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Nitrogen transfer between decomposing leaves of different N status

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Abstract

Nitrogen movement among microsites is thought to be an important control on patterns of ecosystem-level N cycling. In particular, N transfer between decomposing leaves may explain why litter mixtures sometimes decompose differently than would be predicted from the decomposition dynamics of each species separately. We evaluated how N moves between leaves of differing N status in leaf-pair microcosms. We collected litter from six species of trees from French Guiana (three with high N concentration, three with low) and ^{15}N-labeled the microbial communities growing on each species. We then established microcosms with one labeled and one unlabeled leaf in a fully factorial design (each species with every species, ^{15}N on each species) and measured ^{15}N transfer over 28 days. There was substantial transfer of the ^{15}N label in all cases, averaging between 15% and 30% of the ^{15}N originally on the labeled leaf. Net N transfer from high-N to low-N leaves resulted from greater gross ^{15}N transfer from high-N to low-N leaves than in reverse. Gross ^{15}N transfer was controlled entirely by the N status of the source leaf, rather than by the difference in N-status of the leaves or by the characteristics of the sink leaf. For example, as much ^{15}N was transferred from a high-N leaf to another high-N leaf as to a low-N leaf. These results support the assumption from N mineralization theories that microbes at a specific site have first access to that N and therefore control how much N is available to move to other microsites in the soil system. The strength of the gradient between microsites may then control the rate at which available N moves, but not how much N is available to move. If N transfer among different litter species is important for synergistic effects on decomposition of litter mixtures it would not be driven by the N gradient as is often hypothesized, but by the characteristics of the source leaf.

Keywords: Litter; Nitrogen transfer; Microsites; Decomposition

1. Introduction

Soil may be the most complex environment for life on Earth, with microsites that vary in environmental conditions and resource availability (Brussaard et al., 1997; Schimel and Bennett, 2004; Young and Ritz, 2005). Accordingly soil microbial community structure and functioning are highly spatially variable (Cavigelli et al., 1995; Saetre and Bååth, 2000). Microsites and their associated microbial communities, however, do not merely create random variation that could be averaged to get a picture of how soil functions as a whole. Some microsites carry out unique functions, such as anaerobic microsites allowing denitrification in well-drained soil (Sexstone et al., 1985). Microbial processes in microsites also control the form of N available in the soil solution (NO_3^-, NH_4^+, amino acids) and the physical structuring of those microsites controls the amount and forms of N taken up by other microbes and plant roots (Jingguo and Bakken, 1997; Schimel and Bennett, 2004). To fully understand the processes regulating the overall patterns of N dynamics in soil, we need to understand the functioning of this "microbial landscape", i.e. how does the multitude of processes occurring in physically segregated microsites interact spatially and biologically to create the emergent property of ecosystem-level N cycling that we observe?

One component of the whole soil system that is notably patchy and where microsite interactions may be important is the litter layer. The litter layer typically contains materials of widely varying chemistry and resource availability in close proximity, particularly in species-rich

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plant communities (Perez-Harguindeguy et al., 2000; Hättenschwiler, 2005). This can produce sharp gradients in microbial functioning, community composition, and resource needs (Wagener and Schimel, 1998). Interactions among these microenvironments are presumably a major reason why mixtures of leaves often decompose differently as a whole than would be predicted from the dynamics of each species separately (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Sometimes litter mixtures decompose faster than would be predicted, suggesting that resources from a high-resource leaf can prime microbial attack on lower resource material (Chapman et al., 1988; Wardle et al., 1997; Salamanca et al., 1998). Less frequently litter mixtures decompose more slowly than would be predicted from the dynamics of the separate species, suggesting that inhibiting chemicals can move and inhibit microbial growth and activity on other leaves (Hättenschwiler et al., 2005). While these ideas have been discussed in a number of papers, there is only limited experimental evidence for chemical movement between individual leaves in a litter mixture. Budget calculations based on initial and final nutrient concentrations, and mass loss during decomposition, suggest net nutrient transfer between leaves in some two-species litter mixtures commonly towards the species of low nutrient status (Staaf, 1980; Briones and Ineson, 1996; Salamanca et al., 1998). However, the actual movement of materials from leaf to leaf in a decomposing litter mixture has never been experimentally demonstrated, and the mechanisms controlling movement have not been explored.

