Soil Biology & Biochemistry 70 (2014) 211–220

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Slower rates of litter decomposition of dominant epiphytes in the canopy than on the forest floor in a subtropical montane forest, southwest China

Su Li [a,b], Wen-Yao Liu [a,*], Da-Wen Li [c], Ze-Xi Li [a,b], Liang Song [a], Ke Chen [a,b], Yun Fu [d]

[a] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, Yunnan 650223, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] National Forest Ecosystem Research Station at Ailao Mountains, Jingdong, Yunnan 676209, China
[d] Biogeochemistry Laboratory, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, Yunnan 650223, China

ARTICLE INFO

Article history:
Received 31 July 2013
Received in revised form
25 December 2013
Accepted 29 December 2013
Available online 7 January 2014

Keywords:
Bryophyte
Fern
Lichen
Litter decomposition
Nutrient release
Subtropical forest

ABSTRACT

Epiphytes constitute a substantial proportion of the canopy biomass in subtropical montane forests, and their decomposition has not been adequately addressed, especially in the canopy relative to the forest floor compartments. The rates of litter decomposition and nutrient release of five epiphytes (macrolichens *Everniastrum nepalense*, *Nephromopsis ornata* and *Usnea florida*, moss *Homaliodendron flabellatum*, and fern *Phymatopteris connexa*) and two tree species (*Castanopsis wattii* and *Lithocarpus xylocarpus*) were quantified over a two-year period using litterbags in the canopy and on the forest floor in an evergreen broad-leaved forest in the subtropical Ailao Mountains in southwest China. After two years, all litter in the canopy decayed 15–30% slower than on the forest floor, with 17–69% and 2–51% of initial masses remaining respectively. Nutrient concentration varied regularly as decay proceeded in the canopy while nutrient amount underwent regular variation on the forest floor. Decay rate and nutrient release differed significantly among functional groups and the order of decay rate was lichen > tree > fern > bryophyte. Lichens had the fastest decay rates, and the fruticose *U. florida* decayed faster than the other two foliose species. The rate of lichen decomposition was significantly correlated with morphology and initial N and P concentrations. The bryophyte species had the lowest decay rate, but with relatively rapid release of N and P, while the fern had high net N and P immobilization. K was rapidly released from litter. Ca and Mg eventually decreased with variable concentrations during decomposition. Our results highlight the potential importance of nonvascular epiphytes in increasing nutrient availability, especially N and P, in the canopy soil environment, and the probable role of epiphytic bryophytes and ferns in accumulating organic matter.

1. Introduction

Litter decomposition is a fundamental ecological process and provides a major source of nutrients for biological activities in terrestrial ecosystems (Swift et al., 1979). The decomposition of litter is closely related to environmental conditions, litter quality and decomposing organisms (Swift et al., 1979; Cornwell et al., 2008). In forest ecosystems, the majority of decomposition studies have focused on the forest floor. However, litter can remain attached to the canopy and litter decay can begin before reaching the ground (Fonte and Schowalter, 2004). In addition, canopy habitat has low nutrient sources compared with the forest floor (Clark et al., 1998; Hietz et al., 2002; Cardelús and Mack, 2010). Therefore, the decomposition of litter in the canopy is particularly important in subtropical and tropical forests, in which canopy epiphytes comprise a substantial proportion of the entire flora (Coxson and Nadkarni, 1995; Fonte and Schowalter, 2004; Watkins et al., 2007; Cardelús et al., 2009; Cardelús, 2010).

Although little is known about litter decomposition in the canopy, some aspects of decay are unique to this habitat. For example, litter can be removed from the canopy quickly by wind, rain and animal activities (Nadkarni and Matelson, 1991). The contribution of litter to canopy nutrient cycling is therefore not only closely linked with the length of litter retention in the canopy but also with the decomposition rate. If litter decay fast enough, this would potentially increase the total nutrient input to the canopy environment (Cardelús and Mack, 2010). Some studies in the tropics and temperate zone have demonstrated that the decay

* Corresponding author. Tel.: +86 871 65153787; fax: +86 871 65160916.
E-mail addresses: lis@xtbg.ac.cn (S. Li), liuwy@xtbg.ac.cn (W.-Y. Liu).

0038-0717/$ – see front matter Crown Copyright © 2014 Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.soilbio.2013.12.031

of tree and epiphytic bryophyte litter in the canopy is slower than on the forest floor (Clark et al., 1998; Lindo and Winchester, 2007; Cardelús, 2010). The slower decay in the canopy is in general largely due to unique environmental features of canopies, such as lower humidity (Cardelús and Chazdon, 2005), frequent and rapid drying events (Coxson and Nadkarni, 1995) and lower diversity of decomposers (Vance and Nadkarni, 1990; Lindo and Winchester, 2007; Rousk and Nadkarni, 2009). Nevertheless, the litter decomposition rates and nutrient release patterns of epiphytes in the canopy remain unclear, with no available data for epiphytes (especially ferns) of subtropical forests (Hsu et al., 2002; Xu and Liu, 2005; Wang et al., 2008; Chen et al., 2010; Li et al., 2011).

Epiphytes contribute 2–4% to the total biomass in forest ecosystems and often play a disproportionately important role in nutrient cycling (Coxson and Nadkarni, 1995; Liu et al., 2002; Antoine, 2004; Clark et al., 2005; Caldiz et al., 2007; Wang et al., 2008; Campbell et al., 2010; Tan et al., 2011). Litter decomposition of epiphytes provides an important source of nutrients for the forest ecosystems, e.g. 30–90% of the annual new N input comes from decomposing litter of cyanolichens and 5–14% from chlorolichens in N-limited forests (Pike, 1978; Knops et al., 1996; Antoine, 2004; Caldiz et al., 2007; Campbell et al., 2010). Therefore, an in-depth understanding of the decomposition of epiphytes will greatly contribute to understanding their ecosystem functions. To date, only a few studies have focused on epiphytic lichens in temperate and boreal forests (Esseen and Renhorn, 1998; Coxson and Curteanu, 2002; Holub and Lajtha, 2003; Caldiz et al., 2007; Campbell et al., 2010; Asplund et al., 2013; Asplund and Wardle, 2013), and no work has been done on the decomposition of epiphytes in subtropical forests. The available data indicate that epiphytic lichens decay rapidly and their decay is primarily influenced by initial chemical and morphological characteristics (Esseen and Renhorn, 1998; Caldiz et al., 2007; Campbell et al., 2010; Asplund and Wardle, 2013). Nonvascular epiphytes are also proved to decay faster than terrestrial nonvascular species (Moore, 1984; Clark et al., 1998; Lang et al., 2009; Campbell et al., 2010; Asplund et al., 2013; Asplund and Wardle, 2013).

In southwest China, montane moist evergreen broad-leaved forests in high altitude (2000–2600 m) are an important global vegetation type, characterized by high humidity and high epiphyte abundance (You, 1983; Wu and Zhu, 1987; Xu and Liu, 2005; Li et al., 2011). Epiphytes play a vital role in biodiversity conservation (Li et al., 2013), hydrological cycle (Liu et al., 2002) and nutrient transformation (Liu et al., 2000; Wang et al., 2008; Han et al., 2010) in subtropical forests. For example, studies in the Ailao Mountains show that more than 600 epiphytic species occur in this area (Li et al., 2013), and the total epiphytic mass is about 11.0 t ha^{-1} in the primary forests (Liu et al., 2002; Wang et al., 2008). However, information on epiphyte litter decomposition and nutrient release is limited.

To investigate the decomposition rates and nutrient release of epiphyte litter in subtropical forests, we compared the decay of five epiphytes and two trees in the canopy and on the forest floor in a primary forest in the Ailao National Nature Reserve (677 km^2), one of the largest tracts of natural evergreen broad-leaved forests in China (Li et al., 2013). Our main objectives were to characterize changes in decay rate and nutrient release of epiphyte litter (1) between canopy and forest floor habitats (2) among species in subtropical forests. Acting on knowledge of the differences between canopy and forest floor compartments (Vance and Nadkarni, 1990; Coxson and Nadkarni, 1995; Cardelús and Chazdon, 2005; Rousk and Nadkarni, 2009) and the variations in physical and chemical characteristics among litter types (Pike, 1978; Hietz et al., 1999; Dahlman et al., 2003; Cardelús and Mack, 2005, 2010), we hypothesized that (1) litter will decay more slowly in the canopy than on the forest floor and (2) epiphyte litter will decay faster than tree litter in both compartments.

