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Mixing litter from deciduous and evergreen trees enhances decomposition in a subtropical karst forest in southwestern China

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ABSTRACT

In the karst region of southwestern China, mixed evergreen and deciduous broad-leaved forest is typical vegetation, differing remarkably from the evergreen broad-leaved forest developed in non-karst regions in the same latitudinal zone. Litter input from deciduous trees influences the characteristics of the litter layer, which could affect decomposition dynamics. We evaluated the role of deciduous trees in regulating the decomposition of mixed leaf litter in a karst forest. Four species richness treatments (one, two, four and six species) were designed to evaluate the decomposition rates of litter mixtures for two years. The ratio of deciduous to evergreen species numbers was 1:1 in all mixtures. Litter mass loss was positively correlated with initial nitrogen concentrations and negatively correlated with carbon:nitrogen ratios, suggesting that mass loss was controlled by nitrogen concentration of the litter mixture. Litter mixing accelerated the mass loss by 5.0% and enhanced nutrient release by 4.8%–26.2% for different elements. Synergistic effects in the four-species mixture were usually strongest and increased over time. Although individual litter species within the mixtures showed idiosyncratic responses to litter species richness, mixing effects enhanced decomposition of evergreen litter species more than deciduous species. This study suggests that species composition was more important than species richness in driving non-additive effects on decomposition in this forest. Deciduous trees in karst ecosystems significantly contribute to nutrient cycling, through enhancing the decomposition of evergreen leaf litter.

1. Introduction

Karst topography is widespread globally and covers about 12% of the world's land area (Liu, 2009). The karst landscape of southwestern China, occupying more than 500 000 km^2, is one of the most typical landscapes developed on carbonate bedrock in the world and is characterized by extremely slow soil formation from the underlying limestone and very shallow and patchy soils with a low water retention capacity (Zhu, 1997; Liu, 2009). It may take more than 10 000 years to form 1 cm of topsoil in the area (Wei, 1996), and the mean depth of topsoil on karst hills is only about 2–9 cm (Zhang and Wang, 2009; Liu et al., 2013). Because plants grow in a limited soil volume, they have access to smaller amounts of nutrients.

The typical vegetation developed on the carbonate bedrock in the subtropical region of China is mixed evergreen and deciduous broad-leaved forest, which remarkably differs from the representative vegetation type in non-karst regions in the same latitudinal zone, the evergreen broad-leaved forest (Guo et al., 2011). Deciduous trees often dominate karst forests due to better adaptive strategies to drought stress than evergreen trees (Liu et al., 2010, 2011a), and play an important role in nutrient cycling of karst ecosystems. For example, leaves from deciduous species accounted for 35%–66% of annual leaf litter fall in karst forests (Wei et al., 2009; Yu et al., 2011). Leaf litter of deciduous species usually shows higher nutrient concentrations (Liu et al., 2014) and specific leaf area than evergreen leaf litter. The large input of litter from

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deciduous trees into this system substantially influences characteristics of the litter layer, which can affect litter decomposition dynamics, such as nutrient transfer among litter types. However, the role of deciduous trees in regulating the decomposition process of mixed litter in karst forests has not been addressed, and is urgently needed to improve our understanding of nutrient cycling, productivity and stability of karst ecosystems.

Litter mixing effects on decomposition may be additive (i.e., decomposition dynamics of a litter mixture can be predicted from single-species dynamics) or non-additive, depending on the ecosystem under investigation (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Gessner et al., 2010). Several studies have demonstrated that mixing litter can either accelerate or decelerate decomposition (Hector et al., 2000; Gartner and Cardon, 2004; Hättenschwiler and Gasser, 2005; Hättenschwiler et al., 2005). The underlying mechanisms include nutrient transfer among litter types, complementary resource use, stimulatory or inhibitory influences of specific litter compounds, creation of a favorable micro-environment for decomposition and interactions across trophic levels (Hättenschwiler et al., 2005; Gessner et al., 2010). However, effects of litter mixtures from deciduous and evergreen trees on the decomposition process in subtropical karst forests remain unclear. There is little knowledge on litter decomposition rates of different plant species for this area (Wang and Xu, 2013). Given that leaf litter from deciduous species usually has a higher decomposition rate than that from evergreen species (Cornwell et al., 2008), the high richness of deciduous trees, to some extent, could accelerate the nutrient turnover of karst ecosystems even if mixing effects are additive. Non-additive effects on decomposition are also possible in karst forests because mixing litter from deciduous and evergreen species creates a blend of materials with diverse leaf structures, chemical characteristics and alters the micro-environment in which decomposition occurs (Hector et al., 2000; Schimel and Hättenschwiler, 2007). As fast-decomposing species with high litter quality usually accelerate decomposition rates of slow-decomposing species in litter mixtures through nutrient transfer (Hättenschwiler et al., 2005), we firstly hypothesized that leaf litter of deciduous trees would enhance the decomposition of evergreen leaf litter, leading to a positive non-additive effect.

