Reserve Forest. Mature large [> 90 cm dbh (diameter at breast height i.e., 1.37 m)] trees of *Dipterocarpus macrocarpus* Vesq.*, Shorea assamica* Dyer., *Mesua ferrea* L.*, Tetrameles nudiflora* R. Br.*, Castanopsis indica* A. DC. and *Vatica lanceaefolia* Blume. were abundant in this stand.

The average annual rainfall in the area ranges between 2500 and 3600 mm, 70 % of this total being received between July and September. The mean minimum temperature of the coldest month and the mean maximum of the hottest month are 7° C and 36° C respectively. The year has four distinct seasons viz., a cold and dry winter (December-February), a warm pre-monsoon period (March-May), a humid monsoon period (June - September) and a cool post-monsoon autumn (October - November). The soil is a brown, loamy, lateritic ultisol derived from pegmatite rocks. Although the soils in the three selected stands had developed from the same parent material, they differ. The undisturbed forest has a well-developed soil profile with a distinct litter layer and an organic horizon 5 cm deep. In the disturbed sites, the organic horizon was very thin and less distinct because of the absence of a litter layer. Detailed vegetation analyses conducted as described by Phillips (Phillips 1959) have been summarized in Table 1. In each stand, density, frequency and basal area of the constituent tree species (GBH > 30 cm) were estimated in randomly placed quadrats of different sizes: forty 10 m x 10 m quadrats in the undisturbed stand, twenty 15 m x 15 m quadrats in the moderately disturbed stand, and twenty 25 m x 25 m quadrats in the highly disturbed stand. To determine the density of shrubs and herbs twenty quadrats (5 m x 5 m for shrubs and 1 m x 1 m for herbs) were laid down in each stand. Girth at breast height (1.37 m) of all trees was measured.

Materials and methods

Microclimatic parameters were measured at ten random points in each stand during each of the two years and four seasons of the study. The light intensity was measured close to the ground surface using a digital Lux meter (TES 1332); for air temperature and relative humidity a thermo-hygrometer (EXTECH), for soil temperature a SYMAX soil thermometer, were used. The means for each stand are shown in Table 1.

Soil samples were collected from all three stands during the four seasons viz., winter, spring, rainy and autumn. From each stand, three soil cores (5.5 cm diameter) were collected randomly from a soil depth of 0 - 15 cm. After litter, stones, pebbles and large pieces of plant material were removed, the samples were sieved (2 mm mesh) and used to determine soil physico-chemical properties. Soil texture, water-holding capacity and moisture content were determined as described by Anderson & Ingram (1993). Soil organic carbon (SOC) was determined by dichromate oxidation and titration, and the total Kjeldahl nitrogen (TKN) was estimated following the semi-micro Kjeldahl procedure by acid digestion, distillation and titration (Anderson & Ingram 1993). To determine the phosphorus concentration, the soil sample was digested using a tri-acid mixture (Jackson 1985), followed by a colorimetric test (molybdenum blue method) with ammonium molybdate and stannous chloride (Jackson 1985). 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.

In each of the three stands, root biomass sampling was undertaken at seasonal intervals (winter, spring, rainy and autumn) from winter 2004 to winter 2006, using the soil-core method (Bohm 1979; Vogt *et al.* 1996). Ten randomly located soil-core samples were collected from two depth ranges (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 poly-bags and stored in deep freeze at -20 °C for later analysis.

In each sample, fine roots (< 2 mm diameter) were separated by wet-sieving (Bohm 1979); larger roots were picked out by hand. Live and dead roots were hand-sorted on the basis of colour and texture (Persson 1982). When it was difficult to distinguish live from dead roots, the roots were cut with a razor and examined under magnification for colour and cohesion between cortex and periderm. The diameter of roots was measured by using a vernier caliper, and they were categorized into four diameter classes (viz. < 1 mm, 1 - 2 mm, 2 - 5 mm and 5 - 10 mm) for further analysis.

Cleaned live and dead root samples were oven-dried at 80 °C ± 5 °C for 48 h and weighed to find the dry-matter content. Annual root production, by diameter class and depth, was estimated by sum-

Table 1. Mean annual root mass (0 - 30 cm), vegetation, microclimate and soil (0 - 15 cm) physico-chemical characteristics of disturbed and undisturbed forest stands.

