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Fine Root Biomass and Production in Tropical Moist Forest of Eastern Nepal

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ABSTRACT

The fine root biomass (< 5 mm diameter) was estimated from two soil depths (upper: 0-15 and lower: 15-30 cm) during summer, rainy and winter seasons in the undisturbed stand (US) and disturbed stand (DS) of tropical moist forest of Sunsari district in eastern Nepal. Soil samples were analyzed also for their physico-chemical characteristics. In the upper soil depth, soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP) and potassium (K) were 3.07%, 0.24%, 626.6 $\mu\text{g g}^{-1}$, and 346.3 $\mu\text{g g}^{-1}$ respectively in US and 1.8%, 0.14%, 618.3 $\mu\text{g g}^{-1}$, and 268.1 $\mu\text{g g}^{-1}$ respectively in DS. Similarly, annual mean soil microbial biomass: carbon (MB-C), nitrogen (MB-N) and phosphorus (MB-P) were 558.4 $\mu\text{g g}^{-1}$, 50.7 $\mu\text{g g}^{-1}$, and 12.3 $\mu\text{g g}^{-1}$ respectively in US and 438.5 $\mu\text{g g}^{-1}$, 39.9 $\mu\text{g g}^{-1}$, and 9.7 $\mu\text{g g}^{-1}$ respectively in DS. Annual mean fine root biomass (FRB), fine root production (FRP) and turnover rate was 6.6 Mg ha^{-1} , 5.2 $\text{Mg ha}^{-1} \text{ year}^{-1}$, and 0.78 respectively in US; and 3.4 Mg ha^{-1} , 2.9 $\text{Mg ha}^{-1} \text{ year}^{-1}$, and 0.86 respectively in DS. In comparison to upper depth, FRB decreased in lower depth by 50% in US and 55% in DS. Distinct seasonality was observed in FRB in both the stands. It was maximum in rainy and minimum in summer season. Variations in FRB due to difference in stand, season and depth were significant ($P < 0.001$). In US, FRB showed significant negative correlations with SOC, TP, MB-C and MB-N whereas, FRP showed significant positive correlations with them except TP. In DS, none of the soil variables showed significant correlations with FRB but SOC, TN, MB-C and MB-N showed significant negative correlations with FRP.

Key Words: Forest Disturbance; Fine Root Dynamics; Soil Characteristics; Seasonal Variation; Tropical Forest.

INTRODUCTION

Fine root is one of the dynamic components of below-ground biomass. The root having <5 mm diameter is generally considered as fine root (Espeleta and Clark 2007, Maycock and Congdon 2000, Rieger et al. 2013). Fine roots of <2 mm diameter size are even exemplified as more active component. Fine roots influence the soil organic matter and nutrient cycling in the terrestrial ecosystems (Hendricks et al. 2006). The contribution of fine roots in the carbon and nutrients input to soil is equivalent to or even higher than that from leaf litter in tropical moist forests (Roderstein et al. 2005).

Fine roots comprise about 30% of the aboveground

biomass (Noordwijk et al. 1996). So far the production is concerned fine roots contribute over 33%, or even between 40-85% of the net primary production (Hendricks et al. 2006, Hoffmann and Usoltsev 2001). In tropical moist forests, fine roots (≤ 2 mm diameter) comprise up to 50% of the net primary production (Gill and Jackson 2000). It happens because the production and turnover of fine roots flux a considerable amount of carbon to the ecosystems. It becomes clear from the turnover rate of 0.56 yr^{-1} in forest ecosystems (Gill and Jackson 2000). After analyzing the global data, Finér et al. (2011) also reported turnover rate of 0.77, 1.21, and 1.44 yr^{-1} for boreal, temperate, and tropical forests respectively.

Fine roots absorb water and nutrients from soil. They show quick response to changes in water and nutrient availability (Espeleta and Clark 2007). Vertical distribution of fine root is dependent on the soil environment and stand age (Yuan and Chen 2010). Fine root dynamics is usually influenced by soil properties like depth, bulk density, moisture, temperature, clay, nutrient content, and soil microbial biomass (Joslin et al. 2006). Plant species composition, genetic properties and seasonality are also the determining factors for the growth and development of the fine root (Barbuiya et al. 2012, Espeleta et al. 2009, Lei et al. 2012).

Soil nutrients like nitrogen, phosphorus and potassium have strong influence on fine root biomass. In general, soil nutrients show negative relationships with fine roots (Jimnez et al. 2009). Hendricks et al. (2006) found a negative relationship between N availability and fine root biomass. Lima et al. (2010) also found an opposite trend between fine root biomass, and soil moisture, N and P availabilities. Fine roots increase their surface area in water and nutrient deficient soils mainly for nutrient absorption (Kochsiek et al. 2013). The reduction in fine root biomass with nutrient availability may be due to the decrease in carbon share in root production or increased turnover rates (Hendricks et al. 2006). However, the contribution of fine root to NPP remains constant with decreasing nutrient availability (Meier and Leuschner 2008).

There exist two views regarding the effect of nitrogen on fine root production. According to some studies, nitrogen fertilization increases the fine root production and turnover (Uselman et al. 2007, Pei et al. 2012, Yuan and Chen 2012), whereas other studies found uncertain and opposite results (Maycock and Congdon 2000, Nadelhoffer 2000).

Most of the research in tropical forests is confined to aboveground systems only. Only few studies are concerned with the belowground components of tropical forests (Girardin et al. 2013, Ibrahima et al. 2010, Noguchi et al. 2014, Powers and Peréz-Aviles 2013). Fine root dynamics and their governing factors are still underdeveloped in tropical moist forests (Kochsiek et al. 2013). Fine roots contribute significantly to forest soil C flux and help in the reduction of elevated carbon dioxide concentration in the atmosphere. In order to quantify the forest carbon stock accurately, fine root biomass, production and turnover rate should be estimated carefully. Therefore, the present study was designed to know the status of fine root dynamics in tropical moist forest of eastern Nepal, especially to address the

following questions: What is the status of fine root biomass and production along the soil depth and turnover rate in context of forest disturbance? How does the seasonality affect the fine root biomass and production? How are the soil characteristics correlated with fine root biomass production?

MATERIALS AND METHODS

Study Area

This study was conducted in the Sal bearing tropical moist forest, located in the Bhabar belt of Sunsari district, eastern Nepal ($86^{\circ} 53' E$ to $87^{\circ} 21' E$ and $26^{\circ} 24' N$ to $26^{\circ} 52' N$) (Figure 1). The northern and southern parts of the forest are bordered by dense settlements whereas western and eastern sides are bounded by rivers. The forest is dominated by *Shorea robusta* Gaertn. Other main associates were *Lagerstroemia parviflora* Roxb., *Terminalia alata* Heyne ex Roth., *Mallotus philippensis* (Lam.) Mull.-Arg., *Adina cordifolia* Benth. and Hook f. ex Bran. and *Dillenia pentagyna* Roxb. Top soil of the study area is typical loam.

The climate is tropical monsoonal. The year is divisible into three distinct seasons: (i) dry and warm summer season (March to May); (ii) wet and warm rainy season (June to October); and (iii) dry and cool winter (November to February). The mean monthly minimum temperature ranges from 10.9 to $25.3^{\circ}C$ and maximum temperature ranges from 22.6 to $33.2^{\circ}C$. The average annual rainfall is 1009.6 mm; of which more than 79% occurs during June to September (Figure 2). Relative humidity is high from June to September (Figure 3). Data on rainfall, temperature and humidity were considered for the period 2005-2014, and were recorded from the Department of Meteorology, Koshi Basin, Dharan in Sunsari district, Nepal.

