Interspecific variation in leaf litter production, decomposition, and nitrogen and phosphorus loss from decomposing leaves in a humid subtropical forest ecosystem of northeastern India

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Abstract: Studies providing direct experimental evidence of species impact on litter dynamics in forest ecosystems are limited. The decomposition processes in subtropical forests are also poorly understood. We studied variation in quality and quantity of leaf litter production, decomposition, and N and P loss from decomposing foliar litter in three tree species as well as a mixed-species plot in a subtropical broad-leaved forest of northeastern India. The annual leaf litter production was highest in *Rhododendron arboreum* Sm. (7293 $kg\cdot ha^{-1}\cdot year^{-1}$) followed by *Myrica esculenta* Buch.-Ham. ex D. Don (6902 $kg\cdot ha^{-1}\cdot year^{-1}$), mixed plots (6808 $kg\cdot ha^{-1}\cdot year^{-1}$), and *Neolitsea cassia* (L.) Kosterm (6299 $kg\cdot ha^{-1}\cdot year^{-1}$). The annual N and P inputs through litter were highest in the mixed plot (N, 111.0 $kg\cdot ha^{-1}\cdot year^{-1}$; P, 4.8 $kg\cdot ha^{-1}\cdot year^{-1}$) and lowest in the *Rhododendron* plot (N, 65.6 $kg\cdot ha^{-1}\cdot year^{-1}$; P, 2.9 $kg\cdot ha^{-1}\cdot year^{-1}$). The highest decay rate was recorded for *Neolitsea* ($k = 0.89$) and lowest for *Myrica* ($k = 0.53$) litter. The rate of N loss was highest for *Neolitsea* ($k_N = 1.39$) and lowest for *Myrica* ($k_N = 0.68$) species, and P loss was in the order of mixed ($k_P = 1.02$) > *Neolitsea* ($k_P = 0.88$) > *Rhododendron*($k_P = 0.84$) > *Myrica* ($k_P = 0.62$). Acid-insoluble residue, which indicates lignin content and P-related litter chemistry, were correlated with the differential decomposition rates and nutrient loss pattern among the species.

Résumé : Les études qui fournissent des preuves expérimentales directes de l'impact d'une espèce sur la dynamique de la litière dans les écosystèmes forestiers sont peu nombreuses. Les processus de décomposition dans les forêts subtropicales sont également mal compris. Nous avons étudié la variation qualitative et quantitative de la production de litière, sa décomposition et les pertes de N et P dans la litière en décomposition de trois espèces arborescentes ainsi que dans une parcelle d'espèces mixtes dans une forêt feuillue subtropicale du nord-est de l'Inde. La production annuelle de litière de feuilles était la plus élevée pour *Rhododendron arboreum* Sm. (7293 $kg\cdot ha^{-1}\cdot an^{-1}$) suivi de *Myrica esculenta* Buch.-Ham. ex D.Don. (6902 $kg\cdot ha^{-1}\cdot an^{-1}$), de la parcelle mixte (6808 $kg\cdot ha^{-1}\cdot an^{-1}$) et de *Neolitsea cassia* (L.) Kosterm. (6299 $kg\cdot ha^{-1}\cdot an^{-1}$). Les apports annuels de N et P ($kg\cdot ha^{-1}\cdot an^{-1}$) dans la litière étaient les plus élevés dans la parcelle mixte (N : 111,0 $kg\cdot ha^{-1}\cdot an^{-1}$; P : 4,8 $kg\cdot ha^{-1}\cdot an^{-1}$) et les plus faibles dans la litière de *Rhododendron* (N : 65,6 $kg\cdot ha^{-1}\cdot an^{-1}$; P : 2,9 $kg\cdot ha^{-1}\cdot an^{-1}$). Le taux de décomposition le plus élevé a été observé dans la litière de *Neolitsea* ($k = 0{,}89$) et le plus faible dans celle de *Myrica* ($k = 0{,}53$). Le taux de perte de N était le plus élevé dans la litière de *Neolitsea* ($k_N = 1{,}39$) et le plus faible dans celle de *Myrica* ($k_N = 0{,}68$) tandis que la perte de P suivait l'ordre suivant : espèces mixtes ($k_P = 1{,}02$) > *Neolitsea* (0,88) > *Rhododendron* (0,84) > *Myrica* (0,62). Les résidus insolubles dans l'acide, un indice du contenu en lignine et des caractéristiques chimiques de la litière en lien avec P, étaient corrélés avec les différents taux de décomposition et les patrons de perte de nutriments des différentes espèces.

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Introduction

Litterfall, which is a major biological pathway for element transfer from vegetation to soil, and the two related processes of decomposition and mineralization are critical to the functioning of forest ecosystems (Swift et al. 1979; Prescott et al. 2004). Litterfall has been correlated with climate, seasonal cycle, topography, site quality, and species composition by various workers (Sundarapandian and Swamy 1999; Norgrove and Hauser 2000; Y.S. Yang et al. 2005). The rates of litter decomposition and nutrient loss from the decomposing litter vary significantly among forest types because of changes in microenvironment, quality of litter, and composition as well as activities of the decomposers (Swift et al. 1979; Berg and McClaugherty 2003). Most studies quantifying the rate of litter decomposition are confined to tropical and temperate forest ecosystems (Melillo et al. 1982; Cornelissen 1996; Sundarapandian and Swamy 1999), and our understanding of the decomposition processes in subtropical forest ecosystems remains poor (sensu Xu and Hirata 2005).

