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Foliage decomposition and nutrient release dynamics of *Bambusa balcooa* and *Bambusa pallida* in a 9-year-old jhum fallow

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Abstract—Litter decay and nutrient release rates of leaf and leaf sheath litters of *Bambusa balcooa Roxb.* and *B. pallida* Munro were determined using the litter-bag technique in a 9-year-old jhum fallow in the humid tropics of north east India. C concentration was highest in leaf and leaf sheath litters of *B. pallida*, while N and lignin concentrations were greater in *B. balcooa* litter. Both leaf and scale leaf litters of *B. balcooa* and *B. pallida* showed similar decomposition patterns. The daily decay constants did not differ significantly between the two litter types and among bamboo species studied. Nonetheless, mass-loss rates during decomposition of the leaf and leaf sheath litters of both the species showed positive correlations with incubation period (the time after burying the samples in the soil). In general, until 120 days of incubation, there was N immobilization and later during the study period rapid release occurred. The release of N from *B. pallida* is greater than *B. balcooa* as per K_N values. P was initially being immobilized followed by a gradual release after 120 days of litter decomposition in *B. balcooa*. In *B. pallida*, no definite pattern was observed. The rate of weight loss and N release showed significant positive relationships with lignin and N concentrations and lignin/N, C/P and N/P ratios, and negative relationships with C and P concentrations and C/N ratio. However, release rates of P did not show significant correlations with most chemical compositions of the litter except with initial P concentration, C/P ratio and lignin/N.

Key words: Bamboo; decomposition; humid tropics; litter; nitrogen; phosphorus.

INTRODUCTION

Bamboo constitutes one of the dominant secondary successional vegetation types in the majority of the northeast Indian forests. Out of 18 genera and 128 species of bamboos of India [1], Arunachal Pradesh alone harbours 16 genera and 63 species [2]. Abandoned jhum (shifting agriculture) lands and forest clearings

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form favourable habitats for bamboos to invade, colonize and establish faster when compared to broadleaved native species [3], resulting in pure and/or mixed bamboo forests. Due to its abundance and faster re-growth, these bamboo species meet a variety of socio-economic and ethno-botanic human needs in the region. Nevertheless, the role of bamboos in soil nutrient cycling in degraded sites has been less studied [4–7], unlike other broadleaved forest tree species [8–10]. Recycled nutrients from decomposing plant litter are one of the main nutrient sources for maintaining growth of forest vegetation [11]. Bamboos in this part of the world are mainly distributed in nutrient poor soils. Hence, the nutrient release from litter decomposition may play an important role in re-establishing the nutrient cycling in nutrient poor soils, particularly when the ecosystem is undergoing recovery following disturbance [12]. The objective of the present study was to determine the rates of decomposition and nutrient release through the leaf and leaf sheath litters of two lower altitude (100 to 600 m above sea level (asl)) bamboos, *Bambusa balcooa* Roxb. and *B. pallida* Munro, growing in a 9-year-old jhum fallow in the humid tropics of Arunachal Pradesh, north-eastern India.

MATERIALS AND METHODS

Study site

The study was conducted in a bamboo forest (9 years old) developed on a fallow agricultural land (1.74 ha) located at an altitude of 132 m above sea level in humid tropics of Arunachal Pradesh (26°28′–29°30′N latitude; 91°30′–97°30′E longitude), northeastern India. The average annual rainfall of the place was about 1800 mm with mean maximum and minimum air temperatures 33 and 18°C, respectively. At the time of sampling (February–March) the average soil temperature recorded was 23°C. The climate was monsoonal with three seasons: winter (October–February), spring/summer (March–May), monsoon (June–September). Almost 80% of the total annual rainfall occurs during May–September. The study site was dominated by two fast growing and clump forming bamboo species having average height of 15 to 20 m and a mean culm diameter of 6–9 cm (Table 1).

Table 1.
Characteristics of bamboo species in the study site

Species	No. of clumps per ha	No. of culms per clump	Height (m)	Average diameter (cm)	
				Clump	Culm
Bambusa balcooa	89 ± 7	23 ± 6	19.6 ± 1.2	470 ± 28	9 ± 2
Bambusa pallida	137 ± 11	37 ± 7	15.6 ± 0.8	415 ± 23	6 ± 1

Values are means ± SE ($n = 5$).

