



Consequences of increasing forest use intensity for biomass, morphology and growth of fine roots in a tropical moist forest on Sulawesi, Indonesia

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ABSTRACT

Tropical moist forests in South-East Asia are heavily exploited by timber extraction and forest conversion into agroforestry systems. Twelve forest stands were selected to investigate fine root biomass, morphology, and growth along a gradient of increasing forest conversion from near-natural forest to cacao agroforestry systems in Central Sulawesi, Indonesia. Fine root biomass decreased markedly with increasing forest disturbance. Fine root growth rate showed a weak dependence on forest disturbance, whereas fine root turnover (growth per standing fine root biomass) was higher in the more heavily disturbed stands. Specific root area was higher in the stands with large timber extraction and fine root N concentration was particularly high in the cacao agroforests. These two root morphological traits were positively related to fine root turnover. We conclude that the higher growth activity of fine roots in the moderately and heavily disturbed forests resulted from differences in fine root morphology and N concentration, hence partly compensating for the decrease in fine root biomass with disturbance.

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1. Introduction

Fine roots are a prominent sink for carbon acquired through canopy photosynthesis (Nadelhoffer and Raich, 1992; Hendrick and Pregitzer, 1996; Jackson et al., 1997). Although tree fine roots represent only a few percent of total tree biomass, they can consume 30–50% of the annual primary production (Ruess et al., 1996; Vogt et al., 1996; Xiao et al., 2003). Fast growth and turnover of fine roots make the fine root system a dynamic component of the forest carbon cycle (Silver et al., 2005). Therefore, the fine root system may have a large influence on how forests respond to anthropogenic disturbances (Powers, 2004). Understanding controls of fine root turnover is crucial in order to predict how carbon and nutrient cycling, plant growth and plant productivity vary under environmental change (Eissenstat and Yanai, 1997).

Root morphology plays an important role in balancing costs and benefits of root growth and activity (Espeleta and Donovan, 2002) and therefore can have a strong impact on fine root turnover and, as a result, will affect soil carbon dynamics (Eissenstat, 1992; Eissenstat et al., 2000; Wahl and Ryser, 2000; Comas et al., 2002). Functionally important morphological attributes of fine roots are specific root surface area (SRA), root tip abundance and the degree

and type of mycorrhizal infection (Janos, 1980; Leuschner et al., 2004; Withington et al., 2006; Ostonen et al., 2007). By altering these morphological traits, plants can adapt their nutrient and water exploitation to the spatially and temporally varying distribution of resources in the soil (Fitter, 1996). The cost/benefit ratio of the fine root system can be influenced by changing morphological features at the level of the individual root, or the entire root system (Leuschner et al., 2004).

Large areas of the remaining tropical rainforests are being logged and converted to agricultural systems at high rates (Nepstad et al., 1999; Achard et al., 2002). Forest conversion together with selective logging in the remaining stands can have a profound effect on the forest carbon cycle (Raich, 1983; Lal, 2005; Jandl et al., 2006). Even though intensive research has focussed on the effects of forest conversion on soil carbon (e.g. Schroth et al., 2002; Smith et al., 2002; Hairiah et al., 2006; Oelberman et al., 2006), data on the impact of anthropogenic disturbance on the fine root system of tropical forests is scarce (Vogt et al., 1996; Leuschner et al., 2006; Hertel et al., 2007). Furthermore, most of the relevant studies focus on fine root mass, but rarely take fine root productivity and fine root morphology into account. In order to predict the influence of forest conversion on the belowground carbon cycle, a better understanding of the effects of forest use intensity on the morphology of the fine root system and its dynamics is required.

By studying a sequence of forest stands differing in disturbance intensity in the forest margin zone of Sulawesi, Indonesia, we

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analysed the impact of several widespread practices of tropical forest use in South-East Asia on important traits of the fine root system of tropical moist forests. In particular, we addressed the following questions: (1) how are standing fine root biomass and fine root morphological traits affected by increasing forest use intensity? and (2) how does root growth activity respond to different degrees in forest use intensity?

2. Materials and methods

2.1. Study area

We conducted our study in the surroundings of the village of Toro in the western margin zone of Lore Lindu National Park, Central Sulawesi, Indonesia (01°39'S, 120°02'E). The Lore Lindu Park is one of the largest remaining areas of montane tropical rain forest in the region. Our 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 natural forest vegetation in the area is lower montane tropical moist forest. Common genera include *Castanopsis* (Fagaceae), *Chionantus* (Oleaceae), *Dysoxylum* (Meliaceae), *Ficus* (Moraceae) and *Lithocarpus* (Fagaceae) (Gradstein et al., 2007). The soils in the Toro region are predominantly well drained Cambisols (World Reference Base Classification, FAO, 2006) with relatively high fertility, while occasionally also Ferralsols are present with a somewhat lower pH and soil fertility (Häring et al., 2005). Annual mean air temperature in the Toro area is about 23 °C and yearly average precipitation is about 2200 mm (H. Kreilein, unpublished data). Rainfall shows a moderate seasonality with at least 100 mm per month falling throughout the year. Air humidity ranges mostly between 75 and 90% throughout the year.

