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Temporal dynamics of phosphorus during aquatic and terrestrial litter decomposition in an alpine forest

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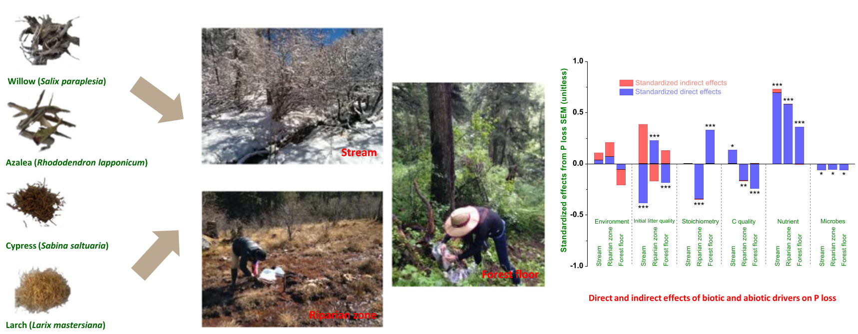
HIGHLIGHTS

- P concentration showed similar temporal dynamics across ecosystem types.
- P loss shared a common hierarchy of drivers between aquatic and terrestrial ecosystems.
- Environment and initial litter quality had both direct and indirect effects on P loss.
- Litter chemical dynamics regulated P loss as a major driver across decomposition stages.
- Microbial diversity had significant but lower effects on P loss compared with other drivers.

GRAPHICAL ABSTRACT



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ABSTRACT

Plant litter decomposition in forested soil and watershed is an important source of phosphorus (P) for plants in forest ecosystems. Understanding P dynamics during litter decomposition in forested aquatic and terrestrial ecosystems will be of great importance for better understanding nutrient cycling across forest landscape. However, despite massive studies addressing litter decomposition have been carried out, generalizations across aquatic and terrestrial ecosystems regarding the temporal dynamics of P loss during litter decomposition remain elusive. We conducted a two-year field experiment using litterbag method in both aquatic (streams and riparian zones) and terrestrial (forest floors) ecosystems in an alpine forest on the eastern Tibetan Plateau. By using multigroup comparisons of structural equation modeling (SEM) method with different litter mass-loss intervals, we explicitly assessed the direct and indirect effects of several biotic and abiotic drivers on P loss across different decomposition stages. The results suggested that (1) P concentration in decomposing litter showed similar patterns of early increase and later decrease across different species and ecosystems types; (2) P loss shared a common hierarchy of drivers across different ecosystems types, with litter chemical dynamics mainly having direct effects but environment and initial litter quality having both direct and indirect effects; (3) when assessing at the temporal scale, the effects of initial litter quality appeared to increase in late decomposition stages, while litter chemical dynamics showed consistent significant effects almost in all decomposition stages across aquatic and terrestrial ecosystems; (4) microbial diversity showed significant effects on P loss, but its effects were lower compared with other

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drivers. Our results highlight the importance of including spatiotemporal variations and indicate the possibility of integrating aquatic and terrestrial decomposition into a common framework for future construction of models that account for the temporal dynamics of P in decomposing litter.

1. Introduction

Phosphorus (P) is a structural and functional element of all organisms because of its role as component of numerous key molecules (Elser, 2012), and it has been recognized as one of the most limited nutrients for primary productivity in terrestrial ecosystems (Elser et al., 2007; Harpole et al., 2011). Unlike nitrogen (N), which can be fixed by some plants such as legumes, the source of P for plants and microorganisms in pristine and undisturbed ecosystems is mainly from mechanical rock weathering, atmospheric deposition and organic matter decomposition (Newman, 1995; Vitousek, 2004). Plant litter comprises the major common sources of energy and nutrients in forested soil and freshwater ecosystems worldwide, and its decomposition plays an important role in regulating the carbon (C) cycle and nutrient dynamics (Berg and McClaugherty, 2014; Gessner et al., 2010). Thus, understanding the factors that control the dynamics of P loss accompanying litter decomposition is of great importance for predicting or modeling P availability and related ecosystem functioning. Although many studies have addressed changes in P mass and concentration along with litter decomposition, in both aquatic and terrestrial ecosystems (Moore et al., 2011; Sohng et al., 2014; Xu and Hirata, 2005), they have been generally carried out independently in a single ecosystem type. In addition, previous studies generally failed to address whether the relative importance of biotic and abiotic factors controlling P loss change at different decomposition stages or not. Therefore, studies that bring aquatic and terrestrial litter decomposition into a common framework to assess P dynamics at a temporal scale are needed, to examine whether commonalities exist across aquatic and terrestrial ecosystems.