Soil sampling and analytical procedures

Topsoil (0–10 cm) under the canopy of *B. balcooa* and *B. pallida* was collected in bulk during February–March, 1999. The soils were sieved through a 2-mm mesh and the initial pH, moisture content (gravimetric method), and concentration of ammonium-N (indophenol blue method) and nitrate-N (phenol disulphonic acid method) were determined within 24 h after sampling. The remaining soil samples were air-dried and analyzed for texture, water holding capacity (WHC), soil organic carbon (SOC), total Kjeldahl nitrogen (TKN) and available-P according to standard procedures [13, 14]. The soil was loamy sand and acidic (pH 5.9–6.5). Water holding capacity and clay content of soils were relatively greater *in B. balcooa* soil (64% and 9.5%, respectively). On the other hand, soil organic C, total Kjeldahl N and available P were higher in *B. pallida* soil (1.9%, 0.46%, 10.69 μg g^{-1}).

Litter sampling and analytical procedures

Freshly fallen foliage litter samples of the two bamboo species were collected from five randomly selected clumps of each species during February–March 1999. The litter was sorted into leaves and leaf sheath and air-dried. Sub samples of litters were oven-dried at 105°C for 24 h in order to determine their dry weights and for moisture correction. Ash content of litter was determined by igniting ground samples in a Muffle furnace at 550°C for 6 h. C content was calculated taking 50% of ash-free weight [14]. Total Kjeldahl N was determined using the semi-micro Kjeldahl procedure and total P was estimated using the molybdenum blue method. Lignin, cellulose and fibre contents were also determined [15]. The data given in Table 2 are the mean values of the five replicated clumps for each species and litter type in the study site.

The sorted foliage litter samples from five clumps of each species were then bulked together to form four categories of samples (2 species × 2 litter type) for further study. Air-dried litter samples equivalent to 10 g of oven-dry weight was placed in a nylon litter-bag (1 mm mesh; 15 cm × 15 cm). Sixty bags were prepared for each litter fraction of a given species. The bags were equally distributed in five clusters in the site. In order to avoid disturbances from grazing animals, the bags were buried in the top 0–5 cm soil layer below the canopy of respective species during March 1999. Five bags per litter type were retrieved at 60 days interval. Each time, the sample from each bag was cleaned of adhering plant parts and soil particles, oven-dried at 105°C for 24 h and weighed. The dried samples were ground and analyzed for N and P using the standard procedures given in Anderson and Ingram [15].

Computation and statistics

Organic matter decay constants for the leaf and leaf sheath litters were computed using negative exponential decay model of Olson [16]:

$$X/X_0 = \exp(-kt),$$

Table 2.
Initial chemical composition of bamboo litter

	B. balcooa		*B. pallida*	
	Leaf	Leaf sheath	Leaf	Leaf sheath
C (%)	44.56^{a} (0.138)	46.71^{b} (0.367)	47.82^{a} (0.129)	48.92^{b} (0.326)
N (%)	1.15^{a} (0.063)	0.34^{b} (0.031)	0.84^{a} (0.049)	0.34^{b} (0.040)
P (%)	0.031^{a} (0.001)	0.032^{a} (0.003)	0.023^{a} (0.001)	0.063^{b} (0.002)
Lignin (%)	31.2^{a} (0.339)	25.1^{b} (0.473)	29.3^{a} (0.375)	20.4^{b} (0.491)
Cellulose (%)	28.26^{a} (0.500)	29.63^{a} (0.438)	30.34^{a} (0.469)	31.05^{a} (0.388)
Fibre (%)	52.08^{a} (0.563)	35.41^{b} (0.491)	49.01^{a} (0.518)	34.31^{b} (0.339)
C/N	38.75^{a}	137.38^{b}	56.93^{a}	143.88^{b}
Lignin/N	26.96^{a}	73.53^{b}	34.52^{a}	58.82^{b}
N/P	37.10^{a}	26.25^{b}	14.78^{a}	5.40^{b}
C/P	1437.42^{a}	1459.69^{a}	2079.13^{b}	776.51^{c}
Lignin/P	1006.45^{a}	784.38^{b}	1273.91^{c}	323.81^{d}

$n = 5$; Values in parentheses denote SE. In each species, the values with similar letters across leaf and leaf sheath categories are not significantly different at $P < 0.05$.

where X is weight remaining at time t, X_0 is initial weight and k is the decay rate coefficient. The times required for 50% (t_{50}) and 99% (t_{99}) decay were calculated as $t_{50} = 0.693/k$ and $t_{99} = 5/k$.