2. Materials and methods

2.1. Site description

The study was conducted in the Xujiaba region (2000–2750 m a.s.l.; 23°35′–24°44′ N, 100°54′–101°30′ E), a core area of the Ailao National Nature Reserve, covering 5100 ha on the northern crest of the Ailao Mountains in Yunnan Province in southwest China (You, 1983). The mean annual rainfall is 1947 mm, with 85% falling in the rainy season (May–October). The mean annual relative air humidity is 85% and annual mean temperature is 11.3 °C (Li et al., 2011).

The montane moist evergreen broad-leaved primary forest accounts for nearly 80% of the total area in Xujiaba. The upper, almost-closed canopy is dominated by *Lithocarpus xylocarpus* (Kurz) Markgr., *Lithocarpus hancei* (Benth.) Rehder, *Castanopsis wattii* (King ex Hook. f.) A. Camus, *Schima noronhae* Reinw. ex Blume and *Stewartia pteropetiolata* Cheng. This forest supports abundant epiphytes, including seed plants (113 species), ferns (117), bryophytes (118) and lichens (178) (Xu and Liu, 2005; Ma et al., 2009a; Li et al., 2013), and the total epiphytic mass is 10.7 t ha^{-1}, composed of 3.94 t ha^{-1} of cryptogams, 2.01 t ha^{-1} of vascular epiphytes and 4.74 t ha^{-1} of dead organic matter (Wang et al., 2008). The nutrient status of canopy soil and floor soil has been reported previously by Wang et al. (2008) and Liu et al. (2010) (Table 1).

2.2. Experimental design

We conducted a habitat × species litter decay study between the canopy and forest floor compartments using three epiphytic groups (fern, moss, lichen) and two dominant host trees in order to determine epiphyte litter decomposition. We chose the fern *Phymatopteris connexa* (Ching) Pic. Serm., moss *Homaliodendron flabellatum* (Sm.) Fleisch., broadly-lobed foliose lichen *Nephromopsis ornata* (Müll. Arg.) Hue, narrowly-lobed foliose lichen *Everniastrum nepalense* (Taylor) Hale ex Sipman, fruticose lichen *Usnea florida* (L.) Weber ex F. H. Wigg. and leaves of *C. wattii* and *L. xylocarpus* for comparison using the litterbag technique.

Freshly fallen leaves of three vascular plants were collected in November–December 2007. Because the lichen and moss litterfall is generally living, moss and lichen materials were collected from the canopy and recent treefalls, as were the case in most previous studies (Caldiz et al., 2007; Campbell et al., 2010; Asplund et al., 2013). Other debris and materials were discarded. All collected materials were dried at 80 °C for 72 h to ensure they were dead and uniformly dry, and then left at room temperature for about 2 h

Table 1
Properties of canopy soil and floor soil in an evergreen broad-leaved forest in the Ailao Mountains, southwest China (Wang et al., 2008; Liu et al., 2010).

	Canopy soil	Floor soil
C (g kg^{-1})	560	136
N (g kg^{-1})	26.4	8.98
P (g kg^{-1})	1.22	1.27
K (g kg^{-1})	2.76	12.5
Ca (g kg^{-1})	2.62	0.48
Mg (g kg^{-1})	0.95	3.04
C/N	21.2	15.2
pH (Wet/Dry season)	3.60/4.30	3.74/3.90
Water content (%, Wet/Dry season)	64.1/53.6	54.1/37.2
Temperature (°C, Wet/Dry season)	13.8/11.9	13.9/10.8

before weighing. Two-hundred aliquots (5 g) of each litter type were weighed to the nearest 0.01 g and sewn into 10 × 20 cm nylon bags made of 1.5 mm mesh. Each litterbag was labeled with a numbered plastic tag.

At the beginning of January 2008, five forest floor plots were located randomly to place litterbags, and in each plot 20 bags of each litter type were staked to the forest floor surface with polyester thread. Accordingly, in order to standardize placement, five large *C. wattii* (dbh > 100 cm) were selected for the placement of litterbags, and 20 bags of each litter type were placed on lower trunk reiterations and limb junctions of each tree. Three replicate bags of each litter type were retrieved randomly from each plot/tree after 2, 5, 8, 12, 18, 24 months. All sampled bags were cleaned to remove extraneous materials, and dried at 80 °C for 48 h and then weighed.

2.3. Chemical analysis

After determining the remaining mass, three within-plot/tree replicate bags of each litter type were pooled as a residual sample to obtain sufficient material for chemical analyses. For each litter type, three residual samples at each retrieval and three initial samples (Table 2) were analyzed. The lichen samples retrieved from the forest floor plots after 24 months were not used for analyses because of insufficient pooled residual materials. The dried samples were ground in a Wiley mill and sent to the Biogeochemistry Laboratory of Xishuangbanna Tropical Botanical Garden for chemical analyses. C and N content were determined using a C/N autoanalyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Germany). The nutrients Ca, K, Mg and P were measured using an ICP-AES (Thermo Jarrell Ash Corporation, USA) after digestion in HNO_3–$HClO_4$ and HCl (Dong, 1996).

2.4. Data analysis

Litter decomposition was calculated as a percentage loss from the original mass. The decay constant (k) was calculated using the exponential model $X_t/X_0 = e^{-kt}$, where X_0 is the initial mass and X_t is the remaining mass at time t (in years) (Olson, 1963). The k values were determined to compare decay rates among the seven litter types. The time required for 50% ($t_{50\%} = 0.693/k$) and 95% mass loss ($t_{95\%} = 3/k$) were also calculated.

ANOVA followed by Tukey's HSD test was used to test differences in mass loss between habitat compartments and among litter types. All data were checked for normality using Shapiro–Wilk test and homogeneity of variances using Bartlett's test, and non-normal data were tested using the non-parametric Kruskal–Wallis test followed by Wilcoxon rank sum test. $P < 0.05$ was used as the significance level and effect with $P \le 0.10$ was considered marginally significant.

The relationships between initial C, N, P contents as well as initial C/N, C/P, N/P ratios in the litter, and the k values were tested by linear regression for all species, vascular and lichen group, respectively. Average values were used for variables and log-transformed as necessary before analysis. All statistical analyses were performed using the statistical package R 2.14.2 (R Development Core Team, 2012).

3. Results

3.1. Litter decomposition

Although the initial chemistries were highly variable among the seven species (Table 2), the decomposition rates of all litter in the canopy were significantly slower than on the forest floor over the two-year period (Kruskal–Wallis $\chi^2 = 37.01$, df = 1, $P < 0.001$; Fig. 1; Table 3). The final mass remaining was 17–69% of the original in the canopy compared with 2–51% on the forest floor. With the notable exception of *N. ornata*, which had 30% less loss in the canopy, the mass loss of most litter in the canopy was about 20% lower than on the forest floor. Constant k was 50–185% lower in the canopy, with a range between 0.17 and 0.94, compared with on the forest floor, with a range between 0.28 and 1.95. Similar patterns were observed for $t_{50\%}$ and $t_{95\%}$. On the forest floor, the greatest mass-loss occurred in the initial eight months, and the litter in the canopy showed similar, albeit less pronounced, patterns.

The rates of decay differed significantly among the seven species (Kruskal–Wallis $\chi^2 = 141$, df = 6, $P < 0.001$) as well as those in the canopy (Kruskal–Wallis $\chi^2 = 87.6$, df = 6, $P < 0.001$) and on the forest floor (Kruskal–Wallis $\chi^2 = 88.9$, df = 6, $P < 0.001$). For multiple comparisons, no significant difference was found between *E. nepalense* and *N. ornata* ($P = 0.083$ in the canopy and 0.74 on the forest floor), *H. flabellatum* and *P. connexa* ($P = 0.32$ and 0.58) in both habitats, and *N. ornata* and *C. wattii* in the canopy ($P = 0.27$). The greatest mass-loss was in *U. florida* and the lowest in *H. flabellatum*. Lichens were almost completely decayed after two years on the forest floor and lost 65–83% of the initial mass in the canopy. *U. florida* decayed the fastest. *E. nepalense* decayed, although not significantly, faster than *N. ornata* in the canopy but slower on the forest floor. In contrast, the mass-loss was less than 50% for the moss and fern; furthermore, 30% of mass-loss in the moss occurred in the final six months on the forest floor. The rates of mass-loss of the two tree species were between these extremes. Thin *C. wattii* leaves decayed about 10% faster than thick *L. xylocarpus* leaves in both habitats.