We evaluated N movement between decomposing leaves of different N status. We hypothesized that when leaves of different N concentrations are in association, there would be a net N transfers from leaves with high N-availability to leaves with low N-availability. This net flow should result from greater gross N-flow from high-N to low-N leaves than from low-N to high-N leaves. We tested this hypothesis by using leaf litter from six species of tropical trees, three of which had relatively high N and three of which had lower N concentrations. We established microcosms containing two leaves, one of which had its decomposer community labeled with ^{15}N while the other was unlabeled. By measuring movement of ^{15}N from the labeled to the unlabeled leaf, we evaluated how source and sink N-availability regulated N movement. This allowed us to evaluate the bi-directional flows of N between leaves of varying N concentration, and to evaluate whether N transfer was controlled by the N-availability in the source leaf, the sink leaf, or by the difference between them.

2. Materials and methods

2.1. Study area

Litter and soil for the microbial inoculum were collected from a tropical forest in the northern part of French Guiana near the Atlantic coast at the Paracou station (5°18′N, 52°53′W, 40 m a.s.l.) that is run by CIRAD-forêt (Département Forêts du Centre de Coopération Internationale en Recherche Agronomique pour le Développement). Mean annual temperature is 25 °C with little seasonal variation, and mean annual precipitation is 2200 mm (Gourlet-Fleury et al., 2004). The climate is characterized by a wet season from December to July, which is normally interrupted in February or March by a short drier period, and a dry season from August to November with monthly precipitation of less than 100 mm. The soil is an oxisol developed on magmatite and shales from the Armina series, with a top soil pH of about 4.5 (Gourlet-Fleury et al., 2004).

We selected litter from six tree species, three with relatively high N concentrations, and three with significantly lower N concentrations (Table 1). Each species had fairly large leaves, ranging in length from 5 to 10 cm and in width from 2 to 5 cm. The chosen species are common components of the lowland tropical forest at Paracou (Gourlet-Fleury et al., 2004). Litter was collected using three litter traps (0.32 m^2 each) underneath a closed canopy of each study species growing in monocultures (20 m × 20 m stands) established in 1984 (see Roy et al., 2005). Litter traps were emptied every 2 weeks from June 2004 to March 2005 and separated into leaf litter of the canopy species, drifted leaf litter from surrounding species, branches, and remaining material (essentially fruit and inflorescence parts) and air dried. Leaf litter from each study species was pooled across litter traps for the entire sampling period and well mixed in order to obtain a representative litter batch for each species from which we drew the leaves used for our experiment. Soil from the upper 5 cm of mineral soil was used for microbial inocula and was collected from all the monoculture plots (including an additional 10 planted tree species) in November 2004, pooled, and air-dried.

2.2. Litter preparation

Litter and soil were returned air-dry from Guiana to Montpellier, France. Overall initial N concentration for each litter species was measured by using a C/N analyzer (Thermo-Finnigan EA1112, Thermo Electron Corporation, Waltham, MA, USA). Approximately 50 leaves of each of the six species of litter were selected at random from the larger sample, as long as they were brown and reasonably intact. A microbial inoculum was prepared by slurrying air-dry soil in deionized water (1:5 ratio by weight) and shaking overnight. The slurries were then allowed to settle for 1 h, and were filtered through a fine mesh gold coffee filter screen (Starbucks, USA) to filter out large particles but allow microbes to pass. The inoculum was turbid with organic matter and suspended clay.

The basic experimental design is shown in schematic in Fig. 1. The leaves of each species were separated into two groups and each group was placed in a plastic container (22 × 15 × 4.5 cm). Inoculum (75 ml) was added to each