Soil Sampling and Analysis

Forest was divided into two stands: i) Central core treated as undisturbed stand (US), and ii) Peripheral part as disturbed stand (DS). Soil samples were collected from seventy randomly established locations (thirty five each in US and DS). At each location the soil was collected from three pits ($10 \times 10 \times 30$ cm each, divided into two strata: upper 0-15 cm and lower 15-30 cm). For each stratum, the soils of three pits were composited and pooled as one replicate. Physico-chemical properties of

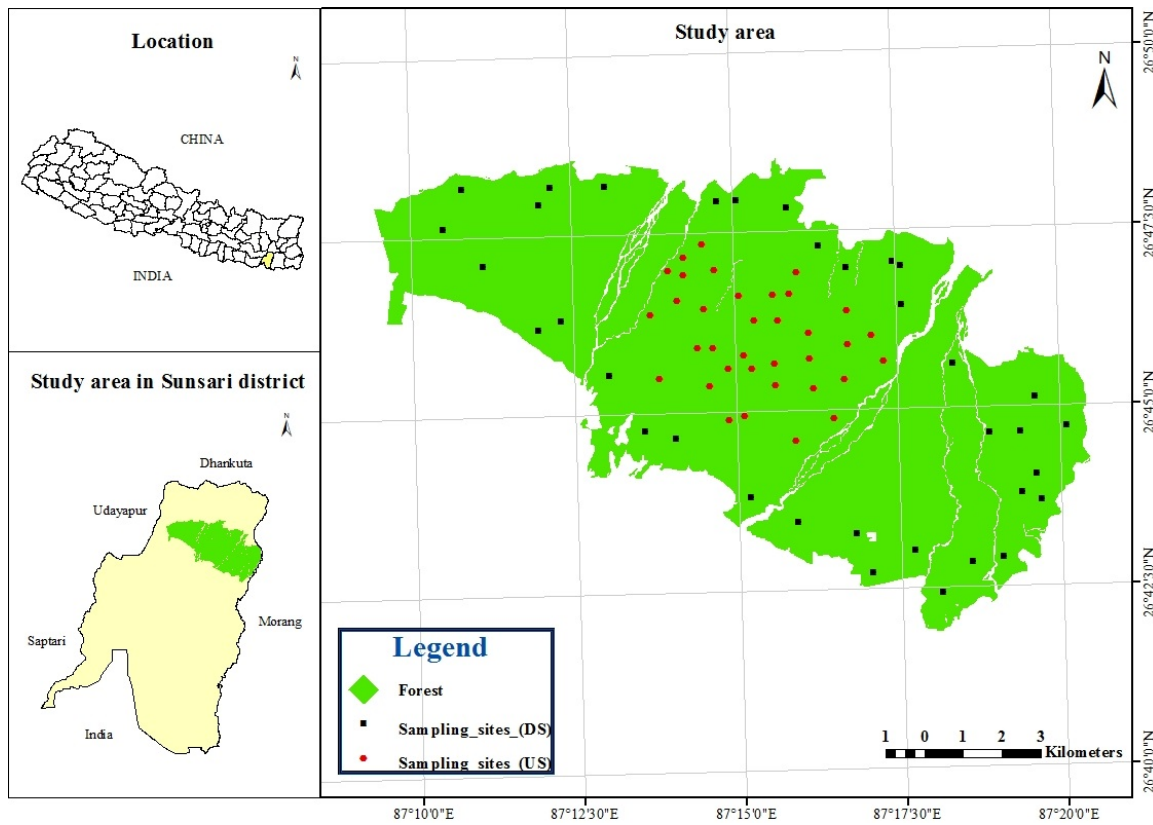


Figure 1. Map of the study area.

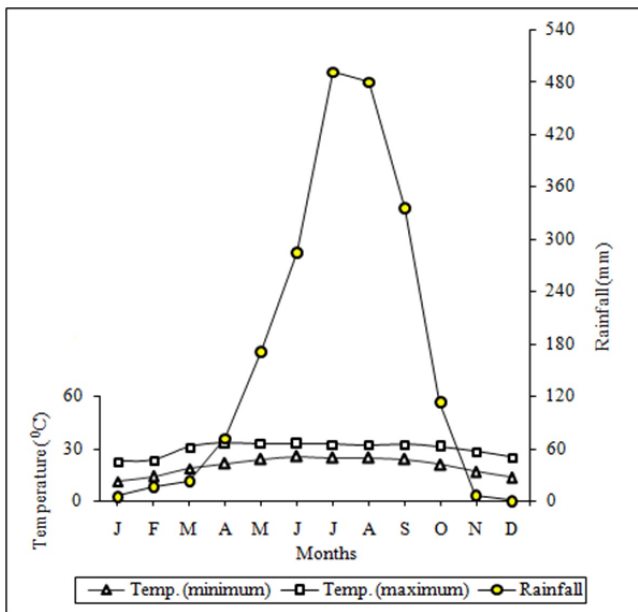


Figure 2. Ombrothermic diagram of the climate of study area.

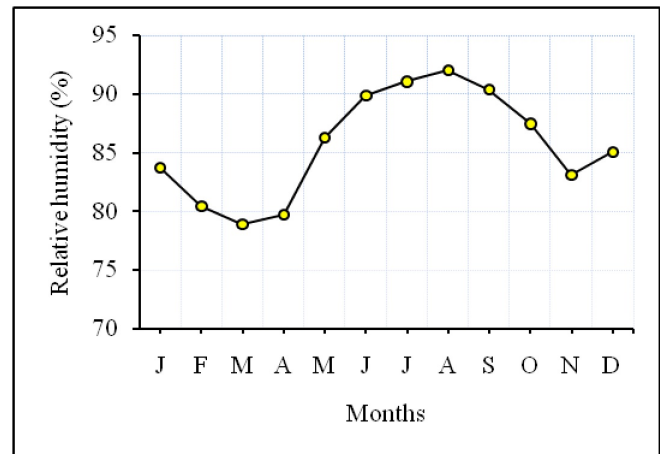


Figure 3. Relative humidity in the study area.

soil samples were determined for both upper and lower strata in the summer season, whereas microbial biomass was estimated only for the upper stratum from the soil

samples collected in May, July and January (2011–2012) representing the summer, rainy and winter seasons, respectively.

Air dried soil samples were sieved through a 2 mm mesh screen and used for further analysis. Texture, moisture, pH, water holding capacity (WHC) and bulk density (BD) of the soil were determined following Piper

(1966). Organic carbon (C) was estimated by dichromate oxidation method (Kalembasa and Jenkinson 1973). Total nitrogen (N) was determined by micro-Kjeldhal method and total phosphorus (P) by ammonium molybdate-stannous chloride blue color method (Jackson 1958). Potassium was estimated by Flame Photometer. Soil microbial biomass C, N and P were estimated by chloroform fumigation extraction method (Vance et al. 1987, Brookes et al. 1985). Carbon stock in soil was calculated by multiplying C concentration (%), soil depth and bulk density of the soil.

Fine Root Estimation

Roots having <5 mm diameter were considered as fine roots. They were collected from seventy randomly established locations, thirty five each in US and DS. Fine root biomass (FRB) was determined from soil monolith (10x10x30 cm³), divided into two depths (0-15 cm and 15-30 cm) at each location in summer (May 2011), rainy (September 2011) and winter (January 2012) seasons.