For all litter, the decay constants were not significantly correlated with initial N and P concentrations or to initial C/N and C/P in both habitat compartments (Table 4), with the exception of initial N ($r^2_{adj.} = 0.18$, $P < 0.034$) and there was a marginally significant relationship between k values and N/P ($r^2_{adj.} = 0.13$, $P = 0.060$) on

Table 2
Initial chemistries of seven litter types in an evergreen broad-leaved forest in the Ailao Mountains, southwest China.

Species	C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	C/N	C/P	N/P
Epiphytic lichen									
Everniastrum nepalense	452 ± 1.20	10.8 ± 0.48	0.99 ± 0.05	3.35 ± 0.29	2.16 ± 0.11	0.63 ± 0.02	42.1 ± 1.87	458 ± 23.1	10.9 ± 0.61
Nephromopsis ornata	433 ± 4.73	9.16 ± 0.50	0.98 ± 0.10	5.36 ± 0.16	4.92 ± 0.52	0.89 ± 0.04	47.5 ± 2.22	452 ± 43.4	9.47 ± 0.48
Usnea florida	439 ± 1.33	8.70 ± 0.10	0.72 ± 0.08	2.53 ± 0.17	2.66 ± 0.15	0.61 ± 0.02	50.4 ± 0.45	623 ± 76.3	12.4 ± 1.51
Epiphytic moss									
Homaliodendron flabellatum	445 ± 0.88	18.6 ± 0.53	2.28 ± 0.05	4.16 ± 0.30	8.74 ± 0.31	1.42 ± 0.05	24.0 ± 0.69	196 ± 4.02	8.15 ± 0.08
Epiphytic fern									
Phymatopteris connexa	466 ± 1.53	6.46 ± 0.12	0.27 ± 0.03	7.22 ± 0.24	5.92 ± 0.42	3.32 ± 0.40	72.2 ± 1.31	1753 ± 148	24.2 ± 1.67
Tree species									
Castanopsis wattii	489 ± 0.88	19.9 ± 0.25	1.41 ± 0.04	12.1 ± 0.20	4.45 ± 0.45	2.13 ± 0.05	24.5 ± 0.26	347 ± 8.64	14.1 ± 0.02
Lithocarpus xylocarpus	505 ± 0.00	16.2 ± 0.16	0.92 ± 0.01	4.27 ± 0.12	5.48 ± 0.19	0.85 ± 0.01	31.1 ± 0.31	551 ± 5.33	17.7 ± 0.09

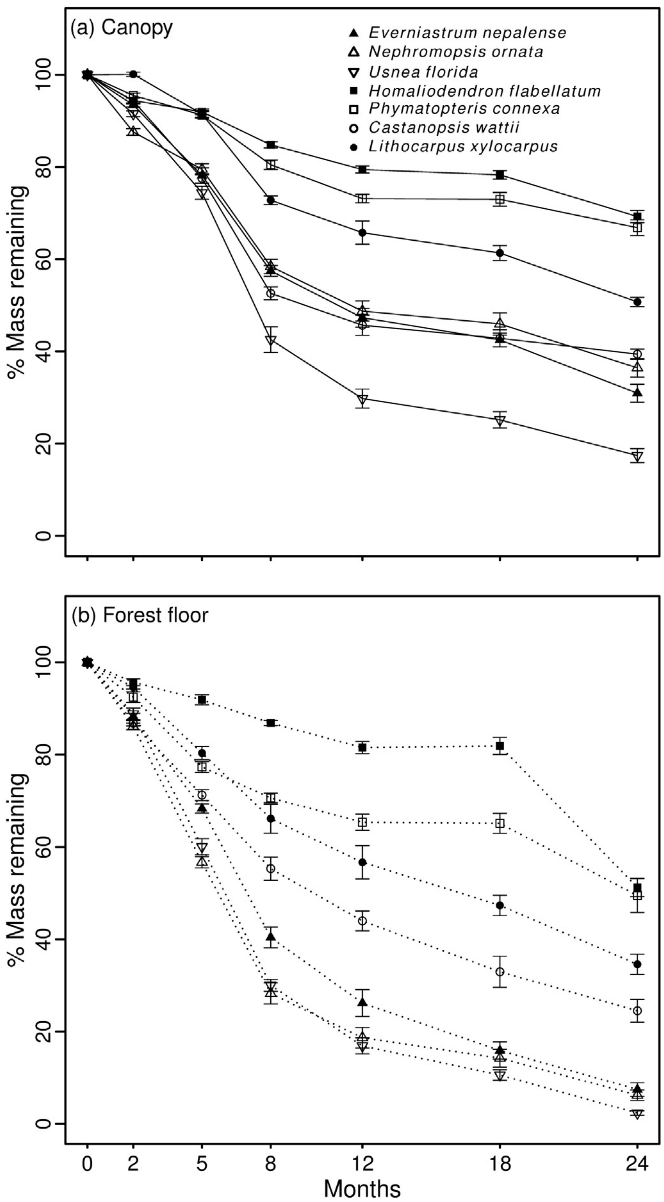

Fig. 1. Mean (±SE) percent initial mass remaining in the canopy and on the forest floor of seven litter types over two years in an evergreen broad-leaved forest in the Ailao Mountains, southwest China.

the forest floor. In the vascular group, there was a significant positive relationship between *k* values and initial N and P, and a strong negative correlation between *k* values and initial C/N, C/P and N/P. The *k* values of the lichen group showed an opposite pattern, and were significantly correlated with initial P, C/N and C/P, and marginally significant with N (on the forest floor: $r^2_{adj.} = 0.34$, $P = 0.060$) and N/P (in the canopy: $r^2_{adj.} = 0.25$, $P = 0.099$; on the forest floor: $r^2_{adj.} = 0.33$, $P = 0.063$).

3.2. Nutrient release

Patterns of nutrient release differed among elements between habitat compartments and among litter types (Figs. 2–4). Overall, nutrients were released faster from litter on the forest floor than in the canopy; and, nutrient release was faster in lichens than in other litter.

Table 3
Decomposition parameters of seven litter types in the canopy (C) and on the forest floor (F) in an evergreen broad-leaved forest in the Ailao Mountains, southwest China.

Species	Habitat	Decay constant *k* (year)	Equation	Coefficient $r^2_{adj.}$	$t_{50\%}$ (year)	$t_{95\%}$ (year)
Everniastrum	C	0.60	$y = 96.7e^{-0.60t}$	0.88***	1.15	4.96
nepalense	F	1.47	$y = 111e^{-1.47t}$	0.82***	0.47	2.03
Nephromopsis	C	0.52	$y = 93.0e^{-0.52t}$	0.80***	1.35	5.82
ornata	F	1.48	$y = 95.4e^{-1.48t}$	0.85***	0.47	2.02
Usnea florida	C	0.94	$y = 95.6e^{-0.94t}$	0.84***	0.74	3.19
	F	1.95	$y = 118e^{-1.95t}$	0.91***	0.36	1.54
Homaliodendron	C	0.17	$y = 97.9e^{-0.17t}$	0.86***	4.00	17.3
flabellatum	F	0.28	$y = 104e^{-0.28t}$	0.72***	2.45	10.6
Phymatopteris	C	0.21	$y = 97.3e^{-0.21t}$	0.81***	3.31	14.3
connexa	F	0.33	$y = 94.5e^{-0.33t}$	0.69***	2.10	9.10
Castanopsis	C	0.50	$y = 91.0e^{-0.50t}$	0.75***	1.37	5.95
wattii	F	0.76	$y = 96.5e^{-0.76t}$	0.80***	0.92	3.96
Lithocarpus	C	0.36	$y = 101e^{-0.36t}$	0.84***	1.94	8.39
xylocarpus	F	0.54	$y = 99.8e^{-0.54t}$	0.81***	1.27	5.50

C concentration was most frequently correlated with decomposition in the canopy while C amount provided significant correlations with the decay for all species in both habitats (Table S1). Litter decomposition was accompanied by increasing C concentration and decreasing C amount in the canopy, but by a more variable concentration on the forest floor (Fig. 2a–b and 3a–b). The change in C concentration was most pronounced for the lichens and least pronounced for the moss and fern.

