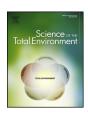
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Foliar litter decomposition in an alpine forest meta-ecosystem on the eastern Tibetan Plateau



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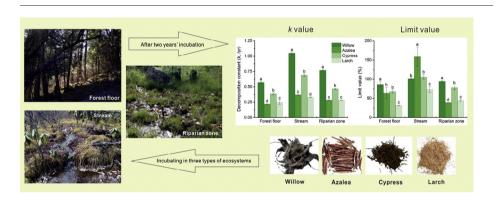
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HIGHLIGHTS

Litter species and ecosystem type significantly affected the decomposition pattern.

- Ecosystem type noticeably affected the litter decomposition rate and extent.
- Micronutrients (e.g., Mn, Ca and Mg) are important litter traits controlling decomposition.
- Local-scale environmental factors may be more crucial than previously thought.

GRAPHICAL ABSTRACT



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ABSTRACT

Litter decomposition is a biological process fundamental to element cycling and a main nutrient source within forest meta-ecosystems, but few studies have looked into this process simultaneously in individual ecosystems, where environmental factors can vary substantially. A two-year field study conducted in an alpine forest meta-ecosystem with four litter species (i.e., willow: Salix paraplesia, azalea: Rhododendron lapponicum, cypress: Sabina saltuaria, and larch: Larix mastersiana) that varied widely in chemical traits showed that both litter species and ecosystem type (i.e., forest floor, stream and riparian zone) are important factors affecting litter decomposition, and their effects can be moderated by local-scale environmental factors such as temperature and nutrient availability. Litter decomposed fastest in the streams followed by the riparian zone and forest floor regardless of species. For a given litter species, both the k value and limit value varied significantly among ecosystems, indicating that the litter decomposition rate and extent (i.e., reaching a limit value) can be substantially affected by ecosystem type and the local-scale environmental factors. Apart from litter initial acid unhydrolyzable residue (AUR) concentration and its ratio to nitrogen concentration (i.e., AUR/N ratio), the initial nutrient concentrations of phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) were also important litter traits that affected decomposition depending on the ecosystem type.

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1. Introduction

Plant litter decomposition is not only one of the most important ecosystem processes for nutrient cycling in the biosphere (Berg and McClaugherty, 2014), but also a main nutrient source within forest meta-ecosystems, defined here as a set of individual ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries (Loreau et al., 2003). Movements of inorganic nutrients, detritus and living organisms may be common within a forest meta-ecosystem, as local individual ecosystems are never totally isolated in space because they receive and lose considerable amounts of dead and living organic matters in many forms and from various processes (Polis et al., 1997). Litter decomposition is one of the potential pathways connecting and driving carbon (C) and nutrient cycling across individual ecosystems, where environmental factors can vary remarkably. As local-scale environmental factors can be of great importance for the litter decomposition process (Bradford et al., 2016), elucidating the spatial and temporal patterns and environmental controls of litter decomposition in different individual ecosystems within a meta-ecosystem is of great importance both for future studies on the connections between these ecosystems and for a better understanding of the effects of environmental factors on the litter decomposition process. However, current studies mainly focus on the process of litter decomposition in a specific ecosystem type, such as on the forest floor (García-Palacios et al., 2016b; He et al., 2016) or in streams (Abril et al., 2016; Ferreira and Canhoto, 2015). Few studies (Nakajima et al., 2006) have explored this process simultaneously in the individual ecosystems within a meta-ecosystem, e.g., integrating both aquatic and terrestrial ecosystems into the same litter decomposition framework.

Streams are widely spread across forests and represent an active zone of material exchange between land and water, providing the major output pathway of energy and material from forests to downstream areas (Graça et al., 2015). Plant litter is a pivotal component of stream food webs and ecosystem functioning, particularly in forest meta-ecosystems (Gessner et al., 2010; Wallace et al., 1997), and its decomposition in streams can contribute significantly to the global C cycle (Battin et al., 2008; Tranvik et al., 2009). Similarly, riparian zones are important domains in forest meta-ecosystems, because they are transitional zones for nutrient transfer and energy flow between forest and river ecosystems (Chapin et al., 2011). The decomposition of allochthonous organic materials (e.g., foliar litter) in riparian zones is often a critical factor for the continued availability of nutrient resources in such nutrient-limited environments (Aerts and de Caluwe, 1997; Alvarez and Guerrero, 2000). Hence, investigations of litter decomposition in streams and riparian zones compared to forest floors will provide baseline data for further studies of the interconnections between individual aquatic and terrestrial ecosystems within a forest meta-ecosystem.

