Tree species distribution and its impact on soil properties, and nitrogen and phosphorus mineralization in a humid subtropical forest ecosystem of northeastern India

Jenpuiru Kamei, H.N. Pandey, and S.K. Barik

Abstract: The impact of tree species on net N and P mineralization, and soil properties beneath their canopy were studied in a subtropical evergreen broad-leaved forest of northeastern India. Four types of experimental plots were identified based on tree species dominance. The first plot was dominated by *Myrica esculenta* Buch.-Ham. ex D. Don., the second by *Rhododendron arboreum* Sm., the third by *Neolitsea cassia* Koster., and the fourth was a mixed-species plot. Organic carbon content (3.11%) and NH_4^+-N concentration (11.40 $\mu g \cdot g^{-1}$) in the *Rhododendron* plot, pH (4.64) and total N content (0.89%) in the mixed plot, available P (5.16 $\mu g \cdot g^{-1}$) and NO_3^--N (8.63 $\mu g \cdot g^{-1}$) concentrations in the *Neolitsea* plot were significantly higher ($p < 0.001$) than the other plots. All these soil parameters were lowest in the *Myrica* plot. The net N and P mineralization rates in an annual cycle across different plots ranged between 18.83 and 22.14 $\mu g \cdot g^{-1} \cdot month^{-1}$ and between 4.54 and 5.87 $\mu g \cdot g^{-1} \cdot month^{-1}$, respectively. The flux varied significantly ($p < 0.001$) among the plots, the lowest and highest being in the *Myrica* plot and mixed plots, respectively. The differences in soil properties and in net N and P mineralization among different species plots were related to litter quality and yield of the respective species as well as soil microenvironment.

Résumé : L'impact des espèces d'arbres sur la minéralisation nette de N et P ainsi que les propriétés du sol sous leur couvert ont été étudiés dans une forêt tropicale feuillue sempervirente du nord-est de l'Inde. Quatre types de parcelles expérimentales ont été identifiées sur la base des espèces arborescentes dominantes. La première parcelle était dominée par *Myrica esculenta* Buch.-Ham. ex D. Don., la deuxième par *Rhododendron arboreum* Sm., la troisième par *Neolitsea cassia* Koster. et la quatrième était composée d'espèces mélangées. Le contenu en C organique (3,11 %) et la concentration de N-NH_4^+ (11,40 $\mu g \cdot g^{-1}$) dans la parcelle dominée par *Rhododendron*, le pH (4,64) et le contenu en N total (0,89 %) dans la parcelle composée d'espèces mélangées, ainsi que les concentrations de P disponible (5,16 $\mu g \cdot g^{-1}$) et de N-NO_3^- (8,63 $\mu g \cdot g^{-1}$) dans la parcelle dominée par *Neolitsea* étaient significativement plus élevés ($p < 0,001$) que dans les autres parcelles. Tous ces paramètres du sol étaient les plus faibles dans la parcelle dominée par *Myrica*. Les taux nets de minéralisation de N et P dans un cycle annuel variaient respectivement de 18,83 à 22,14 et de 4,54 à 5,87 $\mu g \cdot g^{-1} \cdot mois^{-1}$ parmi les différentes parcelles. La variation du flux parmi les parcelles était significative ($p < 0,001$); le flux le plus faible a été observé dans la parcelle dominée par *Myrica* et le plus élevé dans la parcelle composée d'espèces mélangées. Les différences dans les propriétés du sol et la minéralisation nette de N et P entre les parcelles étaient reliées à la qualité de la litière, au rendement des espèces respectives et aussi aux microenvironnements dans le sol.

[Traduit par la Rédaction]

Introduction

Tree species growing on a uniform parent material (Boettcher and Kalisz 1990; Oostra et al. 2006) can influence the size and distribution of nutrient pools across soil horizons (Binkley 1992; Berendse 1998) through plant uptake, root production and turnover, mycorrhizal activity, rhizodeposition, and quantity and quality of litter produced (Binkley and Giardina 1998; Augusto et al. 2002). While assessing the impact of single individuals of six tree species in a temperate forest on C/N ratio and N transformation, Finzi et al. (1998) found significant difference among the species. Similarly, Zinke (1962) reported that a single *Pinus contorta* Dougl. ex Loud. tree growing on a sand dune along the coast of California modified the sand chemistry underneath its crown. Most such studies aiming to assess the impact of individual species or diversity focus on decomposition processes rather than individual elemental cycles. Therefore, the effects of litter diversity on N and P dynamics have received very little attention (Hobbie 2005; Madritch and Cardinale 2007).

The few studies that relate species effects and nutrient cycling are confined to temperate species such as *Acer*, *Fagus*, *Betula*, *Tsuga*, *Larix*, *Pinus*, and *Quercus* and have generally compared mixed-species stands, sometimes with varying soil texture, making it difficult to isolate species effect (Finzi et al. 1998; Côté et al. 2000; Templer et al. 2003; Lovett et al. 2004; Brüggemann et al. 2005). Although some of the stud-

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Fig. 1. Distribution and canopy cover of tree species in the 10 m × 10 m *Myrica esculenta* plots: 1, *Myrica esculenta* (14); 2. *Rhododendron arboreum* (13); 3, *Symplocos javanica* (2); 4, *Ficus nerifolia* Sm. (1); 5, *Eurya acuminata* DC. (1); 6, *Dendropanax japonicum* Seem. (1); 7, *Photinia integrifolia* Lindl. (1); and 8, *Viburnum simonsii* Hook. f. & Thomson (1). The values in parentheses are the numbers of individuals of the species in the plots. The solid circles are the tree stems, the solid lines are the exposed margins of the canopies, and the broken lines are the margins of the canopies beneath other tree(s).

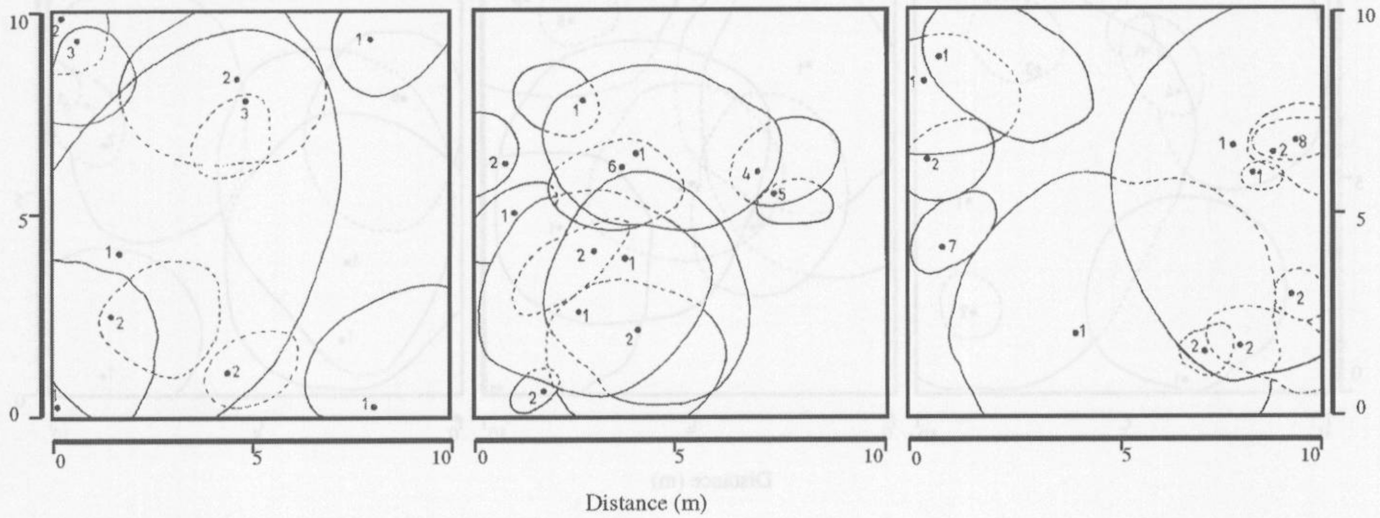
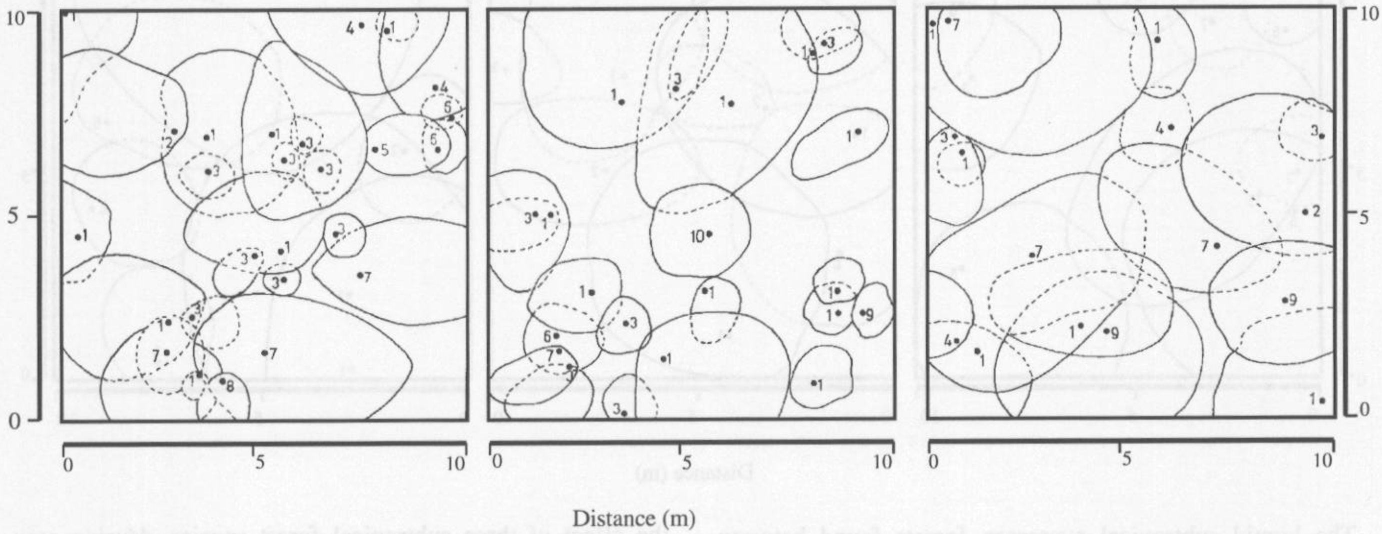