N concentration increased considerably with time, with final increase 2–3 times of the original, and was strongly correlated with mass loss for most species (Fig. 2c–d). The exception was the moss in which N concentration decreased significantly from 18.6 to 15.1 mg g^{-1} ($F = 42.2$, df = 1, $P = 0.003$) in the canopy and remained largely stable on the forest floor. In contrast, the amount of N eventually decreased in most species, but with short immobilization phases (Fig. 3c–d). An exception was the fern, which had the lowest initial N, and tended to immobilize N in both habitats and its N immobilization was more pronounced on the forest floor. More than 50% of the initial N remained in all species except for *U. florida* in the canopy and more than 50% remained in the moss, fern and *L. xylocarpus* on the forest floor. Moreover, highly significant relationships were found between C/N and decay rate, with similar, more regular patterns for all species (Fig. 4a–b). In particular, the C/N of decomposing moss increased over time in the canopy.

P (Fig. 2e–f and 3e–f), C/P (Fig. 4c–d) and N/P (Fig. 4e–f) also exhibited similar patterns. Final P concentration converged at 1.0–1.5 mg g^{-1} in both habitats, owing to increased P in litter with lower initial content. For example, a consistent increase was observed in the decomposing fern in the canopy, ranging from 0.27 mg g^{-1} for the initial concentration to 0.72 mg g^{-1} for final concentration ($F = 21.1$, df = 1, $P = 0.010$). The sharp decreases in C/P and N/P in

Table 4
Correlation coefficients ($r^2_{adj.}$) between litter decay constants (*k*) and initial chemistries in the canopy (C) and on the forest floor (F) in an evergreen broad-leaved forest in the Ailao Mountains, southwest China.

Species group	Habitat	N	P	C/N	C/P	N/P
All species	C	ns	ns	ns	ns	ns
	F	0.16*(−)	ns	ns	ns	ns
Vascular plants	C	0.87***(+)	0.95***(+)	0.77**(−)	0.77**(−)	0.87***(−)
	F	0.58*(+)	0.68**(+)	0.48*(−)	0.50*(−)	0.65**(−)
Lichens	C	ns	0.40*(−)	ns	0.42*(+)	ns
	F	ns	0.70**(−)	0.43*(+)	0.63**(+)	ns

ns: not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

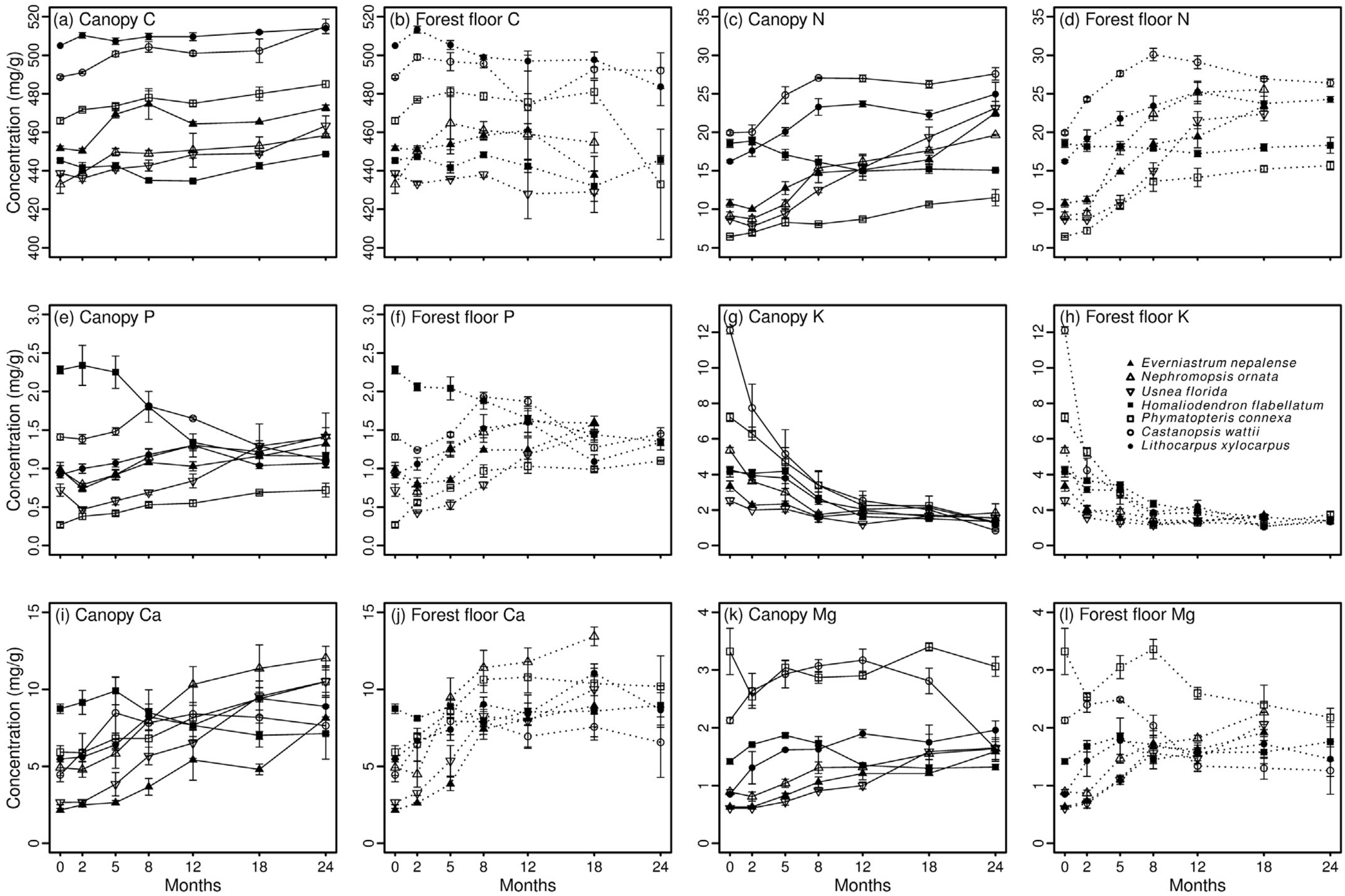

Fig. 2. Changes in nutrient concentrations of seven litter types over two years in the canopy and on the forest floor in an evergreen broad-leaved forest in the Ailao Mountains, southwest China.

decomposing fern indicated that a more rapid immobilization occurred for P than for C and N.

K was the nutrient most rapidly lost from all decomposing litter. About 68–90% of the initial K was lost in the canopy and 63–95% on the forest floor in the first year, matched by a strong decrease in concentration (Fig. 2g–h and 3g–h). Less than 20% was lost in the second year.

Ca concentration was variable but increased consistently in decomposing litter in both habitats (Fig. 2i–j). However, the moss remained a relatively constant Ca concentration on the forest floor. Ca amount was lost slowly and more than 50% was retained in the canopy (Fig. 3i–j). *C. wattii* had a net Ca immobilization in the canopy, reaching 116% of its original.

The change in Mg (Fig. 2k–l and 3k–l) was similar to that of Ca. However, Mg concentration in the *C. wattii* was first increased and then decreased. Mg amount in *L. xylocarpus* displayed a similar pattern, retaining 119% of its original in the canopy and 63% on the forest floor.

4. Discussion

4.1. Comparison of decomposition between canopy and floor habitats

We found the studied litter decayed 15–30% more slowly in the canopy than on the forest floor in subtropical evergreen broad-leaved forests in southwest China, and thus the result is consistent with our first hypothesis. Our observations generally agree with those of Nadkarni and Matelson (1991), Clark et al. (1998) and Cardelús (2010), who concluded that the decay rates of epiphytic bryophyte and tree leaves are 2–3 times higher on the forest floor than in the canopy in tropical forests. In a temperate coniferous forest, however, the decay rate of cedar litter is only 3% lower in the canopy (Lindo and Winchester, 2007). Thus, the variation in the decomposition rate between canopy and forest floor compartments probably was related to the type of forest ecosystem at a large-scale. Based on the above findings, we propose a hypothesis that the variations in litter decomposition between canopy and forest floor habitats may decrease with large-scale climatic gradient from tropical to temperate forests.

The slower decomposition observed in the canopy can be explained in part by lower humidity (Cardelús and Chazdon, 2005), frequent and rapid drying events (Coxson and Nadkarni, 1995) and lower diversity of decomposers (Vance and Nadkarni, 1990; Rousk and Nadkarni, 2009). Cardelús (2010) also noted that litter decomposition depends on P availability in the canopy and carbon quality on the forest floor.