Although litter decomposition is controlled by such diverse chemical properties of litter as N concentration and C/N ratio (McClaugherty and Berg 1987; Tian et al. 1992; Contrufo et al. 1995), P concentration and C/P ratio (Schlesinger and Hasey 1981; Kwabiah et al. 2001), concen-

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tration of lignin or acid-insoluble residue and lignin to nutrient ratio (Melillo et al. 1982; Berg and McClaugherty 1989; Sariyildiz and Anderson 2003), and soluble phenolic contents (Palm and Sanchez 1991; Tian et al. 1992), no single litter-quality parameter is known to regulate the decomposition process (Berg and McClaugherty 2003). Much information exists on rates of litter decomposition and N mineralization or release in different forest ecosystems (Prescott et al. 2000). However, very few studies have evaluated the relationship between P loss from decomposing litter and litter quality (Kuperman 1999; Kwabiah et al. 2001; Xu and Hirata 2005). Because >90% of the P absorbed by plants comes from recycling, it is necessary to have a thorough understanding of the factors impacting P loss from decomposing litter, most of which is attributed to P mineralization or release that has important implications for soil P availability particularly in P-limited systems.

The interspecific variation in the quality and quantity of litter production and its impact on stand nutrient cycling is much less studied. The knowledge on species-specific litter properties and its interaction with the prevailing microenvironment is essential to understand the pattern of decomposition and nutrient release in a forest ecosystem. Although constituent species characteristics have been described by several workers as an important determinant of litter nutrient content, nutrient and litter input to the forest floor, and rates of decomposition and nutrient mineralization in forest ecosystems, no direct experimental evidence is available in this regard.

The humid montane subtropical broad-leaved forests of northeastern India are characterized by a distinct patchy distribution of canopy tree species in the community (Barik et al. 1992). Such distribution patterns of tree species provide an excellent opportunity to study the interspecific variation in litter dynamics in in situ conditions. In an earlier paper (Kamei et al. 2009), the impact of tree species on soil properties and net N and P mineralization beneath their canopy were studied in these forest stands. Total litter production was estimated, and litter chemistry and microenvironment were related to soil N and P mineralization rates. In the present work, our aim is to study the quality and quantity of the leaf litterfall as well as the rate of litter decomposition under different dominant tree species. We addressed the following three research questions: (*i*) how different canopy tree species differ in the quantity of leaf litter production; (*ii*) how species differ in their litter quality and the rates of mass, N, and P loss during decomposition; and (*iii*) which litter quality parameters have the greatest influence on the decomposition, and N and P loss across the species. The study also aimed to bridge the data gap on litter dynamics in subtropical forest ecosystems.

Methods

Study site

The study was carried out in a protected stand of montane subtropical broad-leaved forest at Swer (25°25′N, 91°47.47′E; altitudinal range 1910–1975 m a.s.l.) approximately 10 km from Cherrapunjee in East Khasi Hills district of Meghalaya, northeastern India. The forest stand is well protected as a sacred grove and covers an area of 12 ha. 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, during the study period i.e., 2004–2005.

Experimental design

Because 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), viz., plots dominated by (*i*) *Myrica esculenta* Buch.-Ham. ex D. Don, (*ii*) *Rhododendron arboreum* Sm., (*iii*) *Neolitsea cassia* (L.) Kosterm, and (*iv*) mixed species, were demarcated. In the mixed plots, *Elaeocarpus lancifolius* Roxb., *Magnolia pterocarpa* Roxb., *Persea odoratissima* (Nees) Koster were the dominant or codominant species. Three replicates of each of the above four types of experimental plots were laid down in the forest for detailed study. The site attributes of the plots, such as angle and aspect of slope, elevation, soil texture, and structure of the forest, were similar. However, the plots were different in terms of species composition, tree density, and soil chemical characteristics. The detailed attributes of the experimental plots have been described in Kamei et al. (2009).

Litterfall

Litterfall was measured at monthly intervals from September 2004 to September 2005 in all the experimental plots. Prior to the commencement of the sampling in August 2004, permanent littertraps of 1 m length × 1 m breadth × 0.15 cm height were laid randomly in each plot with the help of split bamboos to check litter loss by water runoff during rainy season. The litter present in each quadrat was collected, and the ground surface was cleared. Freshly fallen litter was collected from each quadrat at monthly intervals. The litter samples were brought to the laboratory and sorted into leaf litter of the dominant tree species, leaf litter of other species, woody litter (<20 mm in diameter), and miscellaneous litter (flowers, fruits, bark, and other unidentified plant detritus). The separated samples were washed under a fine jet of water to remove adhering soil particles. While washing, care was taken to gently remove the soil particles to minimize the element loss or any other alteration in chemical properties of the litter. The samples were oven-dried at 80 °C for 48 h and weighed. Samples of a given category of the litter were finely ground in a cyclotec (Tecator) and stored for chemical analyses. The annual production figures were presented based on values recorded between October 2004 and September 2005.

