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SPATIAL AND TEMPORAL VARIABILITY OF FINE ROOT ABUNDANCE AND GROWTH IN TROPICAL MOIST FORESTS AND AGROFORESTRY SYSTEMS (SULAWESI, INDONESIA)

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Abstract. Selective logging and forest conversion into agroforestry systems are widespread at the margins of tropical moist forests in South-east Asia, typically creating gradients of forest disturbance intensity from the edge to the interior. We studied the effect of increasing forest use on the temporal and spatial variability of fine root mass and fine root production in a sub-montane tropical moist forest in central Sulawesi. We selected four forest types which represent a disturbance gradient from undisturbed forest to selectively logged forest with small or large timber extraction, and to agroforestry plantations under natural shade tree cover. Increasing intensity of forest use led to a significant decrease in fine root biomass and necromass. Even the extraction of only a limited number of small-diameter stems had a significant negative impact on the fine root biomass. Spatial variability of fine root biomass or necromass within the stands did not differ along the disturbance gradient, and neither did the relative seasonal variation in fine root mass. Fine root production was significantly less in the heavily disturbed forest stands than in the undisturbed forest. Fine root biomass and fine root production were strongly correlated with canopy cover and basal area of the stands, whereas soil physical or chemical conditions were of secondary importance. We conclude that mild to moderate disturbances of tropical moist forests have a significant negative effect on total fine root biomass and carbon fluxes associated with root production, whereas spatial and temporal patterns of the fine root system remain largely unaffected. *Accepted 21 August 2007*.

Key words: *canopy cover*, *fine root biomass*, *fine root necromass*, *forest disturbance*, *seasonality*, *sequential coring*.

INTRODUCTION

In many tropical countries, forest destruction and conversion to agricultural land is continuing at high rates. Indonesia has one of the highest rates of tropical forest loss in the world. Nearly half of Indonesia's forests are fragmented by roads or other access routes, or are encroached upon by plantations. Forest clearance by small-holder farmers is a significant cause of deforestation. Many protected areas suffer from illegal logging and agricultural encroachment by the local communities. In the margin zones of most Indonesian national parks and forest reserves, rattan (*Calamus* sp.) extraction, selective logging, and the creation of small-scale crop plantations are common activities (FWI/GFW, 2002). Because the area of disturbed forest increases rapidly, we need a better understanding of the ecological consequences of forest disturbance in the aboveground as well as the belowground system. Research on the structure and functioning of disturbed tropical forests mostly focuses on aboveground aspects, and the rhizosphere and pedosphere are often ignored. Studies that have focussed on belowground effects of forest disturbance in the tropics, have mostly dealt with natural disturbances such as hurricanes (Sanford 1990, Parrota & Lodge 1991, Silver & Vogt 1993, Denslow *et al*. 1998, Ostertag 1998). Only recently has the effect of anthropogenic disturbance on the belowground system of tropical forests been studied (Arunachalam et al 1996, Sundarapandian & Swamy 1996, Yang *et al*. 2004, Upadhaya *et al*. 2005, Leuschner *et al*. 2006). These studies have mainly focused on differences in fine root mass, fine root production, and the depth distribution of roots between undisturbed and heavily disturbed forests or planted systems. The objectives of the present study are (1) to investigate the spatial and temporal variability in fine root abundance and fine root production of a tropical sub-montane forest, and (2) to analyze how this variability is affected by mild to moderate forest-use intensities and by conversion into agroforestry systems. We hypothesized that increasing

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forest disturbance enhances spatial and temporal variation in the fine root system, following changes in canopy structure and tree species composition. Greater heterogeneity of the fine root system is expected to lead to higher spatial variability of water and nutrient fluxes and carbon sequestration. We further assumed that increasing forest disturbance will reduce the stand average of fine root biomass and associated carbon sequestration through fine root production.

METHODS

Study area. The Lore Lindu National Park, with a size of approximately 229 000 ha, comprises one of the largest remaining montane rain forests of Sulawesi. We conducted our study in the surroundings of Toro village (Kulawi valley) in the western margin zone of the Lore Lindu Park (01°30′S, 120°02′E). In the Toro valley, the surrounding forests are owned by the local community, although they are part of the Lore Lindu National Park. The village head negotiated a contract with the National Park authorities under which the surrounding forests are managed as community forests by the villagers. The forest area concerned is mapped and classed into forest-use types that allow different forms of sustainable forest use, including rattan extraction, selective logging of large-diameter or small-diameter stems, and, locally, conversion to agroforestry systems under a remaining rain forest cover. The forest margin zone is characterized by a gradient of decreasing forest-use intensity with distance from the forest edge.