Soil monoliths were washed over a jet of water and any adhering materials were removed manually. All fine roots were handpicked with forceps without separating them into live and dead mass. Fine roots were divided into two size classes (smaller: 0-2 and larger: 2-5 mm diameter) for the estimation of biomass. Summer, rainy and winter season values were averaged to obtain annual mean fine root biomass. Fine root production (FRP) was estimated as the differences between maximum and minimum biomass values. The fine root turnover was calculated as a ratio of its production and annual mean biomass (Srivastava et al. 1986).

The fine roots of < 2 and 2-5 mm diameter of all sampling locations were mixed separately. Carbon and total ash were determined by combustion method for both size classes of fine roots. The concentration of N was analyzed diameter wise by micro-Kjeldahl method following Jackson (1958). Concentration of C and N were multiplied with the biomass of fine roots in each diameter class and thus stock of C and N in fine root was estimated.

Statistical Analysis

First the FRB and FRP data were tested for outliers, and normality (Shapiro-Wilk test). Data of all three seasons and their mean value showed almost normal trend, therefore, they were correlated with soil environmental variables. A Pearson correlation matrix was used to

correlate FRB and FRP with soil moisture, water holding capacity, bulk density, pH, soil organic C, total N, total phosphorus, potassium, organic matter, and microbial biomass: carbon, nitrogen and phosphorus from upper soil stratum of undisturbed and disturbed forest stands. Regression analysis was done only between correlated variables and fine root parameters as the dependent variables. Three ways ANOVA was performed to know the effect of stand, season and depth on the mean fine root biomass. Further, Post Hoc test (LSD) was performed for season which had more than three groups (summer, winter and rainy) and had significant effect on dependent variables. Analysis was done using IBM SPSS Statistics, ver. 20 package.

RESULTS

Environmental Variables

Environmental variables like soil texture, moisture, soil organic carbon (SOC), total N and others were studied from upper and lower strata in undisturbed and disturbed stands of tropical forest (Table 1). The soil texture was loamy in both the stands. Soil moisture, WHC, SOC, C stock in soil, total N, potassium, phosphorus, and soil microbial biomass decreased along the depth in both the stands whereas BD and pH increased depth wise. The total C stock in the soil (0-30 cm depth) was fairly higher (88.1 Mg C ha⁻¹) in US than DS (59.3 Mg C ha⁻¹). Moreover, it ranged from 61- 67% in upper soil stratum in both the stands.

Spatial Distribution of FRB

Annual mean FRB (< 5 mm in diameter) in 0-30 cm soil depth was almost double in US (6.64 Mg ha⁻¹) than the DS (3.35 Mg ha⁻¹) (Table 2). In both the stands, FRB of <2 mm size class was almost three times greater than that of 2-5 mm size class. FRB of smaller size class combining both stratum was significantly higher (4.96 Mg ha⁻¹) in US than DS (2.55 Mg ha⁻¹) (P < 0.001). Similarly, the biomass of larger fine roots was more than double (1.68 Mg ha⁻¹) in US than the DS (0.80 Mg ha⁻¹). Variation in FRB due to difference in stand was significant (P < 0.001).

Vertical Distribution of FRB

In the present study, 67- 69% of annual mean FRB was present in upper soil stratum in both the stands. Only 31-

Table 1. Environmental variables studied with their units and values in undisturbed and disturbed stands of tropical moist forest in Sunsari district, eastern Nepal.

Variables	Undisturbed stand		Disturbed stand	
	0-15 cm	15-30 cm	0-15 cm	15-30 cm
Sand (%)	45.0 ± 0.6	51.2 ± 0.6	49.8 ± 0.6	51.0 ± 0.7
Silt (%)	37.9 ± 0.7	32.9 ± 0.6	36.4 ± 0.7	37.6 ± 0.6
Clay (%)	17.1 ± 0.8	15.9 ± 0.8	13.8 ± 0.5	11.4 ± 0.4
Soil moisture, average (%)	25.6 ± 0.3	23.9 ± 0.3	17.8 ± 0.4	16.8 ± 0.3
Water holding capacity (%)	47.0 ± 0.8	39.0 ± 1.0	40.4 ± 0.7	37.2 ± 0.9
Bulk density (g cm ⁻³)	1.28 ± 0.1	1.45 ± 0	1.34 ± 0	1.48 ± 0
Soil pH (1: 2.5 w/v H ₂ O)	5.6 ± 0.1	5.8 ± 0.1	6.1 ± 0.1	6.3 ± 0.1
Soil organic Carbon (%)	3.07 ± 0.1	1.34 ± 0.1	1.8 ± 0.1	1.04 ± 0.1
Carbon stock in soil (Mg C ha ⁻¹ soil)	58.9 ± 2.6	29.2 ± 2.1	36.2 ± 2.1	23.1 ± 1.6
Total nitrogen (%)	0.24 ± .01	0.12 ± 0	0.14 ± 0	0.08 ± 0
C:N ratio	12.8	11.2	12.8	13.0
Available Potassium (µg g ⁻¹)	346.3 ± 4.0	291.3 ± 2.2	268.1 ± 1.7	245.8 ± 2.0
Total phosphorus (µg g ⁻¹)	626.6 ± 0.3	621.6 ± 0.4	618.3 ± 0.6	613.5 ± 0.2
Soil organic matter (%)	5.3 ± 0.3	2.3 ± 0.1	3.1 ± 0.1	1.8 ± 0.1
Microbial biomass carbon (µg g ⁻¹)	558.4 ± 7.6	-	438.5 ± 11.8	-
Microbial biomass nitrogen (µg g ⁻¹)	50.7 ± 1.1	-	39.9 ± 0.8	-
Microbial biomass phosphorus (µg g ⁻¹)	12.3 ± 0.2	-	9.7 ± 0.2	-

Table 2. Fine root biomass (Mg ha⁻¹) in undisturbed and disturbed stands of tropical moist forest in Sunsari district, eastern Nepal.

Seasons	0-15 cm soil stratum			15-30 cm soil stratum		
	Size class			Size class		
	< 2 mm	2-5 mm	Total	< 2 mm	2-5 mm	Total
Undisturbed stand						
Rainy	4.81 ± 0.12	1.72 ± 0.09	6.53 ± 0.11	2.28 ± 0.08	0.67 ± 0.09	2.94 ± 0.10
Winter	2.97 ± 0.10	1.05 ± 0.09	4.02 ± 0.11	1.64 ± 0.08	0.50 ± 0.07	2.14 ± 0.09
Summer	2.0 ± 0.09	0.74 ± 0.08	2.74 ± 0.10	1.19 ± 0.05	0.35 ± 0.05	1.54 ± 0.07
Mean	3.26 ± 0.10	1.17 ± 0.09	4.43 ± 0.10	1.70 ± 0.07	0.51 ± 0.07	2.21 ± 0.09
Disturbed stand						
Rainy	2.57 ± 0.10	0.85 ± 0.07	3.42 ± 0.11	1.15 ± 0.07	0.34 ± 0.04	1.49 ± 0.08
Winter	1.65 ± 0.07	0.51 ± 0.06	2.16 ± 0.08	0.77 ± 0.04	0.18 ± 0.03	0.95 ± 0.04
Summer	1.03 ± 0.05	0.34 ± 0.02	1.37 ± 0.06	0.48 ± 0.02	0.19 ± 0.01	0.67 ± 0.02
Mean	1.75 ± 0.08	0.57 ± 0.07	2.32 ± 0.09	0.8 ± 0.04	0.24 ± 0.02	1.03 ± 0.05

33% FRB was recorded in lower stratum. In comparison to upper stratum, FRB decreased in lower stratum by 50% in US and 55% in DS. The FRB of < 2 mm diameter was also higher in upper soil stratum in both US (66%) and DS (69%) as compared to lower stratum. The variation in annual mean of FRB due to depth was significant in both the stands ($P < 0.001$).

