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Decomposition of fine roots of *Pinus kesiya* and turnover of organic matter, N and P of coarse and fine pine roots and herbaceous roots and rhizomes in subtropical pine forest stands of different ages

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Abstract Organic matter accumulation, N and P concentrations of fine (<2 mm diameter) and coarse (2–10 mm) roots of Pinus kesiva and fine roots and rhizomes of ground vegetation, and decomposition of P. kesiya fine roots (<2 mm diameter) were studied in 6-, 15- and 23-year-old P. kesiya forest stands at Shillong, the capital of Meghalaya, India. The mean annual dry weight of *P. kesiya* fine roots did not vary significantly between the stands, but the coarse root mass increased significantly from the 6- to 23-year-old stand. However, herbaceous fine roots and rhizomes showed a reverse trend. Live roots (biomass) showed a higher N and P concentration than the necromass (dead root mass). Nutrient concentrations were greater in the fine roots compared to coarse roots. N and P accumulation was maximum in the 6-yearold stand and minimum in the 15-year-old stand. P. kesiya fine roots decomposed in a three-phased manner in all the stands. The first phase, lasting about 30 days, was characterised by a slow rate of weight loss. This was followed by a rapid phase of weight loss up to 90 days, with an average weight loss of 7.7 mg day-1, and the third phase showed a slow decay pattern (1.2 mg day-1). The weight loss pattern showed a strong seasonal trend; a faster rate of decay in the warm-humid period and a slow rate of decay in the dry-cold period. Nitrogen and P concentration in the decomposing root litter showed a marked decrease and/or increase during decomposition. The study reveals that in the 6-year-old pine stand the roots of herbaceous plants play a more significant role in maintaining the organic matter, N and P status of the soil, while in the older stands pine roots assumed greater significance.

Keywords Fine root decomposition \cdot Pine forest \cdot N and P mineralisation

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Introduction

Fine roots make a substantial contribution to soil organic matter and play an important role in nutrient cycling in forest ecosystems (Aber et al. 1985; Sanchez 1995; Cairns et al. 1997; Lehman and Zech 1998). Root turnover may return 4–5 times more C than the aboveground litter fall (Fogel 1983), and may contribute to 30–40% of the soil organic pool (Heal et al. 1997). The quantity of N added to the soil by roots may be from 18% to 45% greater than that added by the aboveground litter fall in some forest ecosystems (Vogt et al. 1986, 1991), mainly due to their higher annual input and faster turnover rate. Thus root production and turnover are the important processes in the overall cycling of nutrients in the forest ecosystem.

The importance of litter as the dominant pathway of nutrient cycle in forest ecosystems is well recognised (Swift et al. 1979; Vogt et al. 1991; Badre et al. 1998). The studies carried out during the past two decades or so, have generated enough quantitative data to show that at least in the cold temperate forests fine root turnover may contribute more to the organic matter decomposition cycle than the aboveground litter fall (Vogt et al. 1986, 1991). Decomposition and mineralisation patterns of roots may differ from the aboveground litter due to the differences in the resource quality of the two types of litter and differences in the environmental conditions under which they decompose. Litter decomposition and nutrient mineralisation are influenced by a number of factors such as climate, soil moisture content, activities of soil microbes and soil fauna (Badre et al. 1998), chemical composition of the decomposing material (Christensen 1986; Cornu et al. 1997), particularly concentrations of N and lignin, and C/N and lignin/N ratios (Peterson and Rafe 1982; Berg 1984; Vogt et al. 1991).

Pinus kesiya forests are found almost as pure stands over a vast area in north-east India between 800 and 2,000 m altitude. These forests have developed as a result of degradation of primary broadleaved forests by clear felling or selective cutting of trees for shifting cultivation widely practised throughout north-eastern India.

The major objectives of the present research were to study the accumulation of organic matter and nutrients (N and P) in fine and coarse roots of pine trees and in herbaceous roots and rhizomes, decomposition of tree fine roots, and the release of N and P in *P. kesiya* stands of three different ages.

Materials and methods

Site description

The study was carried out in three pure stands of subtropical Khasi pine (*P. kesiya*) forest representing three different ages (6-, 15- and 23-year old), which are located in and around the North-Eastern Hill University Campus, Shillong (latitude 25°34'N, longitude 91°54'E, altitude 1,500 m asl), the capital of Meghalaya, India. The climate of Shillong is monsoonic with distinct warm-wet and cold-dry seasons. During the study period the average annual rainfall was 2,054 mm and mean monthly maximum and mean monthly minimum temperatures were 21.2 and 13.4°C, respectively (Fig. 1). The soils (latosol) which are derived largely from pre-Cambrian igneous rocks (Pascoe 1950) are highly weathered and acidic in reaction.