Leaf litter decomposition

For determining leaf litter decomposition, newly senesced leaves of the single dominant tree species from the three species experimental plots and mixed tree species from mixed-species plot were collected from five random quadrats (1 m × 1 m) laid in each of the permanent plots in June 2004. The collected leaf litters were air-dried at 25 °C for 7 days in the laboratory. Litter decomposition was studied using nylon mesh (1.5 mm × 1.5 mm mesh size) litterbags (15 cm × 15 cm) (Gilbert and Bocock 1960). Ten grams of air-dried foliar litter was placed in each litterbag, and the bag was stitched with nylon thread. Thirty-nine litterbags were buried ca. 1 cm below the litter or soil surface in each replicated species plots during August 2004. Three litterbags of each type were retrieved from each plot at monthly intervals. These were washed gently to remove the adhering soil particles, oven-dried at 80 °C for 48 h, and weighed.

Chemical analyses of litter

The ash content was determined by igniting the litter samples meant for decomposition study as well as for assessment of initial chemical composition 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 content of acid-insoluble residue, indicating lignin content, was determined by the gravimetric method following Peach and Tracey (1956). All chemical analyses were carried out in three replicate samples.

Data analyses

Annual leaf litterfall was the sum of monthly litterfall based on 12 monthly estimations. Similarly, the annual potential nutrient input to the forest floor through leaf litter was computed by multiplying the annual values of leaf fall mass with its corresponding nutrient concentrations.

The negative exponential decay model of Olson (1963) was used to estimate the rates of loss of leaf mass, N, and P during decomposition. The model for estimating mass decay was $-k = (\ln(x/x_0))/t$, where k is the decay rate coefficient; x_0 is the initial dry mass; x is the mass remaining at time t, expressed in years. Nitrogen and P loss constants (k_N and k_P) were calculated by substituting dry mass with N and P contents in the above formula. The time required for 50% (t_{50}) and 99% (t_{99}) decay and mineralization were calculated as $t_{50} = 0.693/k$ and $t_{99} = 5/k$, respectively.

Percent nutrient remaining in undecomposed litter at time t was computed using the formula from Blair (1988):

$$\text{Nutrient remaining}(\%) = \frac{\text{litter mass remaining }(\%) \times \text{nutrient concentration in the remaining mass }(\text{g}/100\ \text{g})}{\text{initial concentration of a nutrient }(\text{g}/100\ \text{g})}$$

The data pertaining to litter mass and decomposition rate were analyzed using two-way analysis of variance (ANOVA; fixed-effects model) to test the variation due to months and species. The variation in chemical composition of leaf litter among the species was analyzed using one-way ANOVA. Linear regression equations and Pearson's correlation coefficient (r) were computed to show the relationship of decay rate, N loss, and P loss with litter quality parameters as well as selected microenvironmental variables using STATISTICA version 6.0 (Stat Soft, Inc., Tulsa, Oklahoma). The microenvironment data on soil moisture and temperature used for correlation analyses were collected during the present study and were presented in detail in Kamei et al. (2009).

Results

Leaf litterfall

The annual leaf litterfall varied significantly ($p < 0.001$) among the species plots and months with the highest value in *Rhododendron* plots (7293 kg·ha^{-1}·year^{-1}) followed by *Myrica* (6902 kg·ha^{-1}·year^{-1}), mixed-species (6808 kg·ha^{-1}·year^{-1}), and *Neolitsea* (6299 kg·ha^{-1}·year^{-1}) plots (Table 1). The leaf litter of the dominant tree species contributed to 57%, 59%, and 55% of the total litterfall in *Rhododendron*, *Myrica*, and *Neolitsea* plots, respectively. The mixed leaf litter in the mixed plot represented 71% of the total litterfall.

Monthly variation in leaf litterfall showed a bimodal pattern in all the experimental plots: one peak in March and another in August (Fig. 1). Leaf litterfall minima occurred in December in all the experimental plots.

N and P return through litterfall

The annual input of N through litter was highest in *Neolitsea* plots with 145 kg·ha^{-1}·year^{-1} followed by the mixed, *Myrica* and *Rhododendron* plots. Annual input of P through litter varied between 4.1 kg·ha^{-1}·year^{-1} and 6.1 kg·ha^{-1}·year^{-1}, and it decreased in the order of *Neolitsea* > mixed > *Rhododendron* > *Myrica* plot (Table 1).

In *Myrica* plots, 70% of N returned from *Myrica* leaf litter alone. The corresponding figures for *Neolitsea* and *Rhododendron* leaf litter were 68% and 65%, respectively. In the mixed-species plot, N return through mixed leaf litter was 88% of the total. The percent contribution of P from different litter fractions was more or less similar to that of N (Table 1).