If the above mechanisms are indeed responsible for litter decomposition, the slow decay in the canopy is probably determined more by air conditions than soil conditions in our area. There are several possible explanations for this. First, similar to Cardelús et al. (2009), recent work in our study region show that canopy soil has a significantly higher water content, higher N availability, higher amounts of fungi and actinomycetes, and

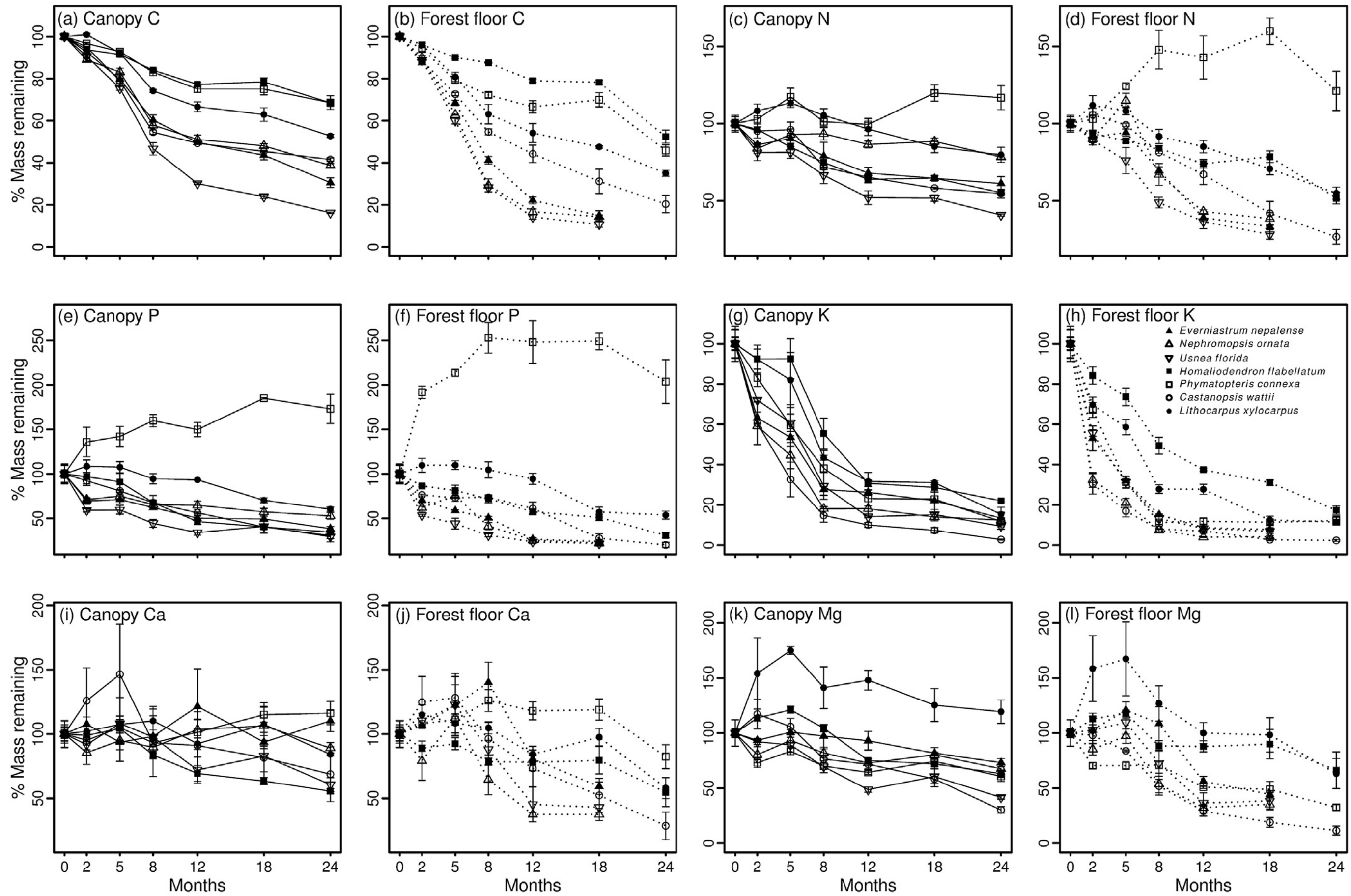

Fig. 3. Changes in nutrient amounts of seven litter types over two years in the canopy and on the forest floor in an evergreen broad-leaved forest in the Ailao Mountains, southwest China.

equivalent P content compared with floor soil (Wang et al., 2008; Liu et al., 2010). However, litter decomposition may not benefit more from the canopy soil properties in this area. Second, the decomposing litter is buried easier by subsequent litter on the forest floor than in the canopy (Nadkarni and Matelson, 1991), and canopy litter is more directly exposed to air. Moreover, canopy soil and bark are usually covered by a thick bryophyte layer in southwest China (You, 1983; Wang et al., 2008), which may also prevent the litter having direct contact with canopy soil. It thus appears reasonable to assume that the conditions of the canopy reduced the positive effect of soil properties on litter decay. In addition, the abundance of canopy micro- and macro-invertebrates associated with litter decay is likely to be lower according to the available evidence (Nadkarni and Longino, 1990; Paoletti et al., 1991; Fonte and Schowalter, 2004; Lindo and Winchester, 2006, 2007, 2008).

While the fern had the highest N and P uptake on the forest floor, the nutrient release from most litter was significantly slower in the canopy than on the forest floor, which was similar to the findings of Clark et al. (1998) and Cardelús (2010). Additionally our regression analyses showed that nutrient concentrations varied more regularly in the canopy than on the forest floor, while nutrient amounts changed more regularly on the forest floor (Table S1). One possible explanation for this result is a higher proportion of mass-loss probably resulted from leaching of nutrients in the canopy, and resulted from a combination of physical processes and microbial and invertebrate consumption on the forest floor (Swift et al., 1979; Fonte and Schowalter, 2004).

4.2. Comparison of decomposition rates among species

In partial support of our second hypothesis, we found the order of litter decay rate was lichen > tree > fern > bryophyte. This finding supports the notion that functional traits, encompassing a wide range of chemical and physical attributes that do not necessarily correlate with each other, play a prominent role in influencing the litter decomposition (Cornwell et al., 2008; Lang et al., 2009; Asplund and Wardle, 2013). Our result is also consistent with that reported from a boreal forest (Taylor and Jones, 1990), and is further illustrated in a study by Cornwell et al. (2008), who suggest a global pattern that ferns decay more rapidly than bryophytes, but more slowly than seed plants. Likewise, bryophytes (Clark et al., 1998; Liu et al., 2000; Lang et al., 2009) and ferns (Quested et al., 2003; Amatangelo and Vitousek, 2009; Ma et al., 2009b) are known to decay significantly more slowly than other vascular litter.

Epiphytic lichens have labile chemical compositions and lack woody or otherwise recalcitrant tissues (Dahlman et al., 2003; Nash, 2008), and therefore their chemical properties would normally facilitate litter decomposition. Moreover, decomposition rates of epiphytic lichens in this study were within or higher than the ranges reported for temperate/boreal hardwoods (Knops et al., 1996), conifer forests (Taylor and Jones, 1990; McCune and Daly, 1994; Esseen and Renhorn, 1998; Coxson and Curteanu, 2002; Holub and Lajtha, 2003; Campbell et al., 2010) and *Nothofagus* forests (Guzman et al., 1990; Caldiz et al., 2007). As with our results, these studies found that litter decay of epiphytic lichens varies

