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Cell-wall degradation and nutrient release pattern in decomposing leaf litter of *Bambusa tulda* Roxb. and *Dendrocalamus hamiltonii* Nees. in a bamboo-based agroforestry system in north-east India

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Abstract—Decomposition dynamics, nutrient mineralization and cell-wall degradation of leaf litter of *Bambusa tulda* and *Dendrocalamus hamiltonii* were studied in bamboo-based traditional agroforestry systems of Arunachal Pradesh. Initial litter chemistry showed the identical leaf characteristics of both the species, but the species cannot be considered as good residue, as both of them had a greater initial C/N ratio (>25). The decay pattern showed three distinct phases during the field incubation period (0–90 days, 90–180 days and 180–270 days). The annual decay rate (k) varied from 3.34 in *D. hamiltonii* to 3.52 in *B. tulda*. N and P release from the decomposing litter was influenced by the seasonal cycle of mineralization and immobilization processes. Net mineralization was rapid during the later stage of decomposition. N and P remaining after 90% of decomposition in the decomposing leaf litter were 8.85–9.45% and 0.47–1.40%, respectively, in *B. tulda* and *D. hamiltonii*. The concentration of lignin increased, whereas cellulose and hemicellulose decreased during decomposition. Overall, the study revealed that *Bambusa* sp. have a higher N content and less lignin and carbon contents in their leaf litter and in addition they decomposed more rapidly than the residues of *Dendrocalamus* sp. Hence, *B. tulda* can be considered more suitable than *D. hamiltonii* for nutrient enrichment in traditional agroforestry and/or in the rehabilitation of the degraded jhum land.

Key words: Bamboo; litter; decomposition; nutrient dynamics; lignocellulose index.

INTRODUCTION

Globally there are 75 genera and 1250 species of bamboo and India has the second-largest bamboo resource in terms of species diversity, habituating 18 genera and 128

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species occupying about 12.8% of total forest area [1], of which north-eastern India harbours about 16 genera and 63 species [2]. *Bambusa tulda* and *Dendrocalamus hamiltonii* are the two predominant bamboo species of this region [3]. Both species are varied in their leaf size, physiological and biochemical properties [3]. Bamboos are grown in home gardens by different ethnic communities of the north-eastern region realizing their potential with short gestation period and recurring economic returns [4]. Young bamboo shoots are regularly harvested for selling or domestic consumption. Both *B. tulda* and *D. hamiltonii* are good soil binders and are light demanding and, thus, form early successional growth after abandonment or shifting agricultural fields in the region [5]. These sturdy species are used for house building, baskets, mats, toys, wall plates, screens, etc., and, therefore, are not expected to be easily biodegradable. Further, the historical success of the bamboo-based traditional agroforestry system appears to be largely due to the 'nutrient pumping action' of bamboos through slow decomposition of its silica rich litter and greater fine root biomass [6]. There is an unstated assumption that the profusely growing surface (fibrous) root systems of bamboo may out-compete the field tree/crops grown in association [7]. Bamboo can tolerate soil conditions ranging from organic-poor to mineral-rich, which makes it valuable for reclaiming degraded land [8]. The bamboos are preferred in shifting cultivation because they contribute a large amount of nutrients to the system. It helps to conserve potassium in degraded jhum lands following a successional pathway [5].

Decomposition of plant litter is one of the most crucial stages in the biogeochemical cycling in an ecosystem [9]. The quality of the plant litter assessed in terms of chemical composition such as nitrogen (N) and phosphorus (P) and major cell-wall compounds, like lignin, cellulose and hemicellulose, affect litter decay and nutrient release [10]. Besides litter chemistry, population and activity of soil organisms and climatic conditions also influence the organic matter decomposition in the soil. Many studies have shown that litter N, lignin, lignin/N, lignocellulose and the C/N ratio are critical determinants of litter decay [11].

Recently gregarious bamboo flowering occurred in northeastern India. *D. hamiltonii* and many *Bambusa* sp. flowered dense and completed their life cycle, adding a greater amount of green litter to the system. Thus, analysis of litter chemistry, organic matter decay and nutrient release is important for the better understanding of the nutrient cycling, even in bamboo-based traditional agroforestry systems. These systems can bring about significant improvement on litter utilization through scientific knowledge and contribute to the development of sustainable practice for bamboo production and utilization. The objective of this study is to determine mass loss, chemical element dynamics of some major nutrients and degradation of cell wall components like lignin, cellulose and hemicellulose during leaf litter decomposition of *B. tulda* and *D. hamiltonii* growing in traditional agroforestry systems.

STUDY SITES AND METHODOLOGY

Study sites

The study was conducted in a bamboo-based agroforestry system practiced by the Nyishis in Nirjuli village of Papumpare district, Arunachal Pradesh, India (26°46′ N latitude, 93°50′ E longitude (Fig. 1), 110–126 m asl). The average area of the agroforestry farms varied between 200 and 400 m^2 in study sites. In this system the farmers grow tree/palm species such as *Livistonia jenkinsiana*, *Areca catechu*, *Psidium guajava*, *Artocarpus heterophyllus*, *Gmelina arborea* and *Mesua ferrea* in combination with different bamboo species. Among the tuber crops associated with the bamboo species are *Manihot esculenta*, *Colocasia* sp., etc., which are widespread and subsistence crops. Vegetables include *Capsicum* sp., *Zingiber* sp., *Solanum tuberosum*, *etc*. Pineapple is a common floor crop, grown along with the vegetables in this system. A number of banana cultivars are also cultivated. Generally, farmers cultivate bamboo and tree species along the boundary and agricultural crops in the middle of the traditional agroforest/home garden systems. The two commonly grown bamboo species are *D. hamiltonii* and *B. tulda.* Although the height and average diameter of *Dendrocalamus* sp. was lower (Table 1) than *Bambusa* sp., plant density, litterfall and number of culms per clump were higher in *D. hamiltonii*. The total litter biomass of the two species *B. tulda* and *D. hamiltonii* was 48 kg/ha and 57 kg/ha, respectively (Table 1), which is 5.33% and 6.33% of the total litter production (900 kg/ha per year) in the traditional agroforestry system. Higher density, diameter and culms might be the factor of more litterfall under *D. hamiltoni*.