Leaf litter chemistry

Carbon content in the leaf litter varied significantly ($p < 0.01$) from a minimum of 437 g·kg^{-1} in *Neolitsea* to a maximum of 475 g·kg^{-1} in *Myrica*. Nitrogen content was significantly ($p < 0.01$) lower in *Rhododendron* and higher in the mixed-species plots. Although phosphorus content was low in all the species, it was maximum in mixed-species leaf litter and minimum in *Rhododendron*. The C/N ratio varied widely from a minimum of 27.8 in *Neolitsea* to a maximum of 51.7 in *Rhododendron*. The acid-insoluble residue content was also low in *Neolitsea* (221 g·kg^{-1}) and high in *Rhododendron* (354 g·kg^{-1}) leaf litter (Table 2).

Leaf litter decomposition and N and P loss

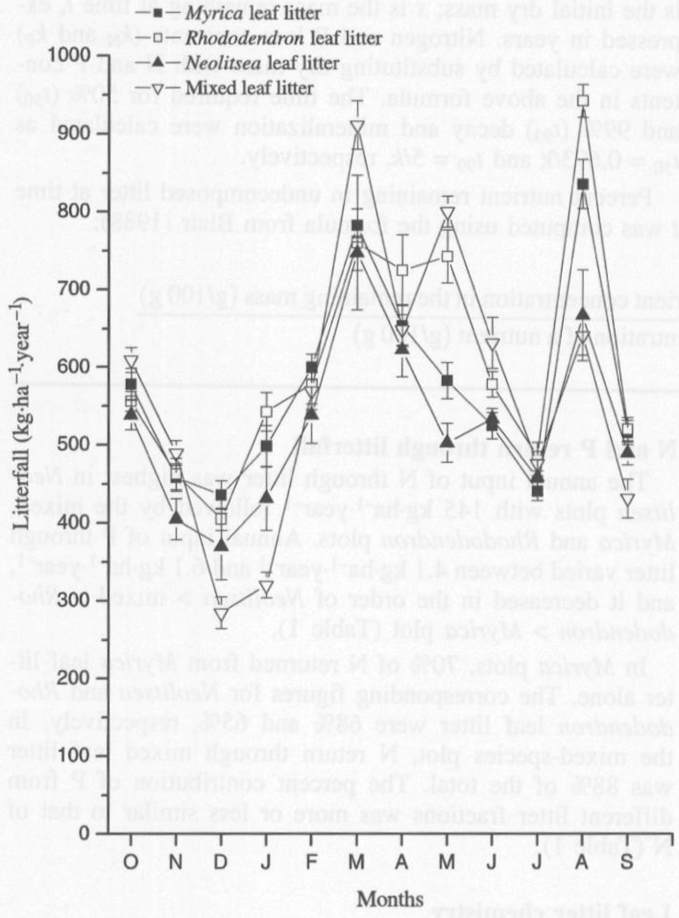
Leaf litter showed two distinct phases of decomposition (Fig. 2). The first phase, which lasted for 30 days, was char-

Table 1. Annual mass ($kg \cdot ha^{-1} \cdot year^{-1}$) and nutrient return ($kg \cdot ha^{-1} \cdot year^{-1}$) for litterfall and total leaf litter on the forest floor in the different experimental plots.

		Mass		Nitrogen		Phosphorus	
Experimental plot	Litter fraction	Litterfall	Total litter	Litterfall	Total litter	Litterfall	Total litter
Myrica	Leaf litter	6902±246	11 732 ± 712	87.7±8.2	124.9±11.6	3.0±0.1	4.1±0.2
Rhododendron	Leaf litter	7293±334	12 827 ± 805	65.6±5.5	101.3±8.0	2.9±0.1	4.3±0.5
Neolitsea	Leaf litter	699±355	11 393 ± 723	98. 9±2.4	144.9±9.6	4.1±0.1	6.2±0.4
Mixed	Mixed leaf litter	6808±262	9535±598	111.0±3.5	125.4±6.0	4.8±0.3	5.6±0.4

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

Fig. 1. Monthly variation in leaf litterfall of dominant species and mixed tree species in the experimental plots. Error bars are SEs ($n = 9$).



acterized by rapid mass loss (12%–33%). This was followed by a slow rate of decay until the end of the study, i.e., 397 days. The decomposition of leaf litter varied significantly ($p < 0.001$) among the months and the species plots with the highest decay rate obtained for *Neolitsea* ($k = 0.89$) followed by mixed-species ($k = 0.85$) and *Rhododendron* ($k = 0.82$); *Myrica* polts were the lowest ($k = 0.53$). The percent mass losses at the end of the study period were 62%, 60%, 58%, and 44% in *Neolitsea*, mixed-species, *Rhododendron*, and *Myrica* plots, respectively. The t_{50} and t_{99} also varied among the different species: highest in *Myrica* and lowest in *Neolitsea* (Table 3).