In the margin zone of Lore Lindu National park, a number of forest use regimes differing in disturbance intensity are widespread. We selected 12 study plots representing four typical stages of forest disturbance ranging from near-natural old-growth forests to cacao agroforestry systems, which replace the former natural forest (Leuschner et al., 2006). Thus, a matrix of 12 plots of 30 m × 50 m size of four different stages of forest use intensity with three replicate plots per forest use type were investigated. The four forest use types were defined as follows: forest use type A is an old-growth natural forest with virtually no human impact; forest use type B is a slightly disturbed forest characterized by the irregular extraction of small diameter stems; forest use type C represents a moderately disturbed forest with selective logging of large-diameter stems at irregular intervals, and forest use type D is an agroforestry system with cacao (*Theobroma cacao*) planted under a sparse shading cover of remaining natural forest trees (Leuschner et al., 2006). Due to the different management intensities, the forest types showed a clear differentiation with respect to the above-ground stand structure. Plots of the forest use type B were only slightly different from those of the undisturbed forest with regard to canopy cover, tree height, stem diameter, stem density and basal area (Table 1). In contrast study plots of forest use types C and D showed markedly lower values in canopy cover, tree height, stem diameter and basal area. Stem density was higher in plots of the forest use type C compared to those of types A and B, but lower in the cacao agroforests (type D). Temperature and moisture conditions in the upper soil were similar in the three forest use types A–C, but agroforestry systems tended to have somewhat higher soil temperature and lower soil water contents (Table 1). Soil morphological and chemical properties showed some variation among the study plots, but there was no trend along the gradient of increasing forest use (Table 1).

Table 1

Above-ground stand structural parameters and characteristics of the upper 10 cm of the soil in the study plots of the four forest use types.

| | Forest use type | | | |
|---|-----------------|------|------|------|
| | A | B | C | D |
| Canopy cover (%) | 90 | 87 | 82 | 77 |
| Mean tree height (m) ^a | 21.3 | 18.1 | 15.2 | 6.1 |
| Mean dbh (cm) ^a | 29.5 | 26.9 | 21.3 | 9.5 |
| Stem density (n ha ⁻¹) ^a | 2474 | 2672 | 3819 | 2106 |
| Basal area (m ² ha ⁻¹) ^a | 52.3 | 47.1 | 39.2 | 21.2 |
| Mean temperature at soil surface (°C) ^b | 20.8 | 20.7 | 21.0 | 22.2 |
| Mean soil water content (vol%) ^b | 35.3 | 33.4 | 37.8 | 28.6 |
| Bulk density of the soil (g cm ⁻³) ^c | 0.99 | 1.11 | 1.08 | 1.20 |
| pH (KCl) ^c | 5.07 | 4.69 | 3.87 | 6.05 |
| Base saturation (%) ^c | 85.0 | 89.6 | 49.2 | 99.5 |
| Soil N (%) ^c | 0.31 | 0.27 | 0.27 | 0.21 |
| Soil C/N (g g ⁻¹) ^c | 9.8 | 9.2 | 11.1 | 10.0 |

Measurements of the canopy cover were done using a convex spherical densiometer at 10 randomly selected locations per stand with four readings per location in the four main aspects (N, E, S, W; i.e. n = 40 per stand).

^a Data from Dietz et al. (2007).

^b Data from L. Woltmann (unpublished).

^c Data from Häring et al. (2005).

2.2. Investigation of fine root biomass, morphology, and C and N concentrations

In order to assess standing fine root biomass, root samples were taken with a soil corer (3.5 cm in diameter) from the first 50 cm of the soil including the organic layer at six randomly selected sampling locations per study plot. To avoid clumping of the locations and to cope with the spatial heterogeneity of the plots, the samples were taken at a minimum distance of four meter from each other. The soil cores were separated into three depths (0–10, 10–20, 20–50 cm). The soil samples were transferred to plastic bags and transported to the laboratory at the University of Palu, where processing of the stored samples (4 °C) took place within 45 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. Only fine roots (roots <2 mm in diameter) of trees were considered for analysis (including roots of the cacao trees in the agroforests). Roots of grasses and herbs, which only were abundant in the agroforestry systems, were easily distinguished from tree fine roots by their smaller diameter, light colour and the absence of a lignified periderm. Live fine roots (biomass) were separated from dead rootlets (necromass) under the stereomicroscope based on 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 fine root biomass of each sample was dried at 70° (48 h) and weighed. The data were expressed as fine root abundance (g m⁻²).