Annual mean air temperature in the Toro area is about 23° C (H. Kreilein, unpublished data). With an annual mean of 2200 mm, rainfall generally shows a low seasonality, but drier or wetter periods may occur due to irregular ENSO (El Niño Southern Oscillation) effects. In 2004 there was an unusual dry period from June to August. In these months the rainfall was only 73 mm/mo, while the average monthly rainfall that year was 143 mm. The natural forest vegetation in the surroundings of Toro is classified as relatively species rich, lower montane, evergreen, tropical moist forest (Pitopang *et al.* 2006). In the natural forest up to 63 tree species per 0.25 ha have been recorded, mostly belonging to the families Meliaceae, Lauraceae, Sapotaceae, and Fagaceae. After increased timber extraction this amount decreased to 53 species per 0.25 ha (Gradstein *et al.* 2007). Natural disturbances such as windthrow or landslides occur only occasionally in this area and were not of great importance during this study.

The selected stands are located on moderately steep slopes (17–39°) at elevations of between 832 and 1130 m a.s.l. The soil types of the investigated stands

TABLE 1. Structural characteristics of the four studied forest-use types (mean ± 1 SE, forest-use type A = undisturbed natural forest, type B = natural forest with little timber extraction, type C = natural forest with substantial timber extraction and type D = cacao plantation under natural shading trees). The soil parameters refer to the topsoil (0–10 cm). ([1] = data from Dietz *et al.* 2006. [2] = data from Häring *et al.*, 2005.) Canopy cover measurements were done with a convex spherical densiometer at 10 randomly selected locations per stand, with 4 readings per location in 4 different directions (N, E, S, W) (n = 40 per stand).

Forest use type	A	B	C	D
Exposition	SE	SE	SW	N
Mean tree height (m)[1]	21.3 ± 1.1	18.1 ± 0.9	15.2 ± 0.9	6.1 ± 0.3
Mean dbh (cm)[1]	29.5 ± 1.2	26.9 ± 1.9	21.3 ± 9.5	9.5 ± 0.1
Stem density (n ha^{-1})[1]	2474 ± 493	2672 ± 553	3819 ± 969	2106 ± 100
Total basal area (m2 ha^{-1})[1]	52.3 ± 4.3	47.1 ± 6.3	39.2 ± 5.5	21.2 ± 4.5
Canopy cover (%)	90 ± 0.3	87 ± 1.0	82 ± 0.3	77 ± 2.5
Bulk density of the soil (g cm^{-3})[2]	0.99 ± 0.12	1.11 ± 0.13	1.08 ± 0.14	1.20 ± 0.06
Organic layer (mm)	14 ± 2.1	13 ± 2.7	10 ± 0.9	8 ± 1
pH (KCl)[2]	5.07 ± 0.51	4.69 ± 0.08	3.87 ± 0.46	6.05 ± 0.27
Base saturation (%)[2]	85.0 ± 4.5	89.6 ± 8.4	49.2 ± 8.4	99.5 ± 0.2
Soil N (%)[2]	0.31 ± 0.05	0.27 ± 0.07	0.27 ± 0.03	0.21 ± 0.05
Soil C (%)[2]	3.03 ± 0.62	2.47 ± 0.62	2.99 ± 0.67	2.10 ± 0.48

are generally well-drained nutrient-rich Cambisols (WRB classification); however, under forest-use type C the soils had a somewhat lower nutrient availability (Häring *et al.* 2005, Table 1).

This study is part of a comprehensive, multidisciplinary research program on the stability of rainforest margins (STORMA) and was carried out on shared study sites. Study sites of 30 m x 50 m were selected, representing four typical stages of forest conversion from primary forests to cacao (*Theobroma cacao*) agroforestry systems in the Lore Lindu region:

Forest-use type A represents old-growth natural forest which shows only minor traces of human impact. There are no major canopy gaps and the mean overall canopy cover is about 90 %. Mean tree height and total basal area are highest in this forest type (Table 1). Although there were no signs of timber extraction in forest-use type A, the extraction of rattan is widespread in all types of forest.

