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Does species richness of subtropical tree leaf litter affect decomposition, nutrient release, transfer and subsequent uptake by plants?

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During leaf litter decomposition, nutrients are released, can be transferred among different litter species, are metabolized by soil organisms and are taken up by plants again. However, it remains unclear to which extent leaf litter species richness affects these processes of nutrient cycling, and whether effects on one of those processes propagate to the subsequent one. We established a common garden decomposition experiment in a Chinese subtropical secondary forest, to trace two essential nutrients during decomposition and their uptake by plants along a litter species diversity gradient. Unlabelled, and ^{15}N and Li (as surrogate for K) labelled leaves of three native tree species were used to create replicated 1-, 2- and 3-species mixtures, each with one species labelled per mixture. Litter mixtures were placed in mesocosms with one growing herbaceous phytometer plant. Over six months, litter and phytometer plants of each mixture were sampled at four points in time and the different process steps of nutrient dynamics were determined. Our results showed species and nutrient specific decomposition dynamics, which propagated through the processes of mass loss, nutrient release and transfer among species, and nutrient uptake dynamics of phytometer plants. However, we found no litter species diversity effects along the different litter decomposition processes. Rather specific diversity effects occurred in few cases at different points in time for mass loss, Li release and transfer dynamics. These effects were not caused by nutrient transfer from labelled to unlabelled litter, suggesting that species identity effects on decomposer dynamics may outweigh effects of nutrient transfer among litter species in mixtures. Further, the observed litter species diversity effects did not affect the ^{15}N uptake of phytometer plants. Hence, the influence of species diversity on nutrient cycling and plant available nutrient stocks is mainly determined by the amount and variety of chemical compounds that different species exhibit and release to the soil.

1. Introduction

The significance of plant biodiversity for terrestrial ecosystem functioning and the delivery of ecosystem services has been pointed out over the last decades, emphasizing a strong biotic control over ecological processes (e.g. Hooper et al., 2005; Cardinale et al., 2012; Tilman et al., 2014). Initially focusing on the consequences of biodiversity loss on productivity, many studies now show that plant species diversity and functional composition of communities strongly affect a large variety of ecosystem properties and processes. Among these, decomposition of dead organic matter is a key function as it affects nutrient cycling, soil formation and carbon storage (Johnson and Todd, 1998; Berg and McClaugherty, 2008). A range of experiments has evaluated the effects of plant diversity on decomposition of leaf litter, demonstrating highly species-specific litter decomposition rates that depend on litter quality traits such as C:N or lignin:N ratios, secondary metabolites or morphological characteristics (e.g. Berg et al., 1992; Cardisch and Giller, 1996; Pérez-Harguindeguy et al., 2000). Decomposition rates of litter species in mixtures often differ from the average ones in their component monocultures, i.e. they are non-additive (e.g. Seastedt, 1984; Chapman et al., 1988; Ball et al., 2008). Thus, some leaves decompose faster (synergistic effects) or slower

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(antagonistic effects) than one would expect from respective monoculture decomposition rates or show idiosyncratic responses (non-linear richness effects) (Gartner and Cardon, 2004; Hättenschwiler et al., 2005a). Litter species richness effects can be caused by (1) an increased attractiveness of low quality litter as a food source for decomposers if mixed with high quality litter, via nutrient transfer among leaves of different species, (2) variations of species-specific litter compounds with either stimulating or inhibiting properties, (3) alteration of microclimate and habitat structures through differences in leaf shapes and toughness, and (4) changes in the abundance or activity of certain decomposer guilds, and (5) feedback mechanisms among different decomposer guilds (reviewed by Hättenschwiler et al., 2005a).

Seeing litter decomposition simply as the rate of mass loss or CO_2-production, as done in most studies, does not adequately reflect the underlying complex, time-dependent phenomena such as leaching of soluble compounds, physical breakup, and biotic shredding, enzymatic breakage of complex compounds, release and transfer of elements among different litter types through leaching and decomposers (e.g. reviewed in Cardisch and Giller, 1996; Berg and McClaugherty, 2008). Potential diversity effects on some of these individual processes, such as the nutrient transfer among litter species in mixtures or the subsequent nutrient uptake by plants, have been rarely considered and remain unclear. Nutrient concentrations of decomposing litter species in mixtures can increase or decrease compared to their respective monocultures (e.g. Briones and Ineson, 1996; McTiernan et al., 1997; Kaneko and Salamanca, 1999). One of the main potential mechanisms is the transport of nutrients among different litter species by leaching and diffusion (Fyles and Fyles, 1993; McArthur, 1994; Briones and Ineson, 1996) or transport by fungal hyphae (Frey et al., 2003; Tiunov, 2009; Lummer et al., 2012) which can improve decomposability of more recalcitrant litter species. Further, nutrients may partially originate from external sources (e.g. Peterson and Rolfe, 1982), such as fungal colonization (Caner et al., 2004) and fungal transport of deposited N from soil (Fahey et al., 2011). Whether subsequent richness effects on litter mass loss and nutrient release rates affect the nutrient uptake by plants still remains unclear.