Based on the contents (mass × concentration) remaining in the litter, N loss from decaying leaf litter was rapid up to 30 days in *Myrica* followed by slow loss up to 397 days at a more or less constant rate. The mixed-species litter followed a similar trend, although the rate of loss was much higher. On the other hand, in *Rhododendron* litter, the rate of loss in the initial 30 days was rapid, slowed down from 30 to 120 days, and increased again until the end. In contrast, *Neolitsea* leaf litter had an initial rapid loss phase of 60 days, following which the N content increased up to 120 days and then was lost at a faster rate until the end. At the end of 397 days, 78% of N was lost from *Neolitsea* leaf litter followed by mixed (75%), *Rhododendron* (70%), and *Myrica* (53%) leaf litter (Fig. 3). The N-loss constant varied between 0.68 and 1.39 with the highest value for *Neolitsea* leaf litter ($k_N = 1.39$), followed by mixed-species ($k_N = 1.29$), *Rhododendron* ($k_N = 1.12$), and *Myrica* ($k_N = 0.68$) (Table 3).

Although the rate of loss of P among different species varied significantly, the pattern of loss was identical in all three species and the mixed-species plots. The loss was faster during the first 30 days, following which there was a no-loss phase up to 90 days, and then there was an increase in P content up to 120 days. After 120 days, the P loss was rapid until the end in all the species (Fig. 4). The fastest P loss was observed in mixed-species (68%) followed by *Neolitsea* (62%), *Rhododendron* (59%), and *Myrica* (49%) leaf litter. The P loss constant was in the order mixed > *Neolitsea* > *Rhododendron* > *Myrica* (Table 3).

Soil moisture and soil temperature were positively correlated ($p < 0.05$) with decay rates as well as rates of N and P loss. Decay rate was significantly correlated ($p < 0.05$) with acid-insoluble residue and P-related litter chemistry, i.e., P and acid-insoluble residue/P ratio. The rate of N loss was significantly correlated ($p < 0.05$) with N, P, C/N ratio, acid-insoluble residue, and ratios of acid insoluble residue with N and P. The rate of P loss was correlated ($p < 0.05$) with N, P, acid-insoluble residue, and ratios of acid-insoluble residue with N and P (Table 4).

Discussion

Litterfall

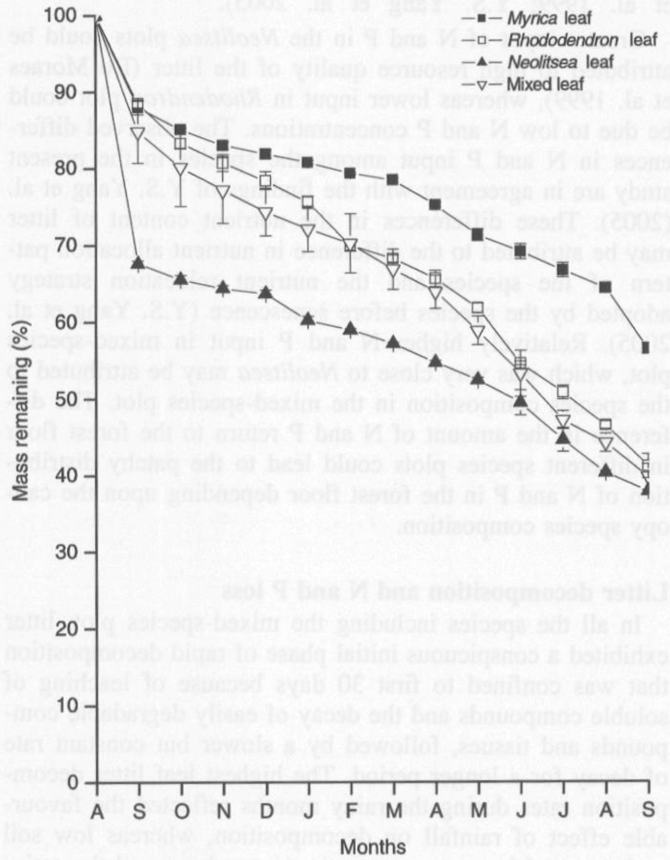
The values of annual total litterfall obtained in the present study (9535–12 827 $kg \cdot ha^{-1} \cdot year^{-1}$) were within the range reported from Amazonian tropical forest (2400–10 300 $kg \cdot ha^{-1} \cdot year^{-1}$) (Cuevas and Medina 1986), tropical evergreen forest (9700–14 200 $kg \cdot ha^{-1} \cdot year^{-1}$) and moist deciduous forest (13 000–15 000 $kg \cdot ha^{-1} \cdot year^{-1}$) (Swamy and Proctor 1994), and tropical dry evergreen forest (13 300–13 500 $kg \cdot ha^{-1} \cdot year^{-1}$) of India (Pragasan and Parthasarathy 2005). Significantly ($p < 0.05$) higher litterfall

Table 2. Initial leaf litter chemistry of the species in the experimental plots.

Litter	C (g·kg⁻¹)	N (g·kg⁻¹)	P (g·kg⁻¹)	Acid-insoluble residue (g·kg⁻¹)	C/N	Acid-insoluble residue/N
Myrica	475.0±0.0	12.7±0.0	0.5±0.0	332.1±0.0	37.4	26.2
Rhododendron	461.6±0.0	9.0±0.0	0.5±0.0	353.6±0.1	51.3	39.3
Neolitsea	436.6±0.1	15.7±0.0	0.7±0.0	221.4±0.0	27.8	14.1
Mixed leaf litter	458.4±0.0	16.3±0.0	0.7±0.0	233.7±0.0	28.1	14.3

Note: Values are means ± SEs (n = 3).