Forest-use type B is a slightly disturbed forest in which small-diameter stems are selectively extracted at irregular intervals. The canopy cover of this forest type is only a few percent less then that of the undisturbed forest, while mean tree height and basal area are markedly lower (Table 1).

Forest-use type C represents moderately disturbed forest, in which large-diameter stems are selectively logged at irregular intervals. Consequently, small- to medium-size canopy gaps occur. In these canopy gaps, young trees with thin stems form thickets. Still the average overall canopy cover is greater than 80 %. The mean tree height and total basal area in this forest-use type are lower then in types A and B (Table 1).

Forest-use type D is an agroforestry system with cacao, planted under a sparse shading cover of remaining forest trees. This forest type is classified as heavily disturbed and has a much lower mean canopy cover, mean tree height and mean basal area then the other forest-use types (Table 1). The maintenance of these cacao plantations is of low intensity, mostly limited to infrequent weed removal. Fertilization is only rarely applied on these stands.

Each of these forest-use types was replicated three times. Due to different management intensities, the four forest types showed a clear differentiation with respect to canopy cover, dbh (diameter at breast height), and basal area of the stands (Leuschner *et al.* 2006), while the species composition of the forest stands remained more or less similar (Pitopang *et al.* 2006).

Root sampling and root analyses. To record fine root bio- and necromass in the four forest-use types we did an inventory at each of the 12 study sites. At six randomly selected sampling locations per study site, root samples were taken with a soil corer (3.5 cm in diameter) from the organic layer and from the mineral soil down to 50 cm soil depth. In order to avoid clumping of the sampling locations and to deal with the spatial heterogeneity of the stands, all sampling locations were at least four meters apart. Each of the soil cores was divided into vertically distributed subsamples (0–10, 10–20, 20–30, 30–40, and 40–50 cm depth). In the laboratory, the samples were soaked in water and cleaned of soil residues using a sieve with a mesh size of 0.25 mm. Large root fractions (> 10 mm in length) were picked out by hand. Only fine roots of trees (roots < 2 mm in diameter) were included in the analyses. Living (biomass, FRB) and dead rootlets (necromass, FRN) were distinguished under the stereomicroscope by color, root elasticity, and the degree of cohesion of cortex, periderm, and stele (Persson 1978, Leuschner *et al.* 2001). Fine root biomass and fine root necromass of each sample were dried at 70° C (48 h) and weighed. The data on fine root abundance was expressed per unit area (g/m^2).

In order to make an estimation of seasonal changes in fine root mass and fine root productivity, fine root sampling with the sequential coring method (Persson 1978, Vogt & Persson 1991, Fahey & Hughes 2004, Yang *et al.* 2004) was carried from February 2004 until February 2005. Because of the large time requirement for fine root seasonality and production analysis in forests, we had to confine this part of the study to four stands, i.e. one stand per forest-use type. The 4 stands selected for the production study give a good representation of the gradient of forest use intensity in the region and represented average values of fine root mass. We sampled 5 times at a 3-monthly interval. However, forest-use type C was an exception; here we sampled only 4 times (May 2004 – February 2005). Due to disturbance of the study site by a natural tree fall, we selected a new stand matching the definition for this particular forest-use type.

At each stand we randomly selected 20 sampling locations spaced at a minimum distance of 4 meters. At each sampling location, the distance to the nearest mature tree was measured to allow for an analysis of the dependence of fine root mass on tree distance. The root samples were taken with a soil corer (3.5 cm in diameter) from the first 20 cm of the soil and divided into two depths (0–10 and 10–20 cm). To prevent effects by the earlier samplings, while at the same time minimizing soil heterogeneity effects, all subsequent samples at the same location were taken at a distance of approximately 30 cm. The soil samples were transported to the laboratory at the University of Palu, where the stored samples (4°C) were processed within 6 weeks. The processing of the roots was done as described above. The fine root fraction (> 10 mm length) obtained with this procedure includes the major part of the biomass, but covers only a small part of the necromass. The fraction of dead fine roots smaller then 10 mm, may account for a large proportion of the total necromass (Bauhus & Bartsch 1996). Therefore on each sampling date, one-third of the samples was additionally subjected to a more detailed analysis of small fine root particles (< 10 mm in length), using a method introduced by van Praag *et al.* (1988) and modified by Hertel (1999). After removal of the larger root particles (>10 mm in length), the residue of the sample was spread evenly on a sheet of filter paper (730 cm^2), marked with 36 squares. Six of the squares were randomly selected and analyzed under the stereomicroscope for even the smallest dead fine root fragments. The mass of small dead root particles was extrapolated to the entire sample by means of the ratio of small dead rootlets to large dead roots (>10 mm in length) that was established in the subsample.

