Patterns of fine root mass and distribution along a disturbance gradient in a tropical montane forest, Central Sulawesi (Indonesia)

Christoph Leuschner[1,3], Maria Wiens[1], Marieke Harteveld[1], Dietrich Hertel[1] & S. Tjitrosemito[2]

[1]*Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, D-37073, Göttingen, Germany.* [2]*Faculty of Science and Mathematics, Institute Pertanian Bogor, 16144, Bogor, Indonesia.* [3]*Corresponding author**

Abstract

Large parts of the remaining tropical moist forests of South-east Asia are encroached at their margins by selective logging, rattan harvesting and the establishment of small agroforest plantations under the rainforest canopy. These slight to heavy disturbances affect aboveground forest structure by reducing wood biomass and canopy cover; however, they may also have a profound impact on the belowground compartment. In a lower montane moist forest of Central Sulawesi, we studied the profile totals of fine root biomass (FRB_{tot}, roots < 2 mm until 50 cm of soil depth) and of fine root necromass (FRN_{tot}), the vertical distribution of fine root mass, and the fine root live/dead ratio by root coring in 12 forest stands that represented a gradient in forest use (or disturbance) intensity (forest use type A: undisturbed natural forest, B and C: slightly or moderately disturbed forests with selective timber extraction, D: heavily disturbed cacao agroforest systems under a remaining rainforest cover; each forest types being replicated three times). FRB_{tot} decreased significantly from forest A to the disturbed B, C and D forests, and reached less than 60% of the FRB_{tot} value of A in the agroforest systems D. A similar decrease with increasing disturbance intensity was found for FRN_{tot}. Forest disturbance intensity had no significant influence on the vertical distribution of fine root biomass in the profiles. According to correlation and principal components analyses, fractional canopy cover was the most important factor influencing FRB_{tot} and FRN_{tot}, whereas diameter at breast height, stand basal area, stem density, soil pH and base saturation had only a minor or no influence on root mass. A reduction in canopy cover from 90% (forest type A) to 75% (types C and D) was associated with a reduction in FRB_{tot} by about 45% which indicates that timber extraction leads not only to canopy gaps but to corresponding 'root gaps' in the soil as well. We conclude that forest encroachment that is widespread in large parts of South-east Asia's remaining rainforests significantly reduces tree fine root biomass and associated carbon sequestration, even if it is conducted at moderate intensities only.

Introduction

In most tropical countries, rainforests are encroached by the local population and converted to agricultural land at constantly high rates (Achard et al., 2002). In many regions of South-east Asia, only small remnants of natural forest remain today, mainly as protected forest in regional or national conservation areas (Schelhas and Greenberg, 1996). However, many of these remaining forest stands are currently encroached

* FAX No: +49-551-39-5701.
  E-mail: cleusch@uni-goettingen.de, cleusch@gwdg.de

at their margins by neighbouring villagers or individuals from distant urban regions who use forest products to increase their income. In Indonesia, many formally protected forests actually consist of a more or less undisturbed core zone far from the edge, and a margin zone several hundred metre to a few kilometre wide with slight to heavy human impact and increasing degradation (Collins et al., 1991).

Rattan extraction, selective logging of a limited number of trees and the creation of small gaps for establishing crop plantations inside the forest are typical activities in the margin zone of most Indonesian national parks and forest reserves (FWI/GFW, 2002). Since these activities in the forest margin zone are primarily controlled by the proximity of access roads and tracks, human impact is rapidly decreasing with growing distance from the forest edge. Typically, a steep gradient of forest use intensity from the forest interior toward the margin exists which is accompanied by an increase in the size and number of canopy gaps. Since there is a steady increase in the proportion of tropical forest which is left in a disturbed state, a better understanding of the effects of low- and moderate-intensity disturbances on soil processes, vegetation and fauna of tropical forests is urgently needed.

The study of the ecological consequences of disturbance in tropical forests has focused on the aboveground compartment. Studies have been undertaken only recently to investigate belowground changes after canopy gap formation in tropical forests (Ostertag, 1998; Sanford, 1989, 1990; Silver and Vogt, 1993; Uhl et al., 1988; Vitousek and Denslow, 1986). Most of these studies refer to gap formation by senescing trees, windbreaks and other natural disturbances in neotropical forests where human impact played a minor role. These results may not be applicable to human-induced disturbances where small gaps are created due to the harvesting of single trees. This situation includes the extraction of wood biomass which is not left in place for decay as is the case during natural disturbances.