Fig. 2. Decay pattern of leaf litter in the experimental plots. Error bars are SEs.



in *Rhododendron* compared with other species could be due to species traits, tree density, and differential response by different species to the prevailing environmental conditions (George and Kumar 1998; Y.S. Yang et al. 2005). The density of *Rhododendron* was highest with 800 trees/ha followed by *Neolitsea* with 600 trees/ha and *Myrica* with 500 trees/ha, confirming the role of tree density in litterfall. Despite higher tree density, lower quantity of litterfall in *Neolitsea* than *Myrica* may be attributed to low leaf biomass content of the former species. Thus, leaf biomass is another factor determining the quantity of litterfall of a given species. The percentages of dominant species leaf litter in the total litterfall did not vary significantly among the species and ranged between 55% and 59%. The contribution of leaf litter including all the species in the plots to the total litterfall ranged between 71% and 81%, which was similar to those reported by Rawat and Singh (1988) from the central Himalayas (77%), by Lian and Zhang (1998) from a sub-

Table 3. Annual decay constant (k), N and P loss constants (k_N and k_P), and time required for 50% (t_{50}) and 99% (t_{99}) decay (in years) of leaf litter in different experimental plots.

Parameter	*Myrica*	*Rhododendron*	*Neolitsea*	Mixed leaf litter
Litter decay				
k	0.53	0.82	0.89	0.85
t_{50}	1.32	0.85	0.78	0.82
t_{99}	9.52	6.13	5.60	5.9
Nitrogen loss				
k_N	0.68	1.12	1.39	1.29
t_{50}	1.03	0.62	0.50	0.54
t_{99}	7.44	4.46	3.61	3.88
Phosphorus loss				
k_P	0.62	0.84	0.88	1.02
t_{50}	1.13	0.83	0.77	0.68
t_{99}	8.12	5.95	5.69	4.90

Fig. 3. The percent content of N in undecomposed leaf litter in the experimental plots. Error bars are SEs.

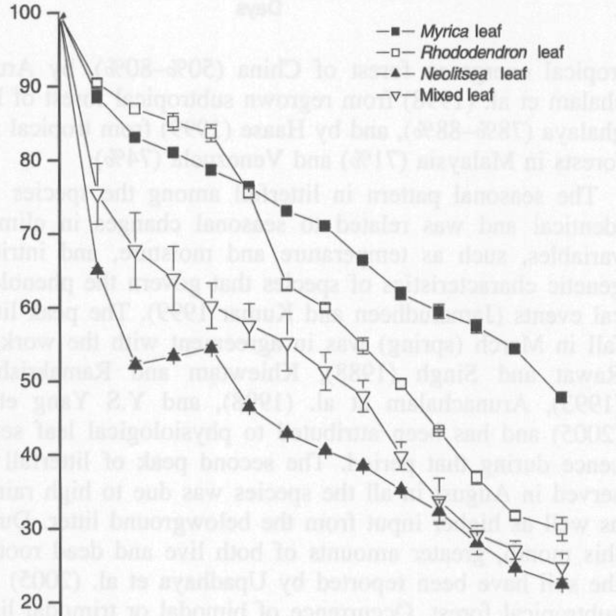
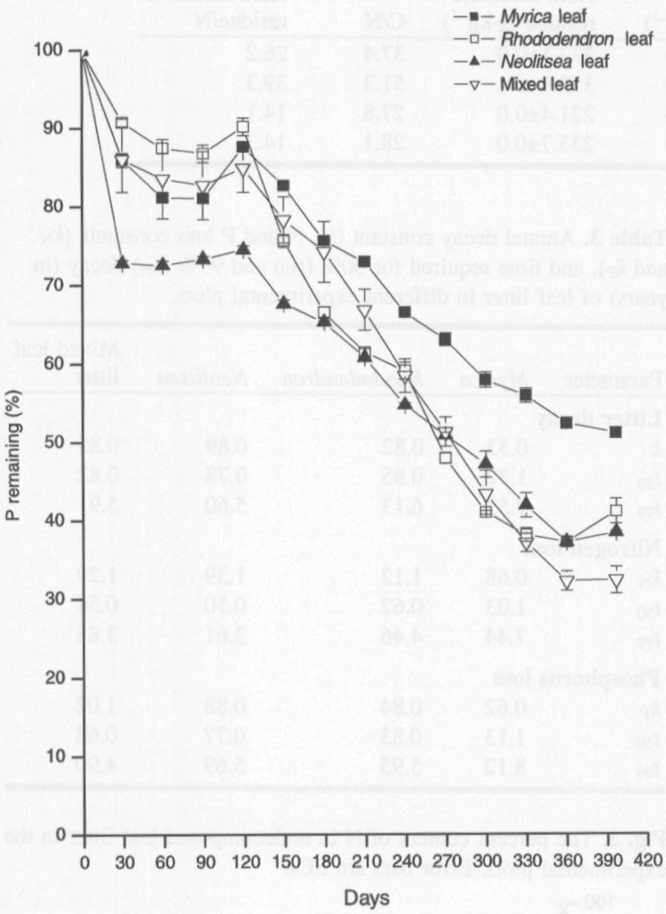


Fig. 4. The percent content of P in undecomposed leaf litter in the experimental plots. Error bars are SEs.



tropical evergreen forest of China (50%–80%), by Arunachalam et al. (1998) from regrown subtropical forest of Meghalaya (78%–88%), and by Haase (1999) from tropical rain forests in Malaysia (71%) and Venezuela (74%).