Fine root production was calculated by analyzing the sequential coring data with the "minimum-maximum method" (Persson 1978, McClaugherty *et al.* 1982). In this approach, the difference between minimum and maximum of total fine root mass (i.e., fine root biomass plus necromass) in the measuring period is calculated and equated with production. In this study, the measuring period lasted from the end of February 2004 until the end of February 2005 (12 months). In principal, we only considered significant differences between seasonal root mass extremes for estimating production. In the case of forest-use type D, however, we deviated from this condition and calculated the production despite a non-significant difference, because it was unlikely that the fine root production in the cacao plantation was zero. Because of the ongoing discussion about the best way of calculating fine root production, we additionally calculated FRP with the balancing transfer method (Fairley & Alexander 1985) and compared the results. However this method is known to be vulnerable to

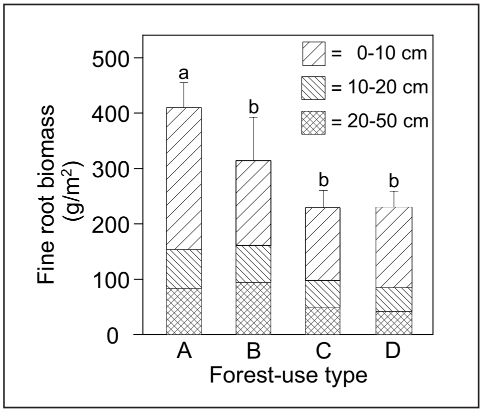

FIG. 1. Fine root biomass and necromass (mean ± 1 SE) in the four forest use types according to the fine root inventory (0–50 cm depth, 3 stands per type, 6 locations per stand). Different letters indicate significant differences between the forest-use types at ($p < 0.05$).

statistical mistakes because it covers even small, not statistically different, seasonal changes in fine root mass (Kurz & Kimmins 1987). The minimum-maximum method, on the other hand, tends to give an underestimation of the FRP (Singh *et al.* 1984, Lehman & Zech 1998, Vogt *et al.* 1998). Surprisingly, we did not find any significant differences in FRP using either the minimum-maximum or the balancing transfer method (Harteveld *et al.*, submitted). Here we will only present the data from the minimum-maximum method, since it has the advantage that the amount of parameters that can cause errors is kept small. Hertel & Leuschner (2002) found in their comparison between four different production estimates, that the sequential coring method in combination with minimum-maximum calculation gave one of the most reliable estimations of FRP.

Statistical analyses. The fine root mass and fine root production data were compared between the forest-use types using Kruskal-Wallis single factor analyses of variance, followed by non-parametric Mann-Whitney two-sample U-tests with a 5% rejection level. These calculations were done with the software package SPSS version 12.01 (SPSS Inc., Chicago, USA).

The dependence of fine root production on canopy cover, mean temperature at the forest floor, mean soil water content, mean tree height, total basal

TABLE 2. Coefficients of variance (CV) for spatial heterogeneity of mean fine root bio- and necromass and temporal variability of fine root bio- and necromass at 5 consecutive sampling occasions within the 4 forest-use types (1 stand per type, n = 20 per stand). FRB = fine root biomass, FRN = fine root necromass.

Forest-use type	CV spatial heterogeneity		CV temporal variability	
	FRB	FRN	FRB	FRN
A	0.33	0.19	0.37	0.36
B	0.27	0.13	0.40	0.24
C	0.29	0.15	0.34	0.25
D	0.41	0.22	0.46	0.28

area, mean dbh, bulk density of the soil, base saturation, pH, and the N and C contents of the soil, was analyzed by single-factor linear, or non-linear, regression analyses (software package Xact version 8, SciLab, Hamburg, Germany).