The mean annual temperature varied between 12 and 37°C, and the average precipitation for the past 5 years varied between 1100 and 1600 mm. Maximum rainfall occurs during June to September (rainy season). However, during the study period (February to November 2003), the temperature and rainfall of the study site ranged between 18 and 28°C, and 11 and 900 mm, respectively (Fig. 2). On the basis of rainfall, the study period was classified in to three seasons,

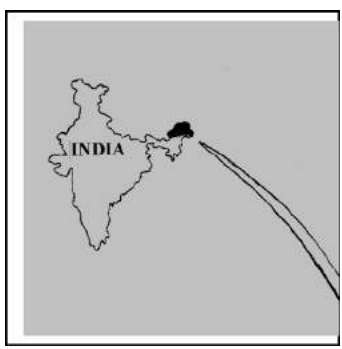

Figure 1. A map of Arunachal Pradesh indicating the study site.

Table 1.
A few structural characters of *Bambusa tulda* and *Dendrocalamus hamiltonii*

Parameter	*B. tulda*	*D. hamiltonii*
Density (shoots/ha)	5600 ± 756	6100 ± 814
No. of culms/clump	25 ± 2	38 ± 5
Height (m)	15 ± 5	16 ± 7
Average diameter of culm (cm)	7.54 ± 2.14	9.72 ± 3.48
Leaf fall (kg/ha^{-1})	48 ± 6	57 ± 7

Values are mean $\pm$ SE ($n = 10$).

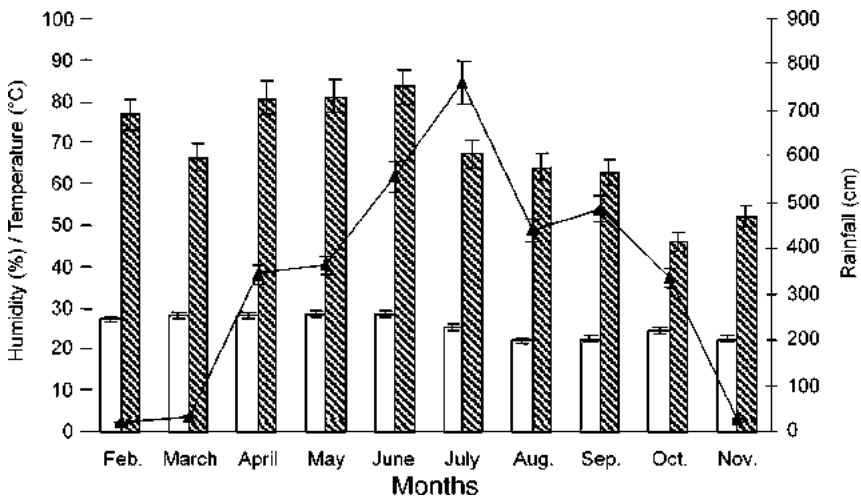

Figure 2. Mean monthly temperature (□), humidity (▨) and rainfall (●) in the study area during the decomposition study.

viz., pre-monsoon (February–April), peak-monsoon (May–July) and post-monsoon (August–October).

Soil analysis

The soil samples have been collected down to 10 cm depth using a soil corer and divided into two parts. One part was air-dried and used for the determination of texture, pH, water-holding capacity (WHC), organic-C, total Kjeldahl nitrogen (TKN), N, NH_4^+ N, NO_3^- N and available-P following standard procedures [12]. Moisture was determined gravimetrically by oven-drying 10 g fresh soil for 24 h at 105°C. Texture and bulk density (BD) were determined by Bouyoucos hydrometric and gravimetric method respectively [12]. Water holding capacity (WHC) was determined by Keens box method using copper cups of 5.6 cm inner diameter and 1.6 cm height. Soil pH was measured in 1 : 2.5 fresh soil/water (w/v) suspensions with an electric digital pH meter (Systronics). Soil organic carbon (SOC) and total Kjeldhal nitrogen were determined, using Walkley and Black's rapid titration and semi-micro Kjeldhal digestion distillation procedures, in air-dried and finely

ground soil samples following Anderson and Ingram [13]. Soil organic matter (SOM) content was obtained by multiplying the organic carbon concentration by 1.724, assuming that the SOM contains 58% of carbon. Ammonium-N, nitrate-N and available-P were determined spectrophotometrically using indophenol blue, phenol disulphonic acid and molybdenum blue methods, respectively, as outlined in Anderson and Ingram [13]. The other part was used in field-moist condition for the determination of microbial biomass C, N and P by chloroform fumigation method [13]. All analyses were using triplicated samples and the mean values are given in the tables and figures.

Litter decomposition

Litter decomposition was studied using the nylon-bag technique [14]. Freshly fallen leaves were collected from both the species in January 2003 and air-dried. Air-dried litter samples (5 g) were kept in 15 cm × 15 cm nylon bags (1 mm mesh size). Sixty bags were prepared for each of the species and the bags were randomly placed in the bamboo-based agroforestry system under the closed canopy of the respective bamboo species in February/March 2003. Before placement, the mouths of the bags were stitched with nylon threads to avoid loss of sample. The bags were placed in a manner such that contact was established with the soil and were covered with a few plant materials, so that cattle and poultry disturbance was reduced.

Five bags were recovered at regular intervals until 90% decomposition was observed. The residual materials were separated carefully from adhering soil particles and oven-dried at 80°C for 48 h and weighed. The net organic matter decay was computed using the negative exponential decay model [15]:

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

where X is the weight remaining at time t, X_0 the initial weight, exp is the base of natural logarithm, k is the decay rate coefficient and t is the time (year). The time required to achieve 50% (t_{50}) and 99% (t_{99}) decay was calculated as $t_{50} = 0.693/k$ and $t_{99} = 5/k$. Monthly weight loss (g/month) from decomposing litter was determined from the difference between the mass remaining in the litterbags in each month and the initial fresh weight.

Chemical analysis

The oven-dried plant materials collected from different months were ground in a Willey-mill and passed through a 0.5-mm sieve before chemical analysis. CHN analyzer (CHNOS 948) determined the nitrogen (N) and carbon (C) content of the leaf litter. P was estimated colorimetrically according to the molybdenum blue method after acid-digesting the plant samples. Major cell-wall component analysis of litter included determination of lignin, cellulose and hemicellulose [16].

