

Variations in fine root growth during age chronosequence of moist tropical forest following shifting cultivation in Mizoram, northeast India

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Abstract: Shifting cultivation is widely practiced in northeast India and reported to affect structure and functioning of the forest. We assessed changes in fine root biomass, production and turnover in different ages of secondary forests (3, 5, 15 and 40 yr old) following shifting cultivation and an old growth forest in Mizoram. The results of this study showed that the fine root biomass, production and turnover varied significantly ($P < 0.01$) during the course of stand development. Fine root biomass and necromass, respectively, ranged between 314 and 111 g m⁻² in 3yr old stand to 834 and 255 gm⁻² in old growth forest. Proportions of very fine root (< 0.5 mm) to total fine root biomass was significantly high (22%) in the 3yr stand which decreased during the course of ecosystem development (13–16%). Higher root categories showed reverse trend with stand development. Maximum fine root biomass (42–53%) recorded in 0–10cm depth, which decreased significantly ($P < 0.05$) with increase in depth in all stands. Enhanced ratio of live root biomass to necromass during the course of stand development indicates increasing root vitality. Turnover of very fine root decreased during stand development while turnover of total fine root increased. We conclude that forest conversion have significant negative impact on fine root dynamics but the increased proportions of fine roots during early stages of stand development speedup the processes of recovery.

Key words: Biomass, developing forest, fine roots, necromass, productivity, turnover.

Introduction

Fine roots are the most dynamic component of the forest ecosystem and account for the bulk transfer of carbon (C) and nutrients from plant to soil (Ruess *et al.* 2006) because of their short lifespan (Norby & Jackson 2000). Fine roots represent approximately 15% of the atmospheric C pool and about one third of the global annual net primary productivity (Jackson *et al.* 1997). Important roles of these fine roots in global C cycling has been well recognised, however, the processes responsible for C sink in terrestrial ecosystems are not well understood (Vargas & Allen 2008). Therefore, estimates of fine root biomass, production and turnover from different ecosystems

from widely distributed tropical forests that represent 30% of the total C stored in living fine roots of the world would be essential for improving global C models.

Fine-root production is one of the most difficult aspects to measure because of time consuming methodological problems that limits the capacity to predict the effects of environmental change on root dynamics (Eissenstat *et al.* 2000; Norby *et al.* 2004). Number of abiotic factors affect fine root production such as seasonality (Lima *et al.* 2010), soil nutrients (Blair & Perfecto 2001), soil temperature and moisture (Metcalf *et al.* 2008). Further, floristic composition (Visalakshi 1994), forest successional stage and soil-use history (Castellanos *et al.* 2001; Jaramillo *et al.* 2003) have also been reported as

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sources of variation for fine-root production.

The long-term change in fine root biomass remains one of the least understood aspects of forest ecology. Studies on changes in fine root biomass overtime using various chronosequence approaches suggests that fine root biomass increases from stand initiation to a maxima at a later stage of stand development, which can vary from canopy closure to maturity (Vogt *et al.* 1983). Studies also reported that variability in site characteristics and species assemblages over time may largely be responsible for the different stand development trends of fine root biomass (John *et al.* 2001; Vogt *et al.* 1987; Yanai *et al.* 2006).

In many tropical countries, forest destruction and conversion to agricultural land is continuing at a high rate that has been reported to affect the structure and functioning of forest ecosystems. Research on the structure and functioning of disturbed tropical forests mostly focuses on aboveground aspects and the belowground part is often ignored. Available studies on the effect of disturbance on belowground system of tropical forests have mainly compared differences in fine root mass, production, and the depth distribution in undisturbed and heavily disturbed forests or planted systems (Arunachalam *et al.* 1996; Barbhuiya *et al.* 2012; Lima *et al.* 2012; Upadhya *et al.* 2005; Yang *et al.* 2004). Knowledge on the dynamics of fine root in the soil profile as a result of changes in land-use pattern would improve our understanding on the consequences of deforestation on both vegetation and global environment change (Jackson *et al.* 2000).

