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Carbon and nitrogen transfer in leaf litter mixtures

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ABSTRACT

The decomposition rate of litter mixtures can differ from that expected on the basis of the decomposition rate of the individual components. This difference may be linked to nitrogen (N) transfer from high-N to low-N components. Transfer of N is probably also associated with transfer of C, but the extent and direction of this C transfer are unknown. This study examined transfer and loss in laboratory microcosms of C and N from two mixed litter species (Scots pine, *Pinus sylvestris* L. and maize, *Zea mays* L.), which have natural isotopic differences in ^{13}C. Half the material was ^{15}N-labelled and the plants were fertilised or unfertilised. Substantial bidirectional transfer of C and N occurred between the litters, with net transfer of C from pine to maize litter and net transfer of N from high-N to low-N litter. Mixtures of fertilised and unfertilised plant litter showed higher than expected C losses and net transfer of N. Mixtures with litters from the same fertilisation treatment had small or insignificant net transfer of N and their C losses did not differ from values estimated using the decomposition rates of the pure litters.
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1. Introduction

Litter decomposition, the process by which the remains of living organisms are separated into their constituent elements, is essential for carbon (C) and nutrient cycling in ecosystems. Overall, it is controlled by the interactions between the decomposer organisms, the properties of the litter, and the abiotic environment (Swift et al., 1979). However, at a more detailed level the interactions are not yet fully understood.

One aspect that has attracted attention recently is the effect of mixing litters on their decomposition. The decomposition rates of mixtures are reported to be frequently higher, but sometimes lower, than the rates expected on the basis of the litter components decomposing separately (Gartner and Cardon, 2004). Studies on litter mixtures that have also examined nitrogen (N) release have suggested that this non-additive effect in litter mixtures could be coupled to the transfer of N between the litters (Chapman et al., 1988; Taylor et al., 1989; Fyles and Fyles, 1993; Briones and Ineson, 1996; McTiernan et al., 1997; Salamanca et al., 1998). Thus rapidly decomposing, high-N litter will release N that is transferred to slowly decomposing, low-N litter in the mixture. Berglund and Ågren (2012) demonstrated that by modifying the C use efficiency of decomposers such a transfer could indeed explain observed changes in decomposition rates for litter mixtures. Transfer of N between components in litter mixtures has also been shown in ^{15}N-labelling studies (Schimel and Hättenschwiler, 2007; Lummer et al., 2012). In addition to N transfer, Lummer et al. (2012) investigated loss of mass by the litters, but found no effect of mixing.

Transfer of N between litters in mixtures is mainly suggested to occur via fungal mycelia (Briones and Ineson, 1996; McTiernan et al., 1997; Tiunov, 2009; Lummer et al., 2012), although transfer without fungal translocation, e.g. by diffusion and leaching, may also be possible (Schimel and Hättenschwiler, 2007). Irrespective of mechanism, it seems that the transfer of N can be bidirectional (Schimel and Hättenschwiler, 2007; Tlalka et al., 2007), although a net flow from high-N to low-N litter is expected.

There is also transfer of C during decomposition. For example, it has been shown that decomposer fungi can transfer C from the litter to the underlying soil while simultaneously transferring N from the soil to the litter layer (Frey et al., 2003). However, it has not been shown whether and in what direction C can be transferred between litters in mixtures. Since N can be transferred bidirectionally as amino acids in fungal mycelia (Tlalka et al., 2007), it is likely that the transfer of N involves transfer of C.

The aim of the present study was to investigate the transfer of both C and N in mixtures of two contrasting litters and to relate such transfers to changes in decomposition rate. Previous studies have only considered N transfer. A microcosm experiment was

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designed in which we observed whether C and N in litter components in a two-species mixture: (i) had been lost in gaseous form, (ii) had been transferred to the other litter component in the mixture, or (iii) remained in the first litter component during decomposition. By mixing the litters from two plant species with natural isotopic differences in ^{13}C, we were able to use their isotopic signature to follow C lost as respiration and C transferred between litters. By labelling half the material with ^{15}N, we were also able to follow the transfer of N between the litters. In addition, we applied fertiliser to plants of both species to obtain litters with different initial N concentrations. Our starting hypothesis was that net transfer of N between the litters would result in a non-additive effect on the decomposition rate. Although it was believed that C transfer would be linked to N transfer, our knowledge of the effects and directions of C transfer was too limited to allow specific hypotheses to be formulated.

2. Materials and methods

2.1. Litter production and isotope labelling

Plant materials were selected from two species (a C_3 plant and a C_4 plant) with different chemistries (see e.g. Table 4.6 in Swift et al., 1979), and hence with different decomposition rates and with natural isotopic differences in ^{13}C. The selected plant materials, needles of Scots pine (*Pinus sylvestris* L.) and leaves of maize (*Zea mays* L.), were grown from seed in a greenhouse with a high N (+) or low N (−) treatment. The plants in the +N treatment were grown in potting soil (Hasselfors Garden Special) and were fertilised with a complete nutrient solution (Wallco Fert. 51-10-43 Mic, 100 mg N/L, Cederroth International AB). The −N plants were grown in a mixture of sand and potting soil, with no additional fertiliser. All plants were watered regularly (2–3 times a week), the −N plants with tapwater and the +N plants with nutrient solution, to maintain non-limiting soil water. Half the plants were labelled with ^{15}N by adding a low dose (20 mg ^{15}N/g N) as $^{15}NH_4NO_3$ (98 atom% N) to the irrigation water. Green leaf materials collected from the living plants were first air-dried and then oven-dried (70 °C) and stored at room temperature until use. To facilitate mixing of the litters, the needles and leaves were cut into pieces (pine needles approx. 20–30 mm, maize leaves approx. 10–15 mm; the different sizes to facilitate separation of the two litters at harvest). Before the start of the experiment, some samples of the two litters were soaked in water and some samples were oven-dried at 105 °C for 24 h to determine wet:dry matter ratio.

2.2. Experimental design

Litter samples corresponding to a total of 0.50 g C were incubated in microcosms consisting of plastic jars (471 cm^3), each with a removable lid that had a 5 mm diameter hole to allow for gas exchange with the air in the room. Equal amounts of C (0.25 g) from the two litters were used in the litter mixtures. In dry matter, this corresponded to 0.96 g litter for the maize (M) microcosms, 0.92 g litter for the pine (P) microcosms, and 0.94 g litter for the mixture microcosms (calculated as 0.50 divided by the C concentration, Table 1). Two litters and two N levels resulted in four sets of single litter microcosms (M+, M−, P+, and P−) and four mixtures of maize and pine (M+P+, M+P−, M−P+, and M−P−). Furthermore, for each of the mixtures there were two different sets, one in which the maize was ^{15}N-