The seasonal pattern in litterfall among the species was identical and was related to seasonal changes in climatic variables, such as temperature and moisture, and intrinsic genetic characteristics of species that govern the phenological events (Jamaludheen and Kumar 1999). The peak litterfall in March (spring) was in agreement with the works of Rawat and Singh (1988), Khiewtam and Ramakrishnan (1993), Arunachalam et al. (1998), and Y.S Yang et al. (2005) and has been attributed to physiological leaf senescence during that period. The second peak of litterfall observed in August in all the species was due to high rainfall as well as higher input from the belowground litter. During this month, greater amounts of both live and dead roots in the soil have been reported by Upadhaya et al. (2005) in a subtropical forest. Occurrence of bimodal or trimodal litterfall patterns have been observed by several workers and have been attributed variously to water stress during summer months, wind, typhoons, and heavy precipitation in the form of rainfall and snow (Xu et al. 2000; W.Q. Yang et al. 2005; Y.S. Yang et al. 2005).

Nitrogen and P return through litter

Litter is the major source of nutrient input in a forest ecosystem. The N input through leaf litter (88–111 $kg \cdot ha^{-1} \cdot year^{-1}$) in the present study is higher than the earlier reports of Rapp et al. (1999) for a Mediterranean forest (27–88 $kg \cdot ha^{-1} \cdot year^{-1}$) and of Y.S. Yang et al. (2005) for a Chinese subtropical forest (35–70 $kg \cdot ha^{-1} \cdot year^{-1}$). However, the values are comparable with those reported for the central Himalayas (76–125 $kg \cdot ha^{-1} \cdot year^{-1}$; Rawat and Singh 1988) and for Brazilian tropical forest (102–153 $kg \cdot ha^{-1} \cdot year^{-1}$; De Moraes et al. 1999). The P input through leaf litter (3–5 $kg \cdot ha^{-1} \cdot year^{-1}$) in the present study is within the range of earlier reports (2.4–8.7 $kg \cdot ha^{-1} \cdot year^{-1}$) for different forest types (Rawat and Singh 1988; Rapp et al. 1999; Y.S. Yang et al. 2005).

Greater input of N and P in the *Neolitsea* plots could be attributed to high resource quality of the litter (De Moraes et al. 1999), whereas lower input in *Rhodendron* plot could be due to low N and P concentrations. The observed differences in N and P input among the species in the present study are in agreement with the findings of Y.S. Yang et al. (2005). These differences in the nutrient content of litter may be attributed to the difference in nutrient allocation pattern of the species and the nutrient relocation strategy adopted by the species before senescence (Y.S. Yang et al. 2005). Relatively higher N and P input in mixed-species plot, which was very close to *Neolitsea* may be attributed to the species composition in the mixed-species plot. The difference in the amount of N and P return to the forest floor in different species plots could lead to the patchy distribution of N and P in the forest floor depending upon the canopy species composition.

Litter decomposition and N and P loss

In all the species including the mixed-species plot, litter exhibited a conspicuous initial phase of rapid decomposition that was confined to first 30 days because of leaching of soluble compounds and the decay of easily degradable compounds and tissues, followed by a slower but constant rate of decay for a longer period. The highest leaf litter decomposition rates during the rainy months reflected the favourable effect of rainfall on decomposition, whereas low soil moisture and low temperature in winter decreased the activity of decomposer organisms, resulting in a slower rate of decomposition. As decay advances, mineralization resulted in the decline of the nutrient in residual litter. Nitrogen showed a decrease phase (net loss) in *Myrica*, *Rhododendron*, and mixed species, whereas it showed a decrease–increase–decrease phase in *Neolitsea* (initially net loss, net gain, and then net loss). Phosphorus demonstrated a decrease–increase–decrease phase (initially net loss, net gain, and then net loss) in all the species plots. The net gain may be attributed to temporary microbial immobilization of N and P during litter decomposition, which minimizes their losses from the ecosystem. In the present study, P was retained more strongly than N indicating that it was probably the most limiting element to the decomposer community (Xu 2006). Because of the presence of a net gain phase between the two consecutive net loss phases, where microbial immobilization takes place, *Neolitsea* seemed to have a better N management strategy than the other species. The decomposition and nutrient

Table 4. Relationship of rates of decay, N loss, and P loss with microenvironment and litter chemistry across the species plots.