Tropical and subtropical forests of Mizoram, India are over-exploited for timber, fuel wood and common agricultural practice like shifting cultivation, which are responsible for the degradation of natural forest. The changes in forest species during the course of ecosystem development in Mizoram has been reported (Singh *et al.* 2015). However, studies on post-disturbance effects on fine root dynamics age chronosequence following shifting cultivation in these moist tropical forests are not available so far. This study would enhance our understanding on dynamics of structural and functional properties of fine root and soil properties during the course of recovery of tropical forests following shifting agriculture. This study hypothesises: (i) that the ratio of live and dead roots increases during the course of stand development, and (ii) that the proportion of very fine roots enhanced at the early stages of recovery during course of stand

development. The objective of the present study is to evaluate biomass, production and turnover of fine roots in different ages of regenerating secondary forest stands following shifting agriculture and an old growth forest of Mizoram, northeast India.

Materials and methods

Study site and the stand

The present study was conducted in Ailawng and Reiek (23°41.749'–23°41.424'N latitude and 92°37.643'–93°36.243'E longitude) areas of Aizawl and Mamit districts of Mizoram, northeast India. The elevation of the study sites range from 970 to 1275 m a.m.s.l. The climate of the area is typically monsoonic with distinct seasons *viz.*, cold and dry winter (December-February), warm pre-monsoon period (March-May), humid monsoon period (June-September) and cool post-monsoon autumn (October-November). The annual mean average rainfall of the area is *ca.* 2350 mm. The ambient air temperature ranges from 20 to 30°C in summer and 11 to 21°C in winter. The forest vegetation falls under three major categories *i.e.*, tropical wet evergreen forest, tropical semi-evergreen forest and sub-tropical pine forest (Champion & Seth 1968).

Developing secondary forest stands with distinct ages (3, 5, 15 and 40 yr) following shifting agriculture and an old growth forest (>100 yr) were selected. In all the sites a sample area of about 0.5 to 1 ha were demarcated. Within each sample area 3–6 randomly located permanent plots measuring 5m×5 m were marked. Soil and root samples were collected from these permanent plots periodically.

Vegetation sampling

In all the stands, vegetation analysis was performed by laying 10 randomly placed 10 m × 10 m quadrats for woody species and 50 cm × 50 cm quadrats for herbaceous vegetation. Density, frequency, abundance, basal cover and importance value of the species were determined (Misra 1968).

Soil analysis

In each stand, soil samples (0–10 cm depth) were collected from five random locations. The soil samples were sieved using 2 mm sieve, air-dried and used for analysis. Soil texture was analysed using soil hydrometer method, pH by electronic pH meter, gravimetric soil moisture content (SMC) by procedure out lined by Anderson & Ingram (1993). Soil bulk density (g cm⁻³) was measured using a

metallic tube of known inner volume and estimating the dry weight of a unit volume of soil (Anderson & Ingram 1993). Total C & N was determined by using CHNS-rapid auto-analyzer.

Sampling and analysis of fine root

Root samples were collected at monthly intervals from October 2012 to September 2013 by excavating 5 soil monoliths (10 cm × 10 cm, 30 cm deep) randomly. Soil monoliths were further divided into three depths (0–10, 10–20 and 20–30 cm). The core samples were brought to the laboratory in sealed polybags and washed over a multiple sieve system. Live and dead roots were separated on the basis of cohesion between cortex, periderm and color, dead roots were dark and spongy while live roots were brown and firm (Persson 1978). The roots were categorized into three different diameter classes (<0.5, 0.5–2, 2–5 mm) for further analysis. All root categories were oven dried at 80 °C for 24h to constant weight.

Computation and statistics

Fine root production was calculated using two methods. The first method (P_1) assumed a single annual pulse of fine root production and computed net production as the sum of differences between annual maximum and minimum root standing crop biomass of different diameter classes (Edwards & Harris 1977; Singh & Singh 1981). The second method (P_2) assumed a rapid fine turnover of fine root to calculated net production as the sum of all the apparent biomass increments for each size classes over the course of a year (McClagherty *et al.* 1982; Persson 1978; Srivastava *et al.* 1986). Fine root turnover (T_1 & T_2) was calculated as the ratio annual net production/annual mean biomass (Singh & Singh 1991; Tripathi *et al.* 1999) using the values of P_1 & P_2 respectively.

Statistical analysis was carried out using the statistical software package SPSS 16.0. Pearson correlation coefficients were used to show the relationships of fine root mass with microclimate and soil physico-chemical properties. The biomass data analysed by analysis of variance (ANOVA) to determine differences between seasons and sites followed by LSD tests to compare significant differences of mean values of fine roots.