Seasonality in FRB

Statistically significant ($P < 0.001$) seasonality was observed in the distribution of FRB in both the stands. FRB of both size classes were maximum in rainy season, followed by winter, and minimum in summer season in both the stands (Table 3). FRB reduced from rainy to

summer season by 55% in US and 59% in DS (Figure 4). Fine root size class also showed distinct seasonality in US with 48% value in rainy, 31% in winter, and 21% in summer season. Same trend was seen in the DS also. However, seasonality did not show effect on the vertical distribution of FRB (Table 3). It ranged between 64-70% in upper stratum in all season in both the stands while in lower stratum the range was from 30-36%.

Table 3. Seasonal variation in fine root biomass (Mg ha^{-1}) in undisturbed and disturbed stands of tropical moist forest in Sunsari district, eastern Nepal.

Season	Size class (mm)	Forest stands	
		Undisturbed	Disturbed
Summer	< 2	3.19 ± 0.12	1.51 ± 0.07
	2-5	1.1 ± 0.09	0.53 ± 0.03
	0-5	4.29 ± 1.04	2.04 ± 0.49
Rainy	< 2	7.09 ± 0.14	3.73 ± 0.12
	2-5	2.39 ± 0.15	1.19 ± 0.08
	0-5	9.48 ± 2.35	4.92 ± 1.27
Winter	< 2	4.61 ± 0.14	2.41 ± 0.08
	2-5	1.54 ± 0.10	0.69 ± 0.07
	0-5	6.15 ± 1.54	3.1 ± 0.86

Fine Root Production and Turnover

FRP was higher by 81% ($5.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) in US than DS ($2.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) (Table 4); the difference was statistically significant ($P < 0.001$). Further, FRP in <2 mm size class was significantly higher ($P < 0.001$) in both the stands in comparison to 2-5 mm size class. Combining both size classes, FRP was higher by 71-73% in upper stratum in both the stands. It revealed that FRP showed less production in the lower stratum.

Table 4. Fine root production ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) in undisturbed and disturbed stands of tropical moist forest in Sunsari district, eastern Nepal.

Soil depth (cm)	Undisturbed stand			Disturbed stand		
	< 2 mm	2-5 mm	Total	< 2 mm	2-5 mm	Total
0-15	2.81 ± 0.08	0.98 ± 0.04	3.79 ± 0.11	1.54 ± 0.07	0.51 ± 0.02	2.05 ± 0.08
15-30	1.09 ± 0.03	0.32 ± 0.02	1.41 ± 0.05	0.67 ± 0.03	0.15 ± 0.01	0.82 ± 0.05
0-30	3.90 ± 0.10	1.30 ± 0.04	5.20 ± 0.15	2.21 ± 0.07	0.66 ± 0.02	2.87 ± 0.09

Turnover rate of fine roots was faster for <2 mm size class in both the stands (Table 5). For both size classes, turnover rate was slower in US than in DS. Considering both strata, average turnover rate of smaller fine roots was 0.75 in US and 0.86 in DS, whereas it was 0.74 and 0.76 for larger size class in US and DS respectively. Moreover, the fine root of both size classes showed faster turnover rate in the upper soil stratum than in the lower stratum in both stands. Turnover time was longer for the fine roots of US than that of DS for both size classes in both strata. Turnover time of smaller fine roots was also shorter in both the stands.

Table 5. Turnover rate and turnover time of fine root in undisturbed and disturbed stands of tropical moist forest in Sunsari district, eastern Nepal.

Soil depth (cm)	Undisturbed stand			Disturbed stand		
	<2 mm	2-5 mm	Mean	<2 mm	2-5 mm	Mean
Turnover rate (year^{-1})						
0-15	0.86	0.84	0.85	0.88	0.89	0.89
15-30	0.64	0.63	0.64	0.84	0.63	0.74
Turnover time (year)						
0-15	1.16	1.19	1.18	1.14	1.12	1.13
15-30	1.56	1.59	1.58	1.19	1.43	1.31

Correlation Between Environmental Variables and Fine Root Biomass

The test of the normality of these variables and fine root data showed normal distribution (Figure 4). Therefore, environmental variables were correlated with fine root biomass and production. In US, FRB showed significant negative correlations with SOC, TP, MB-C and MB-N whereas, FRP showed significant positive correlations

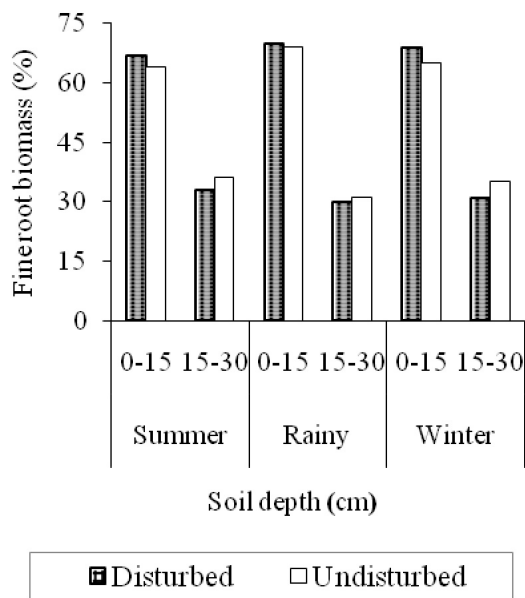


Figure 4. Percent allocation of fine root biomass along the soil depth in different seasons in undisturbed and disturbed stands of tropical moist forest in Sunsari district, eastern Nepal

with them, except TP (Table 6). Regression analysis of FRP with SOC, TN, MBC and MBN in upper soil stratum of US was positive (Figures 5-8). In DS, none of the soil variables showed significant correlations with FRB but SOC, TN, MB-C and MB-N showed significant negative correlations with FRP (Table 7).

Carbon and Nitrogen Stock in Fine Roots

Both carbon and nitrogen stocks in the fine roots were almost two times more in US than the DS (Table 8). Moreover, more than double carbon and nitrogen was found in the fine root of <2 mm size class than that in 2-5 mm size class in both stands. Similarly, both carbon and nitrogen stocks were fairly higher in upper soil than in the lower stratum in both the stands. The carbon stock in lower stratum varied from 31-33% of the total carbon stock in fine roots. Similar pattern was found for nitrogen stock also in the lower stratum.