The effect of initial litter chemistry and rainfall (data obtained from Doimukh Meteorological Station, which is within 1 km radius of the study site) on the decay rate was tested using the linear regression function, $Y = a + bX$ [17]. Polynomial equations were used to characterize the observed decay pattern [18].

RESULTS

Initial litter chemistry

C concentration was about 2–3% higher in the two litter types of *B. pallida*, while N concentrations were greater in *B. balcooa* leaf litter by about 0.3% (Table 2). N concentrations were found to be same in leaf sheath litters of both species. Concentration of P of both the litter types of *B. balcooa* was similar while it was significantly different in the litter types of *B. pallida* showing higher P concentrations in leaf sheath by a difference of 0.040%. Among the species, *B. balcooa* leaf had a higher P concentration (0.008%), whereas the opposite trend was recorded in case of leaf sheath litter (higher by 0.029%). Lignin concentration was larger in *B. balcooa* litters, while the C/N ratio was higher in the other species.

Table 3.
Annual dry matter decay constants of leaf and leaf sheath of two bamboo species

Decay parameter	*B. balcooa*		*B. pallida*	
	leaf	leaf sheath	leaf	leaf sheath
% mass loss day^{-1}	0.40	0.39	0.40	0.40
k (year^{-1})	8.03	5.84	8.03	8.03
t_{50} (days)	31.50	43.31	31.50	31.50
t_{99} (days)	227.27	312.50	227.27	227.27

In general, the leaf sheath had greater C/N and lignin/N ratios. N/P ratio was comparatively higher in leaf samples than in the leaf sheath in both species. Among species, *B. balcooa* registered greater N/P ratios.

Litter decay

Both leaf and leaf sheath litter materials of *B. balcooa* and *B. pallida* showed similar decay patterns (Fig. 1). However, decomposition rate exhibited a significant variation in the two species of bamboo, at least up to 180 days of incubation. In *B. balcooa*, during the initial 120 days of incubation, the rate of decomposition was slow both in leaf (0.14% weight loss day^{-1}) and leaf sheath (0.15% weight lossday^{-1}) litter, and then the decay rate continued to increase until the end of the study period. However, in *B. pallida* the decomposition rate increased rapidly during initial 60 days (0.28% weight loss day^{-1}), which continued up to 120 days (0.23–0.33% weight loss day^{-1}) and then a significant decrease (0.20–0.47% weight loss day^{-1}) was noticed between 120 and 180 days of incubation, afterward both species showed almost similar pattern of decomposition. Nevertheless, the net weight loss rate was almost similar in the two litter types of both the species. The undecomposed litter at the end of the study remained highest in the leaf sheath of *B. pallida* (7%) and in all other cases, only 3% of the initial mass was remaining at the end of the study. The mean weight loss per day was similar in leaves and leaf sheath of *B. balcooa* and *B. pallida* (Table 3). The decay constants (k) did not differ much between the two litter types and among bamboo species studied (Table 3).

Nutrient (N and P) dynamics

The concentration of N fluctuated in the decomposing *B. balcooa* leaves during the study period. However, in the rest of the samples it increased with time (Fig. 2a). Nevertheless, the N immobilization and release rates were different through time. In general, until 120 days of incubation, there was a tendency of N immobilization and then rapid release occurred, which continued throughout the study period (Fig. 3a).

In general, P concentration increased up to 180 days and then decreased rapidly in both species (Fig. 2b). Initially P was immobilized followed by a gradual release