Vegetation and soil analysis

Vegetation analysis was carried out according to Misra (1968). Ten quadrats of 10×10 -m area were laid randomly in each stand to determine tree density, while 20 1×1-m quadrats were laid to determine the density of the herbaceous species.

Five soil samples were collected from each of the four soil depths (0–10, 10–20, 20–30 and 30–40 cm) on a monthly interval between May 1995 and April 1996 from all the three stands by using a soil corer. The soil samples of a given depth were mixed thoroughly, passed through a 2-mm sieve and used for analysis. Soil texture was determined by the Bouyoucos hydrometer method. Moisture content was estimated gravimetrically using freshly collected soil samples. pH was determined in a solution of soil and distilled water (1:2.5 w/v). Organic C was determined by rapid titration method and total Kjeldahl nitrogen (TKN) by micro-distillation method (Allen et al. 1974). Available-P was determined using molybdenum blue after extracting the soil P in 0.5 M sodium bicarbonate solution (Anderson and Ingram 1993).

Accumulation of biomass and nutrients

Roots were sampled using a soil corer (diameter 6.3 cm; length 40 cm) at monthly intervals between May 1995 and April 1996. At each sampling, ten randomly located cores were taken from each of the three forest stands. The cores were subsequently divided into four equal sections each having a 10-cm thickness, starting from the soil surface. The samples were stored in a deep freeze at -20°C until the roots were separated. The roots were retrieved from the soil cores by wet sieving (Bohm 1979) and categorised into fine (<2-mm diameter) and coarse (2- to 10-cm diameter) roots. Roots of herbaceous species and rhizomes of grasses were grouped separately. All the roots were sorted into live and dead fractions on the basis of cohesion between cortex and periderm, colour and presence of live apices (Persson 1978; Vogt and Persson 1991). Live roots were much more resistant than dead ones and did not break easily when bent. Dead roots were often wrinkled and dark in colour in contrast to the smooth and light-coloured live roots. The live and dead roots were dried separately at 80°C to constant weight. Annual root production was determined by summing up all the increments in the live root mass (biomass)

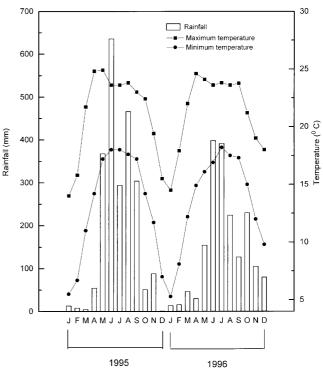


Fig. 1 Monthly variation in rainfall and mean monthly maximum and minimum temperatures during the study period

and concurrent increment, if any, in the dead root mass (necromass) between the sampling dates (Persson 1978). The dried root samples were powdered in a Cyclotec-Tecator and used for nutrient analysis. Total Kjeldahl N was determined by the micro-distillation and total P was analysed using molybdenum blue (Allen et al. 1974). Nitrogen and P accumulation in the live and dead roots was calculated by multiplying the mean dry mass of the two categories of roots with their respective element concentrations.

Root decomposition and nutrient mineralisation

For the decomposition study, tree fine roots (<2 mm) were collected separately from the top soil layer of the three stands during May 1995. The root decomposition experiment was started in July keeping in view the optimum conditions prevailing in this month for root decomposition and renewal of fine roots. They were carefully washed under a gentle flow of tap water to remove the adhering soil particles and organic debris. Due to difficulty in collecting a large amount of newly senesced tree fine roots, only air-dried live roots measuring <2-mm diameter were used for the decomposition experiment. The rate of weight loss and release of nutrients were studied by the litter bag method as outlined by McClaugherty et al. (1984). Sixty bags (2-mm mesh, 15×15-cm nylon bags), each with 2 g air-dried root material, were prepared for each stand. They were buried in soil at a 5-cm depth at four places in each of the three stands on 1 July, 1995. Subsamples of air-dried root materials were used for determining initial dry weight. Four bags were retrieved from each stand at 30-day intervals, the roots were washed gently to remove the adhering soil particles and dried at 80°C for 48 h and weighed. Loss in weight and the rate of N and P release during decomposition were determined using weight and element concentrations of the root samples obtained from the litter bags. Root samples used for initial dry weight determination were analysed for ash content, total P, total Kjeldahl N, lignin and cellulose (Allen et al. 1974). Ash content was determined by igniting the oven-dried root material at 500°C for 6 h in a muffle furnace.

