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Mixed leaf litter decomposition and N, P release with a focus on *Phyllostachys edulis* (Carrière) J. Houz. forest in subtropical southeastern China

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Abstract

As an important non-wood forest product and wood substitute, Moso bamboo grows extremely rapidly and hence acquires large quantities of nutrients from the soil. With regard to litter decomposition, N and P release in Moso bamboo forests is undoubtedly important; however, to date, no comprehensive analysis has been conducted. Here, we chose two dominant species (i.e., *Cunninghamia lanceolata* and *Phoebe bournei*), in addition to Moso bamboo, which are widely distributed in subtropical southeastern China, and created five leaf litter mixtures (PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50) to investigate species effects on leaf litter decomposition and nutrient release (N and P) via the litterbag method. Over a one-year incubation experiment, mass loss varied significantly with litter type ($P < 0.05$). The litter mixtures containing the higher proportions (≥80%) of Moso bamboo decomposed faster; the remaining litter compositions followed Olson's decay mode well ($R^2 > 0.94$, $P < 0.001$). N and P had different patterns of release; overall, N showed great temporal variation, while P was released from the litter continually. The mixture of Moso bamboo and Phoebe bournei (PE80PB20 and PE50PB50) showed significantly faster P release compared to the other three types, but there was no significant difference in N release. Litter decomposition and P release were related to initial litter C/N ratio, C/P ratio, and/or C content, while no significant relationship between N release and initial stoichiometric ratios was found. The Moso bamboo–*Phoebe bournei* (i.e., bamboo–broadleaved) mixture appeared to be the best choice for nutrient return and thus productivity and maintenance of Moso bamboo in this region.

Keywords: litterbag; litter decomposition; litter mixture; mixed mode; Moso bamboo; nutrient return; N release; P release

Introduction

Leaf litter decomposition plays an important role in nutrient cycling and productivity in terrestrial ecosystems [1,2]. It can improve soil fertility through the release of litter nutrients and the maintenance of soil organic matter. According to the study by Wardle et al. [3], the decline of old-growth forest is often associated with reductions in litter decomposition rates and P release from litter. A better understanding of leaf litter decomposition rate and nutrient release is undoubtedly important for forest management as well as regional carbon budgets [4,5].

Generally, leaf litter decomposition rates are affected by climate, litter quality (i.e., plant species traits) and the composition of the decomposer community [4,6–8]. Among the multiple drivers, differences in species traits are the predominant direct regulator of litter decomposition rates [9,10]. For example, deciduous tree leaves decompose more rapidly than evergreen tree leaves because deciduous tree leaves have higher nutrient concentrations and lower lignin concentrations [11,12]. Similarly, the decomposition rates of herbaceous litter were higher than that of tree litter due to higher nutrient concentrations in the herbaceous litter [13]. Litter decomposition is thus commonly correlated with the C/N ratio in litters [9,14,15]. Consequently, C/N or lignin/N rates are often used as an index of quality or decomposability of litter (e.g., see [5]).

Previous studies have also noted that litter decomposition of a single species does not sufficiently represent natural litter decomposition processes [16] because there is a different decomposition pattern when leaves of that species decay alone compared to when they decay mixed with other species' leaves [17].

Phyllostachys edulis (Carrière) J. Houz., also called Moso bamboo, is a non-wood forest product and wood substitute; it plays an increasingly important role in socioeconomic development. It is one of the fastest growing plant species in the world, with growth rates ranging from 30 to 100 cm

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per day during the growing season [18]. The extremely high growth rate of this species requires rich nutrients availability in the soil. Therefore, an exploration of the pattern of decomposing litter and nutrient release is inevitably needed. To our knowledge, decomposition experiments on Moso bamboo have only been conducted in pure stands (see e.g., [19]); no comprehensive research has been conducted to examine leaf litter decomposition and nutrient release of Moso bamboo in mixed stands. Clarifying the mass loss and nutrient release of mixed leaf litter decomposition with a focus on Moso bamboo can provide a theoretical basis for the improvement of bamboo forest productivity by guiding appropriate choices of associated species.