This paper investigates the effects of variable intensities of forest use on the tree fine root system of tropical lower montane moist forests in Central Sulawesi, Indonesia. We studied the profile totals, the vertical distribution and the live/dead ratio of fine roots (diameter <2 mm) in a gradient from negligibly disturbed forest (natural forest) to selectively logged, slightly disturbed forest, to moderately disturbed forest, and finally to a heavily disturbed cacao agroforest system with remaining forest shade trees which replaces the natural forest in many areas of the region. These four forest use types are characteristic elements of the forest margin zone in Sulawesi and in other parts of South-east Asia. We related the root system properties to stand structural and canopy characteristics in order to analyse putative interactions between canopy and fine root system. We tested the hypothesis of Wilczynski and Pickett (1993) that increasing canopy gaps after disturbance are associated with gaps in the root system as well, leading to reduced total fine root biomass in the disturbed forests.

Material and methods

Study sites

The study was conducted in the surroundings of the village of Toro in the province of Donggala, Central Sulawesi, Indonesia (01°30′ S, 120°02′ E). Toro is located on the western fringes of Lore Lindu National Park, one of the last larger areas of tropical montane forest in the region which is protected since 1993. The study sites are situated in rugged terrain on moderately steep slopes (17–39°) in the lower montane belt (elevation 815–1130 m a.s.l.). The soils in the Toro region derived either from sedimentary rocks or from tertiary intrusives; the soil types are predominantly well drained Orthieutric and Hypereutric Cambisols (FAO classification) with relatively high fertility. There is a considerable pedologic heterogeneity in the region; locally, Orthidystric Cambisols and Haplic Ferralsols are also present. The base saturation of the topsoil varied between 34 and 99%, the pH (KCl) between 3.2 and 6.4 (Table 1, unpublished data from Häring). Mean annual air temperature in Toro is about 24 °C, yearly average precipitation is about 2200 mm. Rainfall shows a moderate seasonality with at least 100 mm per month falling throughout the year. Typically, rainfall occurs on 20 to 30 days per month. Air humidity ranges mostly between 75 and 90% throughout the year. December, January and February are often somewhat drier

Table 1. Structural characteristics and soil parameters of the 12 studied plots in the 4 forest use types A–D (structural data from J. Dietz)

Forest type	Plot No.	Exposition	Mean tree height (m)	Mean DBH (cm)	Stem density (n ha^{-1})	Basal area (m^2 ha^{-1})	Canopy cover (%)	pH (KCl)	Base saturation (%)	Organic layer (mm)
A	1	SE	21.9	30.3	2213	60.7	90	4.19	77.1	11
A	2	W	22.9	31.5	1781	47	91	5.95	92.8	18
A	3	N	19.2	26.7	3427	49.1	90	5.07	85	13
B	1	SE	18.9	27.9	1933	48.5	86	4.85	97.6	9
B	2	W	16.3	23.2	2330	35.6	89	4.65	72.8	18
B	3	N	19.2	29.5	3753	57.3	86	4.57	98.3	12
C	1	SE	16.8	22.1	3965	30.6	82	3.23	33.7	10
C	2	W	13.8	21.5	2073	49.5	81	4.75	51.5	8
C	3	N	15.1	20.4	5420	37.4	82	3.52	62.4	11
D	1	SW	5.8	9.6	2214	28.6	80	5.43	99.7	7
D	2	W	5.7	9.5	1907	13.3	78	6.36	99.5	10
D	3	N	6.7	9.4	2198	22.8	72	6.05	99.2	7
A	Mean		21.3±1.1 a	29.5±1.2 a	2474±493 a	52.3±4.3 a	90±0.3 a	5.07±0.51 ab	85.0±4.5 a	14±2.1 a
B	Mean		18.1±0.9 b	26.9±1.9 a	2672±553 a	47.1±6.3 a	87±1.0 b	4.69±0.08 a	89.6±8.4 a	13±2.7 ab
C	Mean		15.2±0.9 b	21.3±0.5 b	3819±969 a	39.2±5.5 a	82±0.3 c	3.87±0.46 a	49.2±8.4 b	10±0.9 ab
D	Mean		6.1±0.3 c	9.5±0.1 c	2106±100 a	21.2±4.5 b	77±2.5 d	5.95±0.27 b	99.5±0.2 c	8±1.0 b

pH and base saturation refer to the topsoil (0–10 cm). Base saturation and pH as measured in spring 2005 by V. Häring. Different letters indicate significant differences among forest use types.

months. The study year (2004) was no ENSO (El Nino Southern Oscillation) year with associated drought periods.

The natural forest vegetation in the region is a fairly species-rich lower montane moist forest with a height of 35–45 m. Common tree genera on the study plots include *Castanopsis* (Fagaceae), *Chionanthus* (Oleaceae), *Dysoxylum* (Meliaceae), *Ficus* (Moraceae) and *Lithocarpus* (Fagaceae) (Pitopang et al., 2006).