Parameters	Soil depth (cm)					
	0–10	10–20	20–30	30–40		
6-year-old stand						
Sand (%) Clay (%) Bulk density (g cm ⁻³) pH Moisture content (mg g ⁻¹) Organic carbon (mg g ⁻¹) Total Kjeldahl nitrogen (mg g ⁻¹) Available-P (mg g ⁻¹)	$\begin{array}{c} 88.5{\pm}1.2\\ 3.2{\pm}0.2\\ 0.73{\pm}.01\\ 5.0{\pm}0.1\\ 300{\pm}22\\ 16.4{\pm}0.3\\ 1.7{\pm}0.1\\ 0.02{\pm}0.002\\ \end{array}$	$\begin{array}{c} 81.2{\pm}0.7\\ 9.6{\pm}0.4\\ 0.90{\pm}0.01\\ 5.1{\pm}0.1\\ 318{\pm}28\\ 11.4{\pm}0.2\\ 1.4{\pm}0.1\\ 0.02{\pm}0.002\\ \end{array}$	72.4 ± 0.7 12.2 ± 0.7 1.05 ± 0.02 5.2 ± 0.1 326 ± 25 9.2 ± 0.8 1.2 ± 0.2 0.01 ± 0.002	$\begin{array}{c} 68.1{\pm}0.7\\ 16.2{\pm}0.5\\ 1.15{\pm}0.02\\ 5.3{\pm}0.1\\ 333{\pm}19\\ 7.8{\pm}0.3\\ 0.8{\pm}0.1\\ 0.01{\pm}0.001\end{array}$		
15-year-old stand Sand (%) Clay (%) Bulk density (g cm ⁻³) pH Moisture content (mg g ⁻¹) Organic carbon (mg g ⁻¹) Total Kjeldahl nitrogen (mg g ⁻¹) Available-P (mg g ⁻¹)	$\begin{array}{c} 91.3 {\pm} 0.4 \\ 1.1 {\pm} 0.1 \\ 0.97 {\pm} 0.002 \\ 5.2 {\pm} 0.1 \\ 307 {\pm} 31 \\ 14.8 {\pm} 0.3 \\ 1.6 {\pm} 0.01 \\ 0.020 {\pm} 0.002 \end{array}$	$\begin{array}{c} 88.5 {\pm} 0.4 \\ 3.2 {\pm} 0.4 \\ 1.01 {\pm} 0.007 \\ 5.3 {\pm} 0.1 \\ 305 {\pm} 27 \\ 11.0 {\pm} 0.4 \\ 1.2 {\pm} 0.02 \\ 0.014 {\pm} 0.002 \end{array}$	$\begin{array}{c} 67.6{\pm}1.2\\ 17.8{\pm}1.2\\ 1.01{\pm}0.02\\ 5.4{\pm}0.1\\ 327{\pm}19\\ 9.2{\pm}0.5\\ 1.1{\pm}0.02\\ 0.013{\pm}0.001\\ \end{array}$	$\begin{array}{c} 49.2{\pm}0.7\\ 30.9{\pm}1.2\\ 1.22{\pm}0.01\\ 5.4{\pm}0.1\\ 339{\pm}16\\ 7.5{\pm}0.2\\ 0.9{\pm}0.02\\ 0.012{\pm}0.001\end{array}$		
23-year-old stand Sand (%) Clay (%) Bulk density (g cm ⁻³) pH Moisture content (mg g ⁻¹) Organic carbon (mg g ⁻¹) Total Kjeldahl nitrogen (mg g ⁻¹) Available-P (mg g ⁻¹)	$78.9\pm1.2 \\ 9.7\pm0.5 \\ 0.95\pm0.01 \\ 5.2\pm0.05 \\ 330\pm4 \\ 10.6\pm0.4 \\ 1.4\pm0.03 \\ 0.020\pm0.0002$	$\begin{array}{c} 77.6 {\pm} 0.7 \\ 11.7 {\pm} 0.3 \\ 1.02 {\pm} 0.01 \\ 5.3 {\pm} 0.006 \\ 325 {\pm} 28 \\ 8.6 {\pm} 0.2 \\ 1.1 {\pm} 0.02 \\ 0.020 {\pm} 0.002 \end{array}$	$52.9\pm1.4 \\ 30.3\pm1.2 \\ 1.07\pm0.007 \\ 5.3\pm0.06 \\ 325\pm26 \\ 7.2\pm0.2 \\ 0.90\pm0.02 \\ 0.010\pm0.0001 \\ \end{array}$	$\begin{array}{c} 38.6{\pm}1.2\\ 39.1{\pm}0.7\\ 1.15{\pm}0.002\\ 5.4{\pm}0.06\\ 324{\pm}18\\ 5.7{\pm}0.3\\ 0.8{\pm}0.03\\ 0.010{\pm}0.001\end{array}$		