	Forest stands		
Parameters	Undisturbed	Moderately disturbed	Highly disturbed
Annual root mass (kg ha^{-1})	8061 ± 225	5156 ± 186	2286 ± 107
Vegetation			
Density (No. ha^{-1})			
Trees	658	369	41
Shrubs	7500	3740	1160
Herbs	15900	38917	40250
Basal area (m^2 ha^{-1})			
Trees	85.55	20.83	5.02
Shrubs	2.61	0.60	0.37
Herbs	0.27	0.44	0.27
Disturbance index (%)	0	54	88
Microclimate[1]			
Air temperature (°C)	22.8	26.4	25.8
Relative humidity (%)	75.0	67.6	69.1
Light intensity (Lux)	2258	10365	17270
Soil temperature (°C)	20.5	23.7	22.8
Soil properties[2]			
Texture			
Sand (%)	58.3 ± 2.4	66.9 ± 0.8	78.8 ± 2.9
Silt (%)	12.0 ± 0.1	10.5 ± 0.3	7.6 ± 0.1
Clay (%)	29.7 ± 2.0	22.5 ± 1.0	13.6 ± 0.3
Textural class	Sandy clay loam	Sandy loam	Sandy loam
Water holding capacity (%)	60.0 ± 2.0	45.77 ± 6.85	40.02 ± 1.16
Bulk density (g cm^{-3})	0.67 ± 0.008	0.83 ± 0.02	0.88 ± 0.008
Moisture content (%)	30.1 ± 2.4	20.0 ± 1.5	18.5 ± 1.4
pH (1:2.5 w/v H_2O)	5.09 ± 0.06	5.41 ± 0.07	6.12 ± 0.11
SOC (%)	1.52 ± 0.11	0.87 ± 0.03	0.62 ± 0.06
TKN (%)	0.61 ± 0.03	0.32 ± 0.04	0.22 ± 0.03
P (%)	0.09 ± 0.001	0.05 ± 0.005	0.04 ± 0.004

[1] Values are the means of ten sampling points during four seasons in two successive years.

[2] ±S.E. (n = 24); values are the means of triplicate samplings during four seasons in two successive years.

SOC = Soil organic carbon, TKN = Total Kjeldahl Nitrogen, P = Phosphorus.

ming the positive increments in live biomass (increments significant at $P < 0.05$) between successive sampling dates (Fairley & Alexander 1985). Turnover of roots was calculated according to Persson (1980):

$$T = P_s - (b_j - b_i),$$

where, T is turnover, P_s is root production and b_i and b_j are estimates of root biomass at the first (b_i) and last (b_j) sampling. Turnover rate (k) was also calculated using the mathematical model of Reiners & Reiners (1970):

$$k = P/(X_m + P),$$

where, P is the annual root production and X_m the mean annual dry weight.

ANOVA was used to test the significance of differences in root biomass and production with stand type, season and soil depth. Pearson correlation coefficients were calculated to show the relationships of root mass with microclimate and soil physico-chemical properties (Zar 1974).

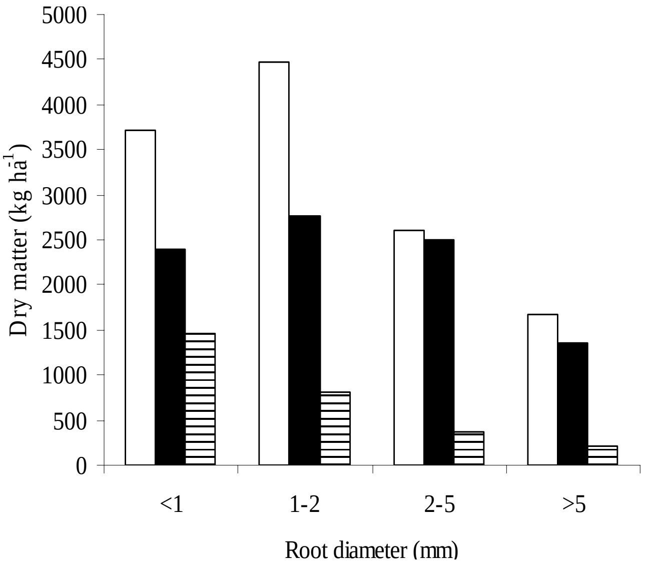

Fig. 1. Variation in root mass (kg ha^{-1}) of four different diameter classes in the undisturbed (□), moderately disturbed (■) and highly disturbed (⊟) stands.