Fig. 2. Distribution and canopy cover of tree species in the 10 m × 10 m *Rhododendron arboreum* plots: 1, *Rhododendron arboreum* (25); 2, *Lyonia ovalifolia* (Wall.) Drude (2); 3, *Persea odoratissima* (1); 4, *Eurya acuminata* (3); 5, *Photinia integrifolia* (7); 6, *Symplocos* sp. (4); 7, *Ficus nerifolia* (1); 8, *Symplocos javanica* (16); 9, *Myrica esculenta* (3); and 10, *Engelhardtia spicata* (1). The values in parentheses are the numbers of individuals of the species in the plots. The solid circles are the tree stems, the solid lines are the exposed margins of the canopies, and the broken lines are the margins of the canopies beneath other tree(s).



ies have reported substantial variation in N (Finzi et al. 1998; Lovett et al. 2002, 2004) and P turnover (Polglase and Attiwill 1992; Rhoades et al. 1994; Campo et al. 2001) due to forest type and influence of individual species, differences among tree species are not consistent among studies, making it difficult to generalize about the species effect (Binkley and Giardina 1998). In other words, the influence of species composition is difficult to predict because the literature does not give a clear picture of how dominant tree species influence various soil properties including the cycling of N and P in the forest (Lovett et al. 2004).

Differences in nutrient availability in stands of different tree species are brought about largely through differences in the decomposability and nutrient mineralization of their foliar litter. Correlations between element transformation and litter-chemistry parameters varied among species, and establishing a general relationship between the two variables has not been possible (Lovett et al. 2004). Although litter decomposition is a major determinant of nutrient cycles, studies directly dealing with N and P mineralization and their correlation with litter chemistry and climatic conditions are rare (Aerts 1997). Further, Vitousek and Sanford (1986) and Aerts (1997) argued that P-related litter-chemistry parameters are important controls of litter decomposition in the tropics. Thus, the factors explaining diversity effects or species influence on N and P cycles remain inconclusive.

Fig. 3. Distribution and canopy cover of tree species in the 10 m × 10 m *Neolitsea cassia* plots: 1, *Neolitsea cassia* (13;, 2, *Prunus jenkinsii* Hook. f. & Thomson (1); 3, *Persea odoratissima* (2); 4, *Psychotria symplicifolia* (1); 5, *Elaeocarpus acuminatus* Wall. ex Mast. (3); and 6, *Glochidion acuminatum* Muell. (2). The values in parentheses are the numbers of individuals of the species in the plots. The solid circles are the tree stems, the solid lines are the exposed margins of the canopies, and the broken lines are the margins of the canopies beneath other tree(s).

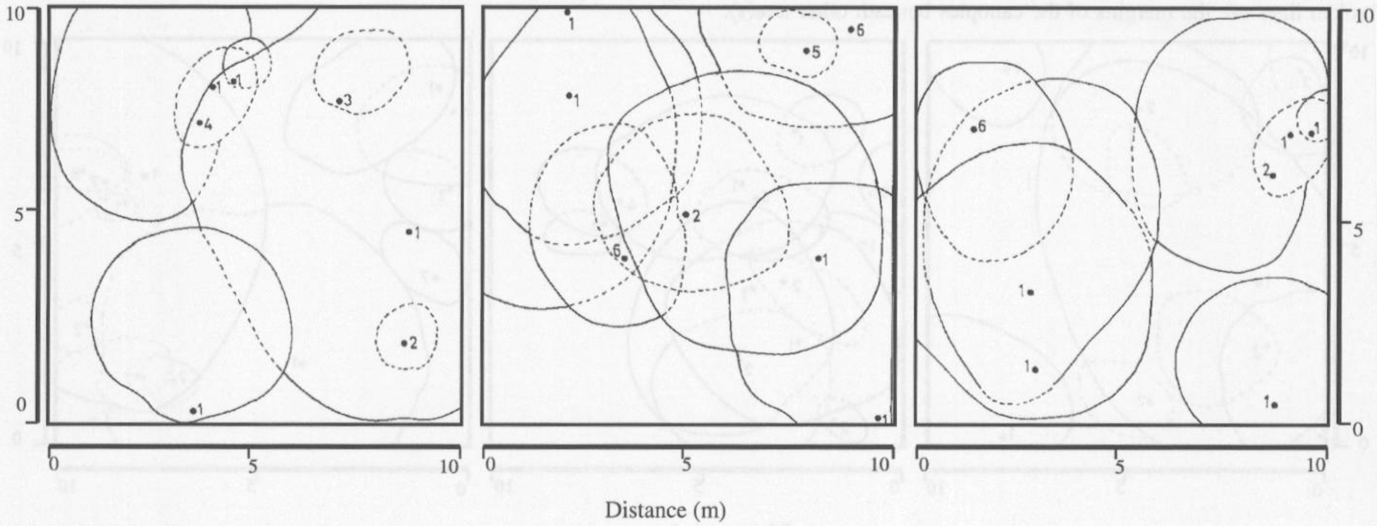
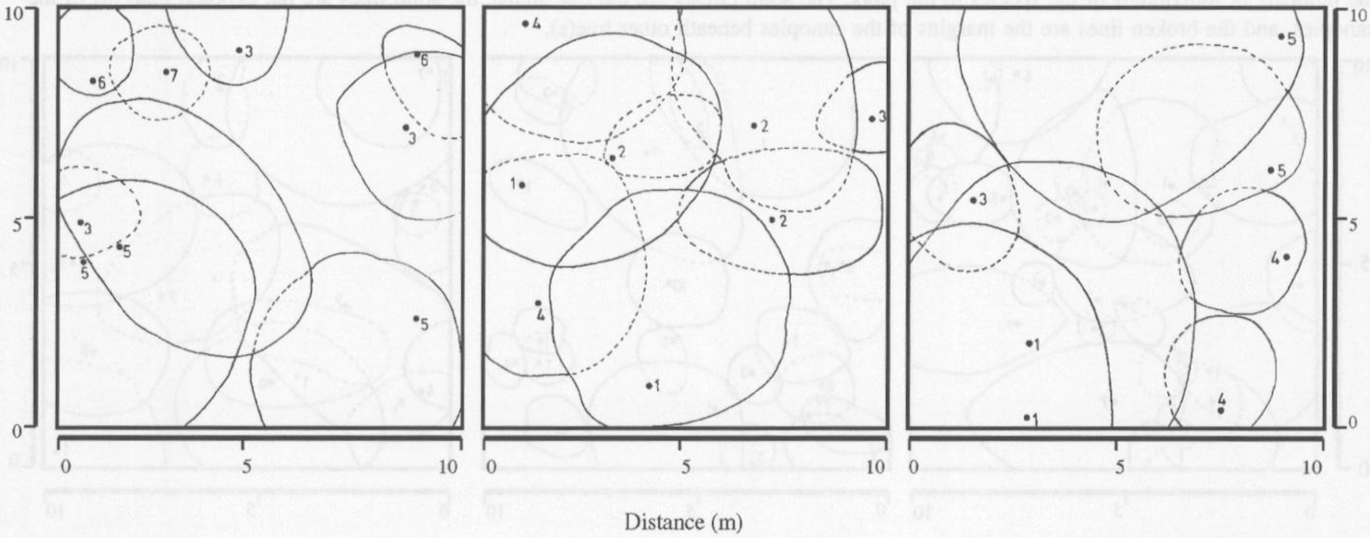


Fig. 4. Distribution and canopy cover of tree species in the 10 m × 10 m mixed plots: 1, *Elaeocarpus acuminatus* (4); 2, *Persea odoratissima* (4); 3, *Glochidion acuminatum* Muell. (6); 4, *Syzygium tetragonum* (3); 5, *Magnolia pterocarpa* (5); 6, *Psychotria symplicifolia* (2); and 7, *Schefflera hypoleuca* (1). The values in parentheses are the numbers of individuals of the species in the plots. The solid circles are the tree stems, the solid lines are the exposed margins of the canopies, and the broken lines are the margins of the canopies beneath other tree(s).



