



Original article

Decomposition dynamics of mixed litter in a seasonally flooded forest near the Orinoco river

Alessia Bastianoni ^{a,*}, Noemí Chacón ^a, Carlos L. Méndez ^b, Saúl Flores ^a^a Laboratorio de Ecología de Suelos, Instituto Venezolano de Investigaciones Científicas, Km 11, Carretera Panamericana, Altos de Pipe, Venezuela^b Laboratorio de Ecosistemas y Cambio Global, Instituto Venezolano de Investigaciones Científicas, Km 11, Carretera Panamericana, Altos de Pipe, Venezuela

ARTICLE INFO

Article history:

Received 12 November 2014

Received in revised form

20 February 2015

Accepted 22 February 2015

Available online 28 February 2015

Keywords:

*Pouteria orinocoensis**Alibertia latifolia**Acosmium nitens*

Riparian forest

Nitrogen

Phosphorus

Total phenolics

ABSTRACT

We evaluated the decomposition of a litter mixture in the seasonally flooded forest of a tributary of the Orinoco river. This mixture was prepared using three litter species, based on the litter fall rate observed over a complete hydro-period (2012–2013). The mixture loading ratio was 0.46 of *Pouteria orinocoensis* (Sapotaceae), 0.38 of *Alibertia latifolia* (Rubiaceae) and 0.16 of *Acosmium nitens* (Fabaceae). The initial chemical composition of each single litter species was also determined. Litterbags (20 × 20 cm, 2 mm opening) containing either each single species or the mixture, were deployed on the flooded forest soil and sampled after 30, 240, 270, 300 and 330 days. There were differences in initial total N and P concentrations, with *A. nitens* (AN) showing the highest nutrient concentrations (%N_{AN} = 1.86 ± 0.19; %P_{AN} = 0.058 ± 0.008) and *P. orinocoensis* (PO) and *A. latifolia* (AL) the lowest (%N_{PO} = 0.92 ± 0.06; %N_{AL} = 1.04 ± 0.04; %P_{PO} = 0.029 ± 0.005; %P_{AL} = 0.032 ± 0.001). Litter from AN showed the greatest mass loss (55%) and fastest decomposition rate ($k = 0.00185 \pm 0.00028$) while litter from AL and the mixture showed the smallest mass loss (24% and 27% respectively) and the slowest decomposition rate ($k_{AL} = 0.00078 \pm 0.00012$ and $k_{MIX} = 0.00077 \pm 0.00006$). Decomposition rates were significantly and positively correlated with initial N ($r = 0.556$, $p < 0.05$) and P concentrations ($r = 0.482$, $p < 0.05$). Nevertheless, there were no significant differences between the expected decomposition rate and the observed decomposition rate of the mixture (additive response). To test the nature of the additivity, an enhancement factor (f) on decomposition rates for each single species was calculated. The species with the highest and smallest value of f were AN and AL, respectively. The fact that two out of the three species had values significantly different from 1, suggests that the additivity detected in our mixture was a consequence of the counterbalancing of the positive and negative effects of each species over the decomposition of the litter mixture.

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1. Introduction

Leaf-litter decomposition plays an important role in maintaining the fertility and productivity of any forested ecosystem (Vitousek and Sanford, 1986; Cuffney, 1988). It is influenced by climatic conditions as well as species diversity, physiological traits, litter chemical composition, and soil characteristics (Klinge et al., 1983; Pérez Harguindeguy et al., 2000; Gartner and Cardon, 2004; Sariyildiz and Anderson, 2005; LeRoy et al., 2007; Hättenschwiler et al., 2008; Cornwell et al., 2008; Yang and Chen,