We studied four types of woody vegetation in the forest margin zone which represent typical stages of a gradient in forest use intensity in the Lore Lindu region:

 (i) Forest use type A is an old-growth natural forest with only minor indication of human impact. Canopy cover is about 90% with no major gaps being present. Timber has been extracted only very exceptionally, and the plots were chosen in patches where no signs of cutting were found. However, extraction of rattan (*Calamus* sp.) was widespread in all types of forest in the region including the natural forest. Today, rattan is very rare even in forest use type A.

 (ii) Forest use type B is a slightly disturbed forest in which small-diameter stems of the lower canopy stratum are being selectively extracted at irregular intervals. Canopy cover is only a few percent lower than in type A.

(iii) Forest use type C is termed a moderately disturbed forest because selective extraction of large-diameter timbers irregularly takes place. As a consequence, small gaps are occurring in the upper canopy (canopy cover about 80%) with the consequence that young trees with small diameters are thriving in the gaps forming small thickets that are mostly in the stem-exclusion phase of stand development (Table 1).

(iv) Forest use type D is an agroforest system with cacao (*Theobroma cacao* L.) planted in the understorey of a sparse cover of remaining rainforest trees that cast shade on the plantation. In contrast to the types A–C, a scattered layer of mainly invasive herbs and grasses covers the soil surface. With respect to forest structure, this vegetation type is classified as 'heavily disturbed'.

All four forest use types are widespread in the Lore Lindu region. 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 (kepala desa) negotiated a contract with the National Park authorities under which the surrounding forests are being managed as community forests by the villagers. The respective forest area is mapped and classed into forest use types which allow different forms of sustainable forest use, including rattan extraction, selective logging of large-diameter or small-diameter stems, and, locally, conversion to agroforest systems under a remaining rainforest cover. Our four forest use types A–D match these management systems of community forestry.

We selected 12 study plots of 50×50 m in the region with each forest use type being represented in triple replication. Selection criteria were (1) good coincidence with the structurally defined four forest use types described above, (2) sufficient comparability of the three replicate stands with respect to forest structure, (3) sufficient spatial homogeneity of the plots, and (4) a defined and temporarily stable management system, i.e. the existence of a non-disputed forest utilization contract between village head and user.

Analysis of aboveground forest structure and soil chemical parameters

The canopy cover of the 12 research plots was measured with a spherical densiometer. At 10 randomly selected locations per plot, readings were done in 4 directions, north, south, east and west. The average of the four readings was used as one measurement.

On all study plots, all stems with a diameter >10 cm were investigated for diameter at breast height (DBH) and tree height (unpublished data of J. Dietz). In addition, three subplots of 5×5 m were randomly selected per plot in which all individuals taller than 2 m were measured. Tree height measurements were taken with the Hagloef Vertex III Ultrasonic device, DBH was recorded with a measuring tape at 1.3 m height. All data were related to ground area and subsequently corrected for slope angle. Cumulative basal area and stem density were then expressed per hectare.

pH (detected in 1 M KCl) and base saturation (sum of basic cations in percent of cation

exchange capacity) were measured in spring 2005 in each four soil pits per study site in the uppermost soil horizon (0–10 cm, all analyses by V. Häring, unpublished data); in addition, organic layer thickness was also determined.

Root sampling and root analyses

Root samples were taken with a soil corer (3.5 cm in diameter) from the organic layer and the mineral soil down to 50 cm soil depth at six randomly selected sampling locations per study plot. The sampling points were located at a minimum distance to each other of 5 m in order to avoid clumping of the locations and to cope with the considerable spatial heterogeneity of many plots. Soil cores were taken at six depths (organic horizon, mineral soil at 0–10, 10–20, 20–30, 30–40 and 40–50 cm depth). The soil samples were transferred to plastic bags and transported to the laboratory at the University of Palu where processing of the samples stored at 4 °C took place within 60 days. In the lab, the samples were soaked in water and cleaned from soil residues using a sieve with a mesh size of 0.25 mm. Large root fractions (>10 mm in length) were extracted by hand. Only fine roots of trees (roots <2 mm in diameter) were considered for analysis. Roots of grasses and herbs, which only were abundant in the agroforestry systems, were easily distinguished from tree fine roots by their smaller diameter and light colour. Live (biomass) and dead rootlets (necromass) were distinguished under the stereomicroscope by colour, root elasticity, and the degree of cohesion of cortex, periderm and stele. A dark cortex and stele, or a white, but non-turgid cortex, or the complete loss of the stele and cortex with only the periderm being present, were used as indicators of root death (Leuschner et al., 2001; Persson, 1978). The collected fine root fraction covered the large majority of the living fine root mass, but it included only a small part of the necromass, because detritus-like fractions of dead roots, that may account for a large portion of the whole necromass (Bauhus and Bartsch, 1996; Hertel, 1999), were recovered only to a small extent with this method. Therefore, one third of the samples was subjected to an additional, more detailed analysis of small fine root necromass particles

