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

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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

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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