RESULTS

Stand totals and spatial heterogeneity of fine root biomass and necromass. The mean total fine root biomass in the soil profiles (0–50 cm) gradually declined with increasing forest-use intensity. With a mean value of 313 g/m^2, forest stands with little timber extraction (type B) had significantly lower profile totals of FRB than the undisturbed forest stand (type A, 408 g/m^2; Fig. 1). More severe forest disturbance, in the form of substantial timber extraction (type C) or conversion to cacao agroforestry systems (type D), led to a further reduction in the profile total of FRB (225 and 229 g/m^2 respectively). In all four forest-use types, the largest part (75–90 %) of FRB and FRN was found in the upper 20 cm of the soil (which includes the organic layer). FRB in the lower profile (20–50 cm) decreased in a similar way from A to D, as did FRB in the upper soil.

Spatial variation of FRB, measured at the sequential coring sites, was moderate in the three forest types A, B, and C, with coefficients of variance (CV) between 0.27 and 0.33 for the 20 sampling locations per stand. The CV value differed only marginally between these three stands, but was approximately 10 % greater in the cacao agroforestry system (Table 2). For necromass the CV values were approximately half of those recorded for biomass, with the largest spatial heterogeneity again found in the cacao agroforestry system.

Regression analysis of the dependence of fine root density on the distance between sampling location and the nearest tree showed no significant relationship, although distance varied between 0.3 and 4.6 m. This indicates a relatively homogeneous distribution of fine root biomass in the horizontal direction in the four stands (Table 3).

Seasonal variation in fine root bio- and necromass. During the 12-month sampling period, the minimum and maximum values of FRB in a stand differed by factors of 1.2 to 1.5 (Fig. 2). In all stands, the seasonal pattern was more pronounced in the uppermost 10 cm of the soil than at 10–20 cm depth. The seasonal variation of FRB as averaged over 20 sampling locations was much larger in the forest-use types A, B, and C than in the cacao agroforestry system; this was also true for FRN. On the other hand, when considering each of the 20 sampling locations separately, the temporal variation in fine root mass was greater in the cacao agroforest than in the forest-use types A, B, and C (Table 2). This indicates that while seasonal minima and maxima in the fine root system of the forest types A-C occurred more or less at the same time in each of the sampling locations, the seasonal changes in the cacao agroforestry system did not occur simultaneously. In general, seasonal peaks of FRB were observed from May to August 2004 and minima in November 2004. The fine root biomass maximum coincided with a three-month period of relatively little rainfall (June to August: mean monthly rainfall 73 mm), while the minimum was observed at the end of a subsequent wetter period of 3 months (September to November: mean monthly rainfall 152 mm,

TABLE 3. Correlation coefficients for linear regression analyses of the relation between fine root biomass density and the distance between sampling location and the nearest tree (1 stand per type, n = 20 per stand).