(<10 mm in length) applying a method introduced by van Praag et al. (1988) and modified by Hertel and Leuschner (2002). After extraction of the large root fractions, the residue of the sample was evenly spread on a large sheet of filter paper (730 cm^2) with 36 squares marked on it. Six of the squares were randomly selected and analysed under the stereomicroscope for even smallest dead fine root fragments. These decaying root particles may represent the main part of the fine root necromass (Bauhus and Bartsch, 1996; Hertel, 1999). The mass of small dead rootlets was extrapolated to the entire sample by means of the ratio of small rootlets to large dead roots (>10 mm in length) that was established in a sub-sample. Fine root biomass (FRB) and necromass (FRN) of each sample were dried at 70 °C for 48 h and weighed. The fine root biomass/necromass ratio was then calculated for each sample. The data were expressed in relation to soil volume as fine root mass density (in g L^{-1}) for different soil depths, and as profile total of FRB or FRN (organic layer plus 0–50 cm of the mineral soil; FRB$_{tot}$ or FRN$_{tot}$ in g m^{-2}).

Statistical analyses

We used the equation proposed by Gale and Grigal (1987) to describe the exponential decrease of fine root biomass with soil depth for all 12 study plots:

$$y = 1 - \beta^d, \tag{1}$$

(y is the cumulative fraction of total fine root biomass from the soil surface to a depth of d cm). β values typically range between 0.80 and 0.99 for tree fine root systems; low β values indicate a more gradual biomass decrease with depth, high β values reflect a more superficial root distribution and a rapid decrease with depth. The surface of the organic layer was used as the zero point of the curves, or, in other words, the thin organic layer was treated as the uppermost soil horizon. The regression fits were calculated with the software package Xact (version 7.12, SciLab, Hamburg, Germany).

Probability of fit to normal distribution was tested by a Shapiro–Wilk test. With only a few exceptions, the root mass and stand structural data showed non-gaussian distribution;

consequently, non-parametric tests were used. The fine root mass data were compared among the four forest use types with one-way Kruskal–Wallis single factor analyses of variance. A non-parametric Mann and Whitney U-test was used for pair-wise comparison of significant differences between the types ($P < 0.05$ in all analyses). These calculations were conducted with the software package SAS, version 8.01 (SAS Institute, Cary, NC, USA).

To analyse the differentiation of the 12 study plots with respect to several stand structural and abiotic characteristics, we conducted a Principal Components Analysis. The matrix species factors were: study plot, canopy cover, basal area, stem density, mean diameter at breast height (DBH), FRB_{tot}, FRN_{tot}, FRB/FRN ratio, and pH(KCl) and base saturation of the upper mineral soil (0–10 cm). The PCA analyses were conducted with the package CANOCO, version 4.5 (Biometris, Wageningen, The Netherlands).

The dependence of FRB_{tot}, FRN_{tot} and FRB/FRN ratio on canopy cover, stem density, and basal area was also analysed by single-factor linear, or non-linear regression analyses (package Xact). The dependence of FRB_{tot} and FRN_{tot} on various biotic and abiotic site factors was further analysed by multiple regression analysis (SAS, version 8.01).

Results

Stand structure

From natural forest with negligible disturbance (forest use type A) to the slightly disturbed forests (type B) and further to the moderately disturbed forests (type C), there was a general decrease in mean tree height (from 21.3 to 15.2 m), in DBH (30–21 cm), in stand basal area (52–39 m^2 ha^{-1}) and in canopy cover (90–82%), despite considerable variation among the three replicate stands of a forest use type and, thus, non-significant differences between types A and B in several cases (Table 1). The forest use type D (heavily disturbed cacao agroforest system) had the smallest mean tree height, mean DBH, stand basal area and canopy cover of all four forest use types. Stem density showed no trend in this sequence of increasing disturbance intensity.

Fine root abundance and distribution patterns

Root coring in the organic layer and the mineral soil to a depth of 50 cm showed highly different profile totals of fine root biomass in the 12 forest stands. Based on each 6 soil profiles investigated per stand, we found a maximum value of 655 g m^{-2} (stand B2) and a minimum of 101 g m^{-2} (B3). With a mean of 408 g m^{-2}, the three natural forest stands (A1–A3) had a significantly larger FRB_{tot} value than all other forest use types. Second were the slightly disturbed forests (B1–B3), followed by the moderately disturbed forests (C1–C3) and the heavily disturbed agroforest systems (D1–D3). The forest use types B, C and D did not differ significantly from each other, although the mean of type B was by 90 g m^{-2} larger than the means of C and D.