Results

Plant composition

Tree species abundance changes during the course of stand development; for example, *Parkia timoriana* and *Psidium guajava* were dominant at 3yr, *Castanopsis tribuloides* and *Parkia timoriana* at 5yr, *Lithocarpus dealbatus* and *Castanopsis tribuloides* at 15yr, and *Alseodaphne petiolaris* and *Castanopsis tribuloides* at 40yr stand. However, in old growth forest (>100yr) most abundant tree species were: *Eurya acuminata* and *Lithocarpus xylocarpus*. Total tree density and basal cover were in decreasing order: old growth forest >40yr>15yr>5>3yr. While the tree density and basal cover increases with increase in fallow age, the density of ground vegetation decreases with the increase in the stand age .

Soil properties

In the old growth forest, soil temperature was significantly ($P < 0.05$) lower than the developing stands. Soil bulk density was highest in 3yr old stand, which declined with the increase in stand age and was lowest in the old growth forest. Soil was loamy sand to sandy loam in texture at all sites. Moisture content was greater in the old growth forest compared to the developing forest stands. The soil was acidic (pH=4.53–4.78) in all stands. The concentration of organic C and N was ~40% less in young stands than that of the old growth forest. C/N ratio did not vary significantly among the study areas (Table 1).

Spatial and temporal variations in fine root mass

Fine root biomass and necromass varied significantly during stand development ($P < 0.05$). During the study period, mean annual fine root biomass ranged from 203 g m⁻² in the 3yr stand to 579 g m⁻² in the old growth forest. However, variations in mean fine root necromass ranged from 111 g m⁻² in the 3yr stand to 255 g m⁻² in the forest (Fig. 1). Both fine root biomass and necromass increased in the following pattern: 3yr<5yr<15yr<40 yr<old growth forest. Total fine root mass ranged from 314 g m⁻² in 3yr stand to 834 g m⁻² in old growth forest stand (Table 2).

Contribution of very fine root (< 0.5 mm) to total fine root biomass was significantly high (22%) in the

Table 1. Vegetation and soil physico-chemical characteristics in upper soil of different developing stands in northeast India.

Parameter	Age of the stands (yr)				Forest site
	3	5	15	40	>100
Vegetation					
Density					
Tree species (no. ha ⁻¹)	369	833	1580	2190	4090
Ground vegetation (no. m ⁻²)	80	72	65	63	58
Tree basal area (m ² ha ⁻¹)	3	8	32	40	75
Soil					
Temperature (°C)	20.8	20.4	19.7	19.0	18.8
Bulk density (g cm ⁻³)	0.98±0.03	0.93±0.03	0.83±0.02	0.81±0.05	0.70±0.05
Textural class	sandy loam	loamy sand	loamy sand	loamy sand	loamy sand
Moisture (%)	28.32±1.6	29.71±1.8	28.76±2.1	32.30±1.7	37.87±1.8
pH	4.69±0.14	4.72±0.31	4.78±0.26	4.65±0.09	4.53±0.11
Organic C (mg g ⁻¹)	24.6±0.19	24.4±0.21	26.8±0.26	35.7±0.20	40.8±0.30
Total N (mg g ⁻¹)	2.2±0.02	2.3±0.02	2.2±0.03	2.9±0.05	3.7±0.26
C/N ratio	11.18±1.1	10.60±1.50	12.18±1.18	12.31±1.17	11.02±2.29

Table 2. Annual mean live and dead root mass (g m⁻², mean ± 1SE) of three diameter classes (30 cm soil depth) in different developing stands in northeast India. Values followed by different superscript letters within columns indicate significant differences ($P < 0.05$) among forest chronosequences.

Stand age (yr)	Root diameter (mm)	Fine root live mass	Fine root dead mass	Total root mass	Ratio of livemass/deadmass
3	<0.5	45±4	40±5	85±8	
	0.5–2	70±8	35±8	105±7	
	2–5	88±11	36±5	124±11	
	Subtotal	203±20 ^a	111±14 ^a	314±34 ^a	1.8
5	<0.5	49±7	54±6	103±10	
	0.5–2	132±12	69±6	201±14	
	2–5	110±10	42±8	152±16	
	Subtotal	291±26 ^b	165±15 ^b	456±45 ^b	1.8
15	<0.5	46±7	50±3	96±9	
	0.5–2	175±16	77±6	252±16	
	2–5	134±12	62±7	196±18	
	Subtotal	355±41 ^c	189±14 ^c	544±60 ^c	1.9
40	<0.5	62±6	70±3	132±12	
	0.5–2	202±14	65±9	267±14	
	2–5	170±18	82±6	252±11	
	Subtotal	434±39 ^d	217±16 ^d	651±65 ^d	2
RF (>100 yr)	<0.5	97±5	104±8	201±16	
	0.5–2	290±16	95±7	385±24	
	2–5	192±16	56±5	248±28	
	Subtotal	579±36 ^e	255±20 ^e	834±62 ^e	2.3