Table 1 Soil characteristics of the three *Pinus kesiya* stands of different ages. Each value (except the values for % sand, % clay and bulk density) is a mean (\pm SE) of 36 samples across the year

The annual decay constant (k) was calculated following the negative exponential decay model of Olson (1963): $k = \ln (x/x_0) t$, where x_0 is the initial dry weight, x is the dry weight remaining at the end of the investigation and t is the time in years. Similarly N and P mineralisation constants, k_N and k_P respectively, were calculated using N and P stocks in the beginning and at the end of the experiment (Singh and Shekhar 1989). The time (in years) required for 50% (t_{50}) and 99% (t_{99}) nutrient mineralisation was calculated as t_{50} =0.93/k and t_{99} =5/k. The data were processed by one-, two- and three-way ANOVA

The data were processed by one-, two- and three-way ANOVA (fixed effect model) to test whether the biomass and nutrient accumulation varied significantly with root size and stand age. Correlation analyses were carried out to determine the effect of initial fine root chemistry on the rate of weight loss.

Results

Vegetation and soil

The density of *P. kesiya* was 11,020 (\pm 394), 3,060 (\pm 46) and 730 (\pm 14) plants ha⁻¹ in the 6-, 15- and 23-year-old stands, respectively. In all three stands ground vegetation was dominated by *Arundinella khasiana*, *Arundinella bengalensis* and *Axonopus compressus* whose densities varied from a low of 75 individuals m⁻² in the 15-year-old stand to a high of 116 individuals m⁻² in the 6-year-old stand.

Soil was sandy and acidic in all stands. The proportion of sand showed a marked decrease with soil depth, but the clay content and bulk density showed a reverse trend. The pH varied from 5.0 in the upper (0–10 cm) soil layer to 5.4 in the lower (30–40 cm) soil layer. Soil organic C, total Kjeldahl N and available P concentrations were low and they did not vary significantly between the stands (Table 1).

Biomass and production of roots

The mean annual dry weight of live and dead fine roots of P. kesiya did not vary significantly between the stands, but that of coarse roots increased significantly (P < 0.01) from the 6-year-old stand to the 23-year-old stand. Herbaceous fine roots and rhizomes declined significantly from the young to the old stands (Table 2). The total annual tree fine root production did not vary significantly between the stands, but herbaceous fine root production declined significantly (P < 0.01) from 589 g m⁻² y⁻¹ in the 6-year-old stand to 322 g m⁻² y⁻¹ in the 23-year-old stand. The coarse root production increased from 169 g m⁻² in the 6-year-old stand to 466 g m^{-2} in the 23-year-old stand (Table 2). Fine root biomass and necromass were maximum during the rainy season and minimum during the spring season in all the forest stands.

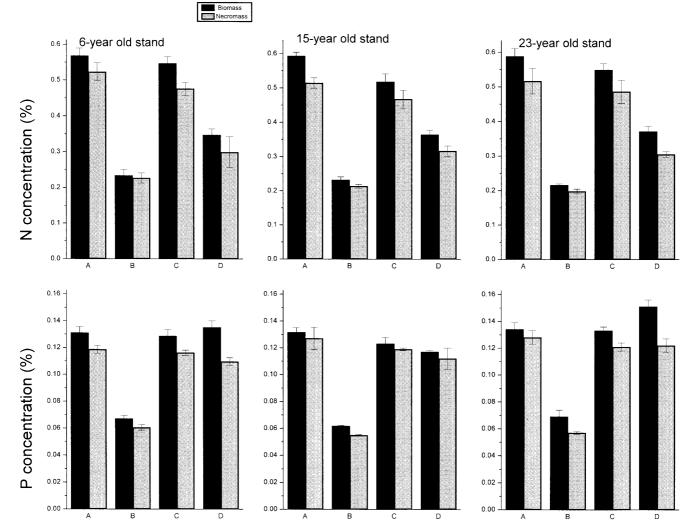


Fig. 2 Mean N and P concentration in biomass and necromass of roots and rhizomes in the three pine forest stands of different ages (A tree fine roots, B tree coarse roots, C herbaceous fine roots, D rhizomes)