In all stands (except for B3), we found more fine root biomass than necromass (FRN) in the profiles. As for FRB_{tot}, the 12 stands showed a large variation in the profile totals of necromass (FRN_{tot}: 54 to 207 g m^{-2} in the organic layer plus 0–50 cm of mineral soil). There was a significant decrease from the natural forests (A) to the slightly disturbed forests (B) and further to the moderately disturbed forests (C, Figure 1). The agroforest systems (D) differed significantly from the type C forests, but not from the type B forests. The average fine root biomass/necromass ratio in the profiles increased from 2.5 in the type A forests to 3.3 in type B and 3.6 in the type C forests (differences not significant). The agroforest systems tended to have the smallest mean FRB/FRN ratio.

In all 12 stands, fine root biomass density decreased exponentially with soil depth from high concentrations in the organic layer (2.5–5.0 g L^{-1}) to low densities at 20–30 cm depth (0.2–0.6 g L^{-1}) and below (< 0.5 g L^{-1} at 30–50 cm, Figure 2a). Exponential functions of the form $y = 1 - \beta^d$ (y = cumulative fine root biomass, d = soil depth) had similar β factors in all stands (0.83–0.91) although root mass was significantly higher in type A than in the other forest use types. Fine root necromass also
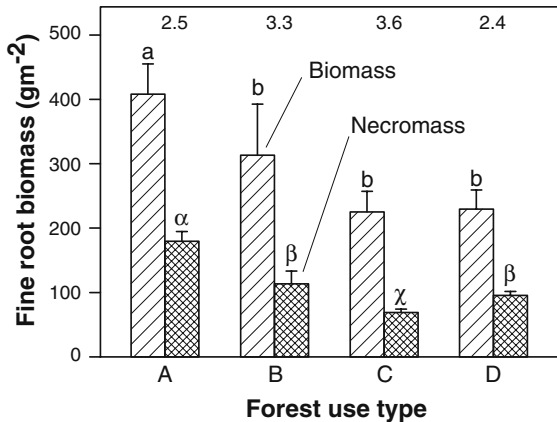
Figure 1. Profile totals of fine root biomass (FRB) and necromass (FRN) in the four forest use types A to D (means + 1 SE of each 3 plots with 6 profiles per plot investigated). Profile total = organic layer plus 0–50 cm of mineral soil. Numbers in headline = mean FRB/FRN ratios of the profiles. Different Latin or Greek letters indicate significant differences in FRB or FRN between the forest use types.

decreased exponentially with depth from high densities in the organic layer (1.0–4.5 g L^{-1}) to low values at 10–20 cm and below (<0.3 g L^{-1}, Figure 2b).

Influence of stand structure and soil acidity on fine root mass

The results of a principle components analysis (PCA) based on stand structural and abiotic characteristics showed a clearer differentiation between the four forest use types (A–D) than between the each three replicate stands within a type: The PCA separated the four forest use types along the first axis (eigenvalue = 0.429) in the sequence A–B–C–D (Figure 3). This axis was related to the parameters canopy cover, DBH and basal area of the stands, and thus expressed the disturbance gradient. Fine root biomass showed a close correlation to these above-ground stand characteristics; in contrast, fine root necromass was less correlated. The factor with the strongest influence on the profile totals of fine root biomass in the 12 stands was canopy cover.

The second axis (eigenvalue = 0.261) coincided with the factors stem density and, in opposite direction, with topsoil base saturation and pH, factors of secondary importance in the explanation of plot similarity. Stem density was particularly high in the larger gaps of the C-type forests where vital tree regrowth occurred. The FRB/FRN ratio was positively related to stem density, but negatively to base saturation.

We fitted an exponential equation to describe the positive relation between canopy cover and FRB_{tot} ($r^2_{adj} = 0.27$, $p < 0.05$). Accordingly, fine root biomass increased by more than 100% from a forest with 75% canopy cover to a stand with 90% cover (Figure 4a). Canopy cover had a similar effect on fine root necromass (Figure 4b). In contrast to the PCA results, we did not find a significant influence of stand basal area on
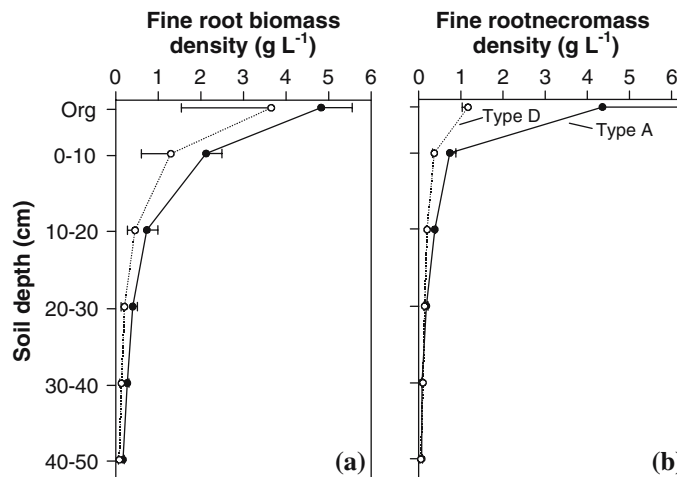