Fig. 1. Mean annual live and dead root mass within soil profile (0–30 cm) during stand development in northeast India. Vertical lines show \pm 1SE.

3 yr stand which decreased during the course of ecosystem development (13–16%). However, the contribution of 0.5–2 mm size roots to total fine root biomass increased from 34% in 3 yr stand to 50% in old growth forest stand. The ratio of root biomass to necromass increased during the course of ecosystem development (1.8 in the 3 yr stand to 2.3 in the old growth forest) (Table 2).

In all studied stands, wide seasonal variations were observed in the amount of total fine root mass with maximum in September and minimum in February–March at all sites. Fine root biomass followed the pattern similar to that of total root mass in all stands, whereas, dead fine root mass did not show consistent pattern (Fig. 2). Higher seasonal fluctuations in the amount of fine root biomass and total fine root mass was observed in younger stands (~40–50% decrease in dry months cf. wet months in young stand) compared to old growth forest throughout the measurement period. The ratio of fine root biomass to dead root mass changed seasonally with maximum (3:1) in the month of September and minimum (1.2:1) in February (Fig. 2). Variations in fine root mass was significant with different seasons ($F=13.6$, $P < 0.01$) and sites ($F=11.7$, $P < 0.01$). Mass of different fine root size categories showed dissimilarities in the seasonal dynamics. Very fine root (<0.5 mm) peaked in the month of September and lowest during April–May. The mean mass for very fine roots ranged between 43 and 149 g m^{-2} in 3 yr stand and old growth forests, respectively. Fine roots (0.5–2 mm) were maximum in the months of August–September and minimum during February–March. Mean mass

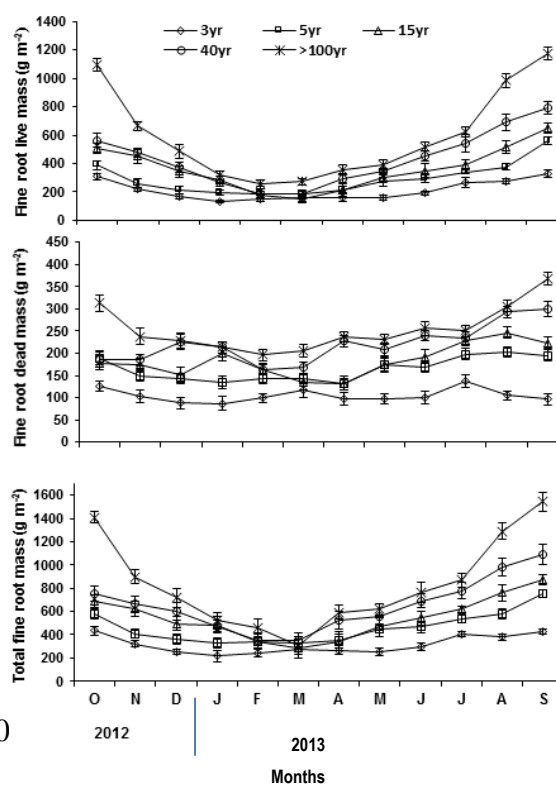


Fig. 2. Monthly changes in live, dead and total fine root mass to 30 cm soil depth during stand development in northeast India. Vertical lines show \pm 1SE.

for fine roots ranged between 137 and 439 g m^{-2} in 3yr and old growth forest, respectively. Maximum mass of 2–5 mm roots was recorded in the month of September–October and the minimum during February–March. The mean mass for this root category ranged from 134 g m^{-2} in 3yr stand to 273 g m^{-2} in old growth forest (Fig. 3).