In this study, we chose two associated species, *Cunninghamia lanceolata* and *Phoebe bournei*, together with *Phyllostachys edulis*, all of which are widely distributed in subtropical southeastern China. We applied five leaf litter combinations to investigate the effect of plant species on leaf litter decomposition and N and P release in Moso bamboo stands so as to optimize the available nutrient supply for the fast growing Moso bamboo via litter nutrient return. Specifically, we intended to examine (***i***) the changes in leaf litter mass loss of the five mixtures, (***ii***) the releasing pattern of N and P, and (***iii***) the relationship between mass loss, N or P release and leaf litter quality.

Material and methods

Site description

This study was conducted in a state-owned forestry station located in Shunchang County in the northern part of Fujian Province in southeastern China (117°30′ E – 118°14′ E, 26°39′ N – 27°12′ N). This area lies in a subtropical monsoon climate. According to the temperature and precipitation microloggers (Onset HOBO U23-001 and RG3-M; Massachusetts, US) installed in 2007 nearby the studying site, the annual mean temperature is 18.7°C with a maximum and minimum temperature of 40.3°C and –6.8°C, respectively, and its annual precipitation is about 1568 mm. The soil is a mountain red soil with a thick soil surface and is classified as Typic Hapludults belonging to Udults suborder of Ultisol order according to the USDA soil taxonomy [20]; soil pH is estimated between 4.36 and 4.81 using potassium chloride (KCl) method [21]. In the top soil layer (i.e., a depth of 0–20 cm), soil organic matter determined using potassium dichromate ($K_2Cr_2O_7$) with external heat and back-titration, and bulk density are 34.30 g/kg and 1.04 g/cm^3, and total nitrogen, total phosphorus and total potassium are 0.81 g/kg, 0.13 g/kg and 16.42 g/kg, respectively. The canopy layers of the forests are dominated by *Phyllostachys edulis*, *Cunninghamia lanceolata*, *Phoebe bournei* and their mixed plant species.

Experimental design

Mass loss and N and P release were observed via the litterbag method [22]. The litterbag's length and width were both 20 cm, with a mesh size of 5 mm.

In this paper, we chose two associated species (i.e., a coniferous species, *Cunninghamia lanceolata* and a broadleaved species, *Phoebe bournei*) that are widely distributed in subtropical southeastern China, together with *Phyllostachys edulis*. We designed five litter combinations (or mixtures) with different proportions of Moso bamboo (i.e., PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50 in Tab. 1) and assessed leaf litter decomposition in this region. The five leaf litter combinations were composed of differing proportions, based on mass, of three species. Freshly senesced leaves of the three species (i.e., Moso bamboo, *Phoebe bournei* and *Cunninghamia lanceolata*) were collected randomly from respective pure stands; the entire leaves were not disrupted and directly used for the decomposition experiment. The mixture proportions were defined according to the relative biomass of leaf litter found in numerous stands in the region. Notably, initial litter chemistry of *Phoebe bournei* and *Cunninghamia lanceolata* were also listed (CL100 and PB100 in Tab. 2) and addressed in "Results" section for the convenience of descriptions and comparisons of leaf litter quality with those of Moso bamboo; however, mass loss and nutrient release of the two single-species litter were not observed and thus not reported in the present paper.

Tab. 1 Denoted leaf litter mixtures and their mass proportions.

Litter mixture	Mass proportion
PE100	100% Moso bamboo
CL100	100% *Cunninghamia lanceolata*
PB100	100% *Phoebe bournei*
PE80PB20	80% Moso bamboo and 20% of *Phoebe bournei*
PE80CL20	80% Moso bamboo and 20% of *Cunninghamia lanceolata*
PE50PB50	50% Moso bamboo and 50% of *Phoebe bournei*
PE50CL50	50% Moso bamboo and 50% of *Cunninghamia lanceolata*

Note: the five litter mixtures used for the incubation experiment were denoted as PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50, respectively. For convenience of descriptions and comparisons of leaf litter quality, single species litters of *Cunninghamia lanceolata* and *Phoebe bournei* were denoted with CL100 and PB100, respectively, and also listed in this table.