Variable	Regression equation	df	*r*
Decay rate versus microenvironment			
Soil moisture	$Y = 36.30 + 2839.6X$	155	0.54
Soil temperature	$Y = 13.735 + 760X$	155	0.48
Rate of N loss versus microenvironment			
Soil moisture	$Y = -0.0013 + 0.11X$	155	0.44
Soil temperature	$Y = -0.0016 + 0.31X$	155	0.39
Rate of P loss versus microenvironment			
Soil moisture	$Y = -0.19 + 0.0013X$	155	0.23
Soil temperature	$Y = -0.25 + 0.0072X$	155	0.41
Decay rate versus litter chemistry			
P	$Y = 0.16 + 0.05X$	35	0.57
Acid-insoluble residue	$Y = 45.4 - 21.85X$	35	–0.55
Acid-insoluble residue/P	$Y = 1269.2 - 881.5X$	35	–0.53
Rate of N loss versus litter chemistry			
N	$Y = 0.55 + 0.41X$	35	0.46
P	$Y = 0.28 + 15.6X$	35	0.72
C/N	$Y = 1.52 - 0.01X$	35	–0.40
Acid-insoluble residue	$Y = 2.06 - 0.33X$	35	–0.71
Acid-insoluble residue/N	$Y = 1.41 - 0.01X$	35	–0.47
Acid-insoluble residue/P	$Y = 1.57 - 0.001X$	35	–0.69
Rate of P loss versu litter chemistry			
N	$Y = 0.50 + 0.25X$	35	0.41
P	$Y = 0.38 + 8.64X$	35	0.58
Acid-insoluble residue	$Y = 1.34 - 0.02X$	35	–0.55
Acid-insoluble residue/N	$Y = 1.00 - 0.01X$	35	–0.38
Acid-insoluble residue/P	$Y = 1.08 - 0.001X$	35	–0.54

Note: Only significant correlations ($p < 0.05$) are presented.

loss patterns in mixed-species plot were identical with *Rhododendron* and *Myrica* species plots, respectively, although decay and loss rates were different.

Although plant species can influence decomposition by impacting the microenvironment in which the litter decomposes, litter quality remains one of the most important factors controlling litter decomposition (Knops et al. 2001). The faster rate of decay in *Neolitsea* and mixed-species plots than *Rhododendron* and *Myrica* plots may be attributed to higher concentrations of N and P, lower concentration of acid-insoluble residue, and lower C/N and acid-insoluble residue/N ratios in the former two litter types than the latter two. It has been established that litter with a low C/N and acid-insoluble residue/N ratios and higher N concentration decomposes more rapidly than those with a high C/N and acid-insoluble residue/N ratio and low N concentration (Upadhyay and Singh 1989; Prescott et al. 1993; Stump and Binkley 1993). The role of initial acid-insoluble residue in slowing the litter decay has been emphasized by Sariyildiz and Anderson (2003). Phosphorus-related litter chemistry such as P concentration, C/P ratio, and acid-insoluble residue/P ratio has also been found to control litter decomposition (Schlesinger and Hasey 1981; Aerts 1997; Kwabiah et al. 2001).

Litter chemistry also appears to be the cause of slower rates of N and P loss in *Myrica* plot, which received litter with a higher concentration of acid-insoluble residue and higher C/N, C/P, acid-insoluble residue /N and acid-insoluble residue/P ratios than in *Neolitsea* and mixed-species plots. The significant positive correlation between decay rate and rates of N and P loss with initial P content and P-related litter chemistry indicated the important role of P in determining the mass loss and nutrient loss. In addition to initial P concentration, N, concentration of acid-insoluble residue and acid insoluble residue/N ratio also influenced the rates of N and P loss.

The rates of decay as well as N and P loss across the species plots were positively correlated with soil moisture and temperature (Table 4). This is in conformity with the findings of many earlier workers, who concluded that the physical environment, especially relative humidity and moisture content and temperature of the upper soil layer are important in litter decay because all these factors influence the biological activity in soil (Meentemeyer 1978; Tripathi and Singh 1992; Hobbie 1996). In addition to poor litter quality, relatively lower moisture content in the soil caused by greater exposure to solar radiation because of a sparse overhead canopy of *Myrica* species could have also contributed towards slower decomposition and nutrient loss. The increased temperature and wind movement have been reported to exacerbate drying of litter, thus slowing down decomposition rates (Prescott et al. 2004). The faster rate of decomposition of *Rhododendron* leaf litter in spite of lower N and higher C/N ratio than the *Myrica* leaf litter could be attributed to greater moisture and organic matter contents due to denser canopy and higher soil pH in the former species plot that might have favoured microbial activities.

Therefore, the present study concludes that the forest patches with different tree species composition show variation in litter production and decomposition pattern. Although litter production is related to species traits, nutrient loss and decay of leaf litter are related to the variation in chemical composition of the litter and soil microenvironment. The variation in leaf litter production, decomposition, and N and P release pattern among the species can contribute to the spatial heterogeneity in nutrient distribution on the forest floor depending on the distribution pattern of tree species in the forest ecosystem.

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