The humid subtropical evergreen forests found between 1000 and 2000 m elevation in the high rainfall areas of eastern Himalayas and northeastern India (Type 8B/C1/C2 as classified by Champion and Seth 1968) are characterized by a distinct patchy distribution of canopy tree species in the community, which is a consequence of segregation of species into different regeneration guilds and spatial and temporal variation in microclimate and microsites on the forest floor (Barik et al. 1992). Therefore, these forests provide ideal conditions to test the hypothesis of whether the canopy tree species distributed in distinct patches impact N and P mineralization and soil properties underneath their canopy. We also evaluated the relative role of litter chemistry and soil characteristics on net N and P mineralization in these forests. The study was designed to assess the effect of three subtropical forest species, *Myrica esculenta* Buch.-Ham. ex D. Don., *Rhododendron arboreum* Sm., and *Neolitsea cassia* Koster., by comparing the net N and P mineralization rates and soil properties in the plots dominated by these species with those in a mixed-species plot. The site attributes of all the experimental species plots such as soil texture, topography, stand age, and mineral soil type were identical, which helped in isolating the species effect.

Materials and methods

Study site

The study was carried out in an old-growth protected stand of subtropical evergreen broad-leaved forest at Swer

Table 1. General attributes of the experimental plots laid for different species in the subtropical broad-leaved forest at Swer.

Parameter	*Myrica* plot	*Rhododendron* plot	*Neolitsea* plot	Mixed plot
Range of slope angle (°)	25–35	25–35	25–35	25–35
Slope aspect	Southeast	Southeast	Southeast	Southeast
Dominant tree species	*Myrica esculenta, Rhododendron arboreum, Symplocos javanica*	*Rhododendron arboreum, Photinia integrifolia, Symplocos javanica*	*Neolitsea cassia, Elaeocarpus acuminatus, Persea odoratissima*	*Magnolia pterocarpa, Elaeocarpus lancifolius, Persea odoratissima*
Individuals·100 m^{-2}	11 (5)	21 (8)	8 (6)	10
Basal area (m^2)	1.29 (1.08)	1.22 (0.94)	1.07 (0.93)	1.38
Canopy cover (%)	73 (62)	79 (51)	81 (76)	81
Dominant DBH class (cm)	30–60	35–60	25–60	40–60
Litter depth (cm)	4	5	4.5	3.5
Textural class of mineral soil	Sandy loam	Sandy loam	Sandy loam	Sandy loam
Clay (%)	12.9±1.5	16.6±0.4	16.2±0.6	16.7±1.1
Sand (%)	66.5±1.0	61.7±0.6	61.1±1.0	61.8±3.7

Note: Values for density, basal area, and canopy cover of tree species are the means of three replicate plots. Values for the dominant tree species are given in parentheses. Values for clay and sand are means ± SEs. DBH, diameter at breast height.

(25°25′N, 91°47.47′E; altitudinal range 1910–1975 m a.s.l.) in East Khasi Hills district of Meghalaya, northeastern India. The area of the forest is 12 ha, and it is naturally regenerated and devoid of human interventions including any artificial regeneration effort. The forest represents the mature stage of community development, which has been maintained and preserved by the local people as a sacred forest from prehistoric times. The estimated age of the forest is >300 years. The soils of the forest are derived from the underlying gneisses, schists, and granites and may be classified as Ultisols (Udults) type. The texture of the soil is sandy loam. The forest floor is characterized by sparse growth of ground vegetation and thick accumulation of litter throughout the year. The climate of the area is seasonal with distinct warm-wet and cool-dry periods. The mean annual rainfall and temperature measured at the nearest meteorological station at Cherrapunjee are 10 754 mm and 23.5 °C, respectively. The forest canopy is composed of *R. arboreum*, *M. esculenta*, *Symplocos javanica* Kurz, *N. cassia*, *Persea odoratissima* (Nees) Koster., *Magnolia pterocarpa* Roxb., *Engelhardtia spicata* Lesch. ex Blume, and *Elaeocarpus lancifolius* Roxb. *Psychotria symplocifolia* Kurz, *Eurya japonica* Thunb., *Jasminum dispermum* Wall. ex Roxb., *Daphne papyracea* Wall. ex Steud., *Ixora subsesillis* Wall. ex G. Don, *Tupidanthus calyptratus* Hook. f., *Viburnum coriaceum* Blume, *Corylopsis himalayana* Griff., and *Gleichinia* sp. were abundant among the shrubs. *Ophiopogon intermedius* D. Don, *Oplismenus burmannii* (Retz.) Beauv., and *Balanophora diocia* R. Br. ex Royle were important herbs in the community.

Experimental design

Since the forest was a mosaic of distinct patches of canopy tree species, experimental plots with different tree species composition were identified and demarcated within the forest for the study. Based on species abundance and cover, four types of experimental plots (10 m × 10 m size) were demarcated: plots dominated by (*i*) *M. esculenta*, (*ii*) *R. arboreum*, (*iii*) *N. cassia*, and (*iv*) mixed species (Figs. 1–4). In the mixed plot, *E. lancifolius*, *Magnolia pterocarpa*, *P. odoratissima* were the dominant or codominant species. Three replicates of each of the above four types of experimental plots were laid down in the forest and studied during 2004–2005. All experimental replicated plots had identical slope, elevation, stand age, and mineral soil, and the sand and clay percentages in the different species plots did not differ significantly (Table 1).

Basal area, canopy cover, and density of tree species (≥5 cm diameter at breast height (DBH)) were measured in each of the experimental plot. Canopy cover was determined by measuring the cover of canopy from the base of the tree (Muller-Dombois and Ellenberg 1974).

Community characteristics of experimental plots

In the *Myrica* plot, the canopy cover was 73%, and *M. esculenta* was the dominant species, constituting 62% of the total canopy cover and 84% of the total basal area. Similarly, in the *Rhododendron* plot, canopy and basal areas contributed by *R. arboreum* were 51% and 77%, respectively. In the *Neolitsea* plot, *N. cassia* contributed 76% to the total canopy cover of the plots and 84% to the basal area. In the mixed plot, canopy cover was 81% (Table 1).

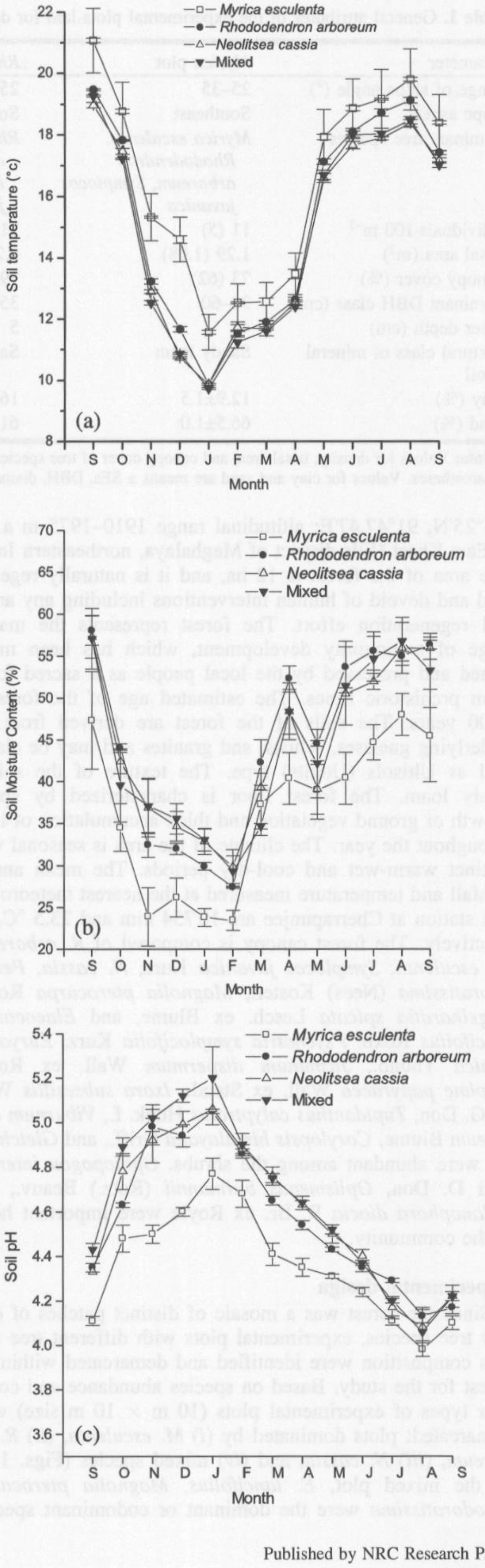
Soil sampling and analyses

Soil samples were collected from the experimental plots at monthly intervals during September 2004 to September 2005. Three replicate samples were collected for the mineral soil layer (0–10 cm depth) from each plot using a steel corer (10 cm diameter). These were mixed thoroughly to obtain one composite sample for each plot. Fresh samples were used for analysis of soil moisture content and soil pH, and the remainder was air-dried and sieved through a 2 mm sieve and stored for further analysis.