Results

Microclimate, vegetation and soil

In the undisturbed forest stand, air temperature, soil temperature and light intensity were significantly ($P < 0.05$) lower than in the disturbed stands (Table 1). Tree species were distributed in four distinct strata in the undisturbed stand. The emergent layer (height > 25 m) included *Dipterocarpus macrocarpus* Vesq., *Shorea assamica* Dyer, *Tetrameles nudiflora* R. Br., *Ailanthus grandis* Prain., *Sapium baccatum* Roxb., *Cinnamomum glanduliferum* Meisn., *Elaeocarpus ganitrus* Roxb. and *Talauma phellocarpa* King. The canopy layer (18 - 25 m) included *Mesua ferrea* L., *Castanopsis indica* A. DC., *Canarium bengalense* Roxb., *Terminalia chebula* Retz., *Talauma hodgsonii* Hk. f. & Th., *Michelia* sp., *Litsea salicifolia* (Roxb.) Hk.f. and *Alstonia scholaris* (L.) R. Br. The sub-canopy (8 - 18 m) had *Baccaurea sapida* Muell and Arg., *Vatica lanceaefolia* Blume., *Dysoxylum reticulatum* King. and *Diospyros variegata* Kurz. etc., and the ground layer (< 8 m) consisted of species like *Sida acuta* Burm.f., *Urena lobata* L. and *Panicum* sp.. A similar stratification pattern of plant species was also observed in the moderately disturbed stand, but with fewer species; whereas in the highly disturbed stand no stratification was observed. The highly disturbed stand was composed of a few sparsely distributed species like *Alangium chienese* Lour., *Baccaurea sapida* Muell & Arg., *Vatica lanceaefolia* Blume. and *Mesua ferrea* L. Tree density and basal area were lowest in the highly disturbed stand (41 trees ha^{-1}, 5.02 m^2 ha^{-1}) and highest in the undisturbed stand (658 trees ha^{-1}, 85.55 m^2 ha^{-1}). Density of shrubs also decreased with the increase in disturbance intensity.

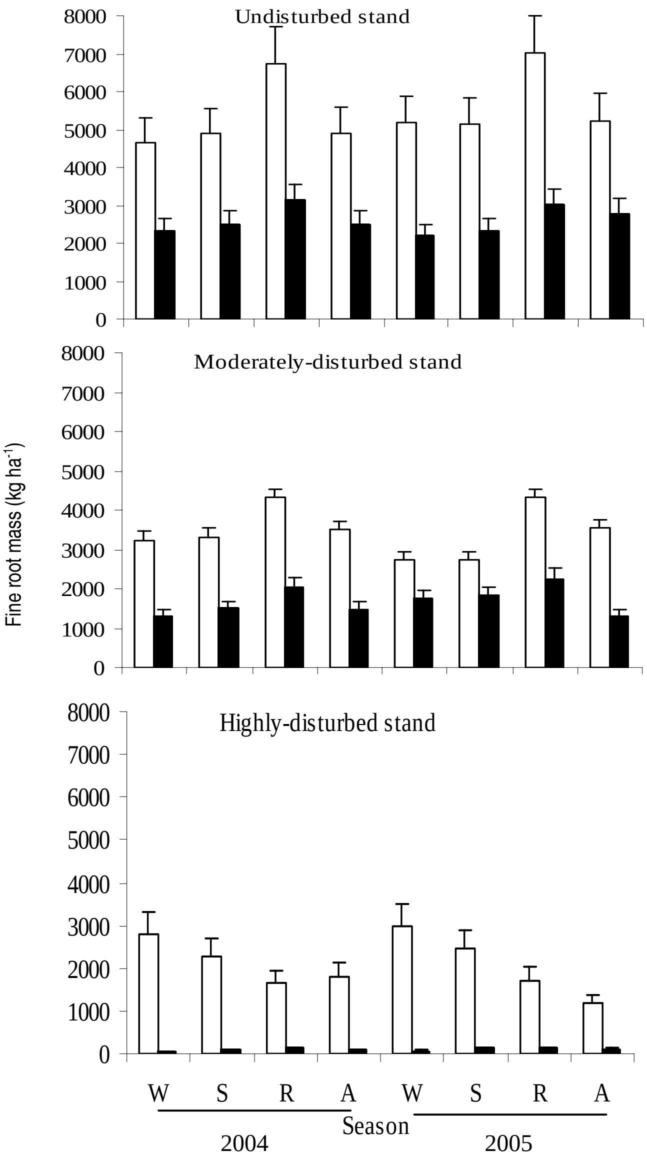

Fig. 2. Distribution of fine roots (< 2 mm) at two soil depths (□ 0 - 15 and ■ 15 - 30 cm) in the three stands. Vertical lines represent standard error (n = 10). W-winter, S-spring, R-rainy, A-autumn. ANOVA test shows significant difference in roots mass ($P < 0.001$, $F = 28.32$) between season, soil depths and stands.

