Soil Biology & Biochemistry 77 (2014) 121–128

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Litter mixture effects on decomposition in tropical montane rainforests vary strongly with time and turn negative at later stages of decay

Olaf Butenschoen*, Valentyna Krashevska, Mark Maraun, Franca Marian, Dorothee Sandmann, Stefan Scheu

J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Berliner Str. 28, D-37073 Göttingen, Germany

ARTICLE INFO

Article history:
Received 2 March 2014
Received in revised form
18 June 2014
Accepted 25 June 2014
Available online 3 July 2014

Keywords:
Ecuador
Litter decomposition
Litter diversity
Litter mixture
Litterbag study
Tropical montane rainforest

ABSTRACT

In a litterbag study in a tropical montane rainforest in Ecuador we assessed the impact of leaf litter species identity and richness on decomposition. We incubated leaf litter of six native tree species in monocultures and all possible two and four species combinations and analysed mass loss over a period of 24 months. Mass loss in monocultures averaged 30.7% after 6 month and differed significantly between species with variations being closely related to initial concentrations of lignin, Mg and P. At later harvests mass loss in monocultures averaged 54.5% but did not vary among leaf litter species and, unexpectedly, did not increase between 12 and 24 months suggesting that litter converged towards an extremely poor common quality retarding decomposition. After 6 months mass loss of leaf litter species was significantly faster in mixtures than in monocultures, resulting in synergistic non-additive mixture effects on decomposition, whereas at later harvests mass loss of component litter species was more variable and leaf litter mixture effects differed with species richness. Mass loss in the two species mixtures did not deviate from those predicted from monocultures, while we found antagonistic non-additive mixture effects in the four species mixtures. This suggests that litter species shared a poor common quality but different chemistry resulting in negative interactions in chemically diverse litter mixtures at later stages of decomposition. Overall, the results suggest that interspecific variations in diversity and composition of structural and secondary litter compounds rather than concentrations of individual litter compounds *per se*, control long term leaf litter decomposition in tropical montane rainforests. Plant species diversity thus appears to act as a major driver for decomposition processes in tropical montane rainforest ecosystems, highlighting the need for increasing plant conservation efforts to protect ecosystem functioning of this threatened biodiversity hotspot.

1. Introduction

Ecosystems worldwide are facing an unprecedented and largely irreversible loss of species diversity, which has been estimated to be 100 to 1000 times higher than average background rates (Butchart et al., 2010). The rapid loss of species diversity has prompted extensive research on biodiversity functioning relationships across a variety of ecosystems (Balvanera et al., 2006; Cardinale et al., 2011). After about three decades of empirical work there is consensus that biodiversity influences a magnitude of ecosystem functions and services including freshwater purification, net primary productivity, pollination and biocontrol (Díaz et al., 2006; Cardinale et al., 2012). In addition, decomposition of leaf litter, a key process controlling the flux of carbon between the biosphere and the atmosphere, is related to various aspects of diversity, and previous studies and syntheses found that mixing of leaf litter often results in synergistic or antagonistic non-additive effects on decomposition (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Srivastava et al., 2009; Cardinale et al., 2012; Handa et al., 2014). Different mechanisms have been reported to explain non-additive mixture effects on decomposition. For example, mixing of leaf litter of divergent physical or chemical quality can result in active translocation and leaching of nutrients and inhibitory compounds between litter species (Schimel and Hättenschwiler, 2007; Lummer et al., 2012; Handa et al., 2014), in changes of community composition and activity of microorganisms

* Corresponding author.
E-mail address: obutens@gwdg.de (O. Butenschoen).

http://dx.doi.org/10.1016/j.soilbio.2014.06.019
0038-0717/

and detritivores (Vos et al., 2011; Chapman et al., 2013), and in the modification of microclimatic conditions (Makkonen et al., 2013). All these mechanisms can alter decomposition rates of leaf litter mixtures, and the contribution of each varies with climate, soil community composition and with leaf litter species included in mixtures.

Due to its eminent importance in the global carbon cycle, considerable efforts were made towards a better understanding of factors driving leaf litter decomposition in tropical forests, and previous studies improved the knowledge on the role of detritivores, leaf litter chemical and physical quality and climate variables (Powers et al., 2009; Wieder et al., 2009; Coq et al., 2010). However, despite supporting the highest diversity of plants on Earth (Joppa et al., 2011) only few experiments have investigated decomposition of leaf litter mixtures in tropical forests. In addition, most studies included only a limited number of leaf litter species and single harvests (but see Giesselmann et al., 2010, 2011). Such experiments may have missed previously observed shifts in magnitude and direction of non-additive leaf litter mixture effects on decomposition in response to alteration in microclimatic conditions, detritivore community composition or changes of leaf litter quality as decomposition proceeds (Gartner and Cardon, 2004; Srivastava et al., 2009; Lecerf et al., 2011). However, these mechanisms might be prevalent in species rich tropical forests as high plant species diversity creates litter mixtures consisting of a large number of compounds that differ in toxicity and degradability (Coley and Barone, 1996; Coq et al., 2010). A variety of compounds each with different decay rates inhibit or promote colonization and feeding activity of detritivores, alter litter quality due to transfer and leaching of nutrient and secondary compounds, and impact trophic interactions at various stages of decomposition with potentially cascading effects on leaf litter decomposition (Hättenschwiler et al., 2005; Gessner et al., 2010). Understanding leaf litter mixture effects on decomposition in tropical forests and information about shifts in magnitude and direction in the long term thus is essential to reliably predict how changes in plant diversity impact carbon cycling and nutrient dynamics in this major component of the global carbon cycle.