Forest-use type	r	p
A	0.028	0.48
B	0.001	0.89
C	0.005	0.78
D	0.018	0.57

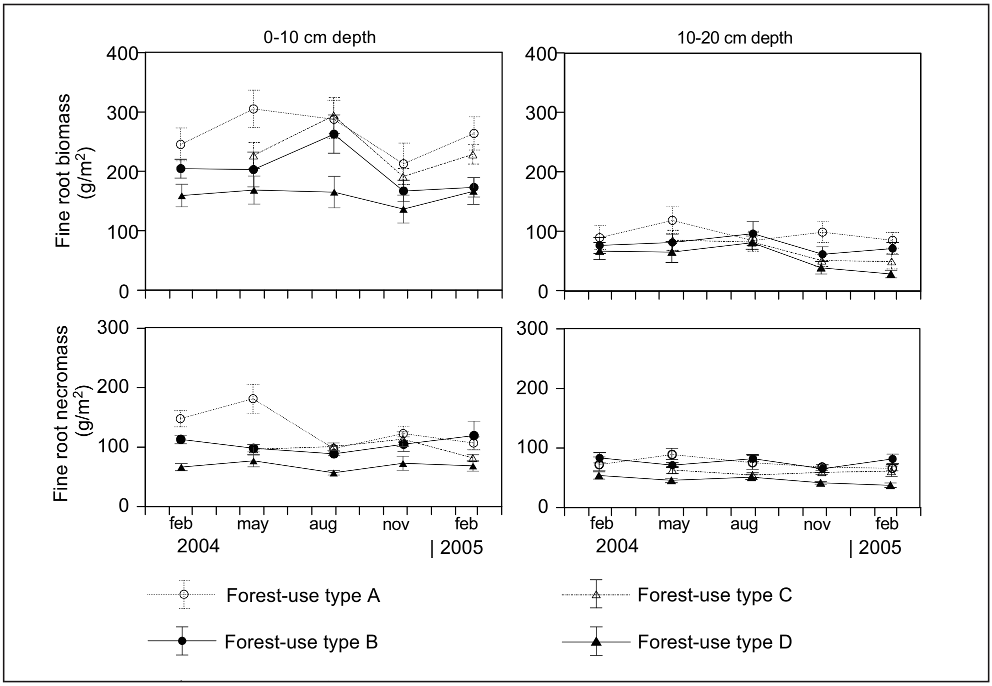

FIG. 2. Seasonal variation in fine root biomass and necromass (mean ± 1 SE) at 0–10 cm and 10–20 cm soil depth in one stand per forest-use type A, B, C, and D. Given are values of 20 soil samples per stand on 4 or 5 occasions.

Table 4). FRB in the three forest-use types A, B, and C was significantly greater during the drier period than in the following wetter period with average rainfall amounts (Table 4). In contrast, there were no significant differences in overall FRB between the relatively dry and wet periods in the cacao agroforest. Seasonality in fine root necromass was less pronounced than in fine root biomass in all 4 forest-use types (Fig. 2). Although maxima and minima did not occur synchronously in the four stands, root necromass in the topsoil (0–20 cm) tended to be less at the end of the relatively dry period (August) than after the wetter period (November, Table 3). However seasonal differences were not significant for FRN.

Fine root production in its dependence on aboveground forest structure and soil conditions. Annual fine root production (FRP) as calculated from the sequential coring data with the minimum-maximum method varied between 563 g/m²/yr in the undisturbed forest and 256 g/m²/yr in the stand with substantial timber extraction (Table 5). FRP in the upper 20 cm

TABLE 4. Fine root biomass and necromass (0–10 cm depth) after a dry period of 3 months (Jun–Aug, 2004) and after the subsequent 3-months rewetting period (Sept–Nov, 2004). In the wet period levels of rainfall were slightly above the average for 2004 (143 mm mo^{-1}). Different letters indicate significant differences between dry and wet periods at $p < 0.05$. (Rainfall data from H. Kreilein, pers. obs.). FRB = fine root biomass, FRN = fine root necromass.

Forest-use type	Dry (73 mm/mo)	Wet (152 mm/mo)
	FRB (g/m²)	
A	287.6 ± 32.0 a	212.7 ± 35.0 b
B	264.2 ± 32.1 a	168.5 ± 18.2 b
C	297.5 ± 30.5 a	194.3 ± 13.8 b
D	167.9 ± 26.7 a	139.4 ± 23.6 a
	FRN (g/m²)	
A	97.4 ± 5.6 a	122.5 ± 12.5 a
B	90.1 ± 3.3 a	106.0 ± 12.1 a
C	103.1 ± 6.1 a	115.7 ± 12.3 a
D	57.8 ± 3.8 a	74.1 ± 11.9 a

TABLE 5. Annual fine root production ($g/m^2/yr$) in the upper 20 cm of the soil (including the organic layer) as calculated from the sequential coring data using the minimum-maximum method (mean ± 1 SE, n = 20). Except for forest-use type D, only significant differences between minima and maxima of fine root mass were considered. Different Roman letters indicate significant differences between the forest-use types at $p < 0.05$ and different Greek letters indicate significant differences between the soil horizons at $p < 0.05$.