Previous studies showed that foliar litter decomposition in aquatic and terrestrial ecosystems can share some common biotic and abiotic drivers (García-Palacios et al., 2016a; Yue et al., 2018). Among which, climate and ambient nutrient availability (Boyero et al., 2011), the chemical traits of foliar litter (Cornwell et al., 2008), and the structure and diversity of decomposer communities that include bacteria, fungi and detritivore invertebrates (Frainer et al., 2014; Heemsbergen et al., 2004) are the most important ones. Recent studies, however, proposed a more important role of local-scale environmental factors during litter decomposition process (Bradford et al., 2016). Environmental factors can directly control litter decomposition process via changes in temperature, moisture and ambient nutrients availability, and indirectly through mediating litter resource quality and decomposer communities (Bradford et al., 2017; Wardle et al., 2004). Because of the contrasting spatiotemporal variations among aquatic and terrestrial ecosystems, differences in the relative importance of drivers between ecosystems are very likely to occur. For example, in forest ecosystems, streams have several fundamental differences from forest floor areas, which may preclude generalizations in terms of litter decomposition and the accompanying P loss pattern. In streams, the buffered temperature, unlimited water availability, abrasion by sediment transport, and consistent nutrient input from upstream may promote P loss as a result of higher leaching or fragmentation effects as well as enhanced microbial activities, while the occurrence of occasionally limited oxygen may also limit the effects of aerobic microbes on P loss (Graça et al., 2015). However, available studies addressing litter decomposition between aquatic and terrestrial ecosystems generally focused on litter mass, C or N dynamics. Because different elements or components have their specific physiochemical characteristics and can be differently mediated by several biotic and abiotic factors during litter decomposition (Berg and McClaugherty, 2014), how the relative importance of different drivers of P release during litter decomposition can vary between ecosystems still remains unclear.

The dominant conceptual model (i.e. the hierarchical model) assessing litter decomposition proposes that the primary controls of decomposition and nutrient release rates are climate, litter quality and decomposer organisms (Aerts, 1997), which only addresses the spatial variations. With the proceeding of decomposition, litter chemical traits can change substantially (Parsons et al., 2014a; Wickings et al., 2012), thus their influence on the decomposition process may vary significantly at different stages of decomposition. Likewise, litter microbial community has been found to undergo substantial successional changes during litter decomposition course (Voříšková and Baldrian, 2013). Moreover, the effects of environmental factors (e.g., temperature and moisture) are also likely to shift among different decomposition stages as a result of seasonal changes (Yue et al., 2016b).These changes along with litter decomposition process highlight the need to take temporal variations into consideration when addressing drivers of P loss in decomposing litter. This is supported by a recent study that suggested that the relative importance of biotic and abiotic drivers can vary significantly among different decomposition stages (García-Palacios et al., 2016b). However, these results were obtained by assessing C and N loss, and we are lack of data on whether P loss shares a similar hierarchy of drivers across aquatic and terrestrial ecosystems at the temporal scale.

To address this scientific question, we conducted a two-year field experiment using litterbag method in both aquatic (streams and riparian zones) and terrestrial (forest floors) ecosystems in an alpine forest on the eastern Tibetan Plateau. We chose four kinds of foliar litter from the dominant tree and shrub species [i.e. willow (*Salix paraplesia*), azalea (*Rhododendronlapponicum*), cypress (*Sabina saltuaria*), and larch (*Larixmastersiana*)] that can represent a wide range of initial litter chemistry. Using multigroup comparisons of structural equation modeling (SEM) method (Grace, 2006) by comparing different litter mass loss intervals (i.e., the groups in SEM), we assessed whether the direct and indirect effects of initial litter quality, litter chemical changes, microbial diversity, and environmental factors on P loss vary among different ecosystem types and decomposition stages. We hypothesize that (1) litter P will show similar loss patterns but a higher loss rate in aquatic than in terrestrial ecosystems, and P loss will share a common hierarchy of drivers across different decomposition stages and ecosystems types; (2) environment and microbial diversity control P loss in the early decomposition stages, while initial litter quality will play a major role in late decomposition stages; and (3) the effects of litter chemistry assessed at different decomposition stages (i.e., litter chemical dynamics) on P loss are significant throughout the litter decomposition process.

2. Materials and methods

2.1. Study area

The experiment was conducted at the Long-term Research Station of Alpine Forest Ecosystems, which is located in the Miyaluo Nature Reserve (31°14′–31°19′N, 102°53′–102°57′E, 2458–4619 m a.s.l.), Li County, Sichuan Province, southwestern China. This region is a transitional and typical winter-cold zone between the Tibetan Plateau and the Sichuan Basin. The long-term (30 years) mean annual temperature is 3 °C ranging from −18 °C to 23 °C, and the mean annual precipitation is 850 mm. The study area is an alpine coniferous forest, with the