Vertical distribution of root mass

Bulk fine root biomass (42–53%) was recorded in 0–10 cm depth which decreased significantly ($P < 0.05$) with increase in depth in all stands. The subsurface soil layers 10–20 and 20–30 cm depth contributes (28–35%) and (19–27%) of fine root biomass respectively. Of the total fine root mass about 27% roots were contained in 0–10 in 5yr stand which increased to 33% in old growth forest. Fine root necromass showed similar pattern i.e. decrease with increase in soil depth (Fig. 4).

The contribution of fine roots in upper depth increased significantly during the course of ecosystem development being minimum (123 g m^{-2}) in

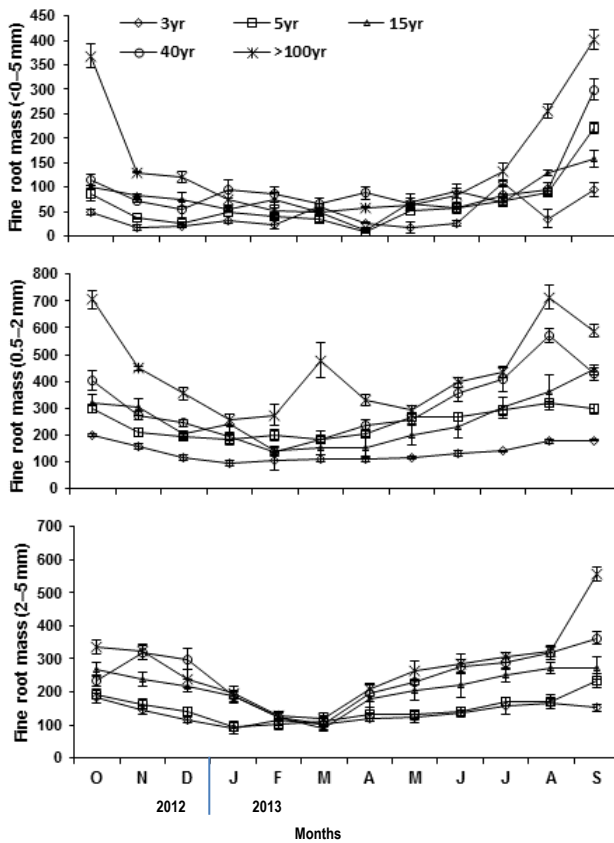


Fig. 3. Temporal changes in different root size classes (<0.5 mm, 0.5–2 mm, 2–5 mm) of fine root mass (g m^{-2}) during stand development in northeast India. Vertical lines show $\pm 1\text{SE}$.

3yr stand and maximum (386 g m^{-2}) in old growth forest. However, amount of fine roots in the surface soil layer increased significantly ($P < 0.01$) from young stand to old growth forest. The decrease in fine root mass with increasing depth was significant ($\text{LSD} = 23.1$, $P < 0.01$) in all the sites. Fine root biomass in upper depth of old growth forest was about 3.15 times higher than that of 3yr stand. This proportion decreased during the course of ecosystem development and it was only 1.1 times when compared to 40yr stand (Fig. 5).

Root production and turnover

Annual production and turnover of roots of various sizes in three soil depths of all stands have been provided in Table 3 & 4. Production of very fine roots (<0.5 mm) was minimum ($92 \text{ gm}^{-2}\text{yr}^{-1}$ and $202 \text{ gm}^{-2}\text{yr}^{-1}$, respectively, through annual max-min biomass and apparent biomass increment) in 3yr stands and maximum ($352\text{--}409 \text{ g m}^{-2}\text{yr}^{-1}$) in old growth forest. The turnover rate of very fine roots

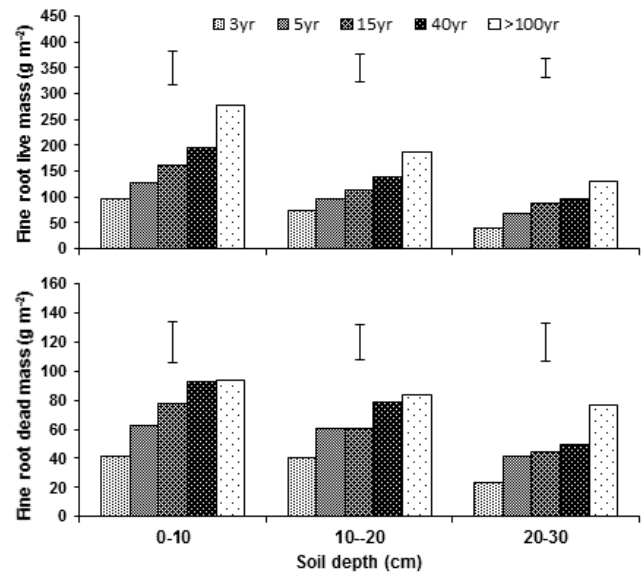


Fig. 4. Variations in mean annual fine root live and dead mass in three soil depths during stand development in northeast India. Vertical bars denote LSD at $P < 0.05$.