Table 6. Pearson's correlation coefficient between the soil variables, and fine root biomass and production in 0-15 cm soil depth of undisturbed stand of tropical moist forest in Sunsari district, eastern Nepal.

	mois	whc	bd	pH	soc	ton	top	pot	som	mbc	mbn	mbp
Fine Root Biomass												
Summer	-0.019	-0.018	0.273	-0.474**	-0.779**	-0.831**	-0.436**	0.209	-0.779**	-0.726**	-0.747**	-0.208
Winter	0.006	0.050	-0.178	-0.077	-0.060	0.036	-0.341*	-0.292	-0.063	-0.101	-0.009	-0.314
Rainy	0.159	0.308	-0.052	-0.124	0.049	0.065	-0.008	-0.043	0.056	0.040	-0.025	-0.047
Mean	0.049	0.168	-0.010	-0.309	-0.374*	-0.332	-0.387*	-0.079	-0.372*	-0.373*	-0.361*	-0.293
Fine Root Production												
0-2 mm	0.270	0.169	-0.336*	-0.042	0.374*	0.398*	0.231	-0.077	0.378*	0.327	0.299	-0.010
2-5 mm	-0.215	0.075	0.181	0.371*	0.221	0.250	0.058	-0.122	0.221	0.230	0.226	0.157
0-5 mm	0.129	0.237	-0.224	0.231	0.564**	0.611**	0.290	-0.173	0.569**	0.521**	0.488**	0.106

*. Correlation is significant at the 0.05 level (2-tailed); **. Correlation is significant at the 0.01 level (2-tailed).

mois = soil moisture, whc = water holding capacity, bd = bulk density, soc = soil organic carbon, ton = total nitrogen, top = total phosphorus, pot = potassium, som = soil organic matter, mbc = microbial biomass carbon, mbn = microbial biomass nitrogen, mbp = microbial biomass phosphorus.

DISCUSSION

Spatial Variation in FRB

The annual mean FRB in the present study (6.6 Mg ha^{-1}) was comparable to that of boreal forest (5.28 Mg ha^{-1}) (Yuan and Chen 2010), and dry forest in Srilanka (5.72

Mg ha^{-1}) (Kurupparachchi et al. 2013). So far the spatial variation, it showed distinct gradient in the content along the disturbance regime. The value decreased due to the effect of disturbance. The lower FRB in DS could be the result of less canopy cover (Harteveld et al. 2007) or a higher fine root turnover (FRT) rate. Similar trend was also reported by Barbhuiya

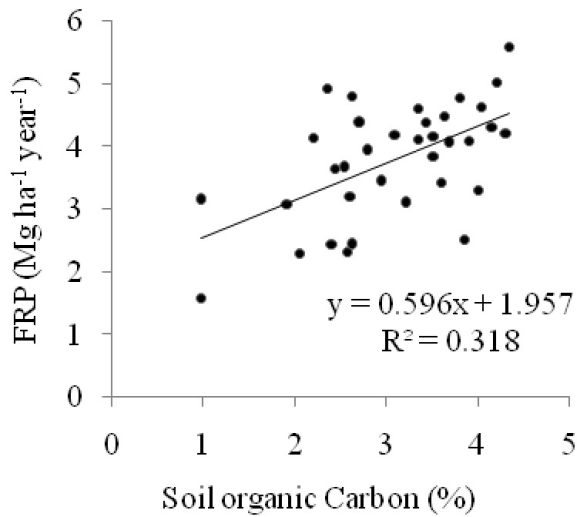


Figure 5. Regression analysis between soil organic carbon and fine root production (FRP)

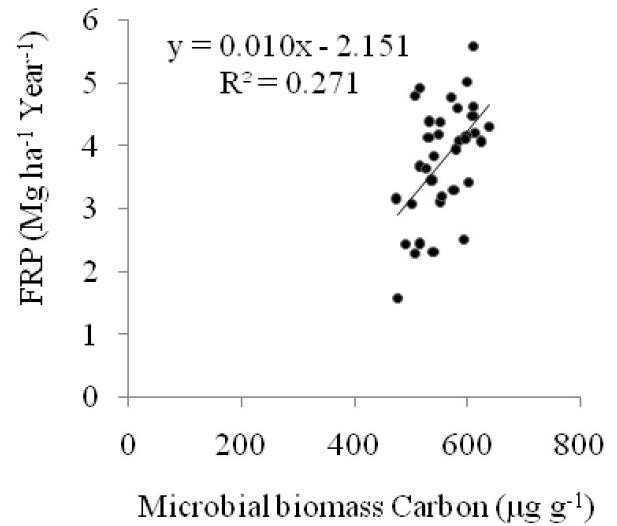


Figure 7. Regression analysis between microbial biomass carbon and fine root production (FRP)

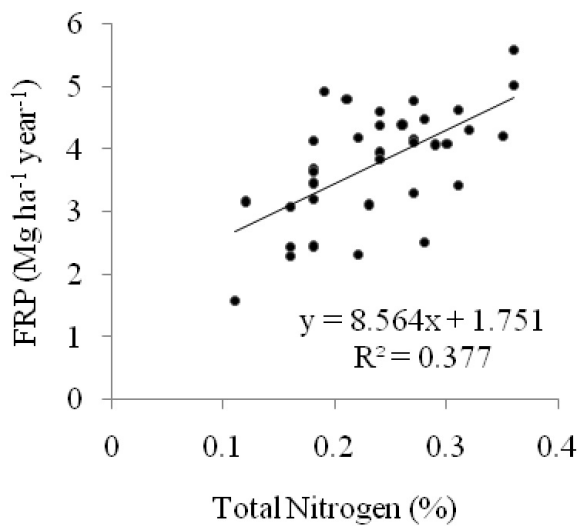


Figure 6. Regression analysis between total nitrogen and fine root production (FRP)

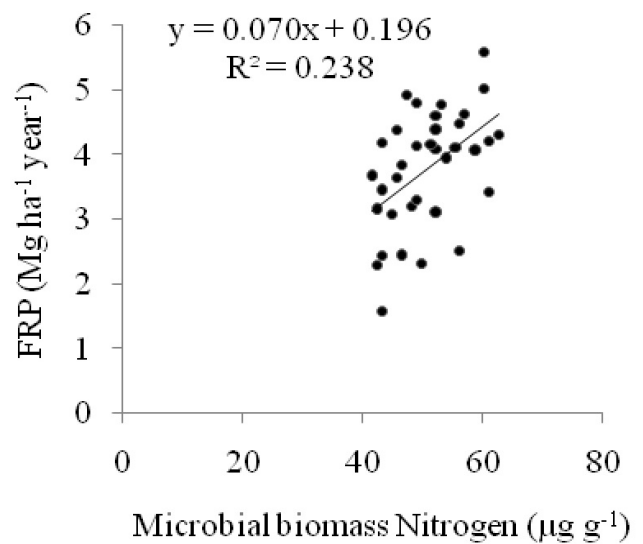


Figure 8. Regression analysis between microbial biomass nitrogen and fine root production (FRP)

et al. (2012) and Leuschner et al. (2009). However, Ibrahima et al. (2010) found opposite trend where FRB was significantly higher in the disturbed than in undisturbed tropical forests. It suggests that fine roots may respond quickly to land-use change (Castellanos et al. 2001), so causing higher FRB in DS.

On the other hand, higher FRB on nutrient-poor stand and a lower FRB in fertile stand may be associated with the differences in soil nutrients, especially available phosphorus and soil nitrogen (Maycock and Congdon

2000). The nutrient deficient soil of DS needs a high standing crop of FRB to fulfill the nutrient requirement of the plants. The cause for the higher FRB in US of the present study may be due to the higher SOC, TN, TP, K and soil moisture at this site (Gautam and Mandal 2013). The significant difference in FRB between US and DS of the present forest reflects that the impact of disturbances on FRB was large, but recovery of fine roots was relatively slow.