For investigating fine root morphology at the 12 forest stands, we took fine root samples with a soil corer from the upper 20 cm of the soil at five randomly selected locations per study site. The samples were divided into two layers (0–10 and 10–20 cm) and transported to the lab in Palu, where the root samples were cleaned as described above. The cleaned samples were transferred to zip-lock bags and transported within a few days to the lab in Göttingen, Germany. In the lab, one intact rootlet per sample and soil depth (n = 120 in total) was used to determine the number of root tips per g of fine root mass by visual counting of intact tips under the stereomicroscope. Additionally, the rootlets were analysed for fine root surface area (cm² g⁻¹) and fine root diameter using a

WinRhizo (Régent, Quebec, Canada) image processing unit. Based on these data and the data on fine root biomass of the respective stands, we calculated tip frequency (number per m² ground area) and root area index (RAI; m² root surface area per m² ground area). RAI and root tip frequency at 20–50 cm soil depth were extrapolated using the morphology data from the 10–20 cm soil horizon.

Additionally, mean fine root C and N concentrations from all four forest use types were established. Root samples from one representative stand per forest use type were taken from the first 20 cm of the soil at 10 randomly selected locations and separated into two depths (0–10 and 10–20 cm). In the lab in Palu, the roots were cleaned as described above and the C and N concentrations measured using a CNH auto-analyser (Vario EL III, Hanau, Germany).

2.3. Analysis of fine root growth activity

An estimate of fine root growth capacity of the different forest use types was obtained by conducting ingrowth core experiments with local soil material in the first 10 cm of the soil according to the methodology described by Persson (1980), Powel and Day (1991) and Majdi et al. (1996). In order to cover a period of more than 1 year, we installed ingrowth cores from January to July 2004 and from August 2004 until May 2005. At 10 randomly selected locations in each of the 12 stands, cores were cut from the topsoil (diameter 55 mm, depth 10 cm) at a minimum distance of 5 m apart from each other. All macroscopically visible live and dead root material (>c. 10 mm length) was extracted by hand. The remaining soil material was replaced into the hole and its edges were marked at the soil surface. Care was taken that the structure and density of the soil samples were conserved as much as possible. The samples were recollected with the soil corer after the respective exposure periods. In the laboratory, root biomass in the cores was extracted as described above. Following Vogt et al. (1998), we calculated fine root regrowth in the cores as the increase in root biomass from the start of root recolonisation (in our study 2 months after installation) until harvest. Fine root growth in the cores during the recolonisation period was extrapolated to 1 year and expressed in g m⁻² year⁻¹. To obtain a balanced estimate of fine root growth rate during a 1-year-period, we averaged the two recolonisation periods. We then extrapolated the data to 20 cm depth using the ratio of standing fine root biomass between the two soil layers. Fine root turnover (year⁻¹) in the ingrowth cores was calculated as annual fine root growth divided by the standing stock of fine root biomass (Aber et al., 1985; Aerts et al., 1992) by relating the fine root growth recorded in the ingrowth cores after a 1-year recolonisation period to the fine root biomass observed in the surrounding, unmanipulated soil at the time of harvest. To measure the standing fine root biomass in the surrounding soil, additional soil cores were taken at approximately 30 cm distance from each of the ingrowth cores. These additional root samples were processed as described above.

2.4. Statistical analysis

All data were tested for Gaussian distribution using a Shapiro–Wilk test. The majority of the datasets showed a non-Gaussian distribution and could not satisfyingly be transformed. Therefore, differences in standing fine root biomass, morphology and fine root growth between the four forest use types or between the different soil horizons were analysed using a non-parametric analysis of variance (Kruskal–Wallis test) and a Mann–Whitney two sample test (*U*-test). These calculations were done with the software package SPSS Version 12.01 (SPSS Inc., Chicago, USA).

The dependence of fine root biomass, root area index, root tip frequency, fine root growth rate and fine root turnover on various above-ground stand structural parameters and soil properties was analysed by single-factor linear or simple non-linear (i.e. with a non-linear polynomial) regression analyses (software package Xact Version 7.12, SciLab, Hamburg, Germany). A one-factorial linear regression analysis was used to analyse the dependence of fine root growth rate and fine root turnover on standing fine root biomass, SRA, root tip abundance, and fine root N concentration.

3. Results

3.1. Fine root biomass

Standing fine root biomass gradually decreased from the undisturbed forest sites (type A) to the cacao plantations under natural shading cover (type D, Table 2). With a mean of 408 g m⁻², the undisturbed forest stands (type A) had a significantly higher standing fine root biomass than all other forest use types ($P < 0.05$). Fine root biomass in the disturbed forest stands with either small timber extraction (type B), large timber extraction (type C) or agroforestry (type D) did not differ significantly from each other, even though the mean fine root biomass of type B was about 90 g m⁻² higher than that of types C and D. In all stands, 70–80% of the profile total of fine root biomass was found in the upper 20 cm of the soil.

3.2. Morphology and C and N concentration of fine roots

Average diameter of the fine root fraction (<2 mm) ranged between 0.61 and 0.85 mm and did not vary markedly with soil depth or forest use type (Table 3). Nevertheless, fine roots in the upper 10 cm of the soil tended to have a somewhat smaller diameter than those at 10–20 cm depth.