Soil texture was determined by the Bouyoucos hydrometer method and soil moisture content by the gravimetric method (Allen et al. 1974). Soil temperature was measured using a digital soil thermometer (Multi-Thermometer).

A digital pH meter (SYSTRONICS-335) was used to determine pH in 1:2.5 *w/v* suspension of soil in deionized water (Anderson and Ingram 1993). Soil organic carbon (SOC) was determined by the colorimetric method

Fig. 5. Monthly changes in (*a*) soil temperature, (*b*) soil moisture content, and (*c*) soil pH in 0–10 cm soil layer of the four experimental plots. Error bars are SEs.



(Anderson and Ingram 1993). Total Kjeldahl nitrogen (TKN) was determined by digesting the air-dried soil samples with concentrated H_2SO_4 followed by distillation and titration (Allen et al. 1974). Available phosphorus (AP) was determined by the ammonium molybdate method (Allen et al. 1974) after extracting air-dried soil P in 0.5 mol/L sodium bicarbonate solution.

Net N and P mineralization were studied in situ with the buried-bag technique (Eno 1960) on a monthly basis from September 2004 to September 2005. At each sampling, paired soil cores were collected from the 0–10 cm soil layer randomly from three points in each experimental plot using a steel corer (10 cm diameter). One of the cores from each pair was sealed in sterilized polyethylene bags after removing roots and larger organic debris and reinserted in the hole created by the soil corer. The other sample was brought to the laboratory and sieved through a 2 mm mesh screen. Initial soil moisture content (SMC), NH_4^+-N, NO_3^--N, and PO_4^{3-}-P concentrations were determined within 24 h of sample collection. NH_4^+-N was determined by the indo-phenol blue method after extracting the fresh soil sample with M NaCl (6%), and NO_3^--N was determined by phenol disulphonic acid method after extracting with deionized water. PO_4^{3-}-P was determined by the ammonium molybdate method (Allen et al. 1974) after extracting fresh soil in 0.5 mol/L sodium bicarbonate solution. After 1 month, the buried bags were retrieved from each plot, and soil samples were analysed for final NH_4^+-N, NO_3^--N, and PO_4^{3-}-P concentrations. Net nitrification rate for each month was calculated by subtracting the initial NO_3^--N concentration from the final concentration. Net N mineralization was calculated as the sum of changes in extractable NH_4^+-N and NO_3^--N over the 1 month period. The increase in the concentration of PO_4^{3-}-P during the field exposure is referred to as net P mineralization.

Litterfall and forest floor litter mass

Litterfall was measured on a monthly basis from September 2004 to September 2005 in all the experimental plots. Prior to the commencement of the sampling in August 2004, 1 m × 1 m × 0.15 m permanent quadrats were laid randomly in each plot using split bamboo stems to check litter loss by runoff water during the rainy season. The litter present in each quadrat was collected, and the soil surface was cleared. Freshly fallen litter was collected from each quadrat at monthly intervals and brought to the laboratory for separation and processing. A small amount of decomposition may have occurred prior to collection of samples but was unavoidable for logistic reasons. The annual production figures were calculated from the values recorded between October 2004 and September 2005.

Litter accumulation or litter mass, also termed standing crop of litter, is the total forest floor material present at a given time. Litter accumulation was estimated by laying three 1 m × 1 m quadrats randomly in each of the experimental plots at the beginning (September 2004) and end of

Table 2. Physicochemical properties of soils of different experimental plots.

Parameters	*Myrica* plot	*Rhododendron* plot	*Neolitsea* plot	Mixed plot	*F*	LSD	*p*
Soil temperature (°C)	16.47±0.50a	15.28±0.54b	14.89±0.52c	14.85±0.54c	147.5	0.23	<0.001
SMC (%)	36.49±0.94a	44.81±1.01bc	44.23±0.90bd	44.07±0.98cd	97.72	1.46	<0.001
pH	4.36±0.02a	4.57±0.03b	4.59±0.03b	4.64±0.03c	169.78	0.035	<0.001
SOC (%)	2.69±0.07a	3.11±0.05b	2.84±0.04ac	2.88±0.05c	15.45	0.16	<0.001
TKN (%)	0.59±0.02a	0.79±0.01b	0.82±0.02c	0.89±0.03d	48.67	0.07	<0.001
C/N	4.75±0.13a	3.95±0.07b	3.56±0.09c	3.45±0.16c	32.30	0.16	<0.001
AP ($\mu g \cdot g^{-1}$)	2.57±0.13a	3.82±0.15b	5.16±0.17c	4.07±0.15b	149.36	0.32	<0.001

Note: Values are means ± SEs ($n = 117$ for soil temperature, SMC and pH, and $n = 45$ for SOC, TKN, C/N, and AP). Within a row, values with the same letter are not significantly different at $p < 0.001$. SMC, soil moisture content; SOC, soil organic carbon, TKN, total Kjeldahl nitrogen; AP, available phosphorus.

the study (September 2005). Litter samples were washed, air-dried, and then oven-dried at 80 °C for 48 h, and the results were expressed on mean dry mass basis.

Litter analyses

For studying leaf litter chemistry, litter in each of the three monodominant species experimental plot was segregated into three categories: (*i*) leaf litter of the dominant species, i.e., *Myrica* leaf litter in case of *Myrica* plot, *Rhododendron* leaf litter in case of *Rhododendron* plot and *Neolitsea* in *Neolitsea* plot; (*ii*) mixed leaf litter including the dominant species in the respective plots with proportional representation of all species present in the plot; and (*iii*) branches (<20 mm in diameter) and miscellaneous litter (flowers, fruits, bark, and other unidentified plant detritus). In the mixed-species plot, litter was segregated into only two categories: (*i*) foliage litter and (*ii*) branches (<20 mm in diameter) and miscellaneous litter (flowers, fruits, bark, and other unidentified plant detritus). All litter samples were brought to the laboratory; segregated samples were washed under a fine jet of water to remove the adhering soil particles, oven-dried at 80 °C for 48 h, and weighed. Samples of given litter types were finely ground in a Cyclotec (Tecator, Sweden) and stored for chemical analyses.

The ash content was determined by igniting the litter sample at 550 °C for 6 h in a muffle furnace. Carbon content was calculated as 50% of the ash free mass (Allen et al. 1974). Total nitrogen was determined by digesting the litter samples with concentrated H_2SO_4 followed by distillation and titration (Allen et al. 1974). Total phosphorus in the litter was colorimetrically determined following the molybdenum blue method after digesting the samples with a mixture of nitric acid, perchloric acid, and sulphuric acid at a ratio of 1:10:2, respectively (Allen et al. 1974). The lignin content (or acid-insoluble residue as argued by Preston et al. 1997; Prescott et al. 2000) was determined by the gravimetric method following Peach and Tracey (1956).

Statistical analyses

The data on soil physicochemical properties, available N and P, and their net mineralization rates were subjected to two-way ANOVA (fixed effect model) to test the variation due to month (soil temperature, moisture, and pH; available N and P; and net mineralization rates) or season (SOC, TKN, AP, and C/N), and tree species. Fisher's least significant difference (LSD) test was carried out for paired comparisons of species plot values. Assumptions of ANOVA were met through tests for normality of variables (Kolmogorov–Smirnov test), homogeneity of group variances (Levene's test), and additivity. The annual litterfall data and soil sand and clay composition data were analyzed using *t* tests to test the difference of means ($n = 3$ replicate plots) in the different species plots. Linear regression equations with Carl Pearson's correlation coefficient (r) showing the relationship between net N and P mineralization and soil physicochemical properties such as SMC, pH, temperature, SOC, TKN, C/N, AP, and litter quality were computed using STATISTICA version 6.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Soil properties

Mean soil temperature varied significantly ($p < 0.001$) among the species plots and months. It declined in the following order: *Myrica* > *Rhododendron* > *Neolitsea* ≥ mixed (Fig. 5*a*). Mean SMC ranged from 36% to 45% with the lowest value in *Myrica* plot. In the *Rhododendron*, *Neolitsea*, and mixed plots, it varied between 44.1% and 44.8% (Table 2). The SMC was high during the rainy season (June–August) and low during the winter months (December–February) (Fig. 5*b*).