Clay content, water-holding capacity and moisture content were greatest in the undisturbed stand, and declined with the increase in disturbance; the soil was acidic (pH = 5.01 - 6.12) in all

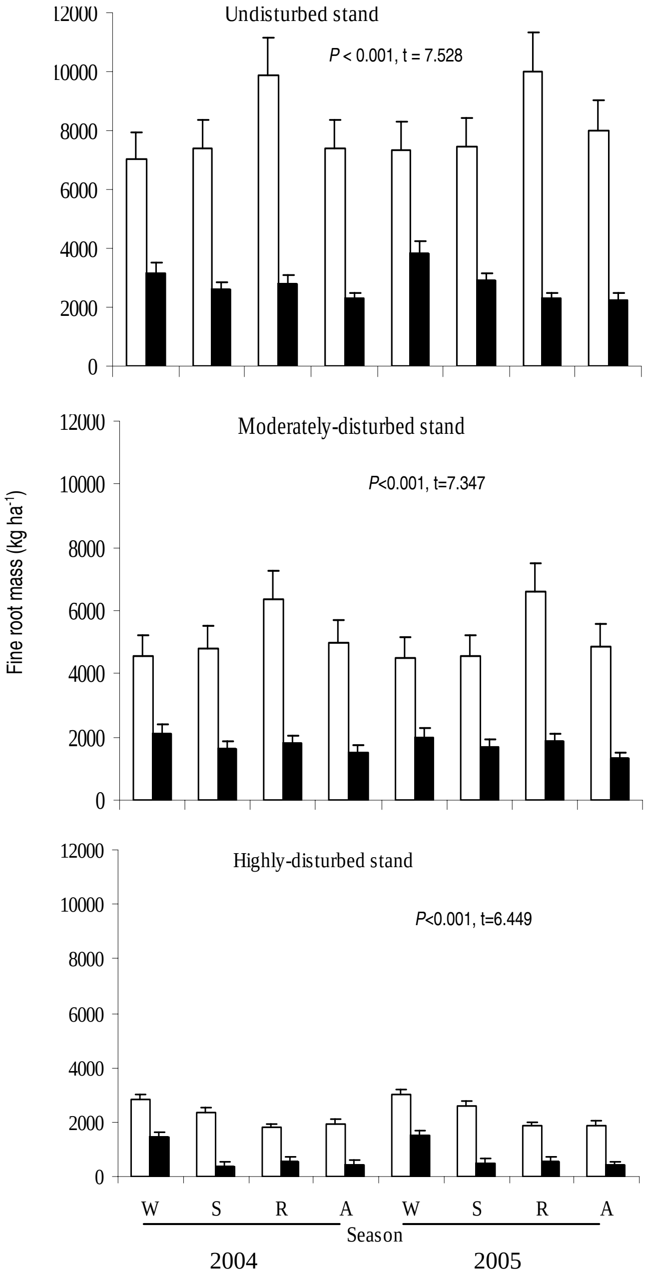

Fig. 3. Seasonal variation in live (□) and dead (■) fine root mass in undisturbed and disturbed stands. Vertical lines represents standard error (n = 10). W-winter, S-spring, R-rainy, A-autumn. Paired t-test showed significant differences in live and dead root mass.

stands. There was a 59 % decline in the concentration of organic carbon in the highly disturbed forest as compared to the undisturbed stand (Table 1). Total Kjeldahl nitrogen and phosphorus concentrations did not differ significantly between moderately disturbed and highly disturbed stands (Table 1).