For each litter mixture, 24 litterbags were placed between O and A horizons in the upper, middle and lower slopes of pure Moso bamboo forests (for more detailed basic characteristics of incubation forests, please see Tab. S1) resulting in a total of 72 litterbags per litter mixture. In total, 360 litterbags were used (i.e., 5 types × 24 replications × 3 slopes) (Fig. 1). The initial weight of each litterbag was 20.00 g.

Sampling and laboratory analysis

Two litterbags from each slope (i.e., a total of six litterbags from the three slopes) for each litter mixture were taken to laboratory on the first three days of each month in the study period. We removed excess debris by hand or flushing, and then the leaf litter was dried at 80°C until it reached a constant weight. The organic carbon (C) concentration of

Tab. 2 Initial litter chemistry of the dominant species and their mixtures in northern Fujian Province of subtropical southeastern China.

Litter mixture	C (g/kg)	TN (g/kg)	TP (g/kg)	Ca (g/kg)	Mg (g/kg)	C/N	C/P	N/P
PE100	159.61 a	6.36 a	0.44 a	5.77 a	4.25 a	25.10 a	365.59 a	14.56 af
CL100	548.57 b	5.00 b	0.24 b	5.19 a	1.46 b	109.78 b	2332.33 b	21.24 b
PB100	530.00 c	10.54 c	1.09 c	2.45 b	1.90 b	50.29 c	486.26 c	9.669 c
PE80PB20	233.69 d	7.19 d	0.57 d	5.11 a	3.78 c	32.48 d	411.96 a	12.68 a
PE80CL20	237.40 d	6.09 ae	0.40 a	5.65 a	3.69 c	39.01 e	599.03 d	15.36 f
PE50PB50	344.80 e	8.45 f	0.76 e	4.11 c	3.07 d	40.81 e	451.75 ac	11.07 d
PE50CL50	354.09 e	5.68 e	0.34 f	5.48 a	2.85 d	62.37 f	1054.17 e	16.90 e

Note: PE100, PE80PB20, PE80CL20, PE50PB50, PE50CL50, CL100 and PB100 denote the same leaf litter mixtures as addressed in Tab. 1. The dissimilar letters indicate significant differences among the litter mixture at the 0.05 level. A log-transformation is performed when the equal variance was not satisfied.

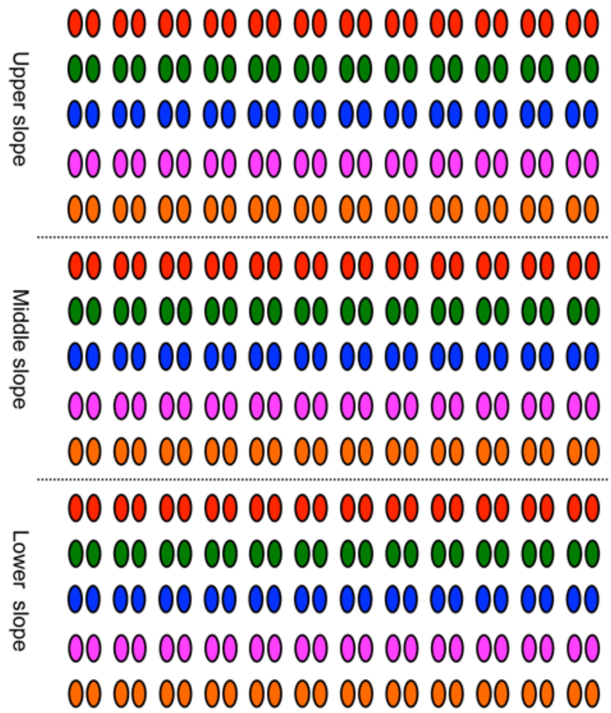

Fig. 1 Sketch map showing incubation litterbags placed in the upper, middle and lower slopes. Each ellipse in red, green, bule, pink and orange denotes litterbag of PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50. The symbols of PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50 represent the same leaf litter mixtures as addressed in Tab. 1.

soil and litter mixture was both measured by wet combustion with $K_2Cr_2O_7$ [23]. Total N and P concentration were measured by the Kjeldahl method [24] and the ascorbic acid method [25], respectively. The atomic absorption was used for both Ca and Mg (atomic absorption spectrophotometer 170-30S; Hitachi, Tokyo, Japan) after an acid wet oxidation in $HNO_3 + HClO_4$ [26].