The soil pH ranged from 4.36 to 4.64. In the *Myrica* plot, soil pH was significantly ($p < 0.001$) lower (4.36) than the other three plots, and the soil in the mixed plots was the least acidic (4.60). Soil pH showed marked seasonality with high values during winter and low values during the rainy season (Fig. 5*c*). The *Rhododendron* plot had the highest SOC (3.1%) followed by the mixed (2.9%), *Neolitsea* (2.8%), and *Myrica* plots (2.7%), but only the value of *Rhododendron* plot was significantly ($p < 0.001$) different with respect to values of the *Myrica*, *Neolitsea*, and mixed plots. Total Kjeldahl nitrogen (%) varied significantly ($p < 0.001$) across the experimental plots (Table 2) with a higher concentration in the mixed plot (0.9%) followed by the *Neolitsea* (0.8%), *Rhododendron* (0.8%), and *Myrica* plots (0.6%). The mixed plot had the lowest C/N ratio (3.45) followed by the *Neolitsea* (3.56) and *Rhododendron* plots (3.95), and the highest value occurred in the *Myrica* plot (4.75); however, the difference between the mixed and *Neolitsea* plots was not significant. Available P ranged from 2.57 to 5.16 $\mu g \cdot g^{-1}$ with the highest and lowest concentrations in the *Neolitsea* plot (5.16 $\mu g \cdot g^{-1}$) and *Myrica* plots (2.57 $\mu g \cdot g^{-1}$), respectively. It varied significantly ($p < 0.001$) among the species plots (Table 2).

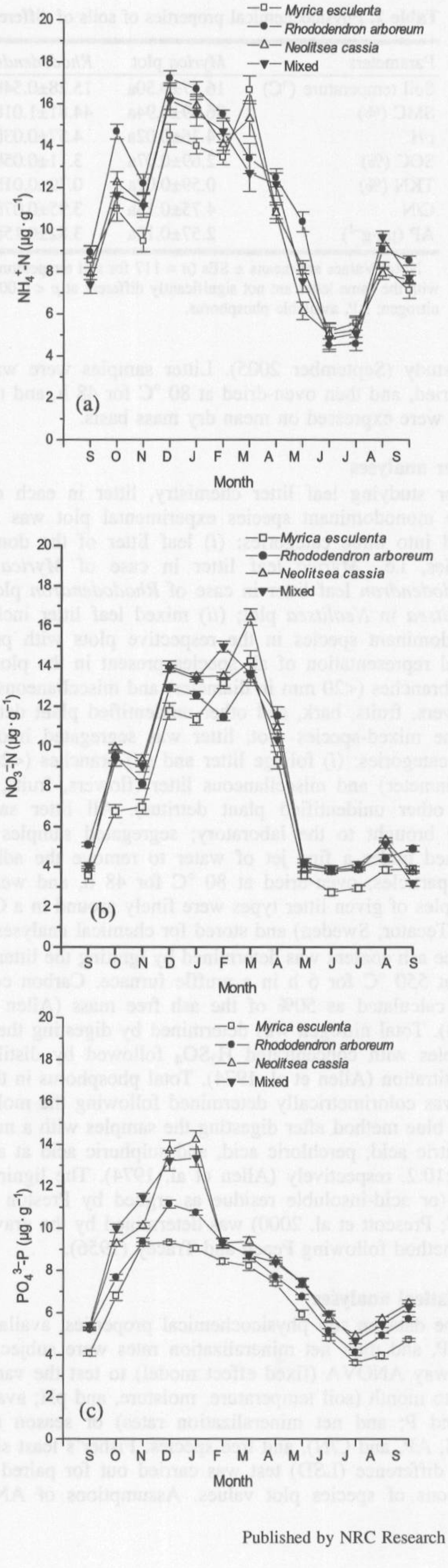


Fig. 6. Monthly changes in (*a*) NH_4^+-N, (*b*) NO_3^--N, and (*c*) PO_4^{3-}-P in 0–10 cm soil layer of the four experimental plots. Error bars are SEs.

Table 3. Annual litterfall (kilograms per hectare per year) and its mean accumulation (kilograms per hectare) on the forest floor in the experimental plots.

Experimental plot and litter fraction	Litterfall	Litter accumulation
Myrica plot		
Leaf litter	6 902	3700±193
Mixed leaf litter	2 858	1000±166
Branches + miscellaneous	1 972	1060±203
Total	11 732	5760±77
Rhododendron plot		
Leaf litter	7 293	4067±196
Mixed leaf litter	3 529	820±151
Branches + miscellaneous	2 006	1260±147
Total	12 827	6147±218
Neolitsea plot		
Leaf litter	6 299	1647±235
Mixed leaf litter	3 120	1577±112
Branches + miscellaneous	975	1320±62
Total	11 393	4544±217
Mixed plot		
Mixed leaf litter	6 808	3260±210
Branches + miscellaneous	2 727	1074±183
Total	9 535	4334±220

Note: Values are means ± SEs, $n = 2$ for litter accumulation.

NH_4^+-N concentrations were significantly ($p < 0.05$) higher in the *Rhododendron* plot than in the other three plots, which were not significantly different from one another. The mean NH_4^+-N values ranged from 10.22 to 11.40 µg·g−1 (Fig. 6*a*). The NO_3^--N concentration varied from 7.24 to 8.63 µg·g−1 with the lowest value in *Myrica* plot, but the values between *Rhododendron* and *Neolitsea* plots and between the mixed and *Neolitsea* plots did not differ significantly (Fig. 6*b*). Based on the PO_4^{3-}-P concentration, the experimental plots can be arranged as *Neolitsea* ≥ mixed > *Rhododendron* > *Myrica* (Fig. 6*c*).

The two forms of nitrogen (NH_4^+-N and NO_3^--N) and PO_4^{3-}-P showed similar seasonal trends. In all four plots, their concentrations were high during the cold-dry period (December–February) and low during the warm-wet period (June–August).

Litterfall and accumulation

Total annual litterfall varied significantly ($p < 0.01$) between the plots with the highest value in *Rhododendron* plot (12 827 kg·ha−1·year−1) followed in decreasing order by the *Myrica* (11 732 kg·ha−1·year−1), *Neolitsea* (11 393 kg·ha−1·year−1), and mixed plots (9535 kg·ha−1·year−1) (Table 3). The amounts of leaf litter of the dominant tree species were 6299 kg·ha−1·year−1 in the *Neolitsea* plot, 6902 kg·ha−1·year−1 in the *Myrica* plot, and 7293 kg·ha−1·year−1 in the *Rhododendron* plot, accounting for 55%–59% of the total litterfall.

Litter accumulation on the forest floor was highest in the

Table 4. Litter chemistry of different categories of litter in the experimental plots.

Experimental plot and litter type	C (%)	N (%)	P (%)	Lignin (%)	C/N	Lignin/N
Myrica plot						
Myrica leaf litter	47.50±0.29	1.27±0.10	0.043±0.001	33.21±0.27	37.40±1.70	26.15±1.22
Mixed leaf litter*	48.33±0.33	1.23±0.10	0.032±0.001	29.42±0.40	39.70±3.16	24.16±1.86
Branches + miscellaneous		0.47±0.02	0.015±0.002			
Rhododendron plot						
Rhododendron leaf litter	46.16±0.17	0.90±0.05	0.04±0.001	35.36±1.16	51.29±3.24	39.29±1.14
Mixed leaf litter*	45.66±0.33	1.03±0.10	0.047±0.001	37.80±0.66	45.05±3.87	37.23±2.89
Branches + miscellaneous		0.53±0.02	0.016±0.003			
Neolitsea plot						
Neolitsea leaf litter	43.66±0.88	1.57±0.02	0.065±0.001	22.14±0.37	27.81±1.07	14.10±0.31
Mixed leaf litter*	45.70±0.25	1.67±0.02	0.067±0.001	17.62±0.33	27.44±0.49	10.58±0.34
Branches + miscellaneous		0.59±0.01	0.025±0.002			
Mixed plot						
Mixed leaf litter	45.84±0.08	1.63±0.04	0.07±0.003	23.37±0.41	28.12±0.71	14.34±0.64
Branches + miscellaneous		0.53±0.02	0.03±0.002			

Note: Values are means ± SEs ($n = 3$).

*Includes leaf litter of dominant tree species in the respective plots.