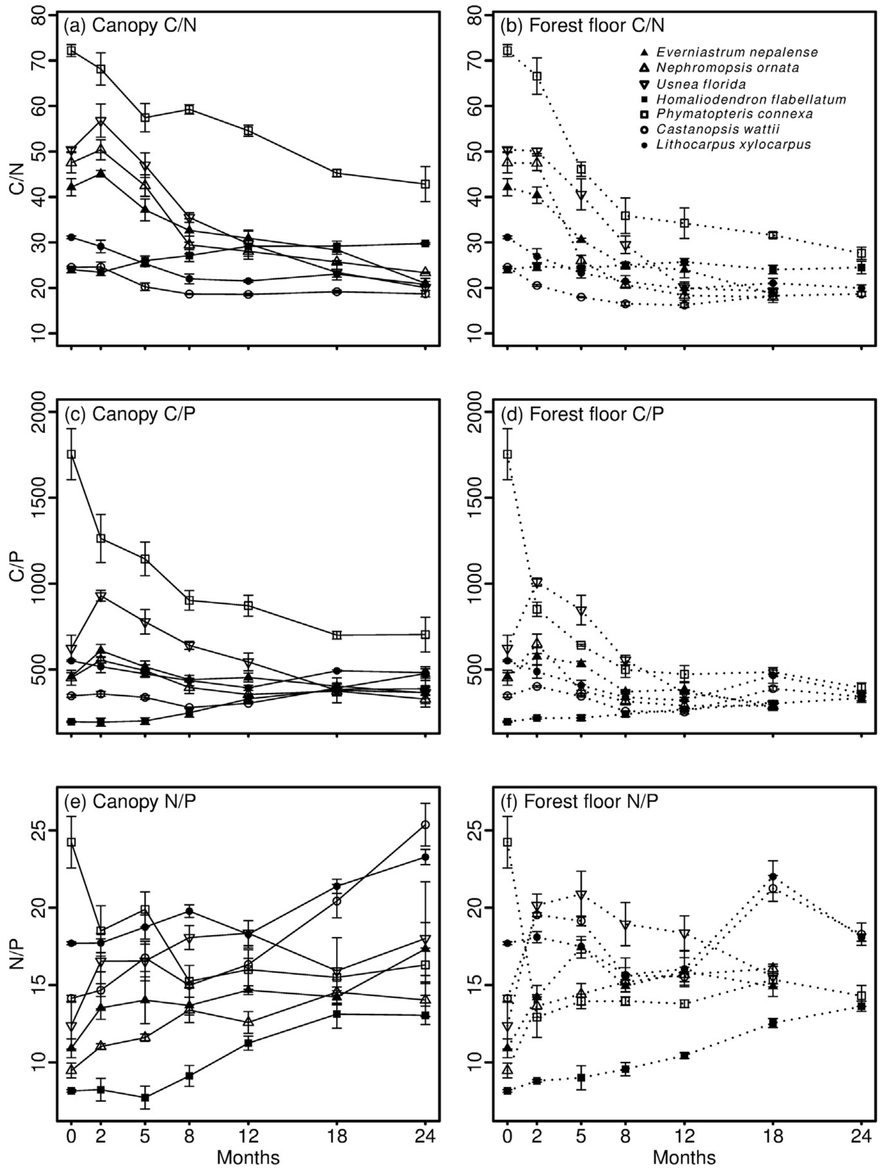

Fig. 4. Changes in ratios of C/N, C/P and N/P of seven litter types over two years in the canopy and on the forest floor in an evergreen broad-leaved forest in the Ailao Mountains, southwest China.

across species and the species-specific differences are related to initial N and C/N (Guzman et al., 1990; McCune and Daly, 1994; Esseen and Renhorn, 1998). In general, lichens with high N concentration and low C/N decay rather quickly. Thallus morphology can also determine lichen decomposition, and fruticose lichens generally decay faster than foliose species. This may be because the higher area/volume ratio can facilitate rapid decomposition and leaching of cellular components despite relatively low N concentration and higher C/N (McCune and Daly, 1994; Esseen and Renhorn, 1998; Coxson and Curteanu, 2002; Campbell et al., 2010). The decomposition of three lichen species in our study site indicates that thallus morphology may be a more important driver than initial N. It should be noted that the initial P as well as N was negatively correlated with lichen mass loss in our study. This result is somewhat contrary to the widely accepted view that P can accelerate litter decomposition (Cornwell et al., 2008; Cardelús, 2010). Similarly, this could be due to the effect of morphology exceeding that of P. In addition, the variation in decay rate between habitats was about 15% for *U. florida*, 23% for *E. nepalense* and 30% for *N. ornata*, indicating that thallus morphology may cause an enhancement of the habitat effect on lichen decomposition (Esseen and Renhorn, 1998; Coxson and Curteanu, 2002; Asplund et al., 2013).

The decay constant of the studied bryophyte was the smallest among functional groups, similar to that of mixed epiphytic bryophytes ($k = 0.31$) on the forest floor in this area (Liu et al., 2000), but significantly higher than those in both habitats in tropical forests (Clark et al., 1998). Further, the lowest decay rate of bryophyte seemed less related to nutrient concentration because it had the highest initial N and P (Liu et al., 2000; Fenton et al., 2010). However, such low rates of decay are largely associated with the secondary metabolites that have high antibacterial and antifungal activity and inhibit decay, although bryophytes lack the lignin that resists decay in tracheophytes (Clark et al., 1998; Lang et al., 2009).

Epiphytic fern also decayed slowly, and its mass loss may be retarded by a relatively thick outer cortex, lower N and P concentrations, and higher concentrations of recalcitrant compounds such as fiber, lignin or tannins (Ganjegunte et al., 2005; Amatangelo and Vitousek, 2009; Richardson and Walker, 2010). However, no literature that addresses the decomposition rate and nutrient release of epiphytic ferns is available for comparison.

In addition, the decay rates of tree leaves in our study were comparable to other reports from the same area and were related to initial lignin, N and P (Liu et al., 2000).

Our results and previous studies provide substantial evidence that the type of plant growth substrate also influences litter decomposition, e.g. litter from nonvascular epiphyte decay faster than that from terrestrial nonvascular species (Moore, 1984; Nadkarni and Matelson, 1992; Clark et al., 1998; Lang et al., 2009; Asplund et al., 2013; Asplund and Wardle, 2013).

The rate of decay of epiphytic fern was lower than terrestrial ferns in the tropics (Russell and Vitousek, 1997; Allison and Vitousek, 2004; Amatangelo and Vitousek, 2009), similar to *Dicranopteris* ($k = 0.25$) in mid-subtropical China (Ma et al., 2009b), and higher than those in the subtropical North America (Hendricks et al., 2002) and the subarctic region (Quested et al., 2003). Further, nitrogen, a key factor determining the litter decomposition, in leaves of epiphytic ferns is slightly lower than those of terrestrial ferns (Watkins et al., 2007). This may indicate that epiphytic fern litter would decay faster than terrestrial fern litter in the same area (Cornwell et al., 2008; Cardelús, 2010; Richardson and Walker, 2010).

4.3. Comparison of nutrient release among species

Our study showed that C and N in epiphytic lichens were readily released during decomposition, accompanied by increasing concentrations. The results concur with those of Taylor and Jones (1990) and Knops et al. (1996) for hair lichens, and Caldiz et al. (2007) for foliose lichens. The rapid N loss from lichens is associated with their higher content of soluble compounds (Dahlman et al., 2003; Nash, 2008). Tree leaves and epiphytic moss showed similar patterns, in accordance with findings by Liu et al. (2000). Notably, N concentration and amount in the decomposing epiphytic fern increased significantly. Its decay pattern is somewhat consistent with those of terrestrial ferns in tropical Hawai'i (Russell and Vitousek, 1997; Allison and Vitousek, 2004), but in contrast to those in subtropical zones where no net N immobilization occurred (Hendricks et al., 2002; Zhao et al., 2006).

Most species lost P more rapidly than N, and the final P concentrations were close to that of soil in both habitats (Wang et al., 2008; Liu et al., 2010). The release patterns of P for moss and trees were also consistent with a previous study in the same area (Liu et al., 2000). The high N and P immobilization in the fern may be attributable to very low initial concentrations, because high C/N and N/P may stimulate their immobilization in microbial biomass (Hietz et al., 2002; Watkins et al., 2007; Cardelús, 2010). Changes in P amount in epiphytic lichens were similar to those in previous studies (Knops et al., 1996; Caldiz et al., 2007; Campbell et al., 2010). In contrast, Moore (1984) reports terrestrial lichen *Cladina stellaris* would retain P and accumulate N during decomposition. The rapid release of P from lichens and moss in this area also indicated that P was very desirable for microorganisms (Liu et al., 2000; Caldiz et al., 2007).

As in many studies (Liu et al., 2000; Hendricks et al., 2002; Zhao et al., 2006; Caldiz et al., 2007; Campbell et al., 2010), K was rapidly released from all studied litter. The amounts of Ca and Mg eventually decreased with variable concentrations in the seven species, analogous to other studies (Liu et al., 2000; Hendricks et al., 2002; Zhao et al., 2006; Caldiz et al., 2007; Campbell et al., 2010). The highly variable patterns may be due to the colloidal materials produced by decomposers, which may absorb more exchangeable nutrients (Caldiz et al., 2007).