Percentage nutrient remaining was calculated as:

$$\text{Nutrient remaining (\%)} = (C/C_0) \times (X/X_0) \times 100,$$

where C is the concentration of each element in the leaf litter at the time of sampling, C_0 is the concentration of initial litter kept for decomposition, X is the mass of dry matter at the time of sampling and X_0 is the initial dry matter of the litter sample kept for decomposition [17]. The ligno-cellulose index was also calculated, as lignin%/(% lignin + % cellulose) [18].

Statistical analysis

The data collected from each parameter during the course of decomposition were analyzed using STATISTICA (version 6.0) to test the statistical significance of variations due to time and species. Correlation analysis [19] was used to study the relationships between different components of the leaf litter sample, and also to characterize the relationship between soil and climatic variables and decomposition and nutrient release ratio.

RESULTS

Initial soil characteristics

The soil under both species was loamy sand (Table 2). Water holding capacity (WHC), soil moisture content (SMC), total Kjeldahl nitrogen (TKN), ammonium and nitrate-N were higher in *B. tulda* soils. Soil pH was relatively lower in *Bambusa* sp. (5.28) as compared to the other species (5.61). Soils of *D. hamiltonii* had more soil organic C (SOC) and available P (Table 2).

Soil microbial biomass C was in the range of 337–432 μg/g in bamboo soil, whereas microbial biomass N and P were 10.58–18.48 μg/g and 4.29–5.34 μg/g, respectively. Microbial biomass C and N were greater in *B. tulda* soils and microbial biomass P was highest in *D. hamiltonii* (2.15 μg/g). The contribution of microbial biomass C to SOC was significantly lower in case of *D. hamiltonii* (2.15) when to compared to that of *B. tulda* (3.17). The contribution pattern of microbial biomass N to total soil N showed a similar trend. Microbial biomass P contribution to soil available P was more in the soils of *D. hamiltonii*. Soils under *Bambusa* sp. held a good population of micro-organisms and, hence, higher microbial activity [20]. A comparison of microbial properties between the two species showed little differences. This may be ascribed to the reason that both the studied species occurred in the same agroforestry system.

Initial chemistry of leaf litter

N concentration in leaf litter of *Bambusa tulda* was *ca*. 5% greater than that of *D. hamiltonii*. Phosphorous concentration was relatively low, varying between 0.09 and 0.11% in both studied species. The initial lignin, carbon and hemicellulose concentrations were greater in *D. hamiltonii* (25.25, 30.67 and 10.43%, respectively). C/N and lignin/N ratios were higher in *D. hamiltonii* leaf litter, and C/P and lignin/P in *B. tulda* (Table 3).

Table 2.
Physico-chemical properties of soil under the canopy of *B. tulda* and *D. hamiltonii*

Soil properties	*B. tulda*	*D. Hamiltonii*
Physical properties		
Textural class	Loamy sand	Loamy sand
WHC (%)	73.46 ± 4.35	75.63 ± 4.29
Moisture (%)	31.68 ± 1.03	21.09 ± 1.26
Chemical properties		
pH (1:2.5 H_2O (w/v))	5.28 ± 0.03	5.61 ± 0.19
Organic C (%)	1.36 ± 0.09	1.57 ± 0.12
Organic matter (%)	2.35 ± 0.47	2.71 ± 0.58
Total N (%)	0.69 ± 0.02	0.52 ± 0.01
C/N	1.97 ± 0.14	3.02 ±0.05
NO_3-N (μg/g)	0.25 ± 0.03	0.17 ± 0.01
NH_4-N (μg/g)	0.44 ± 0.01	0.26 ± 0.01
PO_4- P (μg/g)	11.53 ± 0.87	15.26 ± 0.49
Microbial properties		
MBN (μg/g)	10.58 ± 1.03	18.48 ± 1.57
MBC (μg/g)	337.90 ± 23.18	432.45 ± 25.49
MBP (μg/g)	5.34 ± 0.54	4.29 ± 0.61
MBN/MBP	1.98 ± 0.06	4.31 ± 0.05
MBC/MBN	31.94 ± 2.37	23.40 ± 3.57
MBC/MBP	63.28 ± 5.49	100.80 ± 8.49

Values are mean ± SE ($n = 5$). Abbreviations: WHC, water holding capacity; MBN, microbial biomass nitrogen; MBC, microbial biomass carbon; MBP, microbial biomass phosphorous.

Mass loss

Mass loss occurred periodically and constantly with time (Fig. 3). About 3.8 and 8.5% of initial mass remained after 270 days of field incubation of *B. tulda* and *D. hamiltonii* leaf litter. However, the decay rate showed down during the later stages (180–270 days) as compared to the initial 0–90 and 90–180 days of decomposition. The decay constant during 90–180 days was maximum (5.23–7.80), as compared to initial 90 days (1.21–1.24) and also 180–270 days of incubation (Table 4). In *B. tulda*, highest rate of decomposition (29.4%) was obtained during 90–120 days of incubation, whereas in *D. hamiltonii* the peak value of mass loss (22.8%) was obtained during 120–150 days of field incubation. Over all, decay pattern (Fig. 3) and decomposition constants (3.5, 3.8) did not differ much between the two bamboo species studied.

Carbon and nutrient dynamics in decomposing bamboo leaf litter

N concentration in the decomposing bamboo leaf litter followed a temporal pattern (Table 3). Following an initial drop during the pre-monsoon period, the N concentration in the decaying leaves gradually increased up to 35–70% during 180 days of incubation (Fig. 4). At the onset of post-monsoon period, it again decreased.