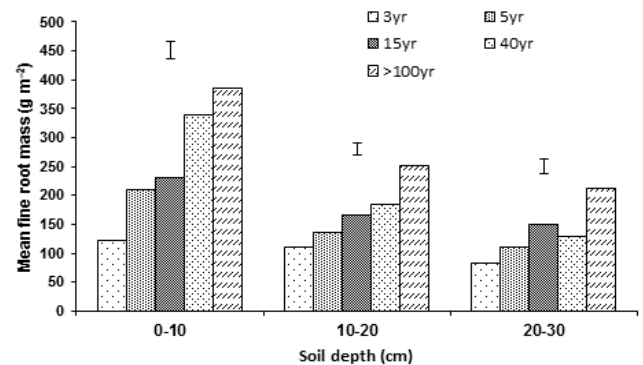


Fig. 5. Variations in mean annual fine root mass in three soil depths during stand development in northeast India. Vertical bars denote LSD, $P < 0.05$.

(<0.5 mm) was fastest in different root categories and highest in the young stands. Productivity and turnover of different fine root categories varied significantly ($P < 0.01$) in different stands. In general, fine root production was significantly ($P < 0.05$) more in the forest stand compared to the developing stands (Table 3). ANOVA showed significant differences in root production in different depths and sites ($F=14.09$, $P<0.001$), indicating significant changes in root production with soil depths and stand age (Table 4). The production of fine roots decreased significantly ($P<0.05$) with the increase in soil depth in all the

Table 3. Annual production ($\text{g m}^{-2}\text{yr}^{-1}$) and turnover (a^{-1}) of different root diameter classes (0–30 cm depth) in different developing stands in northeast India. Values followed by different superscript letters within columns indicate significant differences ($P < 0.05$) among forest chronosequences.

Fallow period (yr)	Root diameter (mm)	Production		Turnover	
		P ₁	P ₂	T ₁	T ₂
3	<0.5	92	202	2.16	4.75
	0.5–2	106	112	0.77	0.81
	2–5	93	121	0.69	0.90
	Total	215 ^a	260 ^a	0.68 ^a	0.83 ^a
5	<0.5	211	235	3.25	3.63
	0.5–2	137	153	0.57	0.63
	2–5	138	140	0.92	0.94
	Total	424 ^b	438 ^b	0.93 ^b	0.96 ^b
15	<0.5	147	189	1.83	2.35
	0.5–2	302	342	1.19	1.35
	2–5	184	198	0.87	0.96
	Total	585 ^c	653 ^c	1.07 ^b	1.14 ^c
40	<0.5	245	306	2.48	3.12
	0.5–2	431	475	1.37	1.49
	2–5	259	344	1.05	1.40
	Total	741 ^d	817 ^d	1.14 ^c	1.25 ^d
RF (>100 yr)	<0.5	352	409	2.36	2.84
	0.5–2	459	760	1.04	1.73
	2–5	437	460	1.59	1.64
Total	1235 ^e	1320 ^e	1.48 ^c	1.52 ^e	

P₁ and P₂ are the values of fine root production calculated as the sum of difference between annual maximum and minimum root standing crop biomass of different diameter classes and the sum of apparent biomass increments for each size classes over the course of a year. T₁ and T₂ are fine root turnover rates calculated as the ratio of annual net production/annual mean biomass using the values of P₁ and P₂ respectively.

stands except in the 3 yr stand. Fine root production of 0–10 cm soil depth ranged from 87 to 519 $\text{g m}^{-2}\text{yr}^{-1}$ through maximum-minimum method and 123–539 $\text{g m}^{-2}\text{yr}^{-1}$ through apparent biomass increment method in the 3yr stand and forest stand, respectively. Turnover of fine roots was significantly ($P < 0.05$) more in the forest compared to the developing stands. In the younger stands, turnover of fine roots was higher in the 20–30 cm soil depth

Table 4. Annual root production ($\text{g m}^{-2}\text{yr}^{-1}$) and turnover (a^{-1}) at different soil depths in developing stands in northeast India. Values followed by different superscript letters within columns indicate significant differences among forest chronosequences at $P < 0.05$.