Most studies on leaf litter mixture effects on decomposition in the tropics have been conducted in lowland forest (Scherer-Lorenzen et al., 2007; Hättenschwiler and Jørgensen, 2010; Barantal et al., 2011). Little is known about how leaf litter species diversity affects decomposition in tropical montane forests (but see Illig et al., 2008), although montane plant species diversity is suggested to be more vulnerable to global change agents than vegetation in lowland tropical forests (Foster, 2001). For instance, most montane vegetation in the tropics occupies relative narrow elevation ranges, and small changes in temperature will require large upslope migration to remain within their climatic envelope (Still et al., 1999). Upslope range shifts of lowland plant species in response to climate change is likely to result in marked changes in plant species composition at higher altitudes (Feeley et al., 2012). Moreover, pathogens and herbivores, but also decomposers likely will shift their altitudinal range in response to shifts in temperature and plant species composition, leading to changes in species interactions (Larsen, 2012).

In this study we investigated leaf litter diversity effects on decomposition in one of the richest and most threatened biodiversity hotspot on Earth, the tropical Andes of Ecuador. In a litterbag experiment we studied leaf litter mass loss of six native tree species incubated in monoculture and all possible two and four species combinations over a period of two years and tested the hypotheses that (1) mass loss of leaf litter mixtures generally deviates from that expected from single species incubation (non-additivity), and that (2) the magnitude and direction of non-additive mixture effects on decomposition change as decomposition proceeds.

2. Material and methods

2.1. Study site

The study area is located in southern Ecuador on the northern fringes of the Podocarpus National Park on the eastern slopes of the Andes, south-east of the province capital Loja. The study site is located in the Reserva Biologica San Francisco in the valley of the Rio San Francisco (3°58″S, 79°04′W) at 2000 m a.s.l. The climate is semihumid with 8–10 humid months per year and a mean annual precipitation and temperature of 3500 mm and 15.7 °C, respectively. The soil is a gley cambisol with a pH ($CaCl_2$) of ~3.5 and a thick organic layer of ~15 cm. The tropical montane rainforest at the study site comprises about 280 tree species with Lauraceae, Melastomataceae and Rubiaceae representing the most species rich families. For more details on geology, geomorphology, climate and species diversity at the study site see Bendix et al. (2013).

2.2. Leaf litter species

Freshly fallen senesced leaf litter of six different tree species that are dominant at the study site [*Myrcia pubescens* (Humb. & Bonpl. ex Willd.), *Dictyocaryum lamarckianum* (H. Wendl.), *Cavendishia zamorensis* (A. C. Sm.), *Clusia* spp. (L.), *Cecropia andina* (Cuatrec.) and *Graffenrieda emarginata* (Ruiz & Pav.)] was collected in September 2008. Leaf litter was air dried at room temperature (~25 °C) and pooled by species and across sampling dates. Leaves with signs of herbivory, fungal attack or galls and atypical texture or colour were excluded from the litter pools.

Three randomly taken subsamples out of each leaf litter species pool were used for the determination of initial litter chemistry (Table 1). Litter was dried at 65 °C for three days and separately milled to powder using a ball mill (MM 400; Retsch GmbH, Haan, Germany) to obtain particles <1 mm. Initial concentrations of carbon (C) and nitrogen (N) were analysed by an element analyzer (Vario EL III, Elementar, Hanau, Germany). Initial concentrations of phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were measured by inductively coupled plasma optical emission spectroscopy (ICP-OES, Optima 5300 DV, Perkin Elmer, USA). A methanol:chloroform:water extraction method was used to separate lignin and cellulose from other litter components (Allen et al., 1974).

2.3. Litterbag experiment

The litterbag experiment started in September 2008. A total of 36 litterbag types including each individual species, and all possible two and four species mixtures with all species equally represented in mixtures were made by weighing 12 g of air dried leaf litter into 20 × 20 cm nylon bags. The mesh size of the litterbags was 4 mm which allowed the dominant soil invertebrate species at the study site access to leaf litter during incubation (Illig et al., 2005). Litterbags were prepared in the laboratory and transported in individual plastic bags to the study site. Three replicates of each litterbag type were randomly assigned to each of four blocks using a full randomized block design (36 litterbag types × 4 blocks × 3 harvests = 432 litterbags). Litterbags were separated from each other by at least 30 cm and randomly distributed within blocks spaced at least 40 m. Litterbags were placed on the soil surface and held in place by nails. The natural litter was evenly distributed around litterbags to provide a continuous litter layer. One replicate of each treatment was retrieved after 6, 12 and 24 months from