Table 3.
Litter chemistry during initial and incubation period of decomposed of bamboo leaf litter

	Period							
	Initial		0–90 days		90–180 days		180–270 days	
	I	II	I	II	I	II	I	II
Carbon (%)	28.52 ± 0.61	30.67 ± 0.02	27.67 ± 0.61	29.31 ± 0.07	25.23 ± 0.42	21.44 ± 0.03	21.52 ± 0.02	22.85 ± 0.13
Nitrogen (%)	1.02 ± 0.04	0.97 ± 0.01	1.19 ± 0.02	0.98 ± 0.01	1.74 ± 0.04	1.31 ± 0.03	1.15 ± 0.09	1.05 ± 0.01
Phosphorous (%)	0.09 ± 0.01	0.11 ± 0.01	0.14 ± 0.01	0.14 ± 0.01	0.09 ± 0.01	0.16 ± 0.03	0.01 ± 0.01	0.05 ± 0.02
Lignin (%)	24.51 ± 0.67	25.25 ± 0.06	25.51 ± 0.67	28.63 ± 0.08	31.70 ± 0.31	35.42 ± 0.12	36.69 ± 0.77	38.19 ± 0.04
Cellulose (%)	22.00 ± 0.01	21.45 ± 0.03	21.05 ± 0.03	25.62 ± 0.14	11.19 ± 0.02	19.41 ± 0.08	7.88 ± 0.16	9.89 ± 0.07
Hemicellulose (%)	6.02 ± 0.01	10.43 ± 0.12	8.78 ± 0.01	8.47 ± 0.07	13.29 ± 0.02	18.33 ± 0.02	7.68 ± 0.11	21.32 ± 1.03
C/N	28.17	31.60	26.02	31.90	16.42	19.20	19.58	21.60
C/P	318.60	280.00	222.50	194.00	169.10	141.00	1809.00	397.00
C/lignin	1.17	1.21	1.07	1.07	0.92	0.670	0.67	0.630
C/cellulose	1.30	1.43	1.32	1.21	1.83	1.16	2.55	2.32
C/hemicellulose	4.74	2.94	3.57	3.04	2.28	1.59	2.54	1.24
Lignin/N	24.03	26.03	21.44	29.21	18.22	27.04	31.90	36.37
Lignin/P	272.33	229.55	182.21	204.50	352.22	221.38	3669	763.80
Lignin/cellulose	1.14	1.18	1.21	1.12	2.83	1.82	4.66	3.86
Lignin/hemicellulose	4.07	2.42	2.91	3.38	2.39	1.93	4.78	1.79

I, *Bambusa tulda*; II, *Dendrocalamus hamiltonii*.

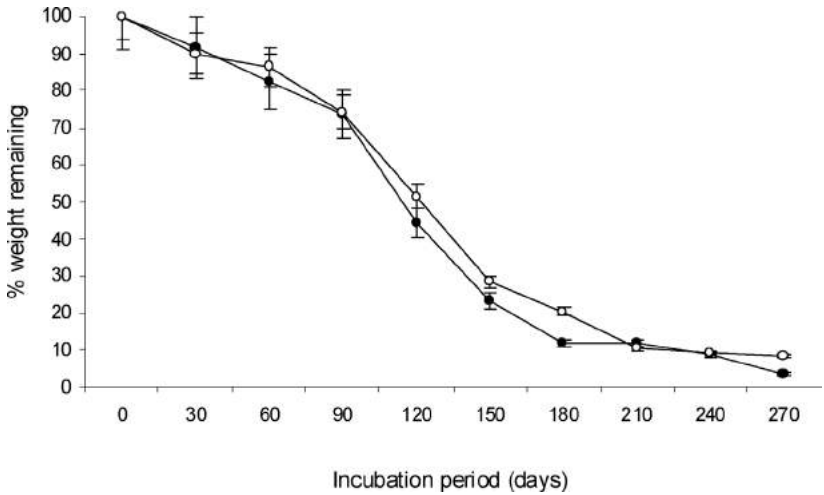

Figure 3. Decay pattern for leaf litter of *B. tulda* (●) and *D. hamiltonii* (○).

Table 4.
Weight and nutrient remaining (%) and annual decay rate constant (k) of bamboo leaf litter

Time (days)	Weight/Nutrient remaining (%)		Decay rate (k, years)		Weight/Nutrient loss rate (% loss/day)	
	I	II	I	II	I	II
Biomass						
0–90	73.62	74.30	1.24	1.21	0.29	0.28
0–180	10.77	20.50	4.52	3.20	0.50	0.44
0–270	7.42	8.47	3.52	3.34	0.34	0.34
90–180	NA	NA	7.80	5.23	0.69	0.60
180–270	NA	NA	1.51	3.57	0.04	0.13
Carbon						
0–90	65.88	70.56	0.12	0.18	0.38	0.33
0–180	8.93	14.45	0.25	0.73	0.51	0.48
0–270	5.65	6.28	0.38	0.57	0.35	0.52
90–180	NA	NA	0.37	1.27	0.63	0.62
180–270	NA	NA	0.65	0.26	0.04	0.09
Nitrogen						
0–90	91.73	73.70	0.66	0.06	0.09	0.29
0–180	19.73	26.36	1.09	0.61	0.45	0.41
0–270	9.45	8.85	1.28	0.70	0.33	0.34
90–180	NA	NA	1.52	1.16	0.80	0.53
180–270	NA	NA	1.66	0.88	0.11	0.19
Phosphorous						
0–90	98.02	81.68	1.69	0.92	0.02	0.20
0–180	21.15	16.57	1.51	0.62	0.44	0.46
0–270	0.47	1.40	5.74	1.99	0.37	0.37
90–180	NA	NA	1.32	0.31	0.85	0.72
180–270	NA	NA	14.20	476	0.23	0.17

NA, not applicable; I, *Bambusa tulda*; II, *Dendrocalamus hamiltonii*.