Rhododendron plot (6147 kg·ha^{-1}) and lowest in the mixed plot (4334 kg·ha^{-1}) (Table 3). Of the total litter accumulation, leaf litter of the dominant tree species was 1647 kg·ha^{-1} in the *Neolitsea* plot, 3700 kg·ha^{-1} in the *Myrica* plot, and 4067 kg·ha^{-1} in the *Rhododendron* plot, ranging from 36% to 66% of the total litter.

Litter chemistry

The mixed leaf litter (including leaf litter of dominant tree species) had a high concentration of C in the *Myrica* plot, high lignin and C/N ratio in the *Rhododendron* plot, the maximum P concentration in the mixed plot, and high N concentration and the lowest lignin/N ratio in the *Neolitsea* plot (Table 4).

The N and P concentrations in branches and miscellaneous litter fractions, which were low compared with those of foliar litter, decreased in the following order: *Neolitsea* ≥ mixed > *Rhododendron* > *Myrica* (Table 4).

Net N and P mineralization rates

Net nitrification rates ranged between 8.60 and 10.45 µg·g^{-1}·month^{-1}. Rates varied significantly between the plots with the lowest rate in the *Myrica* plot (Fig. 7*a*).

Net N mineralization significantly varied ($p < 0.001$) between the plots ranging between 18.83 and 22.14 µg·g^{-1}·month^{-1}. The rate was low in the *Myrica* plot and high in the *Rhododendron*, *Neolitsea*, and mixed plots (Fig. 7*b*).

Net P mineralization rate ranged from 4.54 to 5.87 µg·g^{-1}·month^{-1}. Based on the mean P mineralization rate, the experimental plots may be arranged in the following order: *Neolitsea* ≥ mixed > *Rhododendron* > *Myrica*. The mean net P mineralization rates were minimum in *Myrica* plot and maximum in *Neolitsea* plot (Fig. 7*c*).

Net nitrification, N mineralization, and P mineralization rates showed a sharp drop from the end of rainy season (September) to winter (December–February); thereafter, it steadily increased to a peak in the rainy season (July–August) in all the plots.

Soil moisture, pH, TKN, and AP were positively correlated ($p < 0.001$) and soil temperature and C/N ratio were negatively correlated ($p < 0.001$) with net N and P mineralization rates. Net N mineralization rate was significantly correlated ($p < 0.001$) only with P-related litter chemistry (P, C/P, and lignin/P ratio), whereas net P mineralization rate was positively correlated ($p < 0.001$) with N and P concentrations of litter and negatively correlated ($p < 0.001$) with lignin, C/N, C/P, lignin/N, and lignin/P ratios.

Discussion

Several studies have demonstrated that tree species modify the soil environment in temperate forests or in monospecific tree plantations in the tropics. For example, Boettcher and Kalisz (1990) reported higher pH and mineralizable N in *Liriodendron tulipifera* L. than *Tsuga canadensis* (L.) Carr. stand, and Finzi et al. (1998) found higher C and N pools beneath *Tsuga canadensis* than *Acer saccharum* Marsh. SOC and TKN were higher in the mineral soil under *Ulmus glabra* Huds. than *Fagus sylvatica* L. monoculture plantation in a study by Oostra et al. (2006). However, Powers et al. (2004) found that four emergent tree species viz., *Hyeronima alchorneoides* Allemão, *Lecythis ampla* Miers., *Dipteryx panamensis* Benth., and *Albizia elegans* (Ducke) L. Rico did not affect soil chemistry and nutrient availability in a wet tropical forest of Costa Rica. Thus, the impact of species on soil characteristics has been a matter of debate and seems to vary with forest type, species composition, and climatic conditions. The changes in soil properties beneath the canopy of different tree species observed in the present study indicate differential impacts of the species on soil properties. The differential impact of species on soil properties and net N and P mineralization was evident, when these parameters in monodominant species plots were compared with those of the mixed-species plot. The *Myrica* plot had lower AP, TKN, SOC, NH_4^+-N, NO_3^--N, PO_4^{3-}-P, and pH but higher C/N ratio compared with the *Rhododendron*, *Neolitsea*, and mixed plots. The *Rhododendron* plot had lower pH, TKN, AP, NO_3^--N, and PO_4^{3-}-P and higher SOC, NH_4^+-N, and C/N ratio compared with the mixed plot. The *Neolitsea* plot had lower pH, SOC, TKN, and

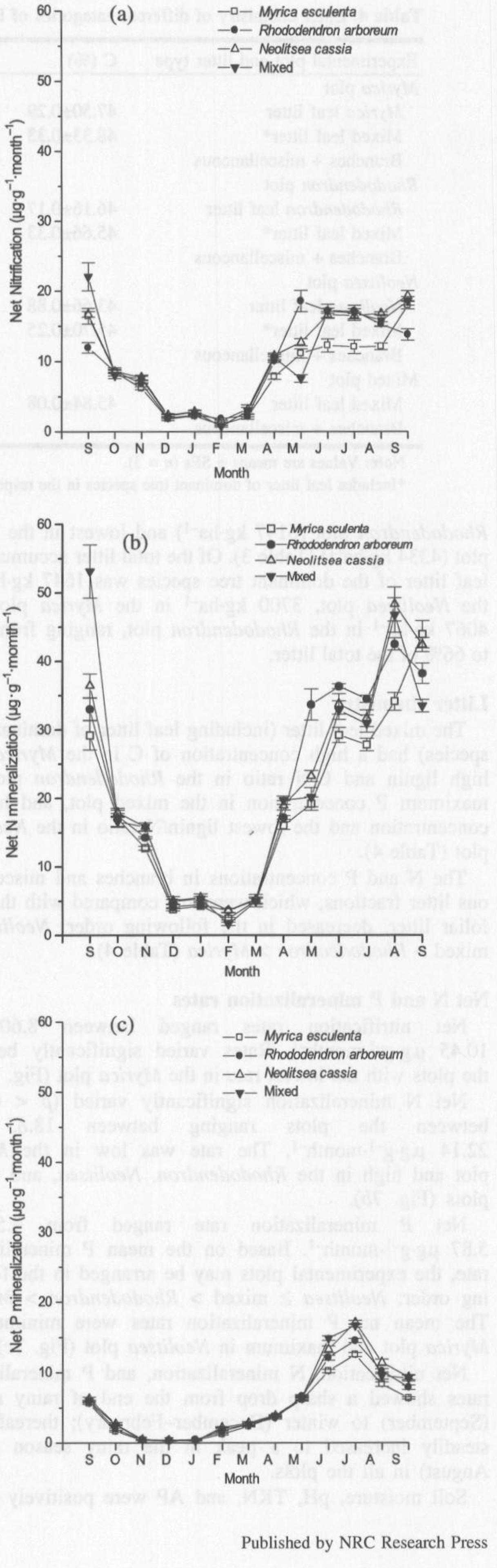


Fig. 7. Monthly changes in (*a*) net nitrification rate, (*b*) net N mineralization rate, and (*c*) net P mineralization rate in the four experimental plots. Error bars are SEs.

NH_4^+-N and higher C/N ratio, NO_3^--N, PO_4^{3-}-P, and AP compared with the mixed plot (Table 2). On the other hand, the physical properties, such as soil temperature and SMC were primarily related to the degree of canopy opening. For instance, in the *Myrica* plot, the canopy was less dense (73%), and the higher temperature and lower moisture content in the upper soil layer were due to greater evaporative loss caused by greater solar radiation.

The size of inorganic N and P pool in soil is influenced by their input through litter, rate of mineralization, uptake by plants and microbes, and losses through processes such as denitrification in case of N. The smaller amounts of inorganic N underneath the N_2-fixing *Myrica* tree could be due to poor growth of nitrifiers owing to the low soil pH and moisture content (Grant 1994); lower net N and P mineralization rates; nonavailability of negatively and positively charged organic functional groups for retention of NH_4^+-N, NO_3^--N, and PO_4^{3-}-P; direct transfer to neighbouring species; and greater leaching losses (Dudley et al. 1996). Compared with the *Myrica* plot, greater inorganic N and P pools in the soil of the other three plots was associated with higher net N and P mineralization rates, higher soil pH, and higher SMC.

During the dry winter season, nutrient concentrations in soil increased, probably because uptake by plants was reduced, leaching losses were minimized, and immobilization in microbial biomass was increased because of slow turnover at low moisture and temperature conditions (Singh et al. 1991). On the contrary, higher nutrient uptake by vegetation, microbial death, microbiovory, and fast turnover were favoured by high temperature and moisture conditions, and increased NO_3^- losses via leaching, denitrification, and runoff (Schmitt and Randall 1994; Maithani et al. 1998; Upadhaya et al. 2005) were probably responsible for the smaller soil nutrient pool during the wet rainy season.