Figure 2. Density (mass per volume) of fine root biomass (a) and fine root necromass (b) in soil profiles of natural forest (Type A) and agroforest (Type D). Mean ± 1 SE of 3 plots per forest use type with each 6 profiles investigated.
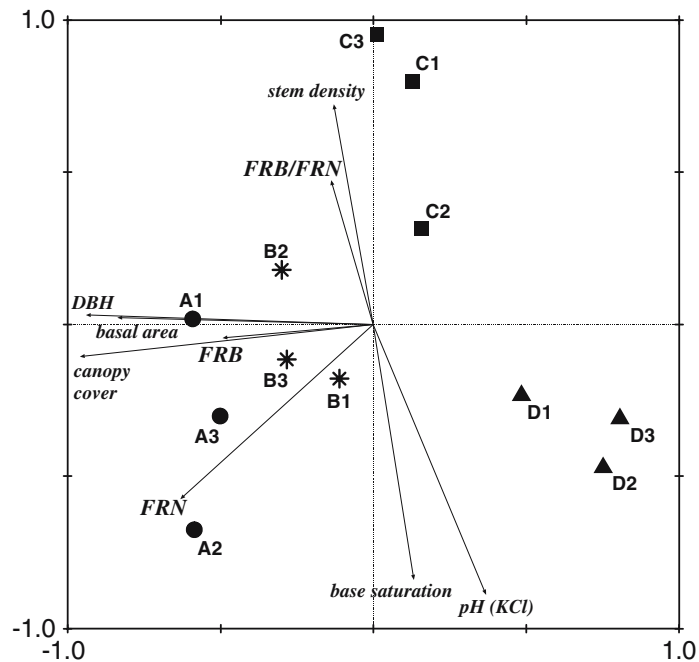
Figure 3. Plot showing the distribution of the 12 study plots (numbered A1 to D3) in PCA axes 1 and 2 together with stand structural and soil chemical variables. Vector length and angle are proportional to the direction and degree of their correlation with the plot ordination scores.
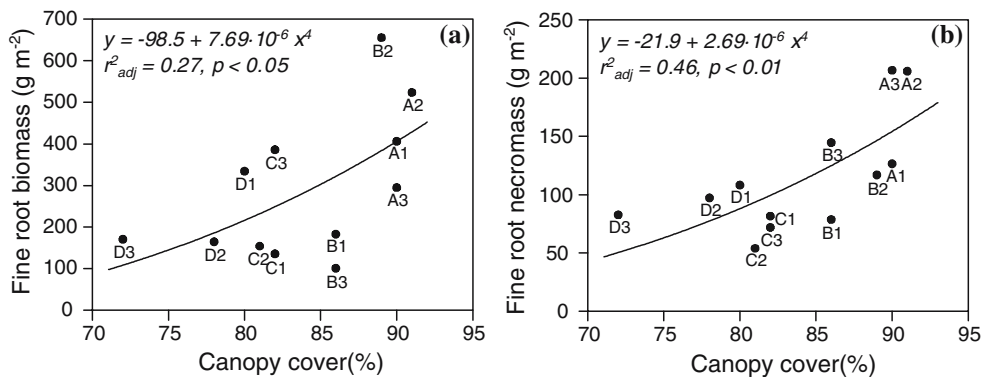

Figure 4. Relationship between canopy cover and fine root biomass (a) or fine root necromass (b) for the 12 studied plots in the four forest use types A to D.

FRB_{tot} in the single-factor correlation analysis (Table 2). A linear multiple regression analysis with stepwise variable selection gave canopy cover as the variable with strongest influence on FRB_{tot}, followed by DBH (Table 3). Fine root necromass was found to be primarily influenced by canopy cover and pH (KCl).