Table 2 Mean monthly biomass and necromass, and production of roots in the three pine forest stands of different ages ($n = 12 \pm SE$)

Categories	Biomass (g m ⁻²)	Necromass (g m ⁻²)	Production (g m ⁻² y ⁻¹)
6-year-old stand			
Tree fine roots Tree coarse roots Herbaceous fine roots Rhizomes	96.4±14.4 44.1±8.3 121.2±20.4 60.9±8.6	96.5±10.5 8.3±4.6 103.2±14.1 64.4±7.3	465.8 169.1 588.5 -
15-year-old stand			
Tree fine roots Tree coarse roots Herbaceous fine roots Rhizomes	109.5±7.2 113.4±25.4 46.4±5.8 24.3±3.5	99.4±8.1 14.8±3.12 47.3±4.8 26.7±2.9	463.1 266.4 268.8
23-yearold stand			
Tree fine roots Tree coarse roots Herbaceous fine roots Rhizomes	109.5±10.4 196.7±27.8 61.6±9.7 44.3±4.4	107.6±12.2 21.5±3.4 42.4±6.4 44.2±5.4	421.2 466.4 321.9

N and P accumulation

Nitrogen and P concentrations in tree fine root biomass tended to be higher than in the necromass. Similarly, fine roots had significantly (P < 0.01) higher concentrations than coarse roots (Fig. 2). Herbaceous fine roots and rhizomes also had higher N and P concentrations in the live fraction than in the dead parts. However, the differences in N and P concentrations between the live and dead roots and between the stands were not significant.

Nitrogen accumulation in tree fine roots did not vary significantly between the stands. However, its accumulation in coarse roots increased from 1.2 kg ha⁻¹ in the youngest stand to 4.7 kg ha⁻¹ in the oldest stand (Fig. 3). Nitrogen accumulation in herbaceous fine roots and rhizomes decreased from young to old stands (Fig. 3). In all cases the live fraction accumulated more N than the dead fraction. Total N accumulation (pine tree + herbs) in the belowground parts declined from 23.3 kg ha⁻¹ in the 6-year-old stand to 22.1 kg ha⁻¹ in the 23-year-old stand (Table 3). In the 6-year-old stand tree roots accumulated 43% of the total N stored in the belowground parts whereas in the 15- and 23-year-old stands the share of tree roots was 70% and 66%, respectively.

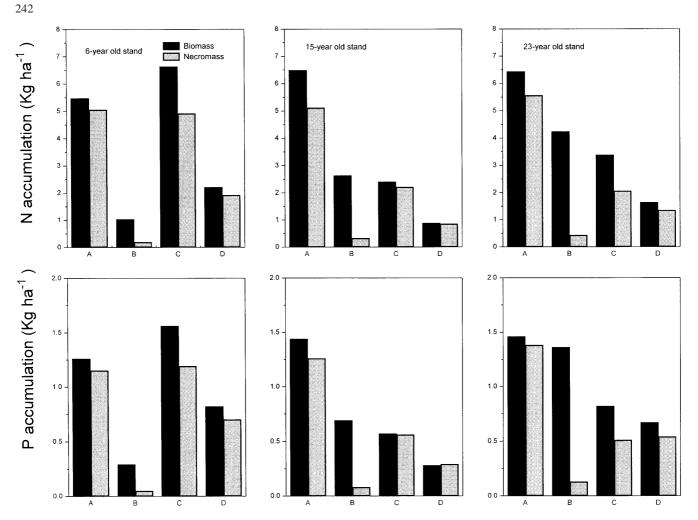


Fig. 3 Nitrogen and P accumulation in biomass and necromass of roots and rhizomes in the three pine forest stands of different ages (A tree fine roots, B tree coarse roots, C herbaceous fine roots, D rhizomes)

 Table 3 Mean accumulation of organic matter, N and P in roots and their turnover in the three pine forest stands of different ages

