Applied Soil Ecology 82 (2014) 44–51

Contents lists available at ScienceDirect

Applied Soil Ecology

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

Leaf litter mixtures and neighbour effects: Low-nitrogen and high-lignin species increase decomposition rate of high-nitrogen and low-lignin neighbours

A. Cuchietti [a,*], E. Marcotti [b], D.E. Gurvich [a,b], A.M. Cingolani [a,b], N. Pérez Harguindeguy [a,b]

[a] Multidisciplinary Institute of Plant Biology, CONICET-UNC, Argentina
[b] School of Exact, Physical and Natural Sciences, National University of Córdoba, Argentina

ARTICLE INFO

Article history:
Received 27 November 2013
Received in revised form 3 May 2014
Accepted 3 May 2014
Available online 9 June 2014

Keywords:
Mixing effects
Species identity
Litter quality
Synergistic and antagonistic effects

ABSTRACT

In natural ecosystems plant litter is typically a mixture of more than one species and the rate of decomposition can be faster (synergistic) or slower (antagonistic) than the average of its component species (non-additive effects). We analysed the decomposition rates of two-species mixtures to determine if there were consistent non-additive effects of litter mixing on decomposition and how do they compare with the effects of species identity on mixture decomposition. Then we tested if non-additive effects were consistently associated with the presence of particular species in the mixture, to the combination of Fast- or Slow-decomposing species, or to initial litter quality of mixtures. We found: (a) that species identity was the primary determinant of the decomposition rate of mixtures, and (b) we detected significant, but weak, non-additive effects which were consistently synergistic in the most chemically heterogeneous mixtures. However, slower decomposing species appeared to increase the decomposition rate of faster decomposing species (30 times out of 41 after 2 months of incubation, and 17 times out of 24 after 9 months of incubation). During the initial stages of decomposition, low-lignin mixtures showed mostly synergistic effects, whereas high-lignin mixtures showed antagonistic effects. At more advanced stages of decomposition, mixtures containing species with highest difference in initial N content had more synergistic effects, whereas those with similar initial N content showed both synergistic and antagonistic effects. Our results confirm previous findings about the importance of chemical heterogeneity of mixtures as a driver of decomposition rates of litter mixtures. We propose that mechanisms related to carbon priming may be related to synergistic effects in most heterogeneous mixtures, while nitrogen interaction with carbon may be resulting in antagonistic effects in homogeneous and Slow-decomposing species mixtures.

1. Introduction

Leaf litter quality is known to be a major driver of species decomposition rates across biomes (Swift et al., 1979; Cadisch and Giller, 1997; Cornwell et al., 2008). During early stages of decomposition, nutrients such as nitrogen and phosphorus, and water-soluble compounds have the largest effects, whereas at later stages, lignin is the primary determinant of decomposition dynamics (Berg and Staaf, 1980; Berg, 2000; Rahman et al., 2013). As a consequence of their structural and chemical attributes, each species, when incubated in isolation, has a characteristic decomposition rate ("decomposability", Pérez Harguindeguy et al., 2013). However, in nature litter typically falls and decomposes in mixtures and physicochemical interactions between decomposing leaves can increase or decrease decomposition up to 30% of their expected mass loss (Hättenschwiler and Gasser, 2005; Hoorens et al., 2010a; Tardif et al., 2013). Previous research has shown that mixtures may decompose faster (synergistic effect Seastedt, 1984; Taylor et al., 1989a; Wardle et al., 1997; Salamanca et al., 1998) or slower (antagonistic effect – Zech and Kogel-Knabner, 1994; Dijkstra et al., 2009) than expected relative to the decomposition rates of their component species in isolation, i.e., non-additive effects. Non-additive effects are mainly driven by the mixture components, such as the presence of Fast- or Slow-decomposing species, the magnitude of the difference in decomposability between the mixture components, the physical characteristics of litter that increase its water retention capacity, or the presence of recalcitrant compounds (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Among the

* Corresponding author. Tel.: +54 3516162084.
E-mail address: anibal.cuchietti@gmail.com (A. Cuchietti).

http://dx.doi.org/10.1016/j.apsoil.2014.05.004
0929-1393/

mechanisms proposed to explain synergistic effects on decomposition in heterogeneous mixtures nutrient transfer from litter of high quality to litter of lower quality has been frequently invoked (McTiernan et al., 1997; Kuziakov et al., 2000) but not always confirmed (Staaf, 1980; Klemmedson, 1992; Hoorens et al., 2003). Antagonistic effects have been mainly related to the presence of recalcitrant compounds such as lignin and phenols which may form resistant complexes with proteins (Hättenschwiler and Vitousek, 2000), inhibiting microbial growth and activities (Schimel et al., 1998). In any case, only a small number of those studies separated the components of the mixture after incubation and were able to test if nutrient transfer had indeed occurred or which element (carbon, nitrogen or other) has changed as result of litter mixing (Staaf, 1980; Hoorens et al., 2010b).

Here we present the results of an analysis of decomposition in two-species mixtures incubated in litter-bags in a common garden experiment. By keeping the number of species constant we avoided richness effects (Pérez Harguindeguy et al., 2008). Initially, we determined if there were consistent synergistic or antagonistic effects on the decomposition of litter mixtures (i.e., non-additive effects, Hättenschwiler et al., 2005) and how important they were compared with the effects of species identity. We then tested whether the observed effects were related to specific combinations of Slow- and Fast-decomposing species or to the decomposability of the other component in the mixtures. We also tested whether non-additive effects were related to initial litter quality or decomposability, or to initial heterogeneity in litter quality of each mixture specifically in their content of carbon, nitrogen, and lignin.