Statistical analysis

Mass loss was calculated by the changes in mass remaining (*MR*, %) at monthly intervals:

$$MR(\%) = \frac{M_t}{M_0} \times 100\% \quad (1)$$

where *MR* is the percentage remaining (%), M_0 is the initial oven-dry mass (kg), and M_t is the oven-dry mass (kg) at month t ($t = 1, 2, 3, \ldots, 12$).

Generally, litter decomposition can be characterized by the Olson's decay mode [27]:

$$y = ae^{-kt} \quad (2)$$

where y is litter mass (kg) at time t ($t = 1, 2, 3, \ldots, 12$), and k is the decomposition rate coefficient.

The nutrients remaining (*NR*) were calculated by the change of nutrient content during litter decomposition:

$$NR(\%) = \frac{N_t M_t}{N_0 M_0} \times 100\% \quad (3)$$

where *NR* is the percentage of remaining nutrients (%), M_0 is the initial oven-dry mass (kg), N_0 is the initial nutrient concentration (g/kg), M_t is the oven-dry mass (kg) at time t, and N_t is the nutrient concentration at time t ($t = 1, 2, 3, \ldots, 12$).

One-way analysis of variance (ANOVA) was used to test the differences in initial litter chemical characteristics among leaf litter mixtures; this was followed by Tukey's honestly significant difference test when ANOVA yielded a significant result. When the statistical assumption of equal variances among groups of datasets was not satisfied, a log-transformation was performed before comparative analysis. Bivariate correlations were performed to examine the relationships between mass loss, N or P remaining and initial litter characteristics. All statistical analyses were performed using the statistical software package SPSS 13.0 for Windows [28]. The level of significance for statistical tests is $\alpha = 0.05$.

Results

Initial litter chemistry

Initial litter chemistry varied dramatically among leaf litter types ($P < 0.001$; Tab. 2). Regarding single-species litter, the litter C concentration of *Cunninghamia lanceolata* (CL100) was the largest (548.57 g/kg), followed by *Phoebe bournei* (PB100) and Moso bamboo (PE100), while total N and P concentrations were both highest in *Phoebe bournei*, followed by Moso bamboo and *Cunninghamia lanceolata*. Thus, *Cunninghamia lanceolata* had significantly higher C/N, C/P, and N/P ratios than the other single species' litters. In contrast, Moso bamboo had the lowest aforementioned ratios among the single leaf litters. However, Moso bamboo and *Cunninghamia lanceolata* had higher Ca concentrations than *Phoebe bournei*. In addition, Moso bamboo had the highest Mg concentration of all the types. The initial litter chemistry of the mixed leaf litter types (PE80PB20, PE80CL20, PE50PB50 and PE50CL50) were all within the range of the corresponding single species.

Changes in mass loss of different litter mixtures

Following Equation (1), we calculated the remaining litter mass in each month for PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50 (Fig. 2). In the first three months, no significant differences in mass loss were found among the five litter mixtures; however, mass loss varied significantly with litter mixtures ($P < 0.05$) from the fourth month to the end of the incubation experiment. Over the entire incubation year, there was a significant difference in mass loss among the leaf litter mixtures ($P < 0.05$). In general, litter combinations containing larger proportions (≥80%) of Moso bamboo litter (i.e., PE100, PE80PB20 and PE80CL20) decomposed faster than those with 50% (i.e., small proportions) of Moso bamboo litter.

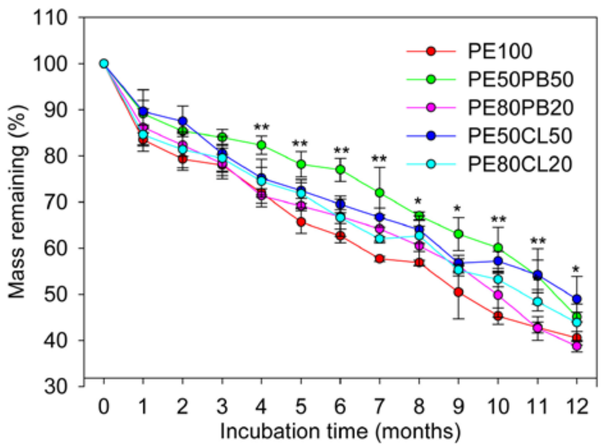

Fig. 2 Litter mass loss in Moso bamboo monocultures and its mixtures with *Cunninghamia lanceolata*, and with *Phoebe bournei*, respectively, during a 12-month period of incubation. Error bar represents standard deviation ($n = 6$). "**" and "*" indicate significant differences among the litter mixtures at the 0.01 and 0.05 levels, respectively, and the more detailed result of analysis of variance is presented in supplementary Tab. S2. PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50 denote the same leaf litter mixtures as described in Tab. 1.