Discussion

Fine root biomass of undisturbed forest

The largest profile totals of fine root biomass of all four land use types in the forest margin zone were found in the natural forest stands with only

Table 2. Correlation coefficients of linear or exponential (*) regressions of canopy cover, basal area and DBH on profile totals of fine root biomass (FRB), fine root necromass (FRN) or the FRB/FRN ratio in the soil profile

Parameter	Source	r	r_{adj}^2	P
Fine root biomass FRB	Canopy cover*	**< 0.58**	0.27	**< 0.05**
	Basal area	0.11	−0.01	0.73
	DBH	0.26	0	0.33
Fine root necromass FRN	Canopy cover*	**0.71**	0.46	**< 0.01**
	Basal area	0.36	0.05	0.24
	DBH	**0.64**	**0.35**	**< 0.05**
FRB/FRN ratio	Canopy cover	0.15	−0.08	0.65
	Basal area	−0.06	−0.1	0.85
	DBH	−0.04	−0.1	0.91

Table 3. Results of a multiple linear regression of several stand structural and abiotic variables on profile totals of fine root biomass or fine root necromass of the 12 plots

Parameter (Y)	Source	F value	P
Fine root biomass	Basal area	0.41	0.55
	Base saturation	0.18	0.67
	Canopy cover	12.03	**0.01**
	DBH	6.07	**0.04**
	pH (KCl)	0.64	0.46
	Stem density	0.29	0.62
	Tree height	3.23	0.12
	Intercept	10.76	**0.01**
Regression model	*$Y = 49.7 \cdot$ canopy cover − 23.8 DBH − 3342 $r^2 = 0.63$, $P = 0.02$*		
Fine root necromass	Basal area	0.21	0.67
	Base saturation	0	0.96
	Canopy cover	13	**0.01**
	DBH	0.92	0.38
	pH (KCl)	6.3	**0.04**
	Stem density	3.53	0.1
	Tree height	0.34	0.58
	Intercept	10.2	**0.01**
Regression model	*$Y = 5.8 \cdot$ canopy cover + 22.9 $\cdot$pH − KCl 488 $r^2 = 0.66$, $P = 0.01$*		

The variables were added in a stepwise manner.

negligible disturbance (forest use type A). Our average fine root biomass totals from a lower montane region (408 ± 66 g m^{-2} for organic layer plus 0–50 cm of the mineral soil, mean ± 1 SE) are in good agreement with data from 55 observations in other tropical moist forests of the globe, which average at 451 (±45) g m^{-2} (in the majority of studies: 0–50 cm depth) although root biomass can differ largely between stands depending on tree species, soil conditions and profile depth analysed (Hertel and Leuschner, 2006).

The average values for old-growth forests from the current study are also close to those obtained from temperate deciduous forests. In a meta-analysis of 129 studies on temperate broad-leaved and coniferous forests, Leuschner and Hertel (2002) reported a mean of 442 (±21) g m^{-2}. The variation in fine root biomass among different stands was considerably lower in our meta-analysis than in earlier ones conducted by Jackson et al. (1996) or Vogt et al. (1996) because we strictly included only data with roots <2 or

3 mm in diameter and only considered live roots, whereas these authors were less rigid in their selection criteria. This data compilation allows to conclude that the average fine root biomass of tropical and temperate forests is rather similar despite striking differences in climate, phenology, aboveground biomass and, most often, leaf area index, attributes which most likely are linked to differences in nutrient demand and nutrient supply between tropical and temperate forests.

Effects of forest disturbance on stand fine root biomass and its distribution

How do selective logging and associated disturbances affect profile totals and spatial distribution of tree fine roots in tropical forests? In theory, human-induced gap formation could act on the fine root system of trees through several causal chains, (1) by altering the thermal and moisture regimes in the gap, (2) by increasing or decreasing nutrient supply through altered litter supply rates and microbial activities, and (3) by changing above-ground stand structure which may interact with the root system.

Our fine root biomass data from 12 forest stands which differed in disturbance intensity and the size of gap fraction showed that moderate to high levels of timber removal lead to a significant and lasting reduction in the profile totals of fine root biomass. However, according to the PCA and the correlation analyses, basal area and its reduction was not the principal structural parameter influencing fine root biomass totals. This is astonishing and may probably be explained by root competition. We hypothesize that competition among fine roots is intense in the topsoil of old-growth forests in tropical and temperate climates. A reduction in stem density with selective logging must cause root dieback in the gaps and thus may partly release the remaining roots from competition. A likely response is enhanced fine root growth by the remaining trees into the gaps, if the openings are sufficiently small. If timber extraction is of low intensity, this effect will partly compensate for the loss in fine root biomass and, thus, may obscure any relation between wood extraction or basal area reduction and a decrease in FRB_{tot}.