The mean specific root area (SRA) in the upper 10 cm of the soil increased from 203 cm² g⁻¹ in the undisturbed forest stands (type A) to 342 cm² g⁻¹ in the forest stands with large timber extraction (type C, Table 3). In the cacao agroforestry sites (type D), we observed intermediate SRA values (258 cm² g⁻¹) that were comparable to those in the forest stands with small timber extraction (type B). At 10–20 cm depth, there was generally less variation in SRA and no significant differences between the forest use types were observed ($P < 0.05$). However, the highest SRA at

Table 2
Standing fine root biomass (g m⁻²) in the upper 50 cm of the soil, including the organic layer, of the forest use types A–D.

| Soil depth (cm) | Forest use type A | Forest use type B | Forest use type C | Forest use type D |
|-----------------|-------------------|-------------------|-------------------|-------------------|
| 0–10 | 255.3 ± 30.0 Aa | 152.5 ± 32.1 Ba | 129.4 ± 22.3 Ba | 144.3 ± 23.3 Aa |
| 10–20 | 71.7 ± 21.0 Bb | 67.1 ± 25.6 Ba | 49.8 ± 10.7 Ba | 44.1 ± 10.0 Bb |
| 20–50 | 81.3 ± 13.9 Ab | 93.5 ± 38.7 ABa | 46.0 ± 10.9 Bb | 41.1 ± 9.1 Bb |
| Profile total | 408.3 ± 47.0 A | 313.2 ± 79.5 B | 225.2 ± 32.1 B | 229.4 ± 29.8 B |

Given are means and standard errors from three plot replicates per forest use types. Different capital letters indicate statistically significant differences between the forest use types, different lower-case letters indicate significant differences between the respective soil horizons or profile totals of the forest types ($P < 0.05$).

Table 3Mean fine root diameter, specific root area and specific root tip abundance at 0–10 and 10–20 cm soil depth (means \pm S.E.) of the four forest use types.

| Forest use type | Soil depth (cm) | Fine root diameter (mm) | Specific root area ($\text{cm}^2 \text{g}^{-1}$) | Specific root tip abundance (n g^{-1}) |
|-----------------|-----------------|-------------------------|--|---|
| A | 0–10 | 0.63 \pm 0.04 Aa | 203.0 \pm 22.3 Aa | 1803 \pm 423 Aa |
| | 10–20 | 0.85 \pm 0.08 Ab | 217.1 \pm 33.2 Aa | 1922 \pm 404 Aa |
| B | 0–10 | 0.61 \pm 0.06 Aa | 237.0 \pm 25.0 ABa | 2298 \pm 442 ABa |
| | 10–20 | 0.69 \pm 0.07 ABa | 223.5 \pm 28.5 Aa | 2360 \pm 516 Aa |
| C | 0–10 | 0.62 \pm 0.06 Aa | 342.2 \pm 62.5 Ba | 3187 \pm 602 Ba |
| | 10–20 | 0.70 \pm 0.08 ABa | 176.6 \pm 26.3 Ab | 2004 \pm 624 Ab |
| D | 0–10 | 0.61 \pm 0.08 Aa | 258.0 \pm 42.5 ABa | 3643 \pm 910 ABa |
| | 10–20 | 0.63 \pm 0.04 Ba | 250.8 \pm 43.9 Aa | 2060 \pm 259 Aa |

Different capital letters indicate statistically significant differences among forest use types in a given soil horizon, different lower-case letters indicate significant differences between the soil horizons in a given forest use type ($P < 0.05$).

Table 4Fine root C and N concentrations (%) at 0–10 and 10–20 cm soil depth (means \pm S.E.).

| Forest use type | Soil depth (cm) | Fine root N (%) | Fine root C (%) | Fine root C:N |
|-----------------|-----------------|---------------------|-------------------|-------------------|
| A | 0–10 | 1.06 \pm 0.04 Aa | 42.5 \pm 1.1 Aa | 40.2 \pm 1.1 Aa |
| | 10–20 | 1.01 \pm 0.05 Ba | 42.3 \pm 0.9 Aa | 42.5 \pm 1.9 Aa |
| B | 0–10 | 1.18 \pm 0.04 Ba | 42.3 \pm 0.6 Aa | 36.9 \pm 1.2 Aa |
| | 10–20 | 1.08 \pm 0.05 Ab | 43.4 \pm 0.6 Aa | 41.1 \pm 1.9 Ab |
| C | 0–10 | 1.17 \pm 0.09 ABa | 45.7 \pm 1.0 Ba | 40.0 \pm 1.3 Aa |
| | 10–20 | 1.04 \pm 0.09 Ab | 44.9 \pm 1.2 Aa | 43.5 \pm 1.6 Ab |
| D | 0–10 | 1.79 \pm 0.11 Ca | 39.0 \pm 1.2 Ca | 22.6 \pm 1.6 Ba |
| | 10–20 | 1.66 \pm 0.10 Ba | 37.2 \pm 1.6 Ba | 23.2 \pm 1.9 Ba |

Different capital letters indicate statistically significant differences among the forest use types, different lower-case letters indicate significant differences between the respective soil horizons of a given forest type ($P < 0.05$).