The significant difference in net N and P mineralization rates observed among the experimental plots is attributable largely to the tree species, which impacted the biological, chemical, and physical conditions of the soils. The large differences in mineralization rates among the different species plots confirm the role of species in mineralization processes. The role of tree species in N mineralization was also emphasized by Binkley and Giardina (1998), Priha and Smolander (1999), and Ste-Marie and Paré (1999). Brüggemann et al. (2005) reported the highest N mineralization and nitrification rates under *Picea abies* (L.) Karst. followed by *F. sylvatica*, *Larix leptolepis* (Sieb. & Zucc.) Gord., *Quercus robur* L., and *Pinus mugo* Turra in a temperate forest. Similarly, nitrification rates have been reported to differ widely among intact forest ecosystems, which range from 0% to 100% of net N mineralization (Binkley 1995). In addition to the impact of tree species, climatic conditions (Pastor and Post 1986), soil characteristics (Ste-Marie and Paré 1999; Côté et al. 2000), stand age (Polglase and Attiwill 1992; Maithani et al. 1998), and elevation (Powers 1990; Knoepp and Swank 1998) have been argued to be other factors that influenced mineralization rate.

Table 5. Relationships of net N and P mineralization rates (micrograms per gram per month) with soil properties and mixed leaf litter chemistry in the experimental plots ($n = 36$).

Parameter	Regression equation	r	p
N mineralization versus soil properties			
Soil temperature	$Y = 52.30 - 2.02X$	–0.79	<0.001
SMC	$Y = 10.13 + 0.26X$	0.71	<0.001
pH	$Y = -30.62 + 11.42X$	0.78	<0.001
C/N	$Y = 30.05 - 2.31X$	–0.76	<0.001
SOC	$Y = 12.16 + 3.14X$	0.48	<0.05
TKN	$Y = 13.12 + 10.51X$	0.81	<0.001
AP	$Y = 16.25 + 1.27X$	0.76	<0.001
N mineralization versus litter chemistry			
N	$Y = 18.80 + 1.73X$	0.30	ns*
P	$Y = 17.35 + 72.71X$	0.65	<0.001
C/N	$Y = 23.00 - 0.05X$	–0.25	ns
C/P	$Y = 24.75 - 0.004X$	–0.75	<0.001
Lignin	$Y = 22.37 - 0.05X$	–0.24	ns
Lignin/N	$Y = 21.71 - 0.02X$	–0.15	ns
Lignin/P	$Y = 23.24 - 0.004X$	–0.59	<0.001
P mineralization versus soil properties			
ST	$Y = 17.36 - 1.07X$	–0.92	<0.001
SMC	$Y = 2.05 + 0.08X$	0.64	<0.001
pH	$Y = -12.22 + 3.87X$	0.80	<0.001
C/N	$Y = 8.66 - 0.86X$	–0.86	<0.001
SOC	$Y = 4.37 + 0.34X$	0.15	ns
TKN	$Y = 2.86 + 3.22X$	0.75	<0.001
AP	$Y = 3.60 + 0.45X$	0.80	<0.001
P mineralization versus litter chemistry			
N	$Y = 3.68 + 1.19X$	0.61	<0.001
P	$Y = 3.51 + 34.49X$	0.92	<0.001
C/N	$Y = 6.77 - 0.04X$	–0.61	<0.001
C/P	$Y = 6.82 - 0.002X$	–0.93	<0.001
Lignin	$Y = 6.49 - 0.04X$	–0.57	<0.001
Lignin/N	$Y = 5.94 - 0.03X$	–0.53	<0.001
Lignin/P	$Y = 6.36 - 0.002X$	–0.89	<0.001

Note: See Table 2 for parameter abbreviations.
*Not significant.

Variation in net N and P mineralization among experimental plots appears to be regulated by a combination of interspecific differences in litter quality, production, and decomposition rate (Melillo et al. 1982; Prescott et al. 1993; Stump and Binkley 1993). Quality of litter is one of the important ways by which species control nutrient cycling. Soils receiving litter with high C/N ratio or lignin have often been predicted to have lower rates of decomposition (Melillo et al. 1982), net nitrification, and net N mineralization (Scott and Binkley 1997). Litter with a high C/N or lignin/N ratio decomposes more slowly than that with a low C/N or lignin/N ratio (Melillo et al. 1982; Prescott et al. 1993; Stump and Binkley 1993). Phosphorus-related litter chemistry (C/P ratio and lignin/P ratio) is also an important control of litter decomposition in the tropics (Aerts 1997). Thus, the faster rate of decay in *Neolitsea* ($k = 0.89$) and mixed plots ($k = 0.85$) than in *Rhododendron* ($k = 0.82$) and *Myrica* ($k = 0.53$) plots may be attributed to higher concentrations of N and P and low C/N and lignin/N ratios. Litter chemistry appears to be the cause of slower rates of mineralization in the *Myrica* plot which received litter with higher acid-insoluble residues and C/N, C/P, lignin/N and lignin /P ratios than in *Neolitsea* and mixed plots. Acid-insoluble residues play an important role in N transformation because they are converted preferentially into persistent humic substances during humification, which makes them unavailable for plants and microbes (Thomas and Prescott 2000). The relative shortage of P in the litter might increase the importance of P as a control of initial litter decay (Aerts 1997). This seems to be true in case of net P mineralization as well, because strong correlations were obtained between net P mineralization and litter quality. Many workers have correlated litter decomposition with climatic changes and leaf litter chemistry (Meentemeyer 1978; Melillo et al. 1982; Aerts 1997). At global scale, climatic factors have been considered as the primary controller of decomposition process, whereas litter chemistry is only of secondary importance. However, in tropical regions, there is a shift from climatic control of litter decay to litter chemistry control. In addition to litter chemistry in the present study, soil microenvironmental factors, such as soil temperature and SMC, influenced the mineralization rate in the *Myrica* plot. Therefore, the weak correlations between net N mineralization and litter quality (N, lignin, and C/N ratio) suggest that microenvironmental factors such as soil temperature, sSMC, pH, and nutrient status also influenced the rate of these soil biological processes (Table 5).

Significant ($p < 0.001$) positive correlations between net N and P mineralization rates and SMC and negative correlations with soil temperature suggest an important role of these factors in net N and P mineralization rates in the soil system and explain the seasonal variation in the mineralization pattern. Chemical properties, such as pH, TKN, and AP, were positively correlated with net N and P mineralization. The only factor that was negatively related was the C/N ratio. Similar observations were also made by Menyailo et al. (2003) in a tropical forest and Latty et al. (2004) in temperate forests.

The low nutrient status of the *Myrica* plot may be attributed to its recalcitrant litter that retards nutrient cycling. On the other hand, the higher nutrient status of *Neolitsea* plot was the result of high-quality litter of the species (low C/N ratio). Myers et al. (1994) also reported that high-quality litter (C/N < 25) releases nutrients at a faster rate during decomposition, whereas low-quality litter (high C/N ratio) immobilizes nutrients. Thus, differences in soil properties and net N and P mineralization rates of the forest floor depend on the distribution pattern of canopy tree species and make the system more heterogeneous. The associations between canopy tree species and the quantity of N and P available to plants through mineralization suggest that forest floor soil N and P dynamics have important implications for the future species composition and growth of the forest.

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References

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos, **79**: 439–449. doi:10.2307/3546886.

Allen, S.E., Grimshaw, H.M., Parkinson, J.A., and Quarmby, C. 1974. Chemical analysis of ecological materials. Blackwell, Oxford, UK.

Anderson, J.M., and Ingram, J.S.I. 1993. Tropical soil biology and fertility: a handbook of methods. CAB International, Wallingford, UK.

Augusto, L., Ranger, J., Binkley, D., and Rothe, A. 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. **59**: 233–253. doi:10.1051/forest:2002020.

Barik, S.K., Pandey, H.N., Tripathi, R.S., and Rao, P. 1992. Microenvironmental variability and species diversity in treefall gaps in a subtropical broadleaved forest. Vegetatio, **103**: 31–40. doi:10.1007/BF00033414.

Berendse, F. 1998. Effects of dominant plant species on soil during succession in nutrient-poor ecosystem. Biogeochemistry, **42**: 73–88. doi:10.1023/A:1005935823525.

Binkley, D. 1992. Mixtures of nitrogen-fixing and non nitrogen-fixing tree species. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malsolm, and P.A. Robertson. British Ecological Society, Oxford, UK. pp. 99–123.

Binkley, D. 1995. The influence of tree species on forest soils: processes and patterns. *In* Proceedings of the Trees and Soils Workshop, Lincoln University, New Zealand, 28 February – 2 March 1994. *Edited by* D.J. Mead and I.S. Cornforth. Lincoln University Press, Canterbury, N.Z. Agron. Soc. N.Z. Spec. Publ. 10. pp. 1–33.

Binkley, D., and Giardina, C. 1998. Why do tree species affect soils? The warp and woof of tree–soil interactions. Biogeochemistry, **42**: 89–106. doi:10.1023/A:1005948126251.