Fallow period (yr)	Soil depth (cm)	Production		Turnover	
		P ₁	P ₂	T ₁	T ₂
3	0–10	87	123	0.70	0.99
	10–20	79	104	0.73	0.94
	20–30	86	107	1.04	1.31
	Total	215 ^a	260 ^a	0.68 ^a	0.83 ^a
5	0–10	192	233	0.91	1.11
	10–20	144	158	1.06	1.16
	20–30	128	158	1.15	1.42
	Total	424 ^b	438 ^b	0.93 ^b	0.96 ^b
15	0–10	214	248	0.93	1.08
	10–20	224	311	1.35	1.87
	20–30	173	229	1.15	1.53
	Total	585 ^c	653 ^c	1.07 ^b	1.14 ^c
40	0–10	420	532	1.23	1.26
	10–20	304	366	1.65	1.79
	20–30	182	312	1.41	1.62
	Total	741 ^d	817 ^d	1.14 ^c	1.25 ^d
RF (>100 yr)	0–10	519	539	1.34	1.39
	10–20	399	475	1.59	1.89
	20–30	217	273	1.03	1.29
Total	1235 ^e	1320 ^e	1.48 ^c	1.52 ^e	

P₁ and P₂ are the values of fine root production calculated as the sum of difference between annual maximum and minimum root standing crop biomass of different diameter classes and the sum of apparent biomass increments for each size classes over the course of a year. T₁ and T₂ are fine root turnover rates calculated as the ratio of annual net production/annual mean biomass using the values of P₁ and P₂ respectively.

while in the 40 yr and forest stand it was more in the 10–20 cm soil depth (Table 4).

Discussion

Variations in fine root mass during stand development

Total fine root mass increased with the increasing age of the stands. Greater fine root mass in the old growth forest site could be attributed to species composition (i.e. higher tree density and

diversity), higher soil moisture and accumulation of greater soil organic matter and relatively undisturbed conditions that all may lead to proliferate roots in the soil and support the dense vegetation cover. However, lower productivity in developing stands may be attributed to decreased soil moisture, organic matter, nutrients and plant cover. The conversions of natural forest into agriculture land have been reported to disrupt the pattern of spatial and temporal controls over nutrient cycling (Arunachalam *et al.* 2001) which may lead to significant losses of nutrients as a result of surface run off during rainy season and consequently lowering fine root mass and productivity in the developing stands. Similar pattern of fine root mass was found in several other studies in boreal (Yuan & Chen 2012), temperate (Jagodziński & Kałucka 2011) and tropical forests (Arunachalam *et al.* 1996; Barbhuiya *et al.* 2012; Upadhaya *et al.* 2005). The range of total fine root mass in the present study is comparable to other reports from different tropical forest of India (Arunachalam *et al.* 1996; Barbhuiya *et al.* 2012; Upadhaya *et al.* 2005).

Temporal changes in the fine root mass in the present study is the outcome of the changing wet and dry conditions of the site as a result of changing temperature and precipitation pattern that is the main characteristics of tropical ecosystems. Studies in other forests have reported similar growth pattern of fine roots and suggesting that fine roots grow and senesce rapidly, probably influenced by soil temperature and humidity (Santantonio & Hermann 1985; Srivastava *et al.* 1986). The variability and periodicity of root growth are due to environmental causes, among which water availability is one of the most important (Vogt *et al.* 1991). In the present study, concentration of maximum fine root mass in the rainy season in all stands (Fig. 4) could be related to favourable temperature and availability of water and nutrients in the soil. In tropical environment, plant mobilizes larger fractions of photosynthate for the formation of active roots to exploit soil nutrients from greater soil volume to increase total production that makes these forests one of the most productive in the world. Similar seasonal trend in root mass have been reported by other workers in similar ecosystems (Barbhuiya *et al.* 2012; Tripathi *et al.* 1999; Upadhaya *et al.* 2005) from different parts of India. The ratio of fine root live mass to dead mass in the present study ranged from 1.8–2.3. This ratio has been considered high by Persson & Stadenberg (2007) that indicates a healthy root system with a

high rate of soil penetration and an efficient uptake function.