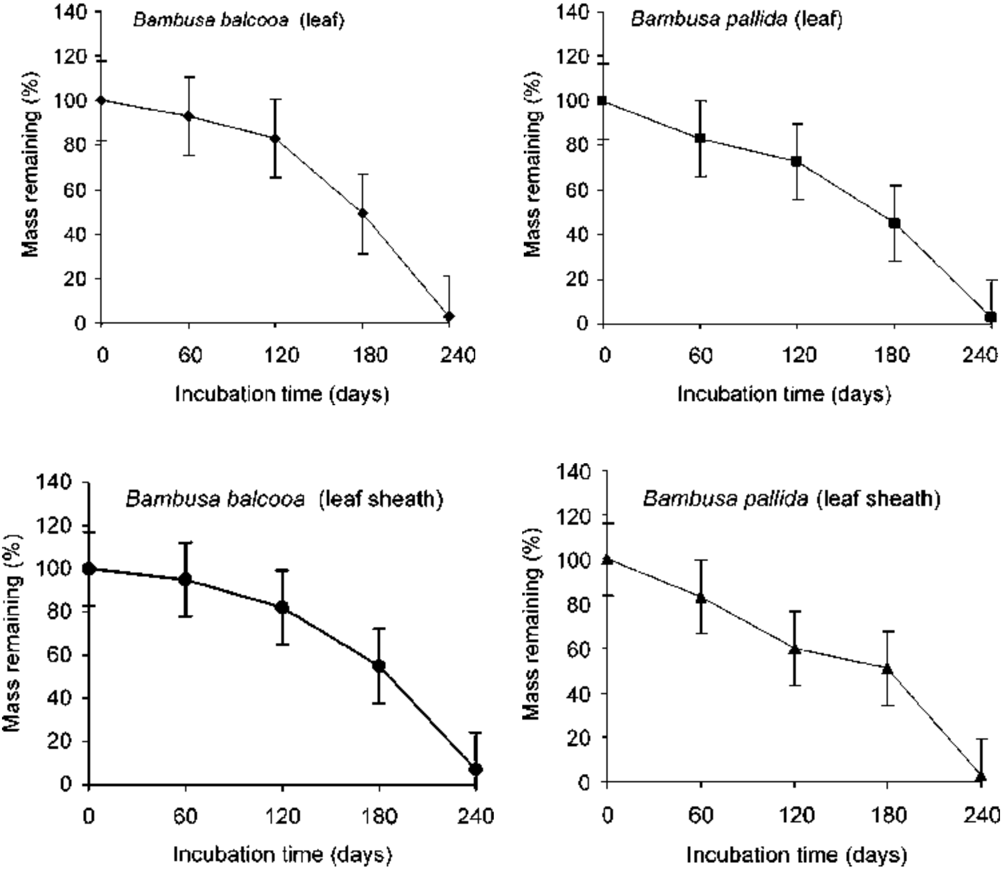

Figure 1. Foliage litter decay pattern in two bamboo species.

after 120 days of litter decomposition in *B. balcooa* and *B. pallida*. P release patterns of leaf litter and leaf sheath were different (Fig. 3b).

Effect of litter quality on decomposition and nutrient release rates

Weight loss and nutrient release rates of different components were correlated with lignin, C, N and P concentrations and ratios of lignin/N and C/P and N/P. We found strong positive correlation of lignin and N concentrations with weight loss and N release rates. However, only P concentration exhibited a significant positive correlation with P release rate (Table 4). The other litter chemical quality variables like lignin/N, C/N, C/P and N/P either exhibited positive or negative correlation with weight loss and nutrient release.