10–20 cm depth was found in type D ($251 \text{ cm}^2 \text{g}^{-1}$), while the lowest SRA value in this soil horizon was found in type C ($177 \text{ cm}^2 \text{g}^{-1}$; Table 3).

In the upper 10 cm of the soil, we found a gradual increase in the number of root tips per root biomass (specific root tip abundance) with increasing forest disturbance. Root tip abundance in this soil horizon varied between 1803 tips g^{-1} in the undisturbed forest stands (type A) and 3643 tips g^{-1} in the cacao plantations (type D; Table 3). In contrast, no significant differences in fine root tip abundance were observed at 10–20 cm depth between the four forest use types ($P < 0.05$). While in the forest stands with minor disturbance (types A and B) mean root tip abundance was similar at both soil depths, root tip abundance in the more heavily

disturbed forest stands (types C and D) was markedly higher at 0–10 cm depth than deeper in the soil.

The C:N ratio of the fine root biomass was significantly lower in the cacao agroforestry stand than in any of the forest stands and in both soil horizons ($P < 0.05$; Table 4). The lower ratio was caused by both a significantly higher N concentration and a significantly lower C concentration in fine roots of type D ($P < 0.05$). Among the stands A, B, and C, fine roots of the undisturbed forest (type A) tended to have the lowest N concentration. This was valid for both soil depths.

3.3. Root area index and root tip frequency at the stand level

The average root area index ($\text{m}^2 \text{m}^{-2}$) in the upper 50 cm of the soil was largest in the undisturbed forest ($8.5 \text{ m}^2 \text{m}^{-2}$; Fig. 1a). Surprisingly, even minor timber extraction reduced RAI significantly by more than 20% ($P < 0.05$). As a result of an increase in specific root surface area, the mean RAI in the forest stand with large timber extraction (type C) and the agroforestry stand (type D) differed not significantly from that in the forest stand with a much lower disturbance level (type B) despite a tendency towards reduced root biomass. The root tip frequency (n m^{-2}) in the upper 50 cm of the soil did not differ significantly between the four forest use types ($P < 0.05$; Fig. 1b). Within the three stands A, B and C, root tip frequency tended to decrease with increasing disturbance intensity from $0.79 \times 10^6 \text{ m}^{-2}$ to $0.64 \times 10^6 \text{ m}^{-2}$. However, the cacao agroforestry stand had the highest number of root tips per square meter ground area (0.80×10^6). The RAI values and the root tip frequency of the most heavily disturbed stands (C and D) were especially high in the uppermost soil horizon (0–10 cm), while the lower soil horizons contained only few tips.

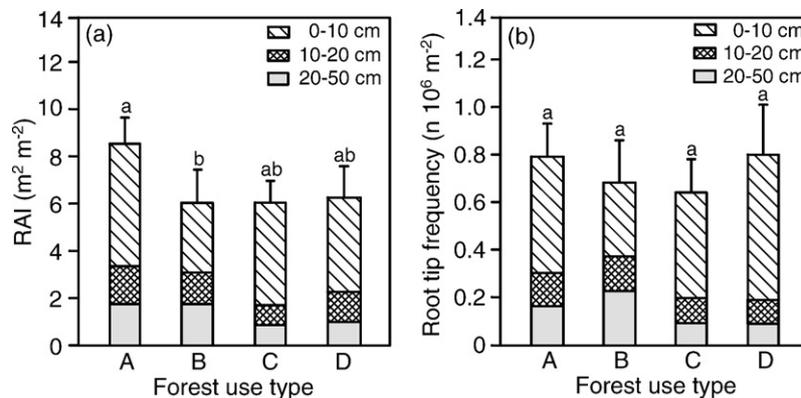


Fig. 1. Mean root area index (RAI) and root tip frequency in the four forest use types at 0–10, 10–20 and 20–50 cm depth. Given are means and standard errors from three plot replicates per forest use types. Different letters indicate statistically significant differences between the forest use types at $P < 0.05$.

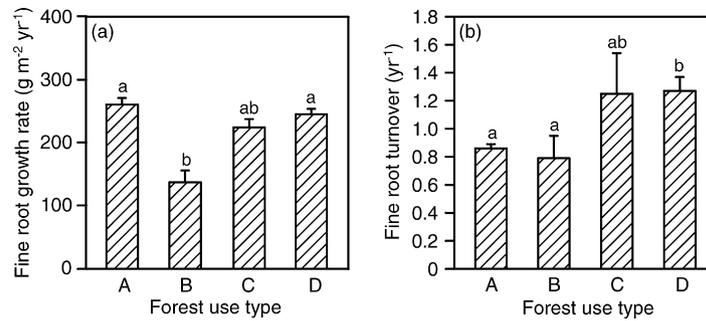


Fig. 2. Fine root growth rate and fine root turnover in the upper 10 cm of the soil, as estimated with the ingrowth core method. Given are means and standard errors from three plot replicates per forest use types. Different letters indicate statistically significant differences between the forest use types at $P < 0.05$.