Parameters	6-year old	15-year old	23-year old
I. Accumulation (kg	g ha ⁻¹)		
Organic matter Nitrogen Phosphorus	4,697 23.28 5.5	4,308 19.16 4.60	5,392 22.1 5.88
II. Annual production	on/input (kg ha ⁻¹)	
Organic matter Nitrogen Phosphorus	12,234 52.48 12.72	9,983 42.22 10.28	12,095 51.52 12.94
III. Turnover rate (y	/ear ⁻¹)		
Organic matter Nitrogen Phosphorus	0.72 0.69 0.70	0.69 0.69 0.69	0.69 0.70 0.70

The P accumulation in fine and coarse roots of *P. ke-siya* increased with stand age. Accumulation of P in herbaceous roots and rhizomes was high (4.3 kg ha^{-1}) in the 6-year-old stand and low (1.7 kg ha^{-1}) in the 15-year-old

stand (Fig. 3). Total P accumulation (pine tree + herbs) was maximum (5.9 kg ha⁻¹) in the 23-year-old stand and minimum (4.6 kg ha⁻¹) in the 15-year-old stand. In the 15- and 23-year-old stands, 63-67% of the total P was present in the pine tree roots while in the 6-year-old stand the pine tree roots contributed only 39% of the total P.

Total input of N to the soil by roots was maximum (52.5 kg ha⁻¹) in the 6-year-old stand and minimum (42.2 kg ha⁻¹) in the 15-year-old stand, whereas the P input was maximum (12.9 kg ha⁻¹) in the 23-year-old stand and minimum (10.3 kg ha⁻¹) in the 15-year-old stand (Table 3).

Initial chemistry and decomposition of fine roots

Carbon, N and P concentrations in the fine roots were similar in all stands, but lignin, cellulose, C/N and lignin/N ratios increased with the stand age (Table 4).

The root decomposition pattern was similar in all the stands (Fig. 4). Initially, during the first 30 days, the decomposition occurred at a slow rate. During this period the average rate of weight loss was 3, 2 and 2 mg day ⁻¹ in 6-, 15-, and 23-year-old stands, respectively. This was followed by a phase of rapid weight loss up to 90 days of

Table 4 Initial chemical composition of fine roots of pine ($n = 5 \pm SE$)

Stand	C (%)	N (%)	P (%)	Lignin (%)	Cellulose (%)	C/N	Lignin/Nitrogen
6-year-old stand	27.66 ± 0.18	0.72±0.01	$\begin{array}{c} 0.048 {\pm} 0.001 \\ 0.053 {\pm} 0.001 \\ 0.053 {\pm} 0.005 \end{array}$	17.40±0.34	34.90±0.21	38.63	24.30
15-year-old stand	25.67 ± 0.30	0.64±0.01		19.38±0.26	38.95±0.96	40.01	30.1
23-year-old stand	25.97 ± 0.25	0.60±0.01		22.61±0.18	39.36±0.28	43.29	37.68

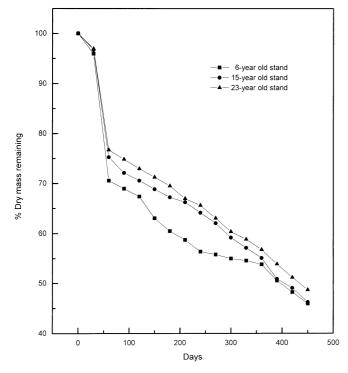


Fig. 4 Weight loss of *Pinus kesiya* fine roots during decomposition in the three pine forest stands of different ages

the study when the average rate was 8.3, 7.0 and 7.7 mg day ⁻¹ respectively. After this the decay process slowed down significantly and it continued at an average rate of 1.2 mg day⁻¹ until day 450. The difference in the rate of weight loss between the stands was not significant.

N and P mineralisation

The average rates of N mineralisation up to day 150 were 53.9, 36.4 and 33.6 μ g day⁻¹ in the 6-,15- and 23-year-old stands, respectively. After 150 days the N concentration in the roots registered an increase indicating a period of nutrient immobilization. During the next phase of decay between 270–450 days, the average rate of N release slowed down to 16.3, 22.4 and 25.8 μ g day⁻¹ in the 6-, 15- and 23-year-old stands, respectively (Fig. 5A). The N mineralisation constant (k_N) varied between 1.50 and 1.59 (Table 5). Annually, about 57–59% of the initial N content present in the roots was mineralised in the three pine stands.