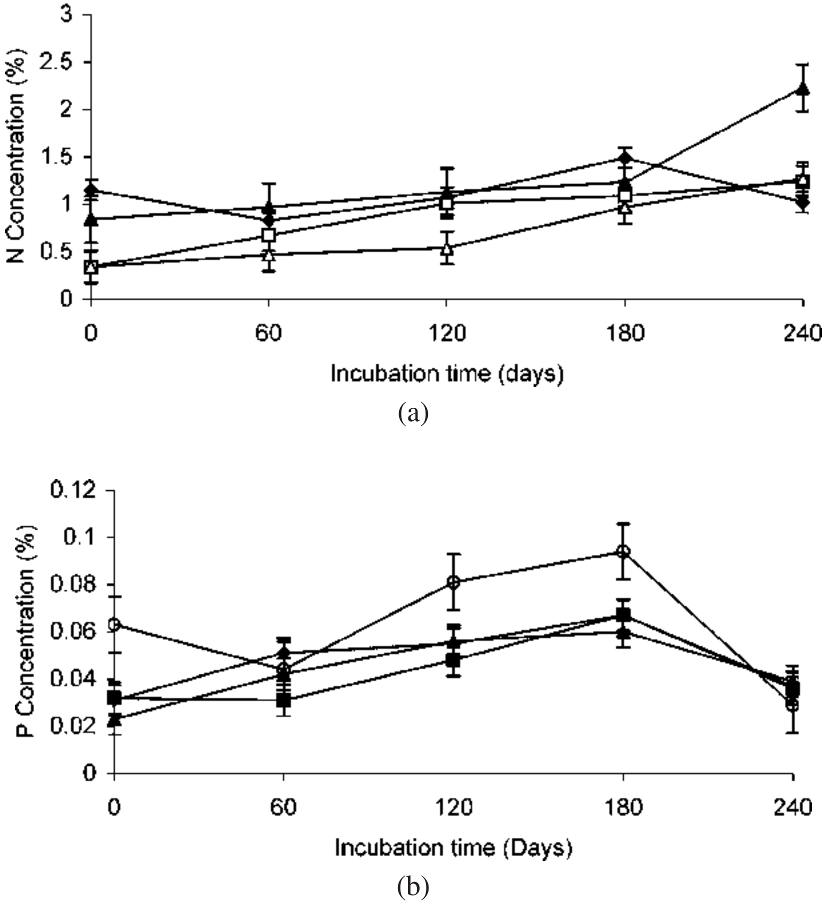

Figure 2. N (a) and P (b) concentration (%) during litter decomposition of *B. balcooa* ((◆) leaf, (■) leaf sheath) and *B. pallida* ((▲) leaf, (◇) leaf sheath).

DISCUSSION

Decomposition dynamics

Overall, the amount of litter remaining at the end of the study period was 3–7%. Nevertheless, the pattern of litter decomposition varied between litter types and species. In *B. balcooa*, the rate of decomposition was slow up to 120 days of incubation. This may be attributed to the time taken by microorganisms to colonize and establish on the litter materials as these litter samples had greater lignin and cellulose contents when compared to *B. pallida* [19, 20]. During monsoon, i.e., after 60–120 days of incubation, the decay rate rose due to greater microbial activity. In this context, several authors have reported faster rate of decomposition during rainy season in the tropics [21]. Relatively higher temperature and moisture conditions during monsoon favoured decomposition of bamboo leaf litter in China