Litter decomposition is usually considered hierarchically regulated by three interacting factors: climate, litter quality, and soil organisms (Bünemann et al., 2004; Coûteaux et al., 1995; García-Palacios et al., 2013). Climate has long been considered the primary broad-scale control on litter decomposition (Coûteaux et al., 1995), while recent work suggests that plant litter traits may predominate (Bachega et al., 2016; Cornwell et al., 2008; Hättenschwiler et al., 2011; Makkonen et al., 2012). For example, Berg et al. (2010) found that manganese (Mn) concentration has a dominant and positive influence on litter decomposition extent (expressed as limit value), governing the estimated stable or very slowly decomposing residual amount of locally collected pine litter. However, more recent studies suggested that local-scale factors may also be of great importance for litter decomposition (Bradford et al., 2014, 2016). Although litter decomposition in streams is generally constrained by the same factors as litter decomposition on forest floors (Wantzen et al., 2008), the environment in streams is characterized by several fundamental differences (e.g., temperature range, water availability, abrasion by sediment transport, and unidirectional transport) from that of terrestrial systems, which may preclude generalizations (Graça et al., 2015). Similarly, in riparian zones, there is considerable evidence for the importance of soil properties, such as temperature and dissolved nutrient concentration, to plant litter decomposition (Pagioro and Thomaz, 1999; van der Valk et al., 1991). Under climatically similar conditions, litter at flooded sites has a higher decomposition rate than at adjacent upland sites (Furch and Junk, 1997; Merritt and Lawson, 1992), but the decomposition of plant litter can also be slowed down in riparian zones that form histosols (Qualls and Richardson, 2000). These unique environmental factors in streams and riparian zones suggest that litter decomposition in these ecosystems may exhibit different decomposition patterns from those on forest floors. The objective of this study was to determine and compare litter decomposition patterns in different ecosystems within an alpine forest meta-ecosystem to test the effects of local-scale environmental factors on the litter decomposition process.

Alpine forests on the eastern Tibetan Plateau are typically cold ecosystems experiencing considerable seasonal freezing and thawing events, and seasonal changes are associated with distinct changes in environmental conditions (Wu et al., 2010, 2014). Distinctive temperature fluctuation patterns are common at this site, and the dynamic changes in freeze-thaw and related environmental factors may contribute differently to litter decomposition in different periods. Given the buffered temperature and strong abrasion effect in streams, as well as the proposed main factors affecting litter decomposition, we hypothesized that (i) the litter decomposition rate will be affected by both litter species and ecosystem type, showing decomposition rates for a given litter species in different ecosystems in the order stream > riparian zone > forest floor; (ii) the litter mass-loss rate can vary among different decomposition periods and can be affected significantly by local-scale environmental factors.

To test these hypotheses, a two-year field litter decomposition experiment was conducted in an alpine forest meta-ecosystem on the eastern Tibetan Plateau, China. The litter decomposition constant, limit value, and mass-loss rate from the foliar litter of four dominant riparian species (willow: *Salix paraplesia* C.K. Schneid, azalea: *Rhododendron lapponicum* (L.) Wahlenb, cypress: *Sabina saltuaria* (Rehder and E.H. Wilson) W.C. Cheng and W.T. Wang, and larch: *Larix mastersiana* Rehder and E.H. Wilson) that vary widely in chemical traits were investigated for two years. We focused on the effects of litter species, ecosystem type, and related environmental factors on the litter decomposition process, the effects of microorganisms were not examined in the present work.

2. Materials & methods

2.1. Site description

The experiment was conducted in the Long-term Research Station of Alpine Forest Ecosystem, which is located in the Bipenggou Valley of 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 typical winter-cold zone situated between the Tibetan Plateau and the Sichuan Basin and is regularly exposed to subfreezing temperatures, with a mean annual temperature of approximately 3 °C and a temperature range from -18 °C to 23 °C. The annual rainfall is approximately 850 mm. The freeze-thaw season starts in November, and water and soils are frozen in the riparian zones of this region from early November to April, with thawing in late April of the following year (Zhu et al., 2013). The alpine forest is a coniferous forest; the dominant tree species in the forest are larch, cypress, and fir (Abies faxoniana Rehder and E.H. Wilson) interspersed with shrubs of azaleas (Rhododendron spp.), willow, and barberry (Berberis sargentiana C.K. Schneid). The herbaceous plants are mainly fern (Cystopteris montana (L.) Bernhardi ex

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