2009; Hättenschwiler and Bracht-Jørgensen, 2010; Moore et al., 2011). Since forest litter usually shows mixed species, several authors have recently highlighted the importance of species diversity in leaf litter as a driver of the decomposition process, because of the interactions that different litter species might have with each other, affecting this process as a whole (Gartner and Cardon, 2004; Hättenschwiler and Bracht-Jørgensen, 2010; Ball et al., 2008; Gessner et al., 2010; Handa et al., 2014). The identity and relative abundance of species in leaf litter influences the physical environment in which decomposition takes place and affects the diversity, abundance and activity of decomposer organisms. In fact, leaves from different species can vary in colour, size, shape and surface area, which influences the retention of moisture and radiative-energy by the litter layer. Thus, mixed litter layers can exhibit different microclimatic conditions when compared to single

* Corresponding author. Present address: Instituto de Ciencias de la Tierra, Facultad de Ciencias, Universidad Central de Venezuela, Venezuela.

E-mail addresses: abastiano@ivic.gob.ve, alessia.bastianoni@ciens.ucv.ve (A. Bastianoni).

species litter layers. The physical properties of the litter layer, also influence the micro-habitat structure, and can affect the activity of the decomposer organisms (Hättenschwiler et al., 2005). All of the above, together with differences in chemical composition among litter species, leads to decomposition rates in litter mixtures that cannot be predicted from those of the component species of the mixture (Hättenschwiler et al., 2005; Gessner et al., 2010).

When mixture decomposition rates can be predicted considering the decomposition rate of the individual species and their loading ratio, the decomposition pattern can be defined as additive (Gartner and Cardon, 2004; Ball et al., 2008; Hui and Jackson, 2009). This implies the lack of interactions among the different litter species. In contrast, when the decomposition rate of the mixture cannot be predicted from those of the component species, a non-additive pattern (NA) is influencing the decomposition dynamics of the mixture, and either positive (synergistic) or negative (antagonistic) interactions among the litter species are taking place. According to several authors there are four mechanisms that can explain the non-additive effects of litter mixture over the decomposition process: (i) decomposition enhancement due to nutrient translocation from nutrient enriched to nutrient impoverished litter, probably through fungal hyphae (Salamanca et al., 1998; Schimel and Hättenschwiler, 2007; Schindler and Gessner, 2009); (ii) complementary resource use by the decomposer organisms of specific compounds present in the different litter species in the mixture (Gessner et al., 2010); (iii) changes in the microclimatic conditions and habitat availability in the mixed litter layer (Hättenschwiler et al., 2005) and (iv) interactions across and within the trophic levels involved in the decomposition process (i.e. leaf-litter detritivores, microbial decomposers, and leaf litter) as suggested by Gessner et al. (2010).

Litter species can also differ in the amount and types of chemical constituents, which can either enhance or inhibit the decomposition process. Thus, when in presence of a chemically diverse litter mixture, the activity of the decomposer organisms can either be enhanced by a nutrient enriched litter species, inhibited due to the presence of a specific compound, like polyphenols, or both (Hättenschwiler et al., 2005; Gessner et al., 2010). Co-occurring stimulating and inhibitory effects can cancel out each other, resulting in decomposition rates equivalent to the expected from an additive response (Hui and Jackson, 2009). According to Gartner and Cardon (2004) and to Ball et al. (2008) the most common response when evaluating decomposition dynamics in litter mixtures is non-additivity. Since the loading ratio of each species in the mixture influences decomposition rates, they proposed the decomposition of litter mixtures should be evaluated considering the proportion of each species in the total litter pool.

Many of the studies carried out in tropical ecosystems evaluate the decomposition of litter mixtures in either tropical forest streams (Rueda-Delgado et al., 2006; Moretti et al., 2007; Ferreira et al., 2012) or tropical forest soils (Schimel and Hättenschwiler, 2007; Hättenschwiler et al., 2008; Barantal et al., 2011; Coq et al., 2011). However in the case of tropical seasonally flooded forests, there seems to be a lack of information regarding the influence of litter mixtures over the decomposition process. Previously, Rosales et al. (2002) evaluated the decomposition of a litter mixture in the floodplain forest of a tributary of the Orinoco river. Nevertheless, the species present in the mixture, their loading ratio and its decomposition pattern were not specified in the mentioned study. Taking into account that tropical flooded forests are very fragile ecosystems subjected to anthropogenic disturbances that can modify their biodiversity and functioning (Rodríguez-Altamiranda et al., 2011), it is of great importance to determine the effect of forest species on key ecosystem processes like litter decomposition. Based on this and considering previous reports made by Scowcroft