4.4. Implications

The importance of epiphytes for subtropical forest ecosystems is becoming increasingly recognized (Liu et al., 2002; Xu and Liu, 2005; Wang et al., 2008; Han et al., 2010; Li et al., 2011, 2013), and they are known to make a disproportionately important contribution to nutrient availability relative to their low biomass (Hsu et al., 2002; Campbell et al., 2010; Chen et al., 2010). This study, together with that of Liu et al. (2000), provides a decomposition pattern for plant functional groups in subtropical forests. Simultaneously, our study confirms the finding that plant litters, regardless of functional group type, decay more slowly in the canopy than on the forest floor (Clark et al., 1998; Lindo and Winchester, 2007; Cardelús, 2010).

Our results demonstrated that epiphytes have significant ecological roles in nutrient cycling in subtropical forests. The highest decay rates of epiphytic lichens are indicative of more rapid nutrient cycling. In our study region, epiphytic lichen biomass tends to be more abundant in secondary forests (Li et al., 2011), and their rapid nutrient-input may be of particular significance in facilitating the restoration of secondary vegetations. Although epiphytic bryophyte had the lowest decay rate, its high biomass (Liu et al., 2002; Wang et al., 2008) and rapid release of N and P may indicate that the decomposition of epiphytic bryophytes is important for biological activities in forest ecosystems, especially for vascular epiphytes in oligotrophic canopy habitats (Clark et al., 1998; Hietz et al., 2002; Cardelús and Mack, 2010).

In the Ailao Mountains, bryophytes contribute to over 60% of total epiphyte biomass while ferns contribute over 10% (Liu et al., 2002; Wang et al., 2008; Xu and Liu, unpublished data). Old-growth trees host the most abundant epiphytes (Xu and Liu, 2005). The slow decay of epiphytic bryophytes and ferns indicates that they can cause a continuous accumulation in the epiphytic organic matter. Consistent with our findings, Coxson and Nadkarni (1995) and Turetsky (2003) suggest that bryophytes are important for the accumulation of C and N in terrestrial ecosystems. The accumulation of epiphyte mass may also partially explain the fact that this primary forest acts as a large carbon sink and old trees sequester the most carbon (Tan et al., 2011).

In addition, the high N and P immobilization in the epiphytic fern may imply that the canopy habitat is N- and/or P-limited for vascular epiphytes in subtropical forests, as found in the tropics (Fonte and Schowalter, 2004; Watkins et al., 2007; Cardelús et al., 2009; Cardelús, 2010).

Although our study first provides some evidence for the importance of epiphyte decomposition in subtropical forests, the impacts of epiphytes on nutrient cycling are not well-known. Further comparative studies regarding the decomposition of epiphytic and terrestrial species are clearly needed and would offer valuable new insights to better understanding forest nutrient cycling.

Acknowledgments

This project was funded by the NSFC–Yunnan Joint Fund, CAS135 Program and West Light Foundation of the Chinese Academy of Sciences. We thank the Management Authority of the Ailao Mountain Nature Reserve for the permission to undertake this research. We are grateful to Wen-Zheng Yang, Jin-Hua Qi and the Ailao Mountains Ecosystem Research Station for their fieldwork assistance. We also thank Biogeochemistry Laboratory of Xishuangbanna Tropical Botanical Garden for assistance with chemical analysis of samples, and Dr. Hai-Shan Niu for advice with statistical analysis. Dr. Pelin Kayaalp helped improve the English for the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2013.12.031.

References

Allison, S.D., Vitousek, P.M., 2004. Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141, 612–619.

Amatangelo, K.L., Vitousek, P.M., 2009. Contrasting predictors of fern versus angiosperm decomposition in a common garden. Biotropica 41, 154–161.

Antoine, M.E., 2004. An ecophysiological approach to quantifying nitrogen fixation by *Lobaria oregana*. The Bryologist 107, 82–87.

Asplund, J., Bokhorst, S., Wardle, D.A., 2013. Secondary compounds can reduce the soil micro-arthropod effect on lichen decomposition. Soil Biology and Biochemistry 66, 10–16.

Asplund, J., Wardle, D.A., 2013. The impact of secondary compounds and functional characteristics on lichen palatability and decomposition. Journal of Ecology 101, 689–700.

Caldiz, M.S., Brunet, J., Nihlgård, B., 2007. Lichen litter decomposition in *Nothofagus* forest of northern Patagonia: biomass and chemical changes over time. The Bryologist 110, 266–273.

Campbell, J., Fredeen, A.L., Prescott, C.E., 2010. Decomposition and nutrient release from four epiphytic lichen litters in sub-boreal spruce forests. Canadian Journal of Forest Research 40, 1473–1484.

Cardelús, C.L., 2010. Litter decomposition within the canopy and forest floor of three tree species in a tropical lowland rain forest, Costa Rica. Biotropica 42, 300–308.

Cardelús, C.L., Chazdon, R.L., 2005. Inner-crown microenvironments of two emergent tree species in a lowland wet forest. Biotropica 37, 238–244.

Cardelús, C.L., Mack, M.C., 2005. Host tree vs. vascular epiphyte nutrient concentrations along the Barva transect, Costa Rica. In: Annual Meeting of the Ecological Society of America, Montreal.

Cardelús, C.L., Mack, M.C., 2010. The nutrient status of epiphytes and their host trees along an elevational gradient in Costa Rica. Plant Ecology 207, 25–37.

Cardelús, C.L., Mack, M.C., Woods, C., DeMarco, J., Treseder, K.K., 2009. The influence of tree species on canopy soil nutrient status in a tropical lowland wet forest in Costa Rica. Plant and Soil 318, 47–61.

Chen, L., Liu, W.Y., Wang, G.S., 2010. Estimation of epiphytic biomass and nutrient pools in the subtropical montane cloud forest in the Ailao Mountains, south-western China. Ecological Research 25, 315–325.

Clark, K.L., Nadkarni, N.M., Gholz, H.L., 1998. Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. Biotropica 30, 12–23.

Clark, K.L., Nadkarni, N.M., Gholz, H.L., 2005. Retention of inorganic nitrogen by epiphytic bryophytes in a tropical montane forest. Biotropica 37, 328–336.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez–Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065–1071.

Coxson, D.S., Curteanu, M., 2002. Decomposition of hair lichens (*Alectoria sarmentosa* and *Bryoria* spp.) under snowpack in montane forest, Cariboo Mountains, British Columbia. The Lichenologist 34, 395–402.

Coxson, D.S., Nadkarni, N.M., 1995. Ecological roles of epiphytes in nutrient cycles of forest ecosystems. In: Lowman, M.D., Nadkarni, N.M. (Eds.), Forest Canopies. Academic Press, California, pp. 495–543.

Dahlman, L., Persson, J., Näsholm, T., Palmqvist, K., 2003. Carbon and nitrogen distribution in the green algal lichens *Hypogymnia physodes* and *Platismatia glauca* in relation to nutrient supply. Planta 217, 41–48.

Dong, M., 1996. Standard Methods for Observation and Analysis in Chinese Ecosystem Research Network-Survey: Observation and Analysis of Terrestrial Biocommunities. Standard Press of China, Beijing (in Chinese).

Esseen, P.A., Renhorn, K.E., 1998. Mass loss of epiphytic lichen litter in a boreal forest. Annales Botanici Fennici 35, 211–217.

Fenton, N.J., Bergeron, Y., Paré, D., 2010. Decomposition rates of bryophytes in managed boreal forests: influence of bryophyte species and forest harvesting. Plant and Soil 336, 499–508.

Fonte, S.J., Schowalter, T.D., 2004. Decomposition in forest canopies. In: Lowman, M.D., Rinker, H.B. (Eds.), Forest Canopies, second ed. Academic Press, California, pp. 413–422.

Ganjegunte, G.K., Vance, G.F., Preston, C.M., Schuman, G.E., Ingram, L.J., Stahl, P.D., Welker, J.M., 2005. Influence of different grazing management practices on soil organic carbon constituents in a northern mixed-grass prairie. Soil Science Society of America Journal 69, 1746–1756.

Guzman, G., Quilhot, W., Galloway, D.J., 1990. Decomposition of species of *Pseudocyphellaria* and *Sticta* in a southern Chilean forest. The Lichenologist 22, 325–331.