3.4. Fine root growth rate

The growth rate of fine roots in the ingrowth cores placed in the upper 10 cm of the soil was significantly higher in the undisturbed forests (type A) than in the forest stands with small timber extraction (type B) ($P < 0.05$; Fig. 2a). In the forest stands with large timber extraction (type C) and the cacao agroforestry stands, on the other hand, fine root growth rate was only marginally lower than in the undisturbed forest stands.

The fine root turnover (fine root growth per standing root biomass; unit: year^{-1}) showed a different pattern (Fig. 2b). With mean values of 0.86 year^{-1} and 0.79 year^{-1} , the fine root turnover in the undisturbed and slightly disturbed stands (types A and B) was markedly lower than in the stands with large timber extraction or agroforestry (types C and D; 1.25 year^{-1} and 1.27 year^{-1} , respectively). Although the mean fine root turnover in type C was relatively high (1.25 year^{-1}), the difference to the

other types was not significant due to a large variation in those stands.

3.5. Influence of stand structure and soil chemistry on fine root parameters

Regression analyses showed significant relationships between stand structure and various fine root parameters (Table 5). The profile total of standing fine root biomass was positively related to the canopy cover of the stands: fine root biomass increased on average by about 80% from a forest stand with 70% canopy cover to a stand with 90% cover. On the other hand, profile totals of RAI and root tips did not demonstrate any direct relationship with the stand structural parameters. While no relationship between stand structure and fine root growth could be detected, we observed a negative relationship between fine root turnover and canopy cover and between fine root turnover and mean tree height of the stands (Table 5). Finally, none of the fine root parameters showed a correlation with the base saturation and pH value of the soil.

3.6. Inter-correlations between different fine root traits

Tests of inter-correlation between the various measured fine root parameters revealed that annual fine root growth in the ingrowth cores at 0–10 cm was positively related to fine root biomass in that horizon (Table 6). None of the other parameters showed statistically significant effects on fine root growth ($P < 0.05$). In contrast to root growth, fine root turnover was negatively related to fine root biomass at 0–10 cm, but positively related to specific root area. Fine root turnover tended to increase with increasing fine root N concentration, but this effect was not statistically significant ($P < 0.05$).

Table 5

Results from linear or simple exponential (*) regression analyses on the influence of above-ground forest structural parameters and soil conditions on standing fine root biomass, root area index (RAI), root tip frequency, fine root growth rate, and fine root turnover in the upper 10 cm of the soil of the four forest use types.

| Parameter | Source | r | r^2_{adj} | P |
|--|------------------|--------------|--------------------|-----------------|
| Fine root biomass (g m^{-2}) | Canopy cover* | 0.58 | 0.27 | <0.05 |
| | Tree height* | 0.42 | 0.09 | 0.17 |
| | Basal area | 0.11 | -0.01 | 0.73 |
| | Base saturation* | 0.16 | -0.07 | 0.62 |
| | pH | -0.08 | -0.09 | 0.81 |
| RAI ($\text{m}^2 \text{m}^{-2}$) | Canopy cover | 0.15 | -0.08 | 0.64 |
| | Tree height | 0.16 | -0.07 | 0.61 |
| | Basal area | -0.05 | -0.10 | 0.88 |
| | Base saturation | 0.12 | -0.08 | 0.71 |
| | pH | 0.22 | -0.05 | 0.50 |
| Root tip frequency (number m^{-2}) | Canopy cover | -0.01 | -0.01 | 0.97 |
| | Tree height | -0.02 | -0.09 | 0.96 |
| | Basal area | -0.25 | -0.03 | 0.43 |
| | Base saturation | 0.16 | -0.07 | 0.63 |
| | pH* | 0.49 | 0.17 | 0.10 |
| Fine root growth rate ($\text{g m}^{-2} \text{year}^{-1}$) | Canopy cover* | -0.02 | -0.10 | 0.92 |
| | Tree height | -0.03 | -0.10 | 0.93 |
| | Basal area | -0.03 | -0.10 | 0.92 |
| | Base saturation | 0.08 | -0.09 | 0.81 |
| | pH* | -0.02 | -0.10 | 0.95 |
| Fine root turnover (year^{-1}) | Canopy cover* | -0.57 | 0.25 | <0.05 |
| | Tree height* | -0.58 | 0.26 | <0.05 |
| | Basal area | -0.27 | -0.02 | 0.41 |
| | Base saturation | -0.14 | -0.08 | 0.67 |
| | pH* | 0.24 | -0.04 | 0.46 |

Statistically significant relationships ($P < 0.05$) are printed in bold.