Table 7. Pearson's correlation coefficient between the soil variables, and fine root biomass and production in 0-15 cm soil depth of disturbed stand of tropical moist forest in Sunsari district, eastern Nepal.

	mois	whc	bd	pH	soc	ton	top	pot	som	mbc	mbn	mbp
Fine root biomass												
Summer	0.045	0.084	0.129	0.110	0.790**	0.875**	0.143	0.063	0.797**	0.748**	0.776**	0.023
Winter	0.323	0.197	0.045	0.010	0.023	0.140	0.171	0.002	0.041	0.038	0.067	0.198
Rainy	0.130	0.108	0.287	0.128	-0.265	-0.182	0.089	0.116	-0.261	-0.260	-0.197	0.056
Mean	-0.087	0.012	-0.188	0.134	0.117	0.273	-0.099	-0.112	0.133	0.112	0.185	-0.153
Fine root production												
0-2 mm	-0.109	0.137	-0.151	0.073	-0.447**	-0.445**	-0.206	-0.103	-0.445**	-0.385*	-0.357*	-0.107
2-5 mm	0.359*	-0.101	-0.275	-0.003	-0.308	-0.256	0.060	0.029	-0.308	-0.356*	-0.327	0.086
0-5 mm	0.126	0.053	-0.292	0.059	-0.557**	-0.524**	-0.135	-0.068	-0.556**	-0.534**	-0.494**	-0.036

* 0. Correlation is significant at the 0.05 level (2-tailed); **. Correlation is significant at the 0.01 level (2-tailed).

mois = soil moisture, whc = water holding capacity, bd = bulk density, soc = soil organic carbon, ton = total nitrogen, top = total phosphorus, pot = potassium, som = soil organic matter, mbc = microbial biomass carbon, mbn = microbial biomass nitrogen, mbp = microbial biomass phosphorus.

Table 8. Carbon and nitrogen stocks (kg ha^{-1}) in fine root at undisturbed and disturbed stands of tropical moist forest in Sunsari district, eastern Nepal.

Diameter (mm)	Undisturbed stand			Disturbed stand		
	Soil depth (cm)			Soil depth (cm)		
	0-15	15-30	Total	0-15	15-30	Total
Carbon stock (kg ha^{-1})						
< 2	1402 ± 28.5	731 ± 21.2	2133 ± 32.7	753 ± 18.1	344 ± 13.7	1097 ± 24.8
2-5	532 ± 26.6	232 ± 20.6	764 ± 34.0	259 ± 13.5	109 ± 7.6	368 ± 16.1
0-5	1934 ± 33.8	963 ± 27.6	2897 ± 44.5	1012 ± 22.3	453 ± 16.5	1465 ± 30.7
Nitrogen stock (kg ha^{-1})						
< 2	29 ± 0.6	15 ± 0.4	44 ± 0.7	16 ± 0.4	07 ± 0.3	23 ± 0.5
2-5	07 ± 0.4	03 ± 0.3	10 ± 0.5	04 ± 0.2	02 ± 0.1	06 ± 0.2
0-5	36 ± 0.6	18 ± 0.5	54 ± 0.8	20 ± 0.4	09 ± 0.3	29 ± 0.6

Vertical Distribution of FRB

FRB decreased significantly along the soil depth in the present study. Similar trend was reported by Richter et al. (2012). Sixty five to 69% FRB in the upper soil stratum observed in the present study was comparable to the findings of Ibrahima et al. (2010) who found 70-82 % FRB in the 0-10 cm soil stratum. Valverde-Barrantes et al. (2007) reported 60% of the fine root in the upper 15 cm soil of tropical forest while Noguchi et al. (2014) found 74% of the FRB within the upper 20 cm soil layers. Other studies reported the presence of 59-91% of

the total FRB in 30 cm soil stratum (Kiley and Schneider 2005, Meinen et al. 2009).

The amount of litter, nutrients and organic matter on the soil surface that finally affect the availability of water might be the cause for the accumulation of fine roots in the upper stratum of the forests. It may be linked to the plant species, physical environment and water availability (Vogt et al. 1981). The higher amount of FRB in upper soil stratum of DS may be a nutrient conservation mechanism under low soil resource availability as mentioned by Jordan (1991).

FRB and Soil Variables

In the US, total fine root biomass was negatively correlated with almost all soil variables suggesting that the soil fertility alone might not be more crucial for plant growth. Moreover, which soil factor is most accountable for the negative correlation between soil variables and fine root biomass would need an additional study. Powers and Peréz-Aviles (2013) observed negative correlations with silt, pH, calcium, magnesium, nitrogen, and phosphorus. Lee et al. (2007) found inverse relationship between FRB and soil nitrogen.

No correlations were found between soil chemical variables, and FRB in European beech forest (Richter et al. 2012). Similarly, no significant correlation was observed between available P and FRB whereas soil N showed negative correlation with FRB (≤ 2 mm) (Maycock and Congdon 2000). The addition of K, and both K and N together decreased FRB (Wright et al. 2011). In the boreal forest, FRB decreased significantly with N and P availability in soil (Yuan and Chen 2010). In contrary, Graefe et al. (2010) found a positive response of N, P, and K fertilization on root growth. Soil nutrients may affect fine root mass either directly by affecting root production or indirectly by influencing the composition of species which differ in underground allocation.

In contrast with a weak positive correlation between FRB and soil moisture content in US, McGroddy and Silver (2000) found a strong positive correlation between them in humid tropical forests. On the other hand, Lima et al. (2010) found an opposite relationship between fine root growth and soil water availability.

Seasonality in FRB

In the present study, distinct seasonality was observed in fine root biomass which was also reported in other studies (Mandal 1999, Pei et al. 2012). The maximum FRB of both root size classes during rainy season in both stands might be associated with the higher nutrient availability and soil moisture. The decrease in the amount of fine roots in winter (by 35–37%) and summer (by 52–55%) seasons indicates a rapid turnover of fine roots. Pei et al. (2012) reported significant increase in FRB from April, which peaked in August and then decreased. Green et al. (2005) also reported higher fine root growth during wet season in tropical forest.

Variation in FRP

FRP in US of present forest ($5.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) was slightly lower than the global average for tropical forests ($596 \pm 478 \text{ g m}^{-2} \text{ yr}^{-1}$), and higher than boreal ($311 \pm 259 \text{ g m}^{-2} \text{ yr}^{-1}$) and temperate ($428 \pm 375 \text{ g m}^{-2} \text{ yr}^{-1}$) forests (Finér et al. 2011). In our study, FRP decreased along the increasing soil depth and disturbance. Similar trend of FRP along the soil depth was also observed by Xiao et al. (2008) and along the disturbance by Harteveld et al. (2007). The spatial pattern of FRP may be associated with the differences in soil N concentration (Uselman et al. 2007), species composition and soil properties (Finer et al. 2011, Yuan and Chen 2012), or canopy cover and stand basal area (Harteveld et al. 2007).

As in US of present forest, the positive correlation between FRP and soil N was also observed in earlier studies (Pei et al. 2012, Yuan and Chen 2012). Some other studies showed negative (Maycock and Congdon 2000), or uncertain (Nadelhoffer 2000) relationship between FRP and soil N. Some previous studies observed positive (Yuan and Chen 2012) or even negative (Uselman et al. 2007) correlation between FRP and soil P as in present US and DS, respectively.

Richter et al. (2012) found no correlation between edaphic factors and FRP. As in this study, Dipesh and Schuler (2013) also found no significant correlation between FRP and soil moisture. These studies suggest that FRP is mainly dependent on soil resources, especially nutrients and moisture. It was also evident from the work of Jimenez et al. (2009), who reported close relationships between FRP and edaphic factors in tropical forest.