Temporal and spatial variation in root mass

The biomass of very fine roots (< 1 mm diameter) was significantly ($P < 0.01$) higher in the highly disturbed stand than in the undisturbed and moderately-disturbed stands (Fig. 1). Total fine-root mass (< 2 mm diameter) was highest (8061 kg ha^{-1}) in the undisturbed stand and lowest (2286 kg ha^{-1}) in the highly disturbed stand (Table 1). In the highly-disturbed stand, fine roots represented about 92 % of the total root mass, while in the moderately and highly disturbed stands their proportion declined to about 74 %. In the undisturbed and moderately disturbed stands, root biomass was greater during the rainy season, and lower biomass was recorded during winter. An opposite trend was, however, observed in the highly disturbed stand, where the biomass was higher during winter and lower during the rainy season (Fig. 2). Variations in the mass of fine roots between seasons were significant ($F = 25.36$, $P < 0.05$) in all the three stands. The proportion of live fine roots was significantly higher than that of dead material, which accounted for 13.8 - 33.5 % of the total mass of fine roots. A greater contribution was recorded during winter and lower during spring and the rainy season (Fig. 3).

Vertical distribution of root mass

Most of the fine roots were present in the surface soil layer (0 - 15 cm), in both the undisturbed and the disturbed stands (66.2 % in the undisturbed and 98.4 % in the highly disturbed) (Fig. 2). The subsurface soil layer (15 - 30 cm) had 4.1 - 33.8 % of total fine-root mass. The decrease in fine-root biomass with increasing depth was significant ($F = 27.09$, $P < 0.01$) in all the three stands. In the top 0 - 15 cm soil layer, the greatest root mass (5462 kg ha^{-1}) was recorded in the undisturbed stand and the lowest (2183 kg ha^{-1}) in the highly disturbed stand. Accumulation of fine roots in the surface soil layer increased significantly ($P < 0.001$) from the highly disturbed to the undisturbed stand (Figs. 2 & 3). The proportion of fine roots to the total root mass in the 0 - 15 cm layer declined from 67 % in the highly disturbed stand to 38 % in the moderately disturbed stand and 26 % in the undisturbed stand. The biomass of fine roots in the undisturbed and moderately disturbed stands increased signifi-

Table 2. Annual production (kg ha^{-1} yr^{-1}), turnover (kg ha^{-1} yr^{-1}) and turnover rate (yr^{-1}) of fine roots at two soil depths in the undisturbed and disturbed stands.

Study stands	Soil depth (cm)	Production 2004	Production 2005	Turnover 2004	Turnover 2005	Turnover rate (k) 2004	Turnover rate (k) 2005
UD	0-15	2361	1869	2868	1904	0.47	0.45
	15-30	785	815	630	960	0.33	0.34
MD	0-15	1091	1596	1161	800	0.34	0.36
	15-30	741	850	689	752	0.31	0.32
HD	0-15	1316	1023	591	799	0.26	0.21
	15-30	85	85	102	152	0.13	0.19

UD-Undisturbed, MD-moderately disturbed and HD-highly disturbed stands.

Table 3. Annual production, turnover and turnover rate of different root diameter classes in undisturbed and disturbed stands.

Study site/ Diameter class (mm)	Annual production (kg ha^{-1} yr^{-1}) 2004	Annual production (kg ha^{-1} yr^{-1}) 2005	Turnover (kg ha^{-1} yr^{-1}) 2004	Turnover (kg ha^{-1} yr^{-1}) 2005	Turnover rate (k) 2004	Turnover rate (k) 2005
Undisturbed stand						
< 1	1711	1521	1659	1517	0.39	0.37
1-2	2759	1306	2354	1490	0.39	0.35
2-5	1663	678	1101	730	0.33	0.24
> 5	1012	670	1085	833	0.23	0.24
Moderately-disturbed stand						
<1	1142	1020	1252	1070	0.33	0.30
1-2	689	1146	530	1167	0.26	0.25
2-5	562	512	601	364	0.20	0.23
>5	461	507	562	867	0.18	0.18
Highly-disturbed stand						
<1	703	1023	765	1239	0.30	0.31
1-2	500	392	619	706	0.30	0.31
2-5	296	99	102	66	0.26	0.28
>5	91	57	68	38	0.24	0.20

cantly ($P < 0.01$) at the onset of the rainy season in both the surface and subsurface soil layers. The mass of dead fine roots in the upper soil ranged from 684 kg ha^{-1} in the highly disturbed stand to 1957 kg ha^{-1} in the undisturbed stand, the corresponding figures for the deeper soil being 41 and 1204 kg ha^{-1} (Fig. 3). The mass of fine roots was higher than that recorded for the other root size classes, and the mass of dead roots decreased at both depths after spring, and increased during the dry season in all the stands. No significant differences in dead root mass were observed between the two soil depths studied.