Our data showed no effect of stem density on FRB_{tot}, but they indicated a principal role of canopy cover on stand fine root biomass, albeit at a low degree of determination ($r^2 = 0.27$). Accordingly, a reduction in canopy cover from 90% (closed natural forest, type A) to 75% (moderately disturbed forest, type C) led to an over-proportional reduction (by 45%) in fine root biomass. Other studies of small, localized disturbances in tropical forests due to natural treefall indicated in most cases a reduction in FRB_{tot} in the gaps compared to intact forest (Denslow et al., 1998; Ostertag, 1998; Sanford, 1989, 1990; Silver and Vogt, 1993). Similarly, Sundarapandian and Swamy (1996) reported a significantly lowered fine root biomass total and also fine root production under open canopies compared to closed canopies in evergreen moist forest in India. The above cited studies further indicate that the decrease in fine root biomass tends to increase with the size of the gap.

The extent of fine root biomass reduction after disturbance seems to depend on time. FRB_{tot} may reach a minimum shortly after a severe disturbance and may recover over periods of months to years (Arunchalam et al., 1996; Herbert et al., 1999). Parrota and Lodge (1991) observed a sharp decrease in fine root biomass after hurricane disturbance in a tropical moist forest in Puerto Rico and concluded that at least one year was required for the re-establishment of the original root mass. The cited results are in general accordance with our data; however, none of the cited studies differentiated between the possible effects of altered canopy cover, basal area and stem density, factors which all might influence fine root biomass.

If canopy cover (or leaf area index), but not stem density, basal area or functional attributes such as stand sapwood area, were indeed the most important variables influencing FRB_{tot}, canopy gaps with reduced leaf area should coincide with reduced fine root densities in the soil. This would partly support the root gap theory of Wilczynski and Pickett (1993) which predicts a less closed 'root canopy' after disturbance of the leaf canopy. Moderate to high levels of timber extraction would thus not only affect canopy density and leaf area but would also have a negative influence on the fine root system and its belowground carbon storage capacity.

Heavy disturbance or near-complete destruction of tropical forests, as occurs with the

establishment of agroforest systems under cover trees or in tree plantations, can also lead to substantial reductions in FRB_{tot}, as is evidenced by our data and the literature reports cited below. Sundarapandian et al. (1999) found a significantly larger fine root biomass in tropical natural forests than in nearby rubber, *Albizia* or *Acacia* plantations. Only in teak plantations, no decrease in FRB_{tot} was found compared to nearby forest. We speculate that canopy cover (or leaf area index) might also be a key factor in this type of disturbance determining the extent of root biomass reduction when converting natural forest to woody plantations.

Reductions in FRB_{tot} as they are occurring in logging gaps or after conversion to agroforest systems could also be driven by altered microclimatic and edaphic conditions in the clearings. In our stands, elevated light transmission to the forest floor in disturbed forests increased daytime temperatures in the topsoil of gaps by 2–3 °C (data not shown); this could have stimulated fine root growth and activity. On the other hand, gaps showed lower night-time temperatures which should have reduced root respiration. Altered temperature regimes may also influence root growth by increasing nutrient availability in the gaps (in particular plant-extractable P, Denslow et al., 1998), although aboveground litterfall typically decreases in gaps. Finally, root dieback and subsequent mineralization pulses in the topsoil due to root decomposition may temporarily have increased nutrient availability in the stands B, C and D. Short-term increases in nutrient supply immediately after gap formation were indeed observed in tropical forests (Denslow et al., 1998).

However, none of the above-discussed changes in soil physical and chemical parameters, which might have stimulated root growth in the disturbed forests, seem to have influenced FRB_{tot} in the forest gaps in the long run in our study, since average FRB_{tot} values decreased, and not increased, with growing disturbance intensity. The assumption that disturbance-driven changes in the soil physical and chemical parameters must have exerted only minor influences on FRB_{tot} in the Sulawesi stands is further supported by comparable vertical fine root distribution patterns in the soil profiles of all four forest use types. This similarity existed despite the fact that temperature, moisture and nutrient supply

are known to be key factors controlling the depth distribution of fine roots in soils (Fitter, 1996; Sainju and Good, 1993).

We conclude that the widespread practise of selective logging and conversion to agroforest systems under tree cover leads to a substantial reduction of fine root biomass in the remaining tropical forests. Disturbed forest may contain only 60% or less of FRB_{tot} as compared to the global average of fine root biomass in undisturbed tropical moist forests. This implies not only lowered average nutrient and water uptake rates in disturbed forests but also reduced carbon storage by the fine root system. The latter effect may seem to be of minor importance when considering the large C losses associated with stem harvesting. However, fine roots typically consume a large fraction of the annual carbon gain of trees (Lauenroth and Gill, 2003) which highlights the outstanding role of fine root growth and turnover in the carbon cycling of forests. Additional studies on fine root production and mortality in logged forests are needed in order to better understand the consequences of forest disturbance for the root-growth-related carbon sink in tropical forests.

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