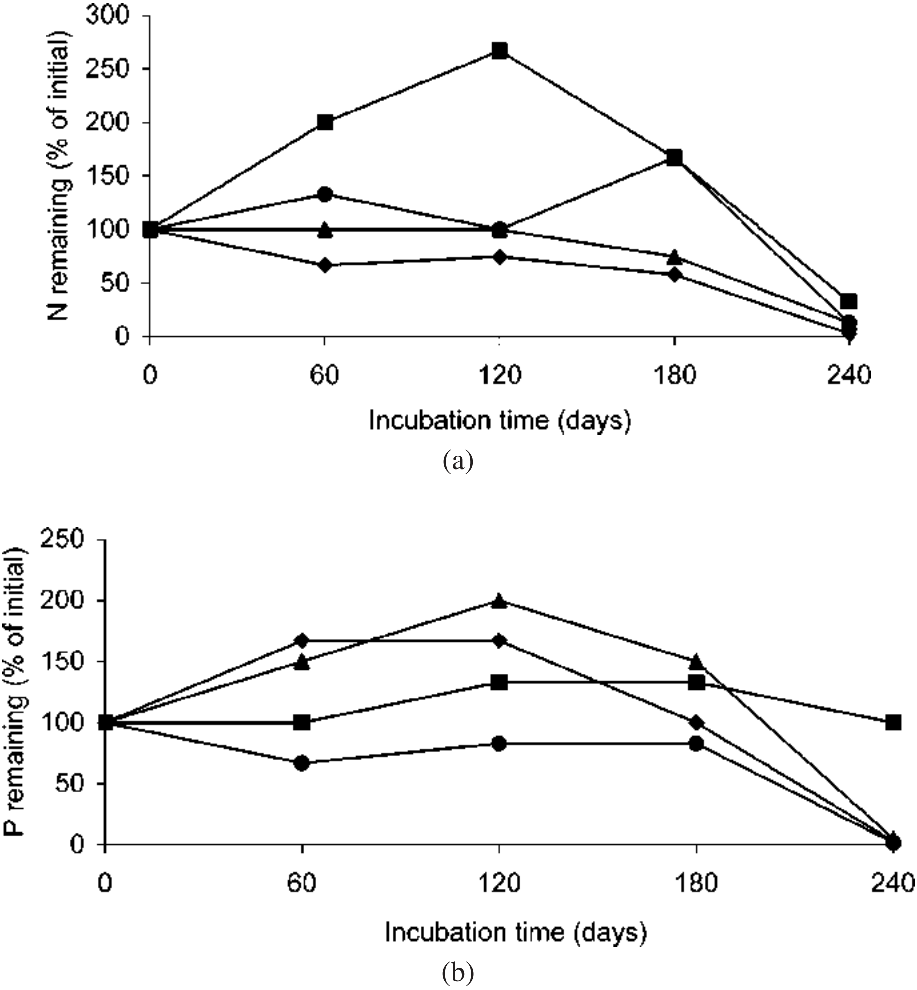

Figure 3. N (a) and P (b) remaining (% of initial) in *B. balcooa* ((◆) leaf, (■) leaf sheath) and *B. pallida* ((▲) leaf, (●) leaf sheath).

[6] and southern Western Ghats of India [7]. Coincidently, we obtained a significant relationship between mass loss and rainfall ($r = 0.451$, df $= 19$, $P < 0.05$).

The C/N ratio of plant litter has frequently been negatively correlated with the decomposition rates [22, 23]. We also observed such a relationship in this study. Among other litter quality parameters, initial N and lignin concentrations influenced the litter decay pattern [24–26]. For instance, the faster rate of decay in leaf litter compared to leaf sheath is attributed to greater initial N in the former (Table 2). Contrary to the most of the reports [27, 28], we found a positive correlation between initial lignin concentration and rate of weight loss during decomposition. This suggests that apart from lignin, other quality parameters, such as cellulose and polyphenols, may have more influence on the decay rate of bamboo litters. For

Table 4.
Relationships of leaf and scale leaf decomposition rate (% weight loss day^{-1}) with its initial chemical composition

Variable	Correlation coefficient (r)	P
Weight loss *versus* initial litter quality		
Lignin (%)	0.907	0.01
C (%)	−0.707	0.01
N (%)	0.632	0.01
P (%)	−0.980	0.01
Cellulose (%)	0.235	NS
Fibre (%)	0.542	0.01
Lignin/N	−0.421	0.05
C/N	−0.693	0.01
C/P	0.949	0.01
N/P	0.754	0.01
Lignin/P	0.930	0.01
N release *versus* initial litter quality		
Lignin (%)	0.958	0.01
C (%)	−0.720	0.01
N (%)	0.985	0.01
P (%)	−0.709	0.01
Cellulose (%)	−0.824	0.01
Fibre (%)	0.256	NS
Lignin/N	0.905	0.01
C/N	−0.991	0.01
C/P	0.633	0.01
N/P	0.651	0.01
Lignin/P	0.108	NS
P release *versus* initial litter quality		
Lignin (%)	−0.103	NS
C (%)	−0.107	NS
N (%)	0.328	NS
P (%)	0.580	0.01
Cellulose (%)	−0.231	NS
Fibre (%)	−0.368	NS
Lignin/N	−0.449	0.05
C/N	−0.190	NS
C/P	−0.601	0.01
N/P	−0.042	NS
Lignin/P	−0.751	0.01

NS, not significant. $n = 4$ (2 species $\times$ 2 litter types).

example, Tripathi and Singh [4] found that roots having low cellulose contents decomposed at a faster rate. Nonetheless, we observed no relationship between cellulose content and litter decay rate in this study. Also, as opposed to the contention of Enriquez *et al*. [29] that the greater the initial P concentration in the litter, the faster would be its decomposition, we observed a negative correlation between initial P and decay rate. This indicates that the decomposer population on bamboo litter was selective to nutrients like N and/or the P levels were low in the litter. Future work needs to test this hypothesis, for a better understanding of the role of P in the regulation of litter decomposition of bamboo residues. The rate of weight loss of bamboo litter in the present study was faster (as indicated by higher annual decay constants, 5.84 to 8.03) compared to those obtained by Tripathi and Singh [4] for bamboo litter (0.43–2.76) in dry tropical bamboo savannas, and by Lugo and Murphy [30] for tree leaf litter (1.28–2.04) in a subtropical forest.