Fine Root Turnover

FRT of the present forest (0.78 in US and 0.86 yr^{-1} in DS) was comparable to that of boreal forests (0.77 yr^{-1}) and less than that of temperate (1.21 yr^{-1}), and tropical (1.44 yr^{-1}) forests reported by Finér et al. (2011). FRT may be affected by the species composition and soil properties mainly nutrients, moisture, and temperature. The FRT increased with the addition of K, and both K and N together in the forest soil (Yavitt et al. 2011), whereas decreased along the intensity of disturbance (Leuschner et al. 2009). Higher FRT in DS of the present forest may be due to lower SOM, TN, TP, K, microbial biomass and moisture in the soil. FRT also depends upon the soil carbon pools (Matamala et al. 2003).

Carbon and Nitrogen Stocks in Fine Root

The C stock and nutrient contents of fine roots vary according to the species composition, type of forest, and diameter class. In the present study, a strong vertical decrease in C stock of fine root with increasing soil depth was observed in both stands. The upper soil stratum had higher percentage allocation (67- 69%) of C stock in the fine roots as compared to the lower stratum. It might be due to the higher WHC and availability of nutrients which enhance the accumulation of more fine roots in the topsoil. Other studies on tropical forests also reported 70-80% of C stocks in fine roots in the upper soil stratum (Hertel et al. 2009, Ibrahima et al. 2010).

The higher N content in the fine roots of upper soil stratum of present study might be linked to the trend in soil N content. Helmisaari et al. (2007) also found a positive relationship between soil N and fine root N content. Nitrogen stocks of fine roots also found to be positively related with root respiration (Pregitzer et al. 1998) or negatively related to longevity of root (Yuan and Chen 2010). The higher value of fine root N stock at US indicated that soil nutrient absorption in this stand was enhanced by higher root metabolism, while the lower fine root N stock at DS was related with low FRB. The higher N stock in the fine root of < 2 mm diameter class reported in this study was as accordance with the finding of Comas and Eissenstat (2009).

In conclusion, fine root dynamics varied with the disturbance of stand, seasons, and soil depth. Further, species composition, soil nutrients and other variables of soil also played a significant role in defining fine root dynamics. The edaphic variables especially SOC, TN, and microbial biomass might have a limiting influence on FRT in tropical moist forests. The significant difference in FRB in two stands of the present forest reflects that the impact of disturbances on FRB was large, but recovery of fine roots was relatively slow.

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REFERENCES

- Barbhuiya, A.; Arunachalam, A.; Pandey, H.; Khan, M. and Arunachalam, K. 2012. Fine root dynamics in undisturbed and disturbed stands of a tropical wet evergreen forest in northeast India. *Tropical Ecology* 53(1): 69-79.
- Brookes, P.C.; Landman, A.; Pruden, G. and Jenkinson, D.S. 1985. Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry* 17: 837-842.
- Castellanos, J.; Jaramillo, V.J.; Sanford, R.L. and Kauffman, J.B. 2001. Slash-and-burn effects on fine root biomass and productivity in a tropical dry forest ecosystem in Mexico. *Forest Ecology and Management* 148: 41-50.
- Comas, L.H. and Eissenstat, D.M. 2009. Patterns in root trait variation among 25 co-existing North American forest species. *New Phytologist* 182: 919-928.
- Dipesh, K.C. and Schuler, J.L. 2013. Fine-root production and aboveground development for Loblolly pine, Silver maple and Cottonwood. *Communications in Soil Science and Plant Analysis* 44(14): 2207-2218.
- Espeleta, J.F. and Clark, D.A. 2007. Multi-scale variation in fine-root biomass in a tropical rain forest: A seven-years study. *Ecological Monographs* 77(3): 377-404.
- Espeleta, J.F.; West, J.B. and Donovan, L.A. 2009. Tree species fine-root demography parallels habitat specialization across a sandhill soil resource gradient. *Ecology*, 90: 1773-1787.
- Finér, L.; Ohashi, M.; Noguchi, K. and Hirano, Y. 2011. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management* 262: 2008-2023.
- Gautam, T.P. and Mandal, T.N. 2013. Soil Characteristics in moist tropical forest of Sunsari District, Nepal. *Nepal Journal of Science and Technology* 14(1): 35-40.
- Gill, R.A. and Jackson, R.B. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147: 13-31.
- Girardin, C.A.J.; Aragão, L.E.O.C.; Malhi, Y.; Huaraca Huasco, W.; Metcalfe, D.B.; Durand, L.; Mamani, M.; Silva-Espejo, J.E. and Whittaker, R.J. 2013. Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles* 27(1): 252-264.
- Graefe, S.; Hertel, D. and Leuschner, C. 2010. N, P and K limitation of fine root growth along an elevation transect in tropical mountain forests. *Acta Oecologica* 36(6): 537-542.
- Green, J.J.; Dawson, L.A.; Proctor, J.; Duff, E.I. and Elston, D.A. 2005. Fine root dynamics in a tropical rain forest is influenced by rainfall. *Plant and Soil* 276: 23-32.
- Harteveld, M.; Hertel, D.; Wiens, M. and Leuschner, C. 2007. Spatial and temporal variability of fine root abundance and growth in tropical moist forests and agroforestry systems (Sulawesi, Indonesia). *Ecotropica* 13: 111-120.
- Helmisaari, H.L. 2007. Roots and Carbon Allocation- Quantity, Quality and Controls. Presentation at Roottrap Session: Belowground Carbon Turnover in European Forests. Finish Forest Research Institute, Helsinki.

