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Nitrogen dynamics within and between decomposing leaves, bark and branches in *Eucalyptus* planted forests

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ABSTRACT

Nitrogen transfer between litter components is often presented as a key mechanism responsible for the synergistic effect of litter mixtures on decomposition rates. The litter cover is a heterogeneous environment stemming from the input of chemically distinct materials and the transfer of nutrients in this patchy environment is likely to fulfil the specific needs of microbial communities in each micro-environment. Our study aimed to gain insight into the factors controlling N dynamics within and between leaves and woody components in the litter cover. We used ^{15}N labelling to discriminate endogenous and exogenous N and to measure N transfers between three types of litter components, viz. leaves and twigs (L + T), bark and branches, in 162 litter bags for more than 2 years in two Congolese *Eucalyptus* forests with contrasting N status (low-N vs high-N litter). Large quantities of N were released from N-rich L + T at the end of the study while early release of leachable N was only observed for the high-N L + T. Exogenous N was only incorporated in N-poor litter components (bark and branches) and a net increase in N compared to the initial quantities only occurred in the low-N bark. The bi-directional N transfers observed between litter components were most likely microbially-mediated rather than driven by abiotic leaching. Nitrogen transfers were controlled by the N status of both source and sink litter components, contrary to the diffusion theory based on concentration gradient. For a given source, more N was transferred to N-rich than to N-poor sink components. Our results suggested that the microbial community might control both the quantity of N available to be transferred to other microsites and the quantity that is actually transferred, presumably because the potential for N immobilization may be limited in N-poor litter components. Interactions among micro-environments can favor chemical convergence from distinct litter components to humified organic matter along the decay continuum.

1. Introduction

In forest ecosystems, litter fall and subsequent litter decomposition constitute major fluxes of energy and matter in the biogeochemical cycles (Sayer, 2006; Swift et al., 1979). Although the role of climatic conditions, litter biochemical composition and decomposer communities in decomposition processes have been extensively studied (Aerts, 1997; Couteaux et al., 1995; Zhang et al., 2008), predicting the decomposition rates of forest litter remains a challenging task. A major reason is probably the patchy nature of litter cover and more particularly, the chemical diversity among plant organs and tree species in forest ecosystems. In most cases, litter mixtures combining several species decompose at different rates from what would be predicted from the dynamics of each species separately (Blumfield et al., 2004; Gartner and Cardon, 2004). Non-additive litter decomposition indicates that interactions can occur between micro-environments stemming from the input of chemically distinct litter components (Cuchietti et al., 2014). In this heterogeneous environment, the transfer of nutrients between decomposing litter components is likely to play a

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major role in the decomposition process, fulfilling the specific needs of microbial communities in each micro-environment (Hättenschwiler et al., 2005). Most of the studies dealing with nutrient dynamics within the litter cover have focused on N transfer between leaves from different species in a natural forest perspective.

Some studies based on budget calculations suggested that net transfers of nutrients between leaves of the litter cover commonly occur from nutrient-rich tree species towards nutrient-poor tree species (Briones and Ineson, 1996; Salamanca et al., 1998). Over recent decades, isotopic studies based on ^{15}N labelling have improved our understanding of the processes driving N dynamics within and between litter components. They demonstrated that the release of endogenous N throughout leaf decomposition is commonly associated with the incorporation of exogenous N in forest ecosystems (Berg, 1988; Blair et al., 1992; D'Annunzio et al., 2008; Setala et al., 1996; Zeller et al., 2000). Schwendener et al. (2005) showed ^{15}N transfers from N-rich to N-poor leaves in mixture, but no synergistic effect on N retention within decomposing leaves. Schimel and Hättenschwiler (2007) showed in ^{15}N-labelled leaf mixtures that N transfers were higher from N-rich to N-poor leaves than the reverse. They also showed that these transfers were controlled by the N status of the source leaf, rather than by the difference in N status between the leaves or by the characteristics of the sink leaves. Their results agree with N mineralization theories (Schimel and Bennett, 2004), which consider that microbes at a specific microsite control how much N is available to move to another microsite in the soil. The composition of microbial communities may therefore be a key factor controlling nutrient transfers. Lummer et al. (2012) recently demonstrated that ^{15}N can be predominantly transferred by saprotrophic fungi in temperate forests, rather than passively by leaching. Their results suggested that N-rich bacterial-dominated litter can be a source of small quantities of N, whereas N-poor fungal-dominated litter can act as an important N source in litter mixtures. They concluded that both absolute and relative differences in initial C:N ratios of co-occurring species in the litter layer need to be considered for understanding N dynamics in decomposing litter mixtures. As far as we are aware, isotopic studies have never been carried out to experimentally quantify nutrient transfers between leaves, bark and branches throughout the decomposition processes in forest ecosystems.