Root production and turnover

Production and turnover of fine roots (1 - 2 mm diameter) were greater in the undisturbed and moderately disturbed stand than in the highly disturbed stand, and ranged between 392 and 2759 kg ha^{-1} yr^{-1} for production, and between 530 and 2354 kg ha^{-1} yr^{-1} for turnover (Table 3). In the moderately disturbed stand, the greatest production and turnover was recorded for very fine roots (< 1 mm diameter). Production and turnover of different size classes varied significantly ($P < 0.001$) between the two years of study. They were greater during 2004 in the undisturbed stand, whereas, in the moderately and highly disturbed stands, they were higher during the second year of study. In general, fine root production was significantly ($P < 0.05$) higher in the undisturbed stand than in the disturbed stands (Table 2).

Fine-root production was greater during the rainy season except in the highly disturbed stand, where the maximum occurred during the dry season. Root production showed significant differences with depth. There were significant interactions among soil depth, stand and root size, indicating that root production in each size class differed with soil depth and stand. The production of fine roots decreased significantly ($P < 0.05$) with increase in soil depth. In the surface soil layer, fine root production ranged between 1316 and 2361 kg ha^{-1} yr^{-1} in the highly disturbed and undisturbed stands respectively.

Fine-root turnover was significantly different between depths over the study period; it was higher in the top soil layer of the undisturbed stand. In the undisturbed and moderately disturbed stands, the fine roots had a greater turnover than the other size classes. On the other hand, in the highly disturbed stand, the very fine roots (< 1 mm) had the greatest turnover (Table 3). In general, the turnover rates of the different size classes of roots decreased as root diameter size increased (Table 3). Whereas turnover time increased with the increase in root size. Fine-root turnover decreased significantly ($P < 0.001$) with the increase in depth and in 2004 ranged from 102 kg ha^{-1} yr^{-1} in the subsurface layer of the highly disturbed stand to 2868 kg ha^{-1} yr^{-1} in the surface soil of the undisturbed stand (Table 2).

Discussion

Significant variations in fine-root biomass in undisturbed and disturbed stands may be attributed to differences in site quality and species composition of the vegetation. The greater fine-root biomass recorded in the undisturbed stand may reflect the higher density and basal area of trees, as well as the higher accumulation of surface litter. The greater fine-root biomass in the undisturbed stand may be related to greater accumulation of soil nutrients, and probably reflects the higher nutrient requirement of the plant's root system, with a large surface area that absorbs nutrients from soil of low bulk density, high soil moisture availability and greater clay content. Lower root mass and production in disturbed stands may be attributed to lower organic matter and nutrients. Small and localized disturbances in tropical forests, such as tree-fall gaps and open canopies, have been shown to be associated with a significant reduction in the biomass of fine roots compared to the undisturbed forest (Arunachalam *et al.* 1996; Silver & Vogt 1993; Sundarpandian & Swamy 1996). Reduction in fine-root biomass in the highly disturbed stand, which had been selectively logged and converted to agricultural land, might also be driven by altered microclimatic and edaphic conditions. Leuschner *et al.* (2006) reported that disturbed forest may contain a biomass of fine roots only 60 % or less of the global average in undisturbed tropical moist forests. Frequent cultivation in the highly disturbed stand may also have contributed to the depletion of soil fertility by losses of soil and nutrients through surface run-off, and this may be a reason for lower mass and production of fine roots in the highly disturbed stand.

The biomass of roots in the top 0 - 15 cm of soil varied among the stands and root-size classes. In the undisturbed stand *ca.* 76 % of fine roots (< 2 mm diameter) were found in the surface soil layer. This high density of fine roots in the top few centimetres of soil is important for the conservation of nutrients within tropical rain forests (Jenik 1978). These surface roots are involved in the uptake of nutrients, either by direct absorption or via mycorrhizal associations. They have access to the highest concentrations of nutrients in the soil at the top of the profile, and to the nutrients returned to the soil in litter fall and through-fall (Maycock & Congdon 2000). Furthermore, the accumulation of litter on the surface soil promotes nutrient availability and thus growth of fine roots in the upper layer of the soil (Cuevas 1995). The vertical distribution of root biomass also varied significantly between the different stands. In particular, the highly disturbed stand had more than 90 % of its fine-root biomass within the uppermost 15 cm of soil, compared with 67 % in undisturbed and moderately disturbed stands. Greenland & Kowal (1960) reported that 86 % of the root biomass in a 40-year-old secondary forest in Ghana occurred in the top soil, while De Castro & Kauffman (1998) found that 71 % of the root biomass in ‘Cerrado denso’ communities of the Brazilian cerrado occurred in the upper soil. The greater proportion of roots near the surface in the highly disturbed stand reflected the greater proportion of herbs in the vegetation. This result was similar to observations in a pasture-land of tropical evergreen forest in Mexico (Jaramillo *et al.*