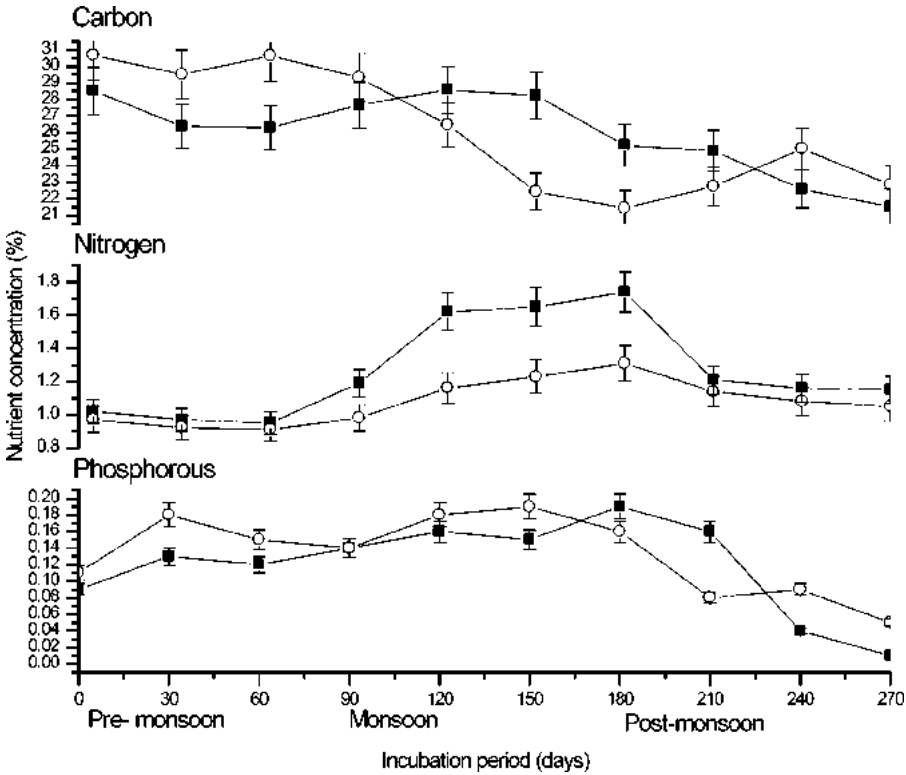

Figure 4. Carbon and nutrient concentrations (%) in the decomposing bamboo leaf litter. (■) *B. tulda*, (○) *D. hamiltonii*.

The N mineralization constant ranged from 0.01 to 0.53, but both the species showing same trend of N mineralization during the course of decomposition. At the end of the study (i.e., 270 days), only 95.98% and 90.93% of initial N remained in the decomposed leaf litter of *B. tulda* and *D. hamiltonii* respectively.

The percentage of P concentration in the remaining mass of decomposing leaf litter was 0.01–0.16% in *B. tulda* and 0.05–0.18% in *D. hamiltonii*. P concentration in the decomposing litter did not have any significant relationship with the weight remaining over time. However, the nutrient remaining of both the bamboo species showed that P immobilization was greater during the initial stages of decay (Fig. 5), whereas it got mineralized during the later stages of leaf decomposition.

C concentration in the decomposing litter samples decreased as the decomposition proceeded and the C remaining in *B. tulda* and *D. hamiltonii* after 90% decomposition was 5.65 and 6.25%, respectively. The concentration of C in bamboo litter did not show significant variation between pre-monsoon and monsoon periods; however, it decreased by 25% during the post-monsoon period (Table 3). Using all the data points from intervening periods, the N and C/N ratio showed a strong regulatory influence on mass loss for the first 180 days. The C/N and C/P ratios decreased until monsoon, whereas the C/cellulose ratio increased until the end of the experiment in

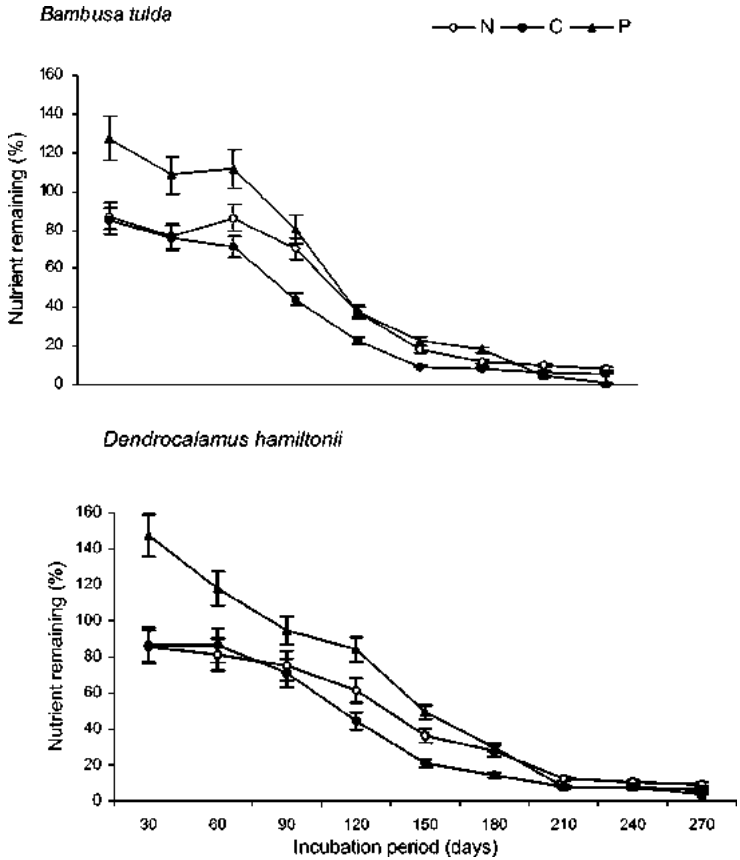

Figure 5. Carbon and nutrient nutrient remaining (%) in the decomposing bamboo leaf litter.

B. tulda (Table 3). The C/lignin ratio decreased during the course of decomposition in both the litter samples. The C/P ratio was maximum during the 180–270 days period in both the bamboo species. Also, litter C showed significant positive correlations with lignin, cellulose and hemicellulose concentrations in both the bamboo species. Hemicellulose also showed significant correlation with most of the other parameters. On the other hand lignin showed significant negative correlation with other chemical parameters in both the bamboo species (Table 5).

Lignin, cellulose and hemicellulose degradation

The initial lignin concentration in leaf litter did not vary significantly between *D. hamiltonii* (25.25%) and *B. tulda* (24.51%). The concentration of lignin increased and tended to remain constant in later stage of decay in both the species (Fig. 6). Lignin and N had a significant positive correlation in *D. hamiltonii* ($y = 25.56x + 5.11$; $r = 0.507$; $P < 0.005$), whereas no relationship existed in *B. tulda* leaf litter.

Table 5.
Correlation matrix among different nutrients and cell wall components of two bamboo leaf litter

Parameter	Carbon	Phosphorous	Lignin	Cellulose	Hemicellulose
B. tulda Roxb					
Nitrogen	0.194	0.495	0.310	−0.231	0.798^{***}
Carbon		0.533^{**}	-0.745^{***}	0.797^{***}	0.099
Phosphorous			-0.361^{*}	0.292	0.528^{**}
Lignin				-0.940^{***}	0.410*
Cellulose					-0.372^{*}
D. hamiltonni Nees					
Nitrogen	-0.851^{***}	0.133	0.712^{***}	−0.324	0.537^{**}
Carbon		0.216	-0.927^{***}	0.670^{***}	-0.806^{***}
Phosphorous			−0.351	0.693^{***}	-0.462^{*}
Lignin				-0.777^{***}	0.811^{***}
Cellulose					-0.878^{***}

$n = 30$; $^{*}P < 0.05$; $^{**}P < 0.005$; $^{***}P < 0.001$.