(1997), Salamanca et al. (1998), Gartner and Cardon (2004), Hui and Jackson (2009) and Barantal et al. (2011) we hypothesized that (i) the decomposition pattern of a litter mixture prepared with litter species in a proportion that matched their natural contribution to the total litter fall, would be additive; and (ii) the presence of species with contrasting chemical composition in the litter mixture could lead to the cancelling out of the positive and negative effects that might be taking place during its decomposition.

2. Materials and methods

2.1. Study zone

Our study site was located at the Mapire river floodplain (Fig. 1), which is a northern tributary of the lower Orinoco river, Venezuela (7° 30'–7° 44' N and 64° 30'–64° 42' E). Annual mean temperature and precipitation are 27.4 °C and 1333 mm respectively, with a dry season between November and April, and a rainy season from May to October (Chacón et al., 2005). Forest communities reflect the longitudinal and perpendicular gradients of flooding depth and duration, associated to topographical variations in the area (Rosales et al., 2002). We selected the forest associated to the maximum flooding zone (MAX), where floods reach up to 12 m and last nearly 8 months (from May to December). During this period, flow of the Mapire river decreases up to a point where the movement of the water surface is negligible, allowing the formation of a transient lake (Vegas-Vilarrúbia and Herrera, 1993a, 1993b). With the beginning of the floods, dissolved oxygen (DO) concentrations also decrease towards the deepest zones of the river and from the surface to the bottom of the transient lake. According to Vegas-Vilarrúbia and Herrera (1993a) DO concentrations at the bottom of the transient lake were low (1.5 mg l⁻¹) and anoxia is plausible within the flooded forest at the sediment–water interface. The alluvial soils in this zone are characterized by a high clay content and low soil organic carbon (C), total nitrogen (N) and phosphorus (P), according to Barrios and Herrera (1994) and Chacón et al. (2005).

The Mapire flooded forest has been classified as an Igapó (i.e. nutrient deficient flooded forests) by Rosales (1988) and Herrera (2013). The main components of the characteristic floristic facies of this area of the forest are *Pouteria orinocoensis* (Aubrév.) T.D. Penn (Sapotaceae), *Couepia paraensis* (Mart. & Zucc.) Benth. (Chrysobalanaceae), and *Acosmium nitens* (Vogel) Yakovlev (Fabaceae). However, other species like *Alibertia latifolia* (Benth) K. Schum (Rubiaceae) are also commonly found. According to Herrera et al. (2009) and Herrera (2013) all species in the Mapire flooded forest are evergreen and several can maintain their leaves under flooded conditions. For instance, *P. orinocoensis* and *Campsiandra laurifolia* (Benth) keep viable leaves under submergence. Nevertheless, species like *A. nitens* lose all of its leaves with the rising of the flood (Herrera et al., 2009).

2.2. Litter collection and chemical characterization

To evaluate the chemical characteristics of the leaf litter that would be used in the litter decomposition experiment (Section 2.3), leaf litter was collected every 15 days throughout the dry season of 2011–2012 (From March 2011 to May 2011 and from November 2011 to March 2012). We used eight litter traps of 0.45 m² fixed at a height of 0.5 m, following a completely randomized design. Since according to Worbes (1997), species in seasonally flooded forest shed most of their leaves at the beginning or the end of the flooding, sampling was carried out during the dry season. Collected litter material was monthly pooled ($n = 7$) and sorted into leaves, seeds, twigs and miscellaneous. Finally, leaves were classified by

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