Boettcher, S.E., and Kalisz, P.J. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. Ecology. **71**: 1365–1372. doi:10.2307/1938273.

Brüggemann, N., Rosenkranz, P., Papen, H., Pilegaard, K., and Butterbach-Bahl, K. 2005. Pure stands of temperate forest tree species modify soil respiration and N turnover. Biogeosci. Discuss. **2**: 303–331.

Campo, J., Maass, M., Jaramillo, V.J., Martinez-Yrízar, A., and Sarukhan, J. 2001. Phosphorus cycling in a Mexican tropical dry forest ecosystem. Biogeochemistry, **53**: 161–179. doi:10.1023/A:1010663516029.

Champion, H.G., and Seth, S.K. 1968. A revised survey of forest types of India. Government of India Press, Delhi.

Côté, L., Brown, S., Paré, D., Fyles, J., and Bauhus, J. 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. Soil Biol. Biochem. **32**: 1079–1090. doi:10.1016/S0038-0717(00)00017-1.

Dudley, J.L., Michener, B., and Lajtha, K. 1996. The contribution of nitrogen-fixing symbioses to coastal heath land succession. Am. Midl. Nat. **135**(2): 334–342. doi:10.2307/2426716.

Eno, C.F. 1960. Nitrate production in the field by incubating the soil in polythene bags. Soil Sci. Soc. Am. Proc. **24**: 277–279.

Ferrari, J.B. 1999. Fine-scale patterns of leaf litterfall and nitrogen cycling in an old-growth forest. Can. J. For. Res. **29**: 291–302. doi:10.1139/cjfr-29-3-291.

Finzi, A.C., Van Breeman, N., and Canham, C.D. 1998. Canopy tree–soil interactions within temperate forests: species effects on soil carbon and nitrogen. Ecol. Appl. **8**: 440–446.

Grant, R.F. 1994. Simulation of ecological controls on nitrification. Soil Biol. Biochem. **26**: 305–315. doi:10.1016/0038-0717(94)90279-8.

Hobbie, S.E. 2005. Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. Ecosystems, **8**: 644–656. doi:10.1007/s10021-003-0110-7.

Knoepp, J.D., and Swank, W.T. 1998. Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians. Plant Soil, **204**: 235–241. doi:10.1023/A:1004375412512.

Latty, E.F., Canham, C.D., and Marks, P.L. 2004. The effects of land-use history on soil properties and nutrient dynamics in northern hardwood forests of the Adirondack Mountains. Ecosystems, **7**: 193–207. doi:10.1007/s10021-003-0157-5.

Lovett, G.M., Weathers, K.C., and Arthur, M.A. 2002. Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. Ecosystems, **5**: 712–718. doi:10.1007/s10021-002-0153-1.

Lovett, G.M., Weathers, K.C., Arthur, M.A., and Schultz, J.C. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? Biogeochemistry, **67**: 289–308. doi:10.1023/B:BIOG.0000015786.65466.f5.

Madritch, M.D., and Cardinale, B.J. 2007. Impacts of tree species diversity on litter decomposition in northern temperate forests of Wisconsin, USA: a multi-site experiment along a latitudinal gradient. Plant Soil, **292**: 147–159. doi:10.1007/s11104-007-9209-5.

Maithani, K., Arunachalam, A., Tripathi, R.S., and Pandey, H.N. 1998. Influence of leaf litter quality on N mineralization in soils of subtropical humid forest regrowths. Biol. Fertil. Soils, **27**: 44–50. doi:10.1007/s003740050398.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology, **59**: 465–472. doi:10.2307/1936576.

Melillo, J.M., Aber, J.D., and Muratore, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology, **63**: 621–626. doi:10.2307/1936780.

Menyailo, O.V., Lehmann, J., Cravo, M.S., and Zech, W. 2003. Soil microbial activities in tree-based cropping systems and natural forests of the central Amazon, Brazil. Biol. Fertil. Soils, **38**: 1–9. doi:10.1007/s00374-003-0631-4.

Muller Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation analysis. John Wiley & Sons, New York.

Myers, R.J.K., Palm, C.A., Cuevas, E., Gunatilleke, I.U.N., and Brassard, M. 1994. The synchronization of nutrient mineralization and plant demand. *In* The biological management of tropical soil fertility (TSBF). *Edited by* P.L. Woomer and M.J. Swift. Wiley-Sayce, Chichester, UK. pp. 81–116.

Oostra, S., Majdi, H., and Olsson, M. 2006. Impact of tree species on soil carbon stocks and soil acidity in southern Sweden. Scand. J. For. Res. **21**: 364–371. doi:10.1080/02827580600950172.

Pastor, J., and Post, W.M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry, **2**: 3–27. doi:10.1007/BF02186962.

Peach, K.A., and Tracey, M.V. 1956. Modern methods of plant analysis. Vol. 1. Springer-Verlag, Berlin.

Polglase, P.J., and Attiwill, P.M. 1992. Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell. I. Return from plant to soil in litterfall. Plant Soil, **142**: 157–166. doi:10.1007/BF00010962.

Powers, J.S., Kalicin, M.H., and Newman, M.E. 2004. Trees species do not influence local soil chemistry in a species-rich Costa Rica rain forest. J. Trop. Ecol. **20**: 587–590. doi:10.1017/S0266467404001877.

Powers, R.F. 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. For. Ecol. Manage. **30**: 19–29. doi:10.1016/0378-1127(90)90123-S.

Prescott, C.E., McDonald, M.A., and Weetman, G.F. 1993. Availability of N and P in the forest floors of adjacent stands of western red cedar – western hemlock and western hemlock – anabilis fir on northern Vancouver Island. Can. J. For. Res. **23**: 605–610. doi:10.1139/x93-080.

Prescott, C.E., Zabek, L.M., Staley, C.L., and Kabzems, R. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Can. J. For. Res. **30**: 1742–1750. doi:10.1139/cjfr-30-11-1742.

Preston, C.M., Trofymow, J.A., Niu, J., and Sayer, B.G. 1997. ^{13}C nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning investigation of the proximate-analysis fractions used to assess litter quality in decomposition studies. Can. J. Bot. **75**: 1601–1613. doi:10.1139/b97-872.

Priha, O., and Smolander, A. 1999. Nitrogen transformations in soil under *Pinus sylvestris*, *Picea abies* and *Betula pendula* at two forest sites. Soil Biol. Biochem. **31**: 965–977. doi:10.1016/S0038-0717(99)00006-1.

Rhoades, C.C., Sanford, R.L., Jr., and Clark, D.B. 1994. Gender-dependent influences on soil phosphorus by the dioecious lowland tropical tree *Simarouba amara*. Biotropica, **26**: 362–368. doi:10.2307/2389229.

Schmitt, M.A., and Randall, G.W. 1994. Developing a soil nitrogen test for improved recommendations for corn. J. Prod. Agric. **7**: 328–334.

Scott, N.A., and Binkley, D. 1997. Foliage litter quality and annual net N mineralization — comparison across North American forest sites. Oecologia (Berlin), **111**: 151–159. doi:10.1007/s004420050219.

Singh, R.S., Srivastava, S.C., Raghubanshi, A.S., Singh, J.S., and Singh, S.P. 1991. Microbial C, N and P in dry tropical savanna: effects of burning and grazing. J. Appl. Ecol. **28**: 869–878. doi:10.2307/2404213.

Ste-Marie, C., and Paré, D. 1999. Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. Soil Biol. Biochem. **31**: 1579–1589. doi:10.1016/S0038-0717(99)00086-3.

Stump, L.M., and Binkley, D. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Can. J. For. Res. **23**: 492–502. doi:10.1139/x93-067.

Templer, P., Findlay, S., and Lovett, G. 2003. Soil microbial biomass and nitrogen transformations among five tree species of the Catskill Mountains, New York, USA. Soil Biol. Biochem. **35**: 607–613. doi:10.1016/S0038-0717(03)00006-3.

Thomas, K.D., and Prescott, C.E. 2000. Nitrogen availability in forest floors of three tree species on the same site: the role of litter quality. Can. J. For. Res. **30**: 1698–1706. doi:10.1139/cjfr-30-11-1698.

Upadhaya, K., Pandey, H.N., Law, P.S., and Tripathi, R.S. 2005. Dynamics of fine and coarse roots and nitrogen mineralization in a humid subtropical forest ecosystem of northeast India. Biol. Fertil. Soils, **41**: 144–152. doi:10.1007/s00374-004-0827-2.

Vitousek, P.M., and Sanford, R.L., Jr. 1986. Nutrient cycling in moist tropical forest. Annu. Rev. Ecol. Syst. **17**: 137–167. doi:10.1146/annurev.es.17.110186.001033.

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology, **43**: 130–133. doi:10.2307/1932049.