The study of such detailed decomposition processes and their underlying mechanisms is methodological challenging and ideally requires 1) a separation of the leaf litter according to species and 2) the use of isotope tracer elements to determine the nutrient sources and sinks. Common tracer elements to follow nutrients through the plant-soil system are stable isotopes like ^{15}N, or rare elements which serve no apparent vital biological function but have similar chemical properties as other elements essential for plant growth. Lithium (Li), for example, can be used to quantify plant uptake of potassium (K) (Gockele et al., 2014) as they share K^+ transport carriers in roots (Fitter, 1986). By using tracers it is also possible to detect and quantify element transfer from labelled (donor) to unlabelled (acceptor) leaf litter (e.g. Schimel and Hättenschwiler, 2007; Lummer et al., 2012). For example, Lummer et al. (2012) revealed nitrogen transfer through fungal hyphae from nitrogen-poor to nitrogen-rich leaf litter. These results challenge the traditional view of nitrogen transfer being one-directional from nitrogen-rich to nitrogen-poor litter species, and suggest that nutrient transfer mechanisms among litter species are not completely understood. Tracer elements have also been used to follow the transport of nutrients from decomposing leaves to soil and plants (e.g. Zeller et al., 2000, 2001) including the uptake by decomposer organisms (e.g. Caner et al., 2004). Zeller et al. (2000, 2001) documented a 1:1 relationship between litter mass loss and nitrogen release. After two years of litter decomposition, 35% of the nitrogen remained in the recalcitrant part of the litter, 50% reached the topsoil and about 2–4% was incorporated into 15–50 year old beech trees (Zeller et al., 2001). However, these studies focused on pure or low-diverse litter mixtures only, neglecting litter mixtures, and macro-nutrients other than nitrogen. Although these studies provide important insights into mechanisms of nutrient dynamics, they are thus only of limited use for the understanding of litter diversity effects on decomposition and nutrient cycling, especially within litter mixtures.

Here, we specifically addressed the question of how litter species richness affects overall litter decomposition rates (i.e. mass loss), nutrient release and transfer among leaves in mixtures and the subsequent uptake by plants. We conducted a field litter decomposition experiment in the subtropics of south-east China and focused on the macro-nutrients N and K, which were represented by the tracers ^{15}N and Li, to include one immobile and one highly mobile element in leaf litter (Briones and Ineson, 1996; Yang et al., 2004). ^{15}N and Li labelled and unlabelled, senescent leaves of three native tree species were incubated in situ as monocultures, 2- and 3-species mixtures in mesocosms and decomposition rates and tracer contents in the labelled and unlabelled litter species were followed over 24 weeks. We further used a phytometer approach to quantify nutrient transfer dynamics from leaves into plants.

We tested three hypotheses: (i) Temporal dynamics for mass loss, nutrient release, transfer and uptake by plants are highly species- and nutrient specific. Due to strong functional links among these processes involved in decomposition, species identity effects will be consistent for these processes. (ii) Litter species richness positively affects litter mass loss and nutrient dynamics. These richness effects will propagate to subsequent processes, and will therefore also be found for nutrient release and uptake by phytometer plants. (iii) In case of litter species richness effects on litter mass loss, nutrient release and the uptake by indicator plants we expect richness effects also on nutrient transfer among litter species. This expectation is based on the fact that nutrient transfer among litter species has been hypothesized to be a key mechanism explaining diversity effects on decomposition processes (Hättenschwiler et al., 2005a).

2. Materials and methods

2.1. Study site

We conducted a litter decomposition experiment from Apr. (2012) to Oct. 2012 in Xingangshan, Jiangxi province in south-east China (29.12″ N, 117.91" E). The climate is subtropical with warm, wet summers and cold, dry winters. Mean annual temperature is 16.7 °C and annual precipitation averages 1821 mm (Yang et al., 2013). The field site was situated on a mountain ridge in a small, natural mixed forest stand with *Castanopsis calesii* (Hemsley) Hayata, *Loropetalum chinense* (R. Brown) Oliver, *Eurya muricata* Dunn, *Lithocarpus glaber* (Thunberg) Nakai and *Castanopsis eyrei* (Champion ex Bentham) Tutcher as dominant tree species (Eichenberg, personal communication). Besides few plants of *Carex* spec., no herb layer existed. The site is situated on an Endoleptic Cambisol (IUSS Working Group WRB, 2015) on silt loam (24% sand, 50% silt and 26% clay) with a mean pH in the topsoil layer (0–5 cm) of 4.7 (Seitz et al., 2015).

2.2. Production of labelled leaf litter

We established a nursery with the native tree species *Sapindus saponaria* Linnaeus, *Quercus acutissima* Carruthers and *Schima superba* Gardner & Champion to produce both labelled and unlabelled leaf litter. A total of approx. 6000 3–6 year old trees of all three species were planted in spring 2011. One third of the trees was watered twice with 200 ml 0.001 M $^{15}NH_4Cl$ and 0.236 M LiCl,