Forest-use type	0–10 cm	10–20 cm	Profile total 0–20 cm
A	353.23 ± 36.54 a α	198.04 ± 19.57 a β	551.27 ± 48.22 a
B	233.42 ± 24.82 b α	163.22 ± 22.79 ab β	396.64 ± 35.19 b
C	200.21 ± 23.35 b α	125.52 ± 15.97 b β	325.74 ± 32.88 b
D	206.88 ± 19.42 b α	133.56 ± 16.81 b β	340.44 ± 23.88 b

of the soil was significantly less in the three disturbed forest-use types (B, C, D) than in the undisturbed forest (type A). The three disturbed forest types did not differ significantly with respect to fine root production (Table 5). Approximately 60 % of the profile total of annual fine root production took place in the upper 10 cm of the soil. In all of the studied forest-use types it was this uppermost soil horizon that showed the largest differences in root production between undisturbed and disturbed forests. Although the forest-use types A and B did not differ significantly from each other, the lower soil layer (10–20 cm) showed a similar decrease from A to D as the topsoil; C and D differed significantly from A in this horizon. The seasonal minimum-maximum differences in fine root mass in the 12-month period were significant at a 5 % confidence level in all forest use types except for the cacao plantation (type D).

Regression analysis of fine root production on parameters of aboveground forest structure (canopy cover, mean tree height, total basal area, mean dbh) and on edaphic variables (soil bulk density, soil water content, soil surface temperature, base saturation, pH(KCl), soil N content) revealed that none of the soil chemical and physical, or the climatological factors had a significant effect on fine root productivity (Table 6). In contrast, fine root production showed a positive relationship to above ground stand structural attributes, i.e., canopy cover, tree height, basal area, and dbh. The strongest correlation was found with tree height and basal area of the stands (Table 6, Fig. 3).

TABLE 6. Correlation coefficients for linear or simple exponential (*) regressions between fine root production and various factors of aboveground forest structure and soil conditions. (n = 4, each point representing 20 replications). Significant relationships are printed in bold ($p < 0.05$).

Source	r	r^2_{adj}	p
Canopy cover*	0.90	0.88	0.04
Tree height*	0.99	0.98	< 0.01
Basal area*	0.99	0.98	< 0.01
dbh*	0.97	0.91	0.03
Soil surface temperature	0.52	– 0.09	0.48
Soil water content	0.20	– 0.44	0.79
Soil bulk density	0.77	0.41	0.22
Base saturation (%)	0.07	– 0.49	0.92
pH (KCI)	0.20	– 0.44	0.79
Soil N	0.41	– 0.25	0.59

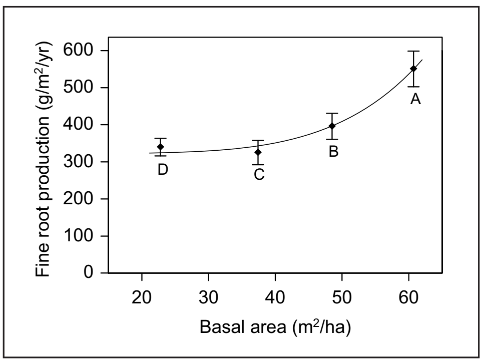

FIG. 3. Relationship between fine root production and basal area of the stands. The different letters indicate the different forest-use types. Regression equation: $y = 322.8 + 2.75^{-0.07} \cdot x^5$ ($r^2_{adj} = 0.99$, $p < 0.01$).

DISCUSSION

Variability of fine root mass along the disturbance gradient. Total fine root biomass and necromass declined significantly with increasing forest disturbance. Remarkably, even the extraction of small-diameter stems caused a significant reduction in both fine root biomass and fine root necromass. A similar reduction in FRB due to anthropogenic forest disturbance or conversion from forest to plantation was found in several other studies in (sub)tropical Asia (Sundarapandian & Swamy 1996, Yang *et al.* 2004, Upadhaya *et al.* 2005). In this study we could also demonstrate a negative effect of forest disturbance on fine root production. A significant decrease in annual fine root production was observed between the undisturbed forest site (forest-use type A) and the three disturbed sites (types B, C and D). Comparable reductions in fine root production were found by Sundarapandian & Swamy (1996) in a comparison of undisturbed and disturbed tropical moist forests in southern India. However estimated fine root production in Sulawesi did not decrease in the sequence B – C – D, although disturbance intensity increased. This contrasts with differences in FRB and FRN, and also with differences in canopy cover and basal area, which both decreased in this sequence. A possible explanation is that the cacao trees in the agroforestry system, which contribute to FRB in forest-use type D, have a relatively high fine root production rate but a lower FRB than the trees of the natural forest. This idea is supported by greater root regrowth in ingrowth cores in the cacao plantation than in the disturbed forests (Harteveld *et al.*, in prep.).

