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

Christoph Leuschner *, Marieke Harteveld, Dietrich Hertel

Plant Ecology, Albrecht-von-Haller Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, D-37073 Göttingen, Germany

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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.

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

* Corresponding author. Tel.: +49 551 395718; fax: +49 551 395701.
E-mail address: cleusch@gwdg.de (C. Leuschner).

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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 (cm^2 g^{-1}) and fine root diameter using a