Han, B., Zou, X.M., Kong, J.J., Sha, L.Q., Gong, H.D., Yu, Z., Cao, T., 2010. Nitrogen fixation of epiphytic plants enwrapping trees in Ailao Mountain cloud forests, Yunnan, China. Protoplasma 247, 103–110.

Hendricks, J.J., Wilson, C.A., Boring, L.R., 2002. Foliar litter position and decomposition in a fire-maintained longleaf pine wiregrass ecosystem. Canadian Journal of Forest Research 32, 928–941.

Hietz, P., Wanek, W., Popp, M., 1999. Stable isotopic composition of carbon and nitrogen and nitrogen content in vascular epiphytes along an altitudinal transect. Plant, Cell and Environment 22, 1435–1443.

Hietz, P., Wanek, W., Wania, R., Nadkarni, N.M., 2002. Nitrogen–15 natural abundance in a montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte nutrition. Oecologia 131, 350–355.

Holub, S.M., Lajtha, K., 2003. Mass loss and nitrogen dynamics during the decomposition of a ^{15}N labeled N_2-fixing epiphytic lichen, *Lobaria oregana*. Canadian Journal of Botany 81, 698–705.

Hsu, C.C., Horng, F.W., Kuo, C.M., 2002. Epiphyte biomass and nutrient capital of a moist subtropical forest in north-eastern Taiwan. Journal of Tropical Ecology 18, 659–670.

Knops, J.M.H., Nash III, T.H., Schlesinger, W.H., 1996. The influence of epiphytic lichens on the nutrient cycling of an oak woodland. Ecological Monographs 66, 159–179.

Lang, S.I., Cornelissen, J.H.C., Klahn, T., van Logtestijn, R.S.P., Broekman, R., Schweikert, W., Aerts, R., 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. Journal of Ecology 97, 886–900.

Li, S., Liu, W.Y., Li, D.W., 2013. Epiphytic lichens in subtropical forest ecosystems in southwest China: species diversity and implications for conservation. Biological Conservation 159, 88–95.

Li, S., Liu, W.Y., Wang, L.S., Ma, W.Z., Song, L., 2011. Biomass, diversity and composition of epiphytic macrolichens in primary and secondary forests in the subtropical Ailao Mountains, SW China. Forest Ecology and Management 261, 1760–1770.

Lindo, Z., Winchester, N.N., 2006. A comparison of microarthropod assemblages with emphasis on oribatid mites in canopy suspended soils and forest floors associated with ancient western red cedar trees. Pedobiologia 50, 31–41.

Lindo, Z., Winchester, N.N., 2007. Oribatid mite communities and foliar litter decomposition in canopy suspended soils and forest floor habitats of western red cedar forests, Vancouver Island, Canada. Soil Biology and Biochemistry 39, 2957–2966.

Lindo, Z., Winchester, N.N., 2008. Scale dependent diversity patterns in arboreal and terrestrial oribatid mite (Acari: Oribatida) communities. Ecography 31, 53–60.

Liu, W.Y., Fox, J.E.D., Xu, Z.F., 2000. Leaf litter decomposition of canopy trees, bamboo and moss in a montane moist evergreen broad-leaved forest on Ailao Mountain, Yunnan, south-west China. Ecological Research 15, 435–447.

Liu, W.Y., Fox, J.E.D., Xu, Z.F., 2002. Nutrient fluxes in bulk precipitation, throughfall and stemflow in montane subtropical moist forest on Ailao Mountains in Yunnan, south-west China. Journal of Tropical Ecology 18, 527–548.

Liu, Y.J., Liu, W.Y., Chen, L., Zhang, H.B., Wang, G.S., 2010. Microbial community and its activities in canopy- and understory humus of two montane forest types in Ailao Mountains, northwest China. Chinese Journal of Applied Ecology 21, 2257–2266 (in Chinese).

Ma, W.Z., Liu, W.Y., Li, X.J., 2009a. Species composition and life forms of epiphytic bryophytes in old-growth and secondary forests in Mt. Ailao, SW China. Cryptogamie Bryologie 30, 477–500.

Ma, Y.D., Jiang, H., Yu, S.Q., Dou, R.P., Guo, P.P., Wang, B., 2009b. Leaf litter decomposition of plants with different origin time in the mid-subtropical China. Acta Ecologica Sinica 29, 5237–5245 (in Chinese).

McCune, B., Daly, W.J., 1994. Consumption and decomposition of lichen litter in a temperate coniferous rainforest. The Lichenologist 26, 67–71.

Moore, T.R., 1984. Litter decomposition in a subarctic spruce-lichen woodland, eastern Canada. Ecology 65, 299–308.

Nadkarni, N.M., Longino, J.T., 1990. Invertebrates in Canopy and Ground Organic Matter in a Neotropical Montane Forest. Biotropica, Costa Rica, pp. 286–289.

Nadkarni, N.M., Matelson, T.J., 1991. Fine litter dynamics within the tree canopy of a tropical cloud forest. Ecology, 2071–2082.

Nadkarni, N.M., Matelson, T.J., 1992. Biomass and Nutrient Dynamics of Epiphytic Litterfall in a Neotropical Montane Forest. Biotropica, Costa Rica, pp. 24–30.

Nash, T.H., 2008. Lichen Biology, second ed. Cambridge University Press, Cambridge.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H., Benzing, D.H., 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. Journal of Tropical Ecology, 373–383.

Pike, L.H., 1978. The importance of epiphytic lichens in mineral cycling. The Bryologist 81, 247–257.

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F., Riemann, P., Gwynn–Jones, D., Kondratchuk, A., Jonasson, S.E., 2003. Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. Ecology 84, 3209–3221.

R Development Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL: http://www.R-project.org/.

Richardson, S., Walker, L.R., 2010. Nutrient ecology of ferns. In: Mehltreter, K., Walker, L.R., Sharpe, J.M. (Eds.), Fern Ecology. Cambridge University Press, pp. 111–139.

Rousk, J., Nadkarni, N.M., 2009. Growth measurements of saprotrophic fungi and bacteria reveal differences between canopy and forest floor soils. Soil Biology and Biochemistry 41, 862–865.

Russell, A.E., Vitousek, P.M., 1997. Decomposition and potential nitrogen fixation in *Dicranopteris linearis* litter on Mauna Loa, Hawaii. Journal of Tropical Ecology 13, 579–594.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Oxford.

Tan, Z.H., Zhang, Y.P., Schaefer, D., Yu, G.R., Liang, N., Song, Q.H., 2011. An old-growth subtropical Asian evergreen forest as a large carbon sink. Atmospheric Environment 45, 1548–1554.

Taylor, B.R., Jones, H.G., 1990. Litter decomposition under snow cover in a balsam fir forest. Canadian Journal of Botany 68, 112–120.

Turetsky, M.R., 2003. The role of bryophytes in carbon and nitrogen cycling. The Bryologist 106, 395–409.

Vance, E.D., Nadkarni, N.M., 1990. Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. Soil Biology and Biochemistry 22, 677–684.

Wang, G.S., Liu, W.Y., Fu, Y., Yang, G.P., 2008. Comparison of physical and chemical properties and microbial biomass and enzyme activities of humus from canopy and forest floor in a montane moist evergreen broad–leaved forest in Ailao Mts., Yunnan. Acta Ecologica Sinica 28, 1328–1336 (in Chinese).

Watkins, J.E., Rundel, P.W., Cardelús, C.L., 2007. The influence of life form on carbon and nitrogen relationships in tropical rainforest ferns. Oecologia 153, 225–232.

Wu, Z.Y., Zhu, Y.C., 1987. The Vegetation of Yunnan. Science Press, Beijing (in Chinese).

Xu, H.Q., Liu, W.Y., 2005. Species diversity and distribution of epiphytes in the montane moist evergreen broad-leaved forest in Ailao Mountain, Yunnan. Biodiversity Science 13, 137–147 (in Chinese).

You, C.X., 1983. Classification of vegetation in Xujiaba region in Ailao Mts. In: Wu, Z.Y. (Ed.), Research of Forest Ecosystems on Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, pp. 74–117 (in Chinese).

Zhao, G.F., Cai, Y.B., Luo, Y.Y., Li, M.H., Yu, M.J., 2006. Nutrient dynamics in litter decomposition in an evergreen broad-leaved forest in East China. Acta Ecologica Sinica 26, 3286–3295 (in Chinese).