The observed decrease in FRB and FRN, and also in fine root production, from the undisturbed forest (A) to the disturbed forests, could be the result of environmental change with canopy opening, or of alterations in the aboveground biomass and structure of the stands. However, in our study the different forest-use types did not differ markedly with respect to environmental parameters, and therefore no relationship between such factors as soil surface temperature, soil water content, or soil C and N content and fine root production were observed. In contrast, we observed a strong dependence of fine root mass and production on structural attributes such canopy cover, mean tree height, total basal area, and mean dbh. In a review of the influence of natural and anthropogenic disturbance on the fine root system in tropical moist forests, Hertel *et al.* (2006) found that changes in the aboveground structure due to disturbance in all cases led to a reduction in fine root mass.

Spatial variability of fine root mass within research sites. Spatial variability of FRB was higher in the shaded cacao agroforest (D) than in the three forest-use types A, B, and C. This might have been caused by the existence of root gaps, i.e., the local thinning of the root system under canopy gaps (Denslow *et al.* 1998, Ostertag 1998). However, if this had been the case, we should have found a negative dependence of FRB on the distance between the sampling location and the nearest tree. Yet, such dependence was not observed in this study. Moreover, the coefficient of variance should have been greater in the disturbed forest-use types B and C than in A, a pattern we also did not find. Similarly, other studies also found no relationship between fine root biomass and distance from the nearest tree in temperate or tropical old-growth forests (Hertel 1999, Muñoz & Beer 2001). We hypothesize that timber extraction and the associated canopy opening did not result in distinct root gaps; rather it may have caused an overall thinning of the root system leading to lowered stand totals of FRB. The observed spatial variability of FRB could also be a result of the spatially highly variable tree species composition in the stands. Thus in the case of the agroforestry system, the variability might originate in differences in rooting patterns between cacao and the shading trees.

Seasonal variability of fine root mass. In central Sulawesi, maximum FRB was observed at the end of the dry period, and the minimum during the subsequent wet period. This contrasts with observations reported from other regions, e.g., in subtropical China or subtropical and tropical India, where the maximum values of FRB were found in the wet season (Khiewtam & Ramakrishnan 1993, Sundarapandian & Swamy 1996, Yang *et al.* 2004, Upadhaya *et al.* 2005). According to Khiewtam & Ramakrishnan (1993), root biomass peaks might correspond to periods of nutrient release during the wet season. In Sulawesi, there might have been more nutrient release during the dry season than during the wetter period. Woltmann & Migge (unpublished data) found an increase in the decomposing soil fauna during the drier period in our study plots. This could be an explanation for the higher amount of roots at the end of the dry period compared to the wet season. Also, it is known that soil moisture can have a pronounced influence on fine root turnover and productivity. However, whether increase in soil moisture has a positive or a negative effect on fine root turnover seems to differ according to location. Some studies report a decrease of fine root turnover with increase in soil moisture (Pregitzer *et al.* 1993, Hendrick & Pregitzer 1996), while others state the opposite (Joslin *et al.* 2000, Jones *et al.* 2003). The fact that we did not observe an increase in root necromass after root biomass decreased from the dry to the wet season might be explained by rapid decomposition processes in the hot climate of Sulawesi.

Seasonal differences in FRB were more pronounced in the upper 10 cm of the soil than in the subsurface layer, a finding also reported by two studies in subtropical north-east India (Khiewtam & Ramakrishnan 1993, Upadhaya *et al.* 2005). Effects of seasonal differences in temperature and rainfall are generally expected to be more distinct in the uppermost part of the soil. In the agroforestry system (type D), significant changes in FRB between the drier and the wetter season were not observed. This might be due to the fact that root systems of tree-based cropping systems not only respond to seasonal changes in soil moisture and temperature but to tree management activities as well. These tree management activities may mask possible seasonal fine root dynamics (Lehmann 2003). In addition, the production of pods could have a negative effect on the fine root production of cacao trees due to competing carbon sinks in the plant (Muñoz & Beer 2001).

Conclusion. We conclude from our results that mild to moderate disturbances of tropical moist forests had a significant negative effect on total fine root biomass and carbon fluxes associated with root production. However, contrary to our hypothesis, spatial and temporal variation in root mass remained largely unaffected by the disturbance regimes.

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