Table 6.
Leaf litter decay constants of different bamboo species

Species	Ecosystem, country	k	Turnover rate	Reference
Ochlandra travancorica Benth	Western Ghats, India	0.23	4.35	[29]
Sinarundinaria nitida Nakai.	Evergreen forest, China	0.40	2.50	[44]
Bambusa balcooa	Eastern Himalaya	5.84	0.17	[45]
Bambusa pallida	Eastern Himalaya	8.03	0.88	[45]
Bambusa tulda Roxb	Eastern Himalaya	3.52	0.28	present study
Dendrocalamus hamiltonni Nees	Eastern Himalaya	3.38	0.30	present study

The cellulose concentration of the bamboo leaves observed after 90% decomposition was 7.88% and 9.89% in *B. tulda* and *D. hamiltonii* leaf litter, respectively (Fig. 6). The fraction of lignin in the lignocellulose (lignocellulose index) component of decaying litter tended to increase linearly as decomposition proceeded (Fig. 7).

The initial hemicellulose concentration was significantly different between *B. tulda* (6.02%) and *D. hamiltonii* (10.43%), which increased to 7.68 and 21.32%, respectively, after 270 days of decomposition (Table 3). However, hemicellulose concentration is negatively correlated ($y = 0.058x + 0.26$; $r = -0.691$; $P < 0.001$) with the litter mass in bamboo species.

The rate of decomposition of *B. tulda* and *D. hamiltonii* was higher than two other species (*B. balcooa* and *B. pallida*) growing in the same climatic zone in this part of the country (Table 6).

Among the different microclimatic factors humidity played the most significant role in weight loss pattern of two bamboo species in agroforestry systems. Litter quality factors, such as C, N, lignin, cellulose and hemicellulose, were also significantly correlated with the weight loss pattern in both bamboo species. On

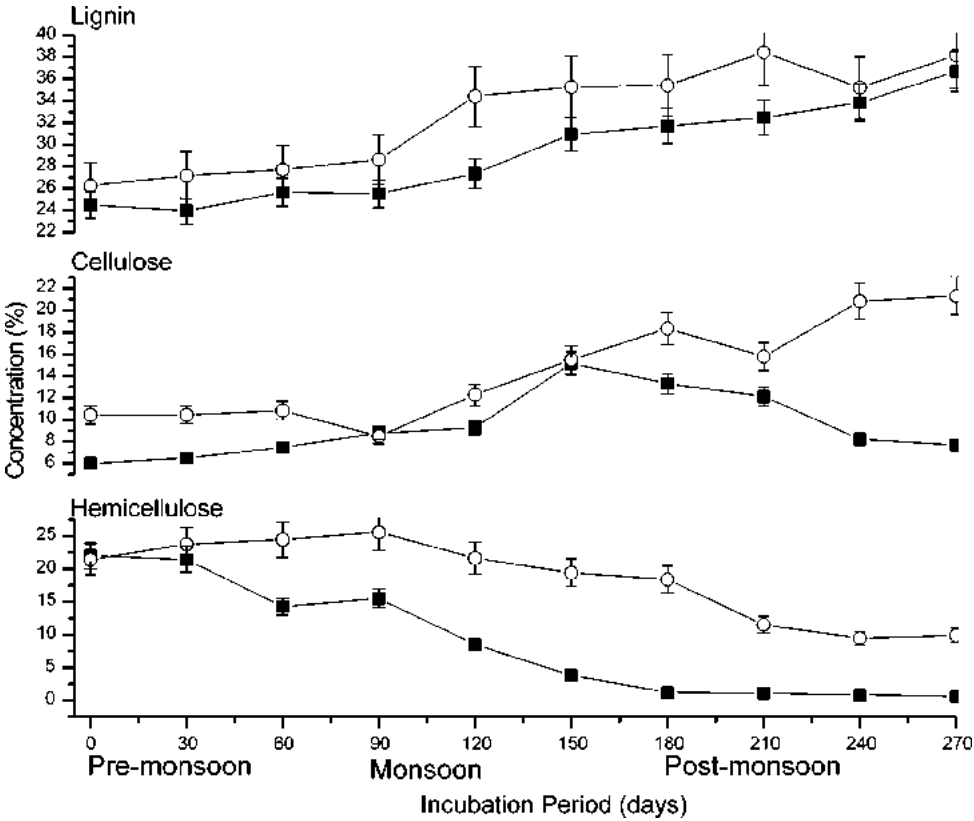

Figure 6. Concentrations (%) of major cell-wall compounds during bamboo leaf decomposition. (■) *B. tulda*, (○) *D. hamiltonii*.

the other hand, the litter chemistry of *B. tulda* showed more a significant relation with the weight loss pattern than that of *D. hamiltonii* (Table 7).

DISCUSSION

Soil properties

Soil moisture content was greater under the *B. tulda* canopy, whereas *D. hamiltonii*, having lower moisture content which might be due to the covered surface area on the ground by the species as it is, had a greater leaf area than the *B. tulda* plant. Between the two studied bamboo species, total N in the soil was greater under the canopy of *B. tulda* than the *D. hamiltonii*. This could be attributed to the type and quality of plant residues and also the composition of decomposer population as well as the decay rate [19]. Microbial C (338–432 μg/g) values were well within those reported by Vance *et al*. [20] for various terrestrial ecosystems (61–1900 μg/g). The soil under both the bamboo species had microbial C/microbial N ratios between 22