We predict that as the heterogeneity of the mixture increases (for example in Slow–Fast mixtures) decomposition rate of the mixture will be greater than expected (synergistic effects). Specifically, we predict that nutrient-rich Fast-decomposing species will transfer nutrients to Slow-decomposing species and thereby increase the decomposition rate of the Slow-decomposing species. Within less heterogeneous mixtures, we expect to find antagonistic effects in Slow–Slow mixtures associated with the presence of recalcitrant compounds, such as lignin. Finally, we predict that if synergistic interactions do occur, after decomposition nitrogen (or carbon) will be lower than expected in at least one of the mixture components. If antagonistic interactions occur, nitrogen (or carbon) will be higher than expected in at least one of the mixture components. In turn, if antagonistic interactions are caused by the formation of nitrogen–lignin resistant complex (Berg, 1986; Camiré et al., 1991), the higher nitrogen in mixtures showing antagonistic interactions should be associated with high initial lignin content in one of the components of that mixture.

2. Materials and methods

2.1. Species selection

We collected leaf material from eight dominant species in the Sierras Chicas, Córdoba Mountains, central Argentina, from May to August 2007, depending on the peak litter fall of each species. The vegetation in the area is characteristic of Chaco montane woodlands (Luti et al., 1979). The climate is temperate/warm temperate, with rainfall concentrated in the warm season (October–April). Annual precipitation is about 850 mm and mean annual temperature is 15 °C (De Fina, 1992). The selected species have leaves that can be clearly classified as either of Fast- or Slow-decomposing species, based on the results of previous studies on decomposition dynamics (Vaieretti et al., 2005). The Fast-decomposing species selected were: *Acalypha communis* Mull. Arg., *Ambrosia tenuifolia* Spreng., *Celtis ehrenbergiana* (Klotzsch) Liebm., and *Zanthoxylum coco* Gillies ex Hook. f & Arn., and the Slow-decomposing species were: *Acanthostyles buniifolius* (Hook. & Arn.) R.M. King & H. Rob., *Lithraea molleoides* (Vell). Engl., *Schizachyrium condensatum* (Kunth) Ness, and *Jarava ichu* Ruiz & Pav. var. *ichu* (Table 1).

2.2. Litter preparation

We collected fresh litter of at least 10 individuals of each of the eight species and determined decomposition rate using the widely used nylon bag technique (Bocok and Gilbert, 1957; Schlesinger, 2000; Vaieretti et al., 2005; Pérez Harguindeguy et al., 2007). We prepared litter-bags following the methodology of Cornelissen (1996) and Pérez Harguindeguy et al. (2013); all litter was air-dried (±0.1 g), weighed, and sealed in 0.3 mm mesh nylon bags. This mesh size excludes most macrofauna which have been shown to contribute little to the decomposition process (Vaieretti et al., 2010) but permits entry of mesofauna, bacteria, protozoa and fungi, the major decomposers in our system. To estimate litter water content, we oven-dried subsamples of air-dried litter at 60 °C for 48 h. Difference in leaf litter mass as a correction factor of the initial dry mass of each sample.

2.3. Decomposition treatments

We made all possible 2-species combinations of the Slow–Slow and Fast–Fast mixtures. Of the 16 possible combinations of Fast–Slow mixtures we randomly selected eight in order to improve the balance in the number of Slow–Slow and Fast–Fast combinations. Overall, we made 20 species combinations: six Slow–Slow combinations, six Fast–Fast combinations, and eight Slow–Fast combinations. We incubated all mixtures, together with individual species samples, on a decomposition bed (1.0 ± 0.1 g for single species; and 0.5 g ± 0.1 of each component species in mixtures). We performed 10 replicates (per period of incubation) of the individual species samples and of each of the two-species combination.

To maintain almost natural and homogeneous conditions during the decomposition process, we incubated all samples simultaneously in a 4 m × 3 m purpose-built decomposition bed (common garden experiment) placed within the area where the litter had been collected. Before placing the litterbags, we cleaned the area by removing the most conspicuous plants, stems and litter. Then, we randomly placed litterbags on the decomposition bed and covered them with natural litter previously removed from the area. We protected the bed from damage by birds and small mammals by placing 3 cm-mesh galvanised metal net over the top of it. Samples remained in the decomposition bed for either 2 or 9 months (total period: January–September 2008, i.e., summer–winter–spring), under the natural temperature and rainfall conditions of the area.

After incubation we retrieved 10 replicates from each species and mixture and stored them at −14 °C until processing in the laboratory. Samples were defrosted and carefully cleaned by manually removing adhering soil and extraneous material. Samples were then dried for 48 h at 60 °C and weighed. Decomposition rate was defined as the percentage of litter mass loss (%LML) during the incubation period.

We were able to separate, and independently weight, only the component species of Slow–Slow and Fast–Slow mixtures. Fast–Fast mixtures were too decomposed and we were unable to identify and separate their component species; hence, they were not included in the analysis of neighbour effect (Hoorens et al., 2010b).

2.4. Litter chemical quality

We determined the initial litter quality of each species and then calculated initial litter quality of mixtures (as the average quality of