The temporal variation in P concentration in the decomposing roots was similar to that of N (Fig. 5B). Dur-

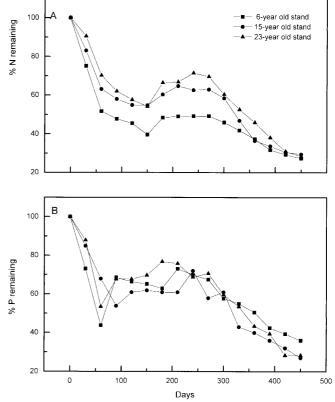


Fig. 5 Nitrogen (A) and P (B) mineralisation during decomposition of *Pinus kesiya* fine roots in the three pine forest stands of different ages

Table 5 Annual decay constant (*k*) and mineralisation constant (k_N) and (k_P) of *P. kesiya* fine roots in the three pine stands of different ages (t_{50} and t_{99} time in years required for 50% and 99% nutrient mineralisation)

Parameters	6-year-old	15-year-old	23-year-old				
	stand	stand	stand				
Root decay							
k	0.88	0.94	0.81				
t ₅₀	1.06	0.99	1.15				
t ₉₉	5.68	5.32	6.17				
N mineralisa	N mineralisation						
$\begin{array}{c} k_{\rm N} \\ t_{50} \\ t_{99} \end{array}$	1.59	1.50	1.54				
	0.58	0.62	0.60				
	3.14	3.33	3.25				
P mineralisation							
$\begin{array}{c} k_{\mathrm{P}} \\ t_{50} \\ t_{99} \end{array}$	1.25	1.61	1.55				
	0.74	0.58	0.60				
	4.0	3.10	3.22				

ing the first 60 days of root decay, P was mineralised at the average rates of 8.3, 5.4 and 7.7 µg day⁻¹ in the 6-, 15- and 23-year-old stands, respectively. The period between 60 and 210 days was characterised by immobilization when the concentration of P in the decaying litter registered a marked increase. A steady decrease in concentration after 210 days indicated resumption of mineralisation which occurred at the rates of 1.5, 1.4 and 1.9 µg P day⁻¹ in the 6-, 15- and 23-year-old stands, respectively. The phosphorus mineralisation constant (k_P) gradually increased from 1.25 in the young stand to 1.61 in the old stand (Table 5). About 51–58% of the initial P present in the roots was mineralised over a year in the three forest stands.

Discussion

The rainy season being the most favourable period for vegetative growth of plants, owing to favourable temperature and better availability of nutrients and water in soil, both tree and herbaceous fine root biomass attained their peaks during this season. Most of the fine root mass in three pine forest stands was distributed in the surface soil layer (John et al. 2001) which might be helpful in rapid absorption of water and nutrients to meet the requirements of the growing plants. As more and more fine roots were converted to coarse roots with age to provide better mechanical support to the trees in the older stands, the coarse root production increased from the 6-year-old stand to the 23-year-old stand, while the fine root production registered a marked decrease. The greater fine root production in the youngest stand compared to the older stands was mainly due to more luxuriant growth of the herbaceous species in the former stand.

Since renewal and death of fine roots take place simultaneously (Persson 1983), they continuously add nutrients to the soil system. Vogt et al. (1991) reported that nutrient concentration in roots is strongly influenced by their diameter. In the present study too, N and P concentrations were root diameter-dependent and decreased sharply from the fine to coarse roots. Nambiar (1987) has reported a similar relationship between nutrient concentration and root diameter in Pinus radiata. The resorption of nutrients from the young live roots during senescence and maturation could be one of the possible reasons for the low N and P concentration in the root necromass as well as in the older roots. The higher nutrient concentration in the herbaceous roots than the rhizomes could be attributed to greater metabolic activities in the former as was also reported by Boral (1993).

Nitrogen and P accumulation in roots is a function of their concentration in the roots and the root mass. However, the latter played a much greater role in determining the nutrient accumulation pattern in the belowground parts than the former. The maximum accumulation of N and P in the 6-year-old stand can be ascribed to the greater root mass in this stand. The decline in the contribution of herbaceous vegetation to the mean N and P

Table 6 Relationship between initial chemical composition and decomposition rate (% weight loss day⁻¹) of fine roots of *P. kesiya*