Despite extensive testing in different ecosystems, the relationship between species diversity and litter decomposition remains controversial (Hättenschwiler et al., 2005; Gessner et al., 2010). Previous studies of litter mixture decomposition in temperate and tropical forests focused on mass loss and nitrogen (N) dynamics, ignoring the cycling of other essential nutrients (Hättenschwiler et al., 2005; Bonanomi et al., 2010). Subtropical karst forests support a remarkably high biodiversity (Zhu, 1993) despite their shallow topsoils, leading to the hypothesis that litter decomposition is important for recycling many essential nutrients so that they are bioavailable for the plant community, but this remains to be determined. We secondly expected that increasing litter species richness would strengthen the synergistic effects on litter decomposition. Moreover, recent studies suggested that incubation time significantly influences the mixing effects, and should be accounted for in the future (Lecerf et al., 2011; Montané et al., 2013; Wu et al., 2013). We also expected that non-additive effects would change with decomposition time in karst forests due to the temporal changes in litter quality, microclimate and dominant decomposers during the decomposition process.

In this study, we selected three deciduous and three evergreen trees with different litter qualities from a typical karst forest in southwestern China, to examine the mixing effects on mass loss and multiple nutrient dynamics of decomposing litter mixtures. Different litter mixing treatments with species numbers in the range of 1–6 were designed to examine how litter species richness affected mixing effects.

2. Materials and methods

2.1. Study site

This study was carried out at Puding Karst Ecosystem Research Station, Chinese Academy of Sciences in Guizhou Province, China (26°16′1″N, 105°46′39″E). Long-term mean annual precipitation and temperature of this region are 1390 mm and 15.1 °C, respectively. Annual precipitation was 1399.5 mm in 2012 and 725.4 mm in 2013, about 70% of which fell during May–August (Fig. S1). Typical vegetation is mixed evergreen and deciduous broad-leaved forest, dominated by *Platycarya longipes*, *Quercus aliena*, *Lithocarpus confinis* and *Itea yunnanensis*. Common species also include *Carpinus pubescens*, *Celtis bungeana*, *Cinnamomum bodinieri*, *Machilus cavaleriei* and *Pittosporum brevicalyx*. *Platycarya longipes*, *Quercus aliena*, *Carpinus pubescens* and *Celtis bungeana* are deciduous trees and the others are evergreen. The deciduous trees shed their leaves every winter and are dormant during the dry period. The mean height of the tree canopy is about 15 m and mean canopy coverage is about 85%. The soil type is limestone soil, according to Chinese soil genetic classification, or similar to Rendoll according to USDA Soil Taxonomy (Soil Survey Staff, 1999). The topsoil in this region is extremely shallow, in the range of 0–30 cm deep. The soil pH in the study area was 6.8 and soil organic carbon (C) concentration was 77.36 g kg^{-1}. Nutrient concentrations in the soil were as follows (all g kg^{-1}): N 5.60, phosphorus (P) 0.68, potassium (K) 14.83, calcium (Ca) 12.07, iron (Fe) 36.40, magnesium (Mg) 9.86, manganese (Mn) 0.63 and sulfur (S) 1.12.

2.2. Plant material and experimental design

Six broad-leaved trees naturally occurring in the karst forests were selected: three deciduous (*C. pubescens*, *P. longipes* and *Q. aliena*) and three evergreen trees (*I. yunnanensis*, *L. confinis* and *M. cavaleriei*). At the beginning of December 2011 when most of the litter fall occurred, fresh and intact leaf litter was directly collected from the forest floor, air-dried for 10 d and stored for a week at room temperature (15–25 °C). The chemical characteristics of these litter types are described in Table 1.

An experiment was conducted using the litter bag method in the field. Each nylon litter bag (15 cm × 20 cm, 1 mm mesh) was filled with 10 g of air-dried leaf litter. Subsamples of initial litter were oven-dried (65 °C for 48 h) to calculate the correction factor for converting air-dried mass to water-free dry mass. This experiment included nine types of litterbags: (1) six monospecific types from each species; (2) a mixture of two species (a deciduous and an evergreen tree, *P. longipes* and *I. yunnanensis*); (3) a mixture of four species (two deciduous and two evergreen trees, *P. longipes*, *Q. aliena*, *I. yunnanensis* and *L. confinis*); and (4) a mixture of all the studied six species (three deciduous and three evergreen trees). The ratio of deciduous:evergreen species numbers was 1:1 in all mixtures. The priority of species selection in the mixtures was based on their dominance in karst forests. For example, *I. yunnanensis* was included in all three litter mixtures and *M. cavaleriei* only in the six-species mixture because *I. yunnanensis* is the most dominant evergreen species in the forest and constitutes the largest proportion of evergreen litter on the forest floor, and *M. cavaleriei* is the least dominant evergreen species. All mixtures were filled with individual litter species in equal proportions. On 23 December 2011, 288 litterbags (nine types × four replicates × eight sampling dates) were placed on the forest floor in four replicate blocks and retrieved every three months during the