Table 6

Results from linear regression analysis of the influence of fine root biomass (g m^{-2}), specific root surface area ($\text{cm}^2 \text{g}^{-1}$), root tip abundance (n g^{-1}), and fine root N concentration on fine root growth rate ($\text{g m}^{-2} \text{year}^{-1}$) and fine root turnover (year^{-1}) in the upper 10 cm of the soil of the four forest use types.

| Parameter | Source | r | r^2 | P |
|-----------------------|---------------------------|--------------|-------------|-----------------|
| Fine root growth rate | Fine root biomass | 0.71 | 0.50 | <0.01 |
| | Specific root area | -0.31 | 0.10 | 0.32 |
| | Root tip abundance | 0.17 | 0.03 | 0.60 |
| | Fine root N concentration | 0.23 | 0.05 | 0.76 |
| Fine root turnover | Fine root biomass | -0.58 | 0.31 | <0.05 |
| | Specific root area | 0.67 | 0.44 | <0.05 |
| | Root tip abundance | 0.14 | 0.02 | 0.68 |
| | Fine root N concentration | 0.63 | 0.40 | 0.18 |

Statistically significant relationships are printed in bold.

4. Discussion

4.1. Standing fine root biomass

Profile totals of fine root biomass decreased gradually with increasing forest use intensity, with a more than 40% reduction in the heavily disturbed stands of types C and D as compared to the undisturbed stands of type A. All disturbed forest stands had significantly lower standing fine root biomasses than the undisturbed forest stands. Interestingly, even the extraction of small timber resulted in a significant decrease in fine root biomass, while no significant differences were found between the three disturbed forest types (B, C, and D). Other studies on the effect of natural or anthropogenic disturbances in tropical forests reported similar reductions in fine root biomass due to disturbance (Silver and Vogt, 1993; Sundarapandian et al., 1996, 1999; Hertel et al., 2007).

The reduction in fine root biomass after selective logging or conversion into cacao agroforestry systems could, in theory, be explained by alterations in the above-ground structure including the reduction of overall canopy cover and basal area, by enhanced soil temperatures in the gaps leading to altered soil moisture and/or nitrogen regimes, or by a decrease in nutrient supply due to a decrease in litter input. According to correlation analyses, there was no significant relationship between the cumulative basal area of the stands and total standing fine root biomass. Thus, the reduction in wood biomass per se due to timber harvest apparently did not cause the root biomass reduction. On the other hand, we found a significant positive relationship between canopy cover and fine root biomass. This would, to a certain extent, confirm the root gap theory of Wilczynski and Pickett (1993), which assumes a thinning of the root “canopy” as a result of a thinning of the leaf canopy. However, as no relationship between fine root biomass and the distance between sampling location and the nearest tree was observed in our stands, we rather hypothesize that an overall thinning of the fine root system in the entire stand must have occurred with a decrease in canopy cover.

4.2. Fine root morphology

Specific fine root surface area in the upper 10 cm of the soil was markedly higher in the moderately disturbed forest stands (type C) than in other forest use types. A higher SRA can either be achieved through smaller root diameters or through lower tissue densities (Eissenstat, 1991). In our study, average fine root diameter did not differ significantly between the forest use types. Therefore, we assume that the particularly high SRA in the topsoil of forest use type C is mainly caused by lower root tissue densities in these stands with abundant regrowth of young, light-demanding trees in the gaps.

Abiotic factors can have a strong influence on fine root morphology. Ostonen et al. (1999) found that differences in soil nutrient and soil water regimes explained about 30% of the observed root morphological differences in different stands of Norway spruce, while Leuschner et al. (2004) observed a significantly higher root tip abundance in nutrient-poor soils compared to nutrient-rich ones. In the present study, on the other hand, we did not find any significant influence of soil chemical parameters on SRA or tip abundance. The lack of influence of soil parameters on root morphology in this study can most likely be attributed to the relatively small differences in soil acidity and nutrient availability between the stands.

Biotic factors like the availability of soluble carbohydrates and the potential growth rate of a tree species can influence the expression of morphological characteristics of fine roots as well.

Roots of fast growing species seem to possess specific adaptations for fast root growth into unexploited soil patches and generally have a higher SRA, a higher root tip abundance, a greater degree of branching and lower concentrations of phenolic substances compared to slow-growing species (Nicotra et al., 2002; Comas and Eissenstat, 2004). The SRA values (203–342 cm² g⁻¹) and root tip abundance values (1803–3643 g⁻¹) found in our study were comparable to those found in Costa Rican montane rainforests of different successional stages, which showed SRA values between 247 and 591 cm² g⁻¹ and tip abundances between 1400 and 3400 g⁻¹ from old-growth to early-successional forests (Hertel et al., 2003).

A tree species inventory of our study plots revealed that relatively more fast growing trees with lower wood density were present in the stands with previous large timber extraction (type C), compared to the other forest stands (M. Kessler, pers. com.). Early-successional species generally have a higher potential growth rate than mid- or late-successional species under high light conditions (Wright et al., 2003; Gilbert et al., 2006). Tyree et al. (1998) found that tropical pioneer species produced significantly more root area and root length per g dry matter investment than shade-tolerant species. Zangaro et al. (2005) also reported a decrease in SRA and root tip abundance toward late successional communities.