Regardless of leaf litter mixture, the overall remaining mass percentages all decreased significantly, and showed negative exponential relationships with month, following the Olson's decay model well ($R^2 > 0.94$, $P < 0.001$; Tab. 3). Despite the variation in mass loss of PE50PB50, its decomposition coefficient was the same as PE50CL50's. After the end of the 12 months, the remaining mass of the litter mixtures were all less than or equal to 50%, except PE50CL50. The smaller decomposition coefficients of PE50PB50 and PE50CL50 suggested that they would require a longer time to fully decompose the leaf litter than the other three litter mixtures (i.e., nealy 7 years vs. 6 years at most).

Nutrient release

One-way ANOVA indicated that N and P had different release pattern across leaf litter mixtures (Fig. 3; $P < 0.001$), with mean remaining N and P percentages of 34.42%, and 51.79%, respectively.

Overall, N loss from litter showed great temporal variation during the one-year incubation (Fig. 3a). In almost all of the leaf litter samples, N released quickly in the first two months, then accumulated until the sixth month, and finally declined again, showing a loss–gain–re-loss decomposition pattern. PE80PB20 and PE80CL20 had faster N release rates at several time points (e.g., over the two-month incubation) ($P < 0.05$). Over the 12 months, remaining N content was not significantly different among the five litter mixtures ($P = 0.166$).

In contrast, P was released from the litter continually and significantly (Fig. 3b). The litter combinations containing *Phoebe bournei* (PE80PB20 and PE50PB50) decomposed faster than both the pure Moso bamboo (PE100) and the mixture with *Cunninghamia lanceolata* (PE80CL20 and PE50CL50; $P < 0.01$).

Relationships between initial litter chemistry, mass loss, and nutrient release

The mass remaining was positively correlated with the initial litter C concentration, C/N and C/P ratios (Tab. 4). Similarly, the remaining P content was positively correlated with the C/N and C/P ratios but negatively correlated with the initial N and P concentrations. However, no significant correlation was found between N remaining and any leaf litter variables.

Discussion

The initial leaf litter chemistry of Moso bamboo, *Cunninghamia lanceolata* and *Phoebe bournei* reflect three different plant types, namely, giant grass, coniferous and broadleaved species. The coniferous species (i.e., *Cunninghamia lanceolata*) had higher C concentrations, but lower nutrient concentrations (e.g., N and P) and thus higher C/N and C/P ratios than broadleaved and giant grass species. Moso bamboo had the lowest C/N and C/P ratios among the three single species (Tab. 2). This is consistent with previous studies [11–13].

Mass loss exhibited a significant difference among the leaf litter mixtures over the whole incubation year ($P < 0.05$),

Tab. 3 Decomposition characteristics of mass loss for the five leaf litter combinations.

Litter mixture	Expression	Decomposition coefficient (K)	R^2	P	$t_{0.5}$ (yr)	$t_{0.99}$ (yr)
PE100	$y = 94.88exp(-0.071t)$	0.071	0.99	<0.001	0.75	5.34
PE80PB20	$y = 97.65exp(-0.069t)$	0.069	0.96	<0.001	0.81	5.53
PE80CL20	$y = 95.26exp(-0.061t)$	0.061	0.98	<0.001	0.88	6.22
PE50PB50	$y = 100.35exp(-0.055t)$	0.055	0.94	<0.001	1.05	6.98
PE50CL50	$y = 96.47exp(-0.055t)$	0.055	0.99	<0.001	1.00	6.92

Note: the symbols of the five litter mixtures (i.e., PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50) denote the same implications as described in Tab. 1.