2003) and a natural grass-dominated tropical ecosystem in Brazil (De Castro & Kauffman 1998).

Seasonal variation in the biomass of fine roots has already been well documented for many tropical and subtropical forests (Arunachalam *et al.* 1996; Silver & Vogt 1993; Sundarpandian & Swamy 1996). Greater root biomass during a rainy season tends to correspond with periods of seasonal growth dynamics, rapid nutrient release, and other environmental factors. Other studies have also demonstrated a large variation in fine-root biomass both within the growing season and from year to year (Persson 1980). Despite the large spatial variations, statistically significant temporal changes have also been reported, suggesting that fine roots grow and senesce rapidly, probably influenced by soil temperature and humidity (Persson 1980; Santantonio & Hermonn 1985).

Annual root production differed significantly between the stands, decreasing with increasing disturbance intensity. This reduction in fine-root production was closely related to a reduction in total basal area, tree height, tree density and canopy cover of the stands. Jones *et al.* (2003) and Hertel *et al.* (2009) have reported similar effects of stand structure on root production. Root production decreased with increase in root diameter, and was maximum in the upper soil horizons (0 - 15 cm). These results support the pattern of root distribution reported by Ford & Dean (1977), who ascribed the high concentration of fine roots in the surface-soil layer of the forests which they studied to higher nutrient concentrations and more moisture retention, resulting from abundant detrital materials on the forest floor and rapid decomposition (Campo *et al.* 1998). The leaf litter forms a shelter for the surface roots, providing a moist microclimate for the development of new roots, and they undergo rapid changes there (Arunachalam *et al.* 1996; Sundarpandian & Swamy 1996).

Root turnover also decreased with increasing depth, root size and disturbance intensity. The annual turnover in the undisturbed stand was similar to the values reported by Persson (1980) in Central Sweden and Usman *et al.* (1999) in evergreen Central Himalayan forest. The turnover rates for the disturbed and undisturbed stands (0.11 - 0.47 year^{-1}) were of the same order as those reported from a wide variety of deciduous forest types (0.19 - 0.64 year^{-1}: Aber *et al.* 1985). Lower turnover in the disturbed stands is in agreement with the contention that plants growing in nutrient-poor environments increase the life span of their roots, thus reducing nutrient loss (Gill & Jackson 2000). The longevity of a root may be inversely related to the availability of resources; root mortality may coincide with depletion in vegetal cover. Growth of roots relatively deficient in nutrients may require metabolic recycling of nutrients internally, leading to the senescence of cortical tissues and perhaps even increase in root turnover. Vogt *et al.* (1996) speculated 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 vary in response to changes in resource availability in the disturbed stands. Fine roots of smaller diameter showed greater turnover rate (0.13 - 0.47 year^{-1}) than coarser roots (0.11 - 0.28 year^{-1}). Essentially similar results have also been reported by Matamala *et al.* (2003), who in their comparisons showed greater turnover by 1 - 2 mm diameter roots than by roots 2 - 5 mm in diameter. Wells & Eissenstat (2001) also found that woody structural roots of large diameter had longer life spans than smaller roots, and these differences appeared to be related to tissue nitrogen content, and rates of root respiration and decomposition.

In conclusion, the fine-root biomass in forest stands differed significantly between seasons and also in relation to tree density and basal area. Fine-root biomass and production were significantly altered by disturbances such as selective logging and clear-felling of trees, as compared to the undisturbed forest stand. These studies also suggest that root turnover increases with increasing nutrient availability and soil organic matter, following the addition of more organic material and better moisture conditions. We conclude that fine-root dynamics plays a key role in nutrient conservation in disturbed stands, and is, therefore, important for the management of these degraded ecosystems, particularly in tropical wet evergreen 'relict' forest in northeast India.

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