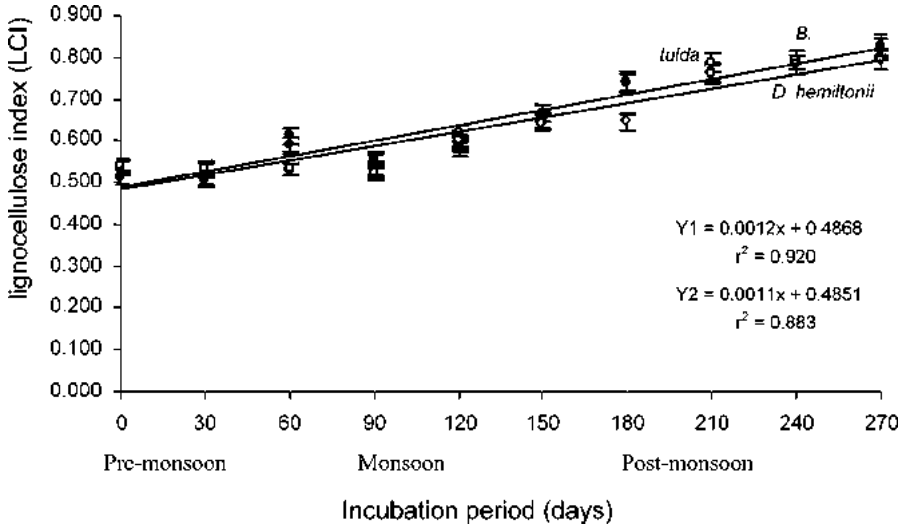

Figure 7. Changes in lignocellulose index (LCI) during leaf litter decomposition of *B. tulda* (Y1) and *D. hamiltonii* (Y2).

Table 7.
Leaf litter decomposition rate (% weight loss) as influenced by climatic variables and initial leaf chemistry

Litter quality	Regression equation		r		F ratio	
	I	II	I	II	I	II
Weight loss *vs*. climatic variables						
Rainfall	$9.09x - 174.35$	$0.05x + 36.25$	0.413	0.368	9.242	9.441
Air temperature	$5.31x - 76.28$	$4.59x - 61.17$	0.481^{*}	0.428	6.228	5.470
Soil temperature	$0.06x + 36.51$	$7.67x - 141.44$	0.493^{*}	0.433	6.037	5.283
Humidity	$-1.74x + 171.32$	$-1.83x + 174.72$	-0.679^{***}	-0.730^{***}	0.920	1.466
Weigth loss *vs*. litter chemistry						
Carbon	$24.18 + 0.04x$	$19.40 + 0.184x$	0.597^{***}	0.480^{*}	5.541	11.17
Nitrogen	$1.46 - 0.0004x$	$-2.04 + 0.128x$	-0.554^{**}	0.258	43.68	52.00
Phosphorous	$0.011 + 0.0001x$	$-3.16 + 0.132x$	0.074	0.264	45.18	54.11
Lignin	$34.22 - 0.11x$	$36.27 - 0.030x$	-0.926^{***}	-0.083	5.55	5.49
Cellulose	$9.57 + 0.14x$	$9.53 + 0.24x$	0.907^{***}	0.541^{**}	18.84	19.75
Hemicellulose	$71+0.09x$	$15.51 + 0.24x$	0.762^{***}	0.584^{***}	3.64	12.13

I, *Bambusa tulda*; II, *Dendrocalamus hamiltonii* (df = 29). $^{*}P < 0.005$; $^{**}P < 0.0005$; $^{***}P < 0.001$.

and 32, which indicates the increased availability of N in the soil. Nonetheless, the microbial biomass in the bamboo soil was dormant, because of the very small microbial C/N ratio (2.13–2.79) [21]. However, microbial P values (4–5 μg/g) were low as compared to the values reported by Brookes *et al.* (1984) for grassland and woodland (12–67 μg/g).

Residue quality

Initial N and lignin concentrations of leaf litter of the two bamboo species are well within the range (0.36–3.90 and 4.5–46.45%, respectively) reported for various tropical tree species [22, 23]. However, *D. hamiltonii*, having more sclerophyllous tissue, had high lignin and low nutrient concentration than *B. tulda*. The cellulose concentration in both the bamboo species was within the range (21.30–31.70%) reported by Bloomfield *et al.* [24] for several tropical tree species. The species can't be considered as good residue as both of them had greater initial C/N ($4 > 25$) ratio (Table 3). In this context, Myers *et al.* [25] reported that the substrates with C/N < 25 are of high quality and release mineral N at a faster rate compared to low quality residues (C/N > 25). The initial P concentration was more in *D. hamiltonii* than in *B. tulda* leaf litter, which indicated that *Dendrocalamus* species might be a better P source than the *Bambusa tulda* leaf litter.

Decay pattern

Decomposition pattern of bamboo was characterized by three distinct phases of weight loss in agroforestry systems. The initial slow rate of decay until 90 days (0.29% weight loss/day) could be attributed to the time lag in colonization and establishment of microbes on the litter mass [26]. The next rapid phase of weight loss (0.65% weight loss/day) may be ascribed to the utilization of readily available energy sources by microbes and loss of water-soluble components and non-structural carbohydrates from the litter [24]. A marked reduction in the decay rate during the third phase (0.09% weight loss/day) might be related to the relatively higher percentage of recalcitrant fractions (lignin) in the decaying leaf tissues (Table 3). These materials are known to control decomposition rate through their own resistance to enzymatic attack and by physically interfering with the decay of other chemical fractions of the cell wall [25].

Within the three-phased decay pattern, seasonal fluctuations were observed (Table 4). A relatively greater rate (54–63% of total weight) of weight loss during the rainy season (90–180 days) could be due to the effect of physical determinants such as temperature and soil moisture content [27–29], and a relatively slow rate (3–12% of initial weight) during the post-rainy season (180–270 days) could be attributed low soil moisture and reduced microbial activity [30]. Similar reports of bamboo decomposition from China [28] and Western Ghats of India [26] have been published. Dickinson and Pugh [31] also mentioned that the decomposition depends upon the fragmentation due to physical forces in the environment in case of microphytes. The amount of rainfall (Fig. 2) being the lowest during the pre-monsoon months (106 mm) compared with the succeeding monsoon period (593 mm), may partly explain why the decay rate during the first 3 months was lower than the decay rate between months 4 and 6 of incubation (Table 4). With the onset of monsoon showers in June, there was a sudden uplift in the decaying process and consequent mass loss (Fig. 3).

The decay rate (k) from different time segments during the study period (0–90, 90–180, 180–270 days) differed due to temporal variation in the decomposition pattern of various litter components [32]. The half-life, or t_{50}, and t_{99} values obtained in *B. tulda* were 0.20 and 1.42 year, respectively, which was comparable to those in *D. hamiltonii* (0.21 and 1.50). Singh *et al.* [33] observed a long half-life period for *Shorea robusta* (8 fortnights) and *Tectona grandis* (14 fortnights). The rate of decomposition of *B. tulda* and *D. hamiltonii* was lower than that of bamboos growing in the Western Ghats [29] and in China [28], whereas it was higher than two other species (*B. balcooa* and *B. pallida*) growing in the same climatic zone in this part of the country (Table 6).