In Congolese *Eucalyptus* plantations, branch and bark components account for about 25% of the litterfall dry mass over the rotation cycle (Laclau et al., 2003a) and 45% of the organic matter left on the forest floor at harvesting (Versini et al., 2014b). Woody components with high C:N ratios are likely to immobilise N in the litter cover and reduce N leaching after forest disturbance (Vitousek and Matson, 1985), as experimentally shown by mixing litter components from *Eucalyptus* plantations in a lysimeter experiment (Gomez-Rey et al., 2008). Gradual release of N from the litter cover synchronized with plant uptake after disturbance may also contribute to explaining very low losses by leaching in planted forests managed in short rotations in tropical sandy soils (Mareschal et al., 2013; Versini et al., 2014a; Muller da Silva et al., 2013). The influence of the initial N concentration of decomposing leaves on net N fluxes (release or accumulation) in litter components throughout the decomposition processes is well documented (Berg and Laskowski, 2005). However, our poor understanding of the factors controlling the N dynamics between leaves and woody components in the litter cover prevent fine-tuning of the fertilization timing in tropical planted forests.

We set out to gain new insight into N fluxes between leaves and twigs (L + T), bark and branches throughout the decomposition of litter components in tropical forest ecosystems. A complete factorial design using litter-bags containing ^{15}N-labelled components was set up in two sites of contrasting N status in the Congo to estimate the dynamics of endogenous and exogenous N in each litter component, and the quantities of N transferred between the litter components. We put forward the hypotheses that i) N release is related to the initial N status of the litter component, and ii) N transfers between litter components are controlled by the N status of the source, as proposed by Schimel and Hättenschwiler (2007).

2. Materials and methods

2.1. Study area

The study was conducted at Kondi in the coastal area of Congo (4° 34′ S, 11° 54′ E, 100 m elevation). The climate is sub-equatorial with a rainy season from October to May and a dry season from June to September. Mean annual rainfall is about 1350 mm, and the mean annual temperature is 25 °C with limited seasonal variations of about 5 °C (Versini et al., 2013). The soil is classified as Ferralic Arenosols (FAO classification). Briefly, this soil is characterized by a homogeneous sandy texture down to more than ten metres, moderately acidic soil pH, and very low quantities of exchangeable base cations and organic matter. The soil mineralogy is dominated by quartz and kaolinite and nutrient bearing minerals are very scarce. A thorough description of the soil at our study area can be found in Mareschal et al. (2011).

The experiment was set up in April–May 2009, between the previous harvest (March 2009) and re-planting *Eucalyptus* trees (June 2009), in two adjacent sites (200 m away) growing on the same soil type. Carbon and nutrient cycling have been intensively studied in these two sites since afforestation of the native herbaceous savannah (e.g. Mareschal et al., 2013; Nouvellon et al., 2012; Versini et al., 2013, 2014b). While the hemicellulose, cellulose and lignin contents in each litter component were of the same order of magnitude for the two sites (considering that only one composite sample per site and per component was analysed), the N concentrations were 35–46% lower in one stand (low-N plot) compared to the other (high-N plot) as a result of contrasting N accumulation patterns for the two *Eucalyptus* clones of each site (Table 1). Further details on *Eucalyptus* clone characteristics and silvicultural backgrounds of each site are given in Versini et al. (2014b).

2.2. Labelling of tree components

^{15}N-labelled litter material was obtained from a previous field trial initiated 20 km from our study area. During this trial, started in 2005, 20 trees of each *Eucalyptus* clone were watered with a ^{15}N-ammonium-nitrate solution (20% ^{15}N atom excess, single application). The labelled trees were cut in March 2009 and three components were distinguished as follows: leaves and twigs <1 cm in diameter (L + T), bark and branches (>1 cm in diameter). The final enrichment levels ($\delta^{15}N$) were 259 and 232‰ for L + T, 440 and 329‰ for bark, and 264 and 193‰ for branches of the low-N and high-N *Eucalyptus* clones, respectively.

2.3. Experimental design

The same tree components (L + T, bark, branches) were collected unlabelled for the two clones at Kondi in March 2009. The N contents were not significantly different for unlabelled and labelled tree components (data not shown). Litter-bags were prepared using a 1 mm nylon mesh, with internal dimensions of 22 cm × 30 cm × 5 cm. This mesh size allowed retention of leaf