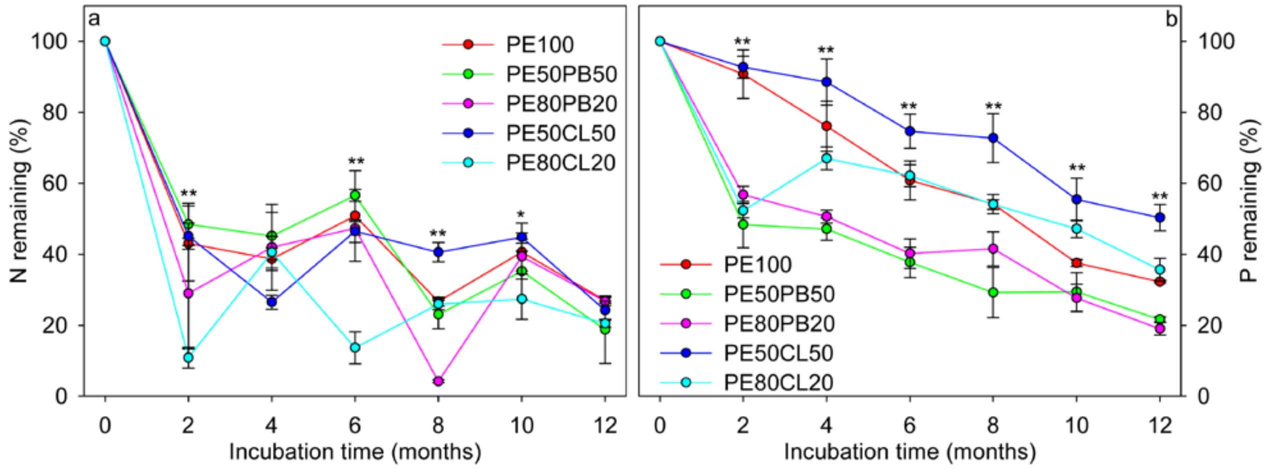

Fig. 3 Litter N (**a**) and P (**b**) content relative to initial nutrient values for the five leaf litter mixtures. Error bar represents standard deviation ($n = 6$). "**" and "*" indicate significant differences among the litter mixtures at the 0.01 and 0.05 levels, respectively, and the more detailed result of analysis of variance is presented in supplementary Tab. S3. PE100, PE80PB20, PE80CL20, PE50PB50 and PE50CL50 denote the same leaf litter mixtures as described in Tab. 1.

Tab. 4 Pearson relationships between initial leaf litter variables and mass loss, remaining N and P content, without considering the leaf litter mixtures, after one year of decomposition.

	C	N	P	C/N	C/P
Mass remaining	0.671	−0.260	−0.208	0.797	0.732
P value	0.006	NS	NS	<0.001	0.002
N remaining	−0.389	−0.364	−0.351	−0.124	−0.038
P value	NS	NS	NS	NS	NS
P remaining	0.262	−0.817	−0.810	0.798	0.895
P value	NS	<0.001	<0.001	<0.001	<0.001

Note: NS denotes "not significant" at 0.05 level.

suggesting that leaf quality (i.e., leaf litter mixture) can affect litter decomposition; the result is in consistence with the report by Sariyildiz and Anderson [29,30], but contradiction to the conclusion of Hilli et al. [31]. Moreover, litter combinations consisting of a large proportion of Moso bamboo decomposed faster (Fig. 2). The faster mass loss of Moso bamboo was most likely caused by the lower litter C: nutrient ratio (Tab. 4). Our results are in accordance with the conclusions that differences in litter decomposition are related to leaf litter quality and varying C/N ratios, C/P ratios and C content (e.g., see [14,32,33]). As addressed by Reich et al. [34] and Hobbie et al. [35], litter calcium concentrations among tree species had a profound effect on soil pH and native earthworm abundance and diversity, and were also key factors in determining species effects on forest floor leaf litter dynamics. From the fourth to the ninth months of the decomposition process, PE50PB50 exhibited lower Ca concentrations (Tab. 2), which may account for the fact that PE50PB50 demonstrated a larger remaining mass percentage than the other four litter mixtures (Fig. 2).