Though rainfall is key to litter decomposition, during the last part of decomposition stages, residue quality of the litter samples played a major role in bamboo litter decomposition. For instance, the slow release of nutrients in *D. hamiltonii* during 180–270 days of incubation may be attributed to higher percentage of recalcitrant fractions like hemicellulose and lignin than the *B. tulda*. These substances are resistant to enzymatic attack and physical interfere with the degradation of other chemical fractions of the cell wall [24]. During the post-rainy season the less mass loss in both the bamboo species may also be due to the low moisture level and reduced microbial activity in the soil [30]. In our study, humidity and temperature also showed significant correlation with weight loss in both the bamboo species.

Nutrient dynamics

The rate of decrease in the N and C concentrations in the initial stage (0–60 days) of both the bamboo species were mainly due to the loss of soluble and easily decomposable compounds, through either leaching (or) assimilation and catabolism by decomposer population [34]. During monsoon, the N concentration in the decomposing leaf litter increased due to intense immobilization activity of microbes, including the N_2-fixing ones, under the most favourable climatic conditions coupled with the rapid decomposition of organic matter compared with the release of nitrogen.

In general, N and C mineralization was higher in *B. tulda* and *D. hamiltonii* after 180 days of incubation. In the initial stages of decomposition (0–90 days), P release in decomposing litter was more in *D. hamiltonii* than *B. tulda* which might be due to more initial P content of the litter (Table 4). Shorter or longer P immobilization periods have also been reported by Gosz *et al.* [35] and Prescott *et al.* [36] for a variety of litter samples. The P mineralization constant (k_p) was maximum during 180–270 days, with its greater value for *B. tulda* plant litter. A slower rate of N mineralization in *D. hamiltonii* indicates the development of nutrient conservation mechanism of the species. N and P release was influenced by the seasonal cycle of immobilization and mineralization. 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 content was also high.

The C/N ratio was greater during the pre-monsoon and lignin/N during the post-monsoon (Table 3). It shows that first phase of decomposition and nutrient release was controlled by the C/N ratio, whereas the last phase was lignin-controlled. Kunhamu [37] also stated that the slow phase of decomposition is lignin-controlled, while the initial rapid mass-loss phase is controlled by N present in soluble compounds. Thus, elemental concentration played great role in bamboo litter decomposition and nutrient mineralization.

Increase in N during the pre-monsoon and monsoon period in the decomposing bamboo leaf litter may be attributed to microbial immobilization [35]. The short-term immobilization and final release observed in this study is in agreement with the report of Jamaludheen and Kumar [35]. A similar release pattern of P was also observed by Bockheim and Jepsen [39] in northwestern Wisconsin and by Bahuguna *et al.* [40] in *Shorea robusta* and *Eucalyptus camaldulensis* leaves in India. Overall, N, C and P release during decomposition was influenced by the seasonal cycle of nutrient immobilization and mineralization processes.

Cell-wall degradation

Lignin in leaf litter is a major factor controlling organic matter decomposition rates. For example, Meentemeyer [41] reported that lignin concentration in plant material is inversely related to its decomposition rate. The high lignin content in the sclerophyllous *Bambusa tulda* and *Dendrocalamus hamiltonii* leaf litter (24 and 25.25%) could be responsible for the slow decomposition rates in the leaf litter. However, as decomposition proceeded, the lignin concentration increased in both the species due to accumulation of recalcitrant lignin is decomposed at a slower rate and thereby dominates the later stages of the decomposition process [42]. The lignin/N ratio showed an increasing trend with incubation time. A negative linear relationship ($r = -0.926$; $P = 0.0001$) between lignin concentration and rate of mass loss has been observed in *B. tulda*. Aber *et al.* [43] reported that the lignin/N ratio exerts a strong influence on organic matter decomposition rates, because N reacts with lignin and forms recalcitrant products that are highly resistant to degradation. Besides lignin some other non-hydrolysable products (e.g., silica) may also accumulate during the course of decay in bamboo species that would affect decomposition *per se*. On the contrary, cellulose and other structural polysaccharides are easily attacked by the microbes after the soluble fraction have been depleted [10]. Evidently, cellulose concentration decreased as the decomposition proceeded in bamboo leaf litter (Fig. 6). Nonetheless, the cellulose concentration of both the bamboo leaf litters was within the values (21.3–31.7%) reported by Bloomfield *et al.* [24] for several tropical tree species. Although hemicellulose is a glucose compound, it takes time to decompose, as it is highly cross-linked with lignin, creating a complex web of bonds which allows slower degradation of cell-wall compounds.

The lignocellulose index (LCI) has also been suggested to be a good measure of the resistance of decaying litter to microbial activity [18], because it describes the fraction of lignin in the lignocellulose components in the residue litter. As decomposition proceeds it is expected that LCI of both the species increased due to increase in the proportion of lignin in lignocellulose. Thus, the lignocellulose index showed a significant positive correlation (Fig. 7) with the litter incubation period in both bamboo species.

CONCLUSIONS

Overall, both *B. tulda* and *D. hamiltonii* leaf litter decomposed slowly, but showed a three-phase decay pattern. Weight loss of bamboo leaves during pre-monsoon and monsoon periods was highly influenced by amount of rainfall, humidity and initial N concentration of the leaf litter, whereas the last phase of decomposition was controlled by lignin content. Amongst the chemical substances, the C/N ratio, lignin and lignocellulose index played a greater role in bamboo litter decay. The nutrient release in both the bamboo species was regulated by the carbon to elemental ratios as it varied during the different period of decomposition. A linear relationship existed between litter mass and nutrient remaining. The leaf litter analysis during the period of decomposition showed that, although the nutrient and cell-wall components of leaf litter were comparable in both the bamboo species, the litter quality of *B. tulda* seems to be comparatively better than that of *D. hamiltonii*. Thus, a marginal difference in decay constant was observed between these two species.

So, addition of bamboo litter can be used in soil nutrient management of the agroforestry systems. It is also recommended that studies on 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 plant regeneration and/or species replacement during secondary succession. Moreover, this would help in developing useful eco-scientific package for managing traditional agroforestry systems.

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