Initial chemical composition	Correlation coefficient: r values			
	First phase (0–30 days)	Second phase (30–90 days)	Third phase (90–450 days)	
Carbon (%)	0.671*	0.726*	-0.584	
Nitrogen (%)	0.747^{*}	0.869^{*}	-0.646*	
Phosphorus (%)	-0.462	-0.551	0.463	
Lignin (%)	-0.690*	-0.945*	0.675^{*}	
Cellulose (%)	-0.716^{*}	-0.811*	0.650^{*}	
C/N	-0.653*	-0.905^{*}	0.602	

* Significant at P < 0.01, n = 6

storage in the old stands was mainly due to the decrease in their biomass in such stands. In all three stands, the amount of N accumulated in the pine tree roots and herbaceous roots was greater than that of P. This is in conformity with the findings of Nambiar (1987) and Khiewtam and Ramakrishnan (1993). Annual N and P input in the soil was also related to the production.

The roots and rhizomes of herbs and grasses played a very important role in organic matter and nutrient dynamics, at least in the young stand where they accumulated 57% of the total N and 67% of the total P storage in the belowground parts. In the older stands, their contribution declined due to their poor growth probably as a result of competition from *P. kesiya* for light, water and nutrients. Finer et al. (1997) reported that roots of herbs and grasses were more abundant in the youngest successional stage in a boreal conifer-broadleaved forest stand. Tree roots played a dominant role in the older stands in this regard.

In all the stands litter decayed at a rapid rate after an initial lag due to the net effect of a large number of processes such as utilization of readily available energy sources by microbes, leaching of water-soluble organic compounds, inorganic salts and non-structural carbohydrates from the decomposing root litter (Bloomfield et al. 1993; Arunachalam et al. 1996; Cornu et al. 1997). With time, the decay rate decreases as the proportion of more resistant materials like lignin and cellulose increases in the decomposing litter (Fogel and Cromack 1977). The variation in litter quality over time thus controls the decay rate. Lignin has been reported to be the most likely constituent which limits weight loss during extended periods of decomposition and forms complexes with proteins present in the cell wall (Fogel and Cromack 1977; Berg and Staaf 1980). Up to day 90, C and N concentrations were positively correlated with decay rate, while lignin, cellulose and C/N ratio were negatively correlated (Table 6). This pattern was, however, reversed after 90 days of decomposition. The weight loss pattern showed a strong seasonal trend. The warm-humid period was characterised by a faster rate of decay while the drycold period was marked by a slow decay rate. Swift et al. (1979) attributed seasonal change in root decomposition rate in the tropical forest ecosystems to the soil moisture condition, ambient temperature and microbial activity.

As the dried fine roots were used for studying decomposition, it is likely that the decomposition rate slowed down because the rhizosphere organisms may have been killed or got separated from the roots during drying. The naturally shed roots may show a faster decomposition than the dried roots as they were attacked almost immediately by decomposers present in the rhizosphere (McClaugherty et al. 1984).

The rapid weight loss during the rainy season was mainly due to leaching while the relative increase in N and P content during the autumn and winter seasons might be the result of microbial immobilization and simultaneous degradation of easily decomposable substances, such as carbohydrates (Anderson 1973; Rutigliano et al. 1998), nutrient input into the soil by precipitation (Bocock 1963) and atmospheric N₂ fixation (Wood 1974). Annually, around 57.6% of N and 51.6% of P content of the roots were mineralised in the three forest stands. These values are comparable with those obtained by Arunachalam et al. (1996) in the semi-evergreen broadleaved forest of Meghalaya. The annual fractional weight loss (0.81-0.94)was within the range reported for the tropical forest ecosystem (0.3-3; Anderson and Swift 1983), teak forest (0.4–2.8; Singh and Shekhar 1989) and montane forest (0.6-1.9; Singh et al. 1984). The values are, however, much higher than those reported from the temperate forest ecosystems (0.16; Fogel and Hunt 1979; 0.09-0.12; McClaugherty et al. 1982; 0.6; Persson 1980).

A comparison of the belowground litter production in the present study with the aboveground litter production reported by Das (1980) in the pine stands of Meghalaya reveals that the contribution by roots to annual organic matter input to the soil in these forest stands is more than by aboveground litter. The data on belowground litter production and nutrient release pattern indicates that coarse and fine roots of pine trees and roots and rhizomes of herbaceous plants play a very significant role in soil nutrient dynamics in the pine forest ecosystem of Meghalaya. The study also reveals that in the 6-year-old pine stand the roots of herbaceous plants play a more significant role in maintaining the organic matter, N and P status of the soil, while in the older stands pine roots assume greater significance.

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