Regardless of leaf litter combination, the leaf litter decomposition followed Olson's decay model (Tab. 3; $R^2 \geq 0.94$, $P < 0.001$), but the coefficient K varied with mixed leaf litter, which is consistent with a previous study [10]; the litter mixtures containing a smaller percentage of Moso bamboo had the smaller decomposition coefficients (PE50PB50 and PE50CL50 vs. other mixtures), suggesting that mixed forest is seemingly an effective method to reduce the rate of carbon emission in comparison with pure Moso bamboo forest. Compared to the values in the study by Zhou et al. [4], the decomposition coefficients of the five litter mixtures in the present paper were small.

N and P demonstrated different release pattern across mixed leaf litters (Fig. 3; $P < 0.001$), and the remaining mean P percentage (51.79%) after one year of decomposition was larger than the remaining N (34.42%), suggesting that P release from leaf litter was slower in the decomposition experiment.

In comparison, N loss from the litters showed high temporal variation (Fig. 3a); N released quickly in the first two months, then accumulated until the sixth month, and finally declined again. However, we found no significant relationships between N remaining and C, N and P concentrations and their stoichiometric ratios. Many studies also suggested that release pattern of N from litter varied highly with litter mixture; for instance, some species showed an increased N loss (see, e.g., [36]), some gained N during the early stages [37] and others showed a multi-staged or complex releasing pattern [38]. Moreover, abundant N deposition has been observed recently in this region [39–41], which may be another reason why N release in this paper showed high variation. Although N release has been commonly correlated to N immobilization [42], stoichiometric litter quality [43,44], and so forth, a full understanding of N release and its mechanism still require more research in the future, especially given the background of increased N deposition occurred in recent years through human activities.

In contrast with the N dynamics, the P contents of all litter mixtures were lower than the initial values during decomposition (Fig. 3b). As noted by previous studies, P loss is often caused by leaching [43,45,46]. In our paper, we found that the intensity of P release was also related to the initial litter C/P and/or C/N ratios. For example, the litter combinations containing *Phoebe bournei* (PE80PB20 and PE50PB50), with a higher C/P ratio, was observed to release more P than the pure Moso bamboo (PE100) or the mixture with a high proportion of *Cunninghamia lanceolata* ($P < 0.01$), suggesting stoichiometric controls of P dynamics [44,47].

Although the leaf litter composed of pure Moso bamboo (i.e., PE100) had the fastest mass loss (Fig. 2), the mixture of Moso bamboo and *Phoebe bournei* exhibited larger nutrient release rates of both N and P release (Fig. 3), suggesting that the Moso bamboo–*Phoebe bournei* (i.e., bamboo–broad-leaved) mixed mode was most likely the optimal species combination in terms of nutrient return from leaf litter to soil. The greater productivity of mixed-species forests has been attributed in part to greater nutrient availability resulting from enhancement of decomposition rates [48]. According to a report by Waring and Schlesinger [49], 69–87% of the annual nutritional requirements of plants come from nutrients mineralized from decomposing litter. The results of the present paper provide a theoretical basis for the choice of appropriate species or mixed mode with a goal of maintaining the productivity of rapidly growing Moso bamboo. Thus appropriate species selection and mixed mode are both extremely important while planting trees. Additionally, cultivators can perhaps improve soil by burying mixed leaf litters from local plant species; the approach can both save cost and prevent fertilizer abuse.

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Authors' contributions

The following declarations about authors' contributions to the research have been made: field survey: LS, LQ, GL; experimental design: LS, SF, ZJ, LQ, GL; laboratory analysis: LS, LQ, GL; data analysis: LS, SF, ZJ, LQ, GL; writing of the manuscript: LS, SF, ZJ, LQ, GL; drawing of the figures: LS, LQ, GL.

Competing interests

No competing interests have been declared.

Supplementary material

The following supplementary material for this article is available online at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.2015.019/0:

1. Tab. S1: characteristics of pure Moso bamboo forests used for incubating leaf litter.
2. Tab. S2: one-way analysis of variance for monthly litter mass remaining among the five litter mixtures during one-year incubation experiment.
3. Tab. S3: one-way analysis of variance for bimonthly remaining nitrogen (N) and phosphorus (P) contents among five litter mixtures during one-year incubation experiment.

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