The growth of cacao trees is characterized by 2–3 flushes per year and root tip abundance therefore often shows an episodic pattern (Kummerow et al., 1982; Sleight et al., 1984). However, as these flushes do not occur simultaneously in all cacao trees of a stand, it is not likely that the high stand average of root tip abundance observed in our study is caused by such a flush in growth. We assume that the high SRA values in the stands of forest use type C are most likely a consequence of the abundance of fast growing, early successional trees in these stands, while the high tip abundance in forest use type D might be related to the dominance of cacao trees and their specific root morphology including particularly high nitrogen concentrations of fine root biomass.

4.3. Root area index and root tip frequency

In a review on fine root mass and surface area, Jackson et al. (1997) found a mean RAI value of 7.4 m² m⁻² for tropical evergreen forests worldwide. With averages between 6.0 and 8.5 m² m⁻², the RAI values observed in our study are close to this estimated global average. No significant differences in root tip frequency were found between the different forest use types and only the undisturbed forest stands and the stands with small timber extraction differed in terms of RAI. This lack of significant variation in RAI and root tip frequency among the forest use types is mainly due to the fact that RAI and root tip frequency are a function of standing fine root biomass on the one hand, and the morphological parameters SRA and tip abundance on the other hand. For example, in the studies of Berish (1982), Berish and Ewel (1988) and Hertel et al. (2003), RAI increased with an increasing participation of late-successional trees despite a decrease in SRA. Fine root biomass significantly decreased along the disturbance gradient, while specific root area and tip abundance increased with increasing forest disturbance. This allows to conclude that the fine root systems in the heavily disturbed stands with an increasing proportion of young early-successional trees were able to partly compensate the loss in biomass by a specific increase in absorbing root surface area.

4.4. Fine root growth and turnover

Fine root growth rate, as estimated with ingrowth cores, seemed to decline with an intensification of forest use and was

distinctly lower in the forest stands with small timber extraction (type B) compared to the undisturbed forest stands (type A). Surprisingly, fine root growth rate increased again with a further intensification of forest use. This was mainly due to the markedly higher fine root turnover in the forest stands of higher disturbance intensity (types C and D) compared to the less disturbed forest use type B, although standing fine root biomass was lower in forest use types C and D than in B.

How can the observed differences in fine root turnover among the forest use types be explained? Given that root morphology affects root maintenance and construction costs, faster fine root turnover is expected in species with roots characterized by a high SRA and low tissue density (Espeleta and Donovan, 2002) as well as in roots characterized by small diameter and little lignification (Eissenstat, 1992; Eissenstat et al., 2000; Wahl and Ryser, 2000; Comas et al., 2002). High turnover values in the more heavily disturbed forest types C and D were positively correlated with SRA. A root system consisting of energetically less expensive roots may not only re-allocate root length more rapidly in favourable soil patches, but might also be more responsive to root pruning (e.g. herbivory or mechanical disturbance) than root systems which invest more in biomass and possibly more in defence compounds (Eissenstat, 1991). Thus, a higher SRA and a more rapid root turnover in the C stands and especially in the cacao agroforestry plots (D) can be judged as an adaptation to the higher disturbance levels in these stands.

Besides SRA and tissue density, N concentration of the roots and mycorrhizal infection can also have a significant impact on fine root dynamics. Tissue N is a key factor in understanding C costs of maintaining fine roots (Pregitzer et al., 2002). Roots with high N concentrations typically have higher respiration rates; therefore, fine root construction and maintenance costs are inversely related (Pregitzer et al., 1998, 2002), which affects fine root longevity. In fact, Withington et al. (2006) found that root C:N ratio was the only root characteristic that significantly correlated with fine root life span for eleven temperate woody species tested in their study. As already has been suggested by Comas et al. (2002), these authors found that fast growing species had higher root N concentrations and lower C:N ratios than slow growing species. We found significantly higher N concentrations in the roots of the cacao plantations compared to the roots of the forest stands and a positive (though non-significant) relationship between fine root N concentration and fine root turnover in the studied stands. Thus, cacao trees replacing rainforest trees are likely to follow a rather opportunistic strategy of high turnover of fine roots which are characterized by high root tip frequencies, SRA and root N concentrations, and thus result in relatively high C and N fluxes from the roots to the soil.

5. Conclusions

The results of our study clearly show that forest disturbance has a profound impact on fine root standing mass, fine root growth rate and fine root morphology in South-east Asian tropical moist forests. Even minor disturbances, like irregular extraction of small-diameter stems, caused a significant reduction of standing fine root biomass. Root morphology of species replacing the extracted natural trees can differ significantly from that of the remaining vegetation. Both the fast growing early-successional species that colonize the gaps as well as the planted agroforestry species (cacao) were found to have a larger SRA and root tip abundance compared to the tree species in the undisturbed natural forest. The larger SRA and root tip abundance in the more heavily disturbed sites levelled out some of the root mass-based differences in RAI and root tip frequency. A higher fine root turnover was observed in

the stands with a higher abundance of young, fast growing species and especially in the cacao agroforestry stands, and seem to be a result of a higher SRA and tip abundance and higher root N concentrations. Hence, we conclude that increasing forest use intensity leads to a decrease in fine root biomass while specific root tip abundance, root N concentration and root turnover increase along the forest conversion gradient.

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