Significantly higher fine root mass in the surface soil layer compared to sub surface soil layer in the present study revealed that the roots are concentrated in the fertile zone of the soil. Upper soil zone in moist tropical forests annually receives nutrients through litterfall return, canopy leachates and stemflow and the mortality of fine roots. So bulk of the nutrients are available during short time span so the proliferation of these roots in surface soil may lead rapidly trap them to meet plant nutrient demand and decreased the probability of runoff losses of nutrients on steep slopes due to torrential rains in wet season. This agrees with the findings from several studies in tropical and sub-tropical ecosystems elsewhere (Arunachalam *et al.* 1996; Barbhuiya *et al.* 2012; Borja *et al.* 2008; Sahu *et al.* 2013; Upadhaya *et al.* 2005; Yang *et al.* 2004;). Greater concentration of fine roots in surface soil of forest compared to developing stands would be due to higher amount of organic matter and nutrients availability in the topsoil of the forest (Table 1). Higher fine root concentrations in the surface soil layer have been reported to be correlated to high nutrient concentrations and soil water (Fu *et al.* 2015). Similar observations were made by Arunachalam *et al.* (1996), Upadhaya *et al.* (2005), Barbhuiya *et al.* (2012) and Noguchi *et al.* (2014) in different tropical ecosystems.

Variations in fine root production and turnover during stand development

In the present study, enhanced fine root production with increasing stand age would be related to the changing pattern of species composition and soil properties with stand age. Positive effect of vegetation structure on root production have been reported in sub-tropical and montane tropical forests (Hertel *et al.* 2009; Jones *et al.* 2003). The fine root productivity in this study indicated that the conversion of an undisturbed forest to cultivable land resulted in about 73% and 59% decrease in productivity in the upper and lower soil depths, respectively. Castellanos *et al.* (2001) reported that conversion of tropical dry forest to pasture resulted in *ca.* 56% decrease in fine root productivity in top 5 cm soil layer. The present fine root production estimates are comparable with the estimates of Arunachalam *et al.* (1996) from subtropical humid forest in north-east India but is higher than those reported by Upadhaya *et al.*

(2005) and Barbhuiya *et al.* (2012) from subtropical and tropical forests of northeast India.

During the conversion of forests to shifting agriculture land or other landuse systems, the topsoils are frequently disturbed and nutrient and surface soil loss would become serious (Ramakrishnan 1992; Ziegler *et al.* 2009). In the present study, the presence of reduced amount of fine roots in the 0–10 cm soil profile in the young stands, compared to the old growth forest, would bring a risk of nutrient loss, especially during the early stage of development due to high annual rainfall, slopes, and fragile soils. A rapid recovery of fine root system that has developed in the surface layer of the soil is, therefore, of much importance in helping nutrient conservation and improving the soil fertility in the young stands. In this respect, high proportion of very fine roots (<0.5 mm) production in younger stands may lead to trap readily available nutrients and accelerates the process of recovery during stand development.

According to Gill & Jackson (2000), fine root turnover rates of world forests were in the range of 0.02 to 2.64 a⁻¹, with an average of 0.56 a⁻¹. Our estimates (0.8–1.46 a⁻¹) is well within the world range but are substantially higher than the global average. Further, our turnover values were higher than those of other tropical and subtropical forests of India (Garkoti 2011; Barbhuiya *et al.* 2012). Higher root turnover might be due to alternating wet and dry conditions of the region, soil physico-chemical characteristics and root intrinsic qualities. Lower turnover in the young stands is in agreement with Gill & Jackson (2000) that the plants growing in nutrient poor environment might increase root life span to avoid nutrient losses. Jackson & Caldwell (1989), speculate that plants might be able to regulate the degree of root proliferation in accordance with their demand for nutrients. Present study suggests that root longevity and turnover may vary in response to changes in resource availability with the developmental stage of the stands.

Conclusion

We conclude that the developing stands increase the proportions of very fine roots with high turnover rates to exploit meagre soil resource (nutrients and water) and to add organic matter and nutrients to the soil through fine root mortality that accelerates the processes of recovery during the early stages of development. This has led to increase root vitality during the course of stand

development as evident from increased ratio of live root biomass to dead root mass. Such studies in secondary tropical forests following shifting agriculture in Mizoram may contribute significantly to their recovery and sustainable management, and would be helpful in predicting and modelling the impact of landuse change on belowground ecology.

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