N and P release

The decreasing trend in N concentration from its initial level in the decomposing materials except of *B. balcooa* leaf may be attributed to leaching. And, the increasing trend in N concentration after 120 days of progressive litter decay as observed in *B. balcooa* may be attributed to (i) microbial immobilization of N [31–34], (ii) throughfall input of atmospheric-N [35, 36] and (iii) atmospheric N_2-fixation [37]. Nevertheless, initial N concentration had a positive correlation with N release rates (Table 4). Tripathi and Singh [4] reported that higher C/N ratios might cause longer immobilization period. This was true for leaf sheath of the two bamboo species (Fig. 2a and 2b) as they, with their greater C/N ratios, showed greater nutrient immobilization during initial stages of litter decomposition as compared to the release rates. Despite variations in N and P concentration in the decomposing litter due to release and/or immobilization, N and P stocks remaining in the litter were positively correlated to its dry mass ($r^2 = 0.48$–0.49, $P < 0.05$). In this context, Cortrufo *et al.* [38] reported no evidence for any increase in nutrient content in the litter, although the nutrient concentration increased owing to immobilization.

In the initial stages of decomposition (0–120 days), P release in decomposing litter decreased or increased depending upon the initial P content of litter (Table 4). Shorter or longer P immobilization periods have also been reported by Gosz *et al.* [39], Berg *et al.* [40], Stohlgren [41] and Prescott *et al.* [42] for a variety of litter samples. In this case, the classic pattern of nutrient immobilization followed by release was always more conspicuous for fast decomposing litter than for litter decaying more slowly [43]. This may also be explained by the role of 'critical' P content in non-woody litters, above which P is released, as suggested by Prescott *et al.* [42], Rustard and Cronan [43] and Eason and Newman [44]. In the present study, initial concentration of P and C/P ratio in litter samples were found to be good predictor of P release as evinced by the significant positive and negative correlations, respectively (Table 4). However, other litter quality parameters, *viz.*, C/N, lignin/N and N did not show significant relationships with P release. In this regard, our results with respect to P release especially, are contrary to the observations made by Tripathi and Singh [4] for bamboo litter in a dry tropical savannah in northern India. Such differences could be due to variations in climatic and other parameters like microbial populations, type of microbial species involved in decomposition and residue quality [45].

In general, nutrient immobilization has been a prominent process during the decomposition of bamboo litter. It may be that the microbial population that colonized these litter fractions could not degrade the organic compounds stored in the litter as quickly because the foliage materials were sclerophyllous and lignin and fibre contents were also high. Myers *et al*. [46] reported that organic residues having C/N ratio < 25 are of good quality and they release nutrients at a faster rate compared to low quality residues (C/N > 25). Obviously, the litter fractions used in this study were all of low quality (C/N $=$ 39–57 for leaf litter and 137–144 for leaf sheath), which may have also influenced the nutrient dynamics during decomposition.

CONCLUSIONS

This study concludes the following: (i) the leaf and leaf sheath litters of both *B. balcooa* and *B. pallida* decomposed at similar decay rates in the humid tropical fallow agricultural land, (ii) N and P release rates differed between the leaf sheath and leaf litter, (iii) P release was faster, showing little difference in decay rate among litter types, whereas N release was rapid only in leaf litter samples, (iv) most of the litter quality parameters showed significant relationships with weight loss and N release patterns, whereas P release was significantly correlated only to initial P content and C/P ratio in litter materials, and finally (v) rainfall influences litter decay and nutrient release.

Given the overall comparable rates of decay and nutrient release, the study suggests that both *B. balcooa* and *B. pallida* have tremendous potential in regulating soil nutrient pool through faster litter turnover and, therefore, can help in soil nutrient restoration *vis-à-vis* ecosystem reconstruction [44]. It is also recommended that studies on the ecological role of bamboos in restoration of degraded sites, particularly in hill slopes, of the humid tropics should address litter decomposition as a key unit for investigation, as this might give some useful information on the patterns and processes of soil nutrient dynamics that would help in understanding the species replacement during secondary succession, and/or to develop useful eco-scientific package for managing bamboo forests in general and jhum fallows in particular.

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