- Hendrick, J.J.; Hendrick, R.L.; Wilson, C.A.; Michell, R.J.; Pecot, S.D. and Guo, D. 2006. Assessing the patterns and controls of fine root dynamics: An empirical test and methodological review. *Journal of Ecology* 94: 40-57.
- Hertel, D.; Hartveld, M.A. and Leuschner, C. 2009. Conversion of a tropical forest into agroforest alters the fine root-related carbon flux to the soil. *Soil Biology and Biochemistry* 41: 481-490.
- Hoffmann, C.W. and Usoltsev, V.A. 2001. Modelling root biomass distribution in *Pinus sylvestris* forests of the Turgai depression of Kazakhstan. *Forest Ecology and Management* 149: 103-114.
- Ibrahima, A.; Mvondo, Z.E.A. and Ntonga, J. 2010. Fine root production and distribution in the tropical rainforests of south-western Cameroon: effects of soil type and selective logging. *iForest - Biogeosciences and Forestry* 3(5): 130-136.
- Jackson, M.L. 1958. *Soil Chemical Analysis*. Prentice Hall, Englewood Cliffs, New Jersey. 498 pages.
- Jimenez, E.M.; Moreno, F.H.; Penuela, M.C.; Patino, S. and Lloyd, J. 2009. Fine root dynamics for forests on contrasting soils in the Colombian Amazon. *Biogeosciences* 6: 2809-2827.
- Jordan, C.F. 1991. Nutrient cycling processes and tropical forest management. pages 90-106, In: Gomez-Pompa, A.; Whitmore, T.C. and Hadley, M. (Editors.) *Rainforest Regeneration and Management*. UNESCO, Paris, France,
- Joslin, J.D.; Gaudinski, J.B.; Torn, M.S.; Riley, W.J. and Hanson, P.J. 2006. Fine-root turnover patterns and their relationship to root diameter and soil depth in a C¹⁴-labeled hardwood forest. *New Phytologist* 172: 523-535.
- Kalembasa, S.J. and Jenkinson, D.S. 1973. A comparative study of titrimetric and gravimetric methods for the determination of organic carbon in soil. *Journal of Science, Food and Agriculture* 24: 1085-1090.
- Kiley, D.K. and Schneider, R.L. 2005. Riparian roots through time, space and disturbance. *Plant and Soil* 269(1-2): 259-272.
- Kochsiek, A.; Tan, S. and Russo, S.E. 2013. Fine root dynamics in relation to nutrients in oligotrophic Bornean rain forest soils. *Plant Ecology* 214: 869-882.
- Kuruppuarachchi, K.A.J.M.; Seneviratne, G. and Madurapperuma, B.D. 2013. Drought induced fine root growth and canopy green-up of tropical dry zone vegetation in Sri Lanka. *Journal of Tropical Forestry and Environment* 3(1): 17-23.
- Lee, E.H.; Tingey, D.T.; Beedlow, P.A.; Johnson, M.G. and Burdick, C.A. 2007. Relating fine root biomass to soil and climate conditions in the Pacific Northwest. *Forest Ecology and Management* 242: 195-208.
- Lei, P.; Scherer-Lorenzen, M. and Bauhus, J. 2012. The effect of tree species diversity on fine-root production in a young temperate forest. *Oecologia* 169: 1105-1115.
- Leuschner, C.; Hartveld, M. and Hertel, D. 2009. Consequences of increasing forest use intensity for biomass, morphology and growth of fine roots in a tropical moist forest on Sulawesi, Indonesia. *Agriculture, Ecosystems and Environment* 129(4): 474-481.
- Lima, T.T.S.; Miranda, I.S. and Vasconcelos, S.S. 2010. Effects of water and nutrient availability on fine root growth in eastern Amazonian forest regrowth, Brazil. *New Phytologist* 187: 622-630.
- Mandal, T.N. 1999. *Ecological Analysis of Recovery of Landslide Damaged Sal Forest Ecosystem in Nepal Himalaya*. Ph.D. Thesis. Banaras Hindu University, Varanasi, India. 197 pages.
- Matamala, R.; Gonzalez-Meler, M.A.; Jastrow, J.D.; Norby, R.J. and Schlesinger, W.H. 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* 302: 1385-1387.
- Maycoc, C.R., and Congdon, R.A. 2000. Fine Root biomass and soil N and P in north Queensland rain forests. *Biotropica* 32(1): 185-190.
- McGroddy, M., and Silver, W.L. 2000. Variations in Belowground carbon storage and soil CO₂ flux rates along a wet tropical climate gradient. *Biotropica* 32(4): 614-624.
- Meier, I.C. and Leuschner, C. 2008. Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biology* 14(9): 2081-2095.
- Meinen, C.; Hertel, D. and Leuschner, C. 2009. Biomass and morphology of fine roots in temperate broad-leaved forests differing in tree species diversity: is there evidence of below-ground overyielding? *Oecologia* 161(1): 99-111.
- Nadelhoffer, K.J. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytologist* 147: 131-139.
- Noguchi, H.; Suwa, R.; de Souza, C.A.S.; da Silva, R.P.; dos Santos, J.; Higuchi, N.; Kajimoto, T. and Ishizuka, M. 2014. Examination of vertical distribution of fine root biomass in a tropical moist forest of the Central Amazon, Brazil. *Japan Agricultural Research Quarterly* 48(2): 231-235.
- Noordwijk, M. van; Lawson, G.; Soumare, A.; Groot, J.J.R. and Hairiah, K. 1996. Root distribution of trees and crops: Competition and/or complementarity. pages 319-364, In: Ong, C.K. and Huxley, P. (Editors) *Tree-Crop Interactions: A Physiological Approach*. CAB International, Wallingford, U.K.
- Pei, Z.-Q.; Xiao, C.-W.; Dongm D. and Zhang, S.-R. 2012. Comparison of the fine root dynamics of *Populus euphratica* forests in different habitats in the lower reaches of the Tarim River in Xinjiang, China, during the growing season. *Journal of Forest Research* 17(4): 343-351.
- Piper, C.S. 1966. *Soil and Plant Analysis*. Hans Publisher, Bombay. 368 pages.
- Powers, J.S. and Pérez-Aviles, D. 2013. Edaphic factors are a more important control on surface fine roots than stand age in secondary tropical dry forests. *Biotropica* 45(1): 1-9.
- Pregitzer, K.S.; Laskowski, M.J.; Burton, A.J.; Lessard, V.C. and Zak, D.R. 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* 18: 665-670.
- Richter, A.K.; Hajdas, I.; Frossard, E. and Brunner, I. 2012. Soil acidity affects fine root turnover of European beech. *Plant Biosystems* 147(1): 50-59.
- Rieger, I.; Lang, F.; Kleinschmit, B.; Kowarik, I. and Cierjacks, A. 2013. Fine root and aboveground carbon stocks in riparian forests: the roles of diking and environmental gradients. *Plant and Soil*. doi: 10.1007/s11104-013-1638-8
- Roderstein, M.; Hertel, D. and Leuschner, C. 2005. Above and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology* 21: 483-492.
- Srivastava, S.K.; K.P. Singh and R.S. Upadhyay. 1986. Fine root

- growth dynamics in teak (*Tectona grandis* Linn. F). Canadian Journal of Forest Research 16: 1360–1364.
- Uselman, S.M.; Qualls, R.G. and Liliencron, J. 2007. Fine root production across a primary successional ecosystem chronosequence at Mt. Shasta, California. Ecosystems 10(5): 703–717.
- Valverde-Barrantes, O.J.; Raich, J.W. and Russell, A.E. 2007. Fine-root mass, growth and nitrogen content for six tropical tree species. Plant and Soil 290: 357–370.
- Vance, E.D.; Brookes, P.C. and Jenkinson, D.S. 1987. Microbial biomass measurements in forest soils: The use of the chloroform fumigation-incubation method in strongly acid soils. Soil Biology and Biochemistry 19: 697–702.
- Vogt, K.A.; Edmonds, R.L. and Grier, C.C. 1981. Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer fine roots in 23- and 180-year-old subalpine *Abies amabilis* stands. Canadian Journal of Forest Research 11: 223–229.
- Wright, S.J.; Yavitt, J.B.; Wurzbarger, N.; Turner, B.L.; Tanner, E.V.J.; Sayer, E.J.; Santiago, L.S.; Kaspari, M.; Hedin, L.O.; Harms, K.E.; Garcia, M.N. and Corre, M.D. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92(8): 1616–1625.
- Xiao, C.W.; Sang, W.G. and Wang, R. 2008. Fine root dynamics and turnover rate in an Asia white birch forest of Donglingshan Mountain, China. Forest Ecology and Management 255: 765–773.
- Yavitt, J.B.; Harms, K.E.; Wright, S.J.; Garcia, M.N. and Mirabello, M.J. 2011. Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. Austral Ecology 36: 433–445.
- Yuan, Z.Y. and Chen, H.Y.H. 2010. Fine Root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. Critical Reviews in Plant Sciences 29(4): 204–221.
- Yuan, Z.Y. and Chen, H.Y.H. 2012. A global analysis of fine root production as affected by soil nitrogen and phosphorus. Proceedings of the Royal Society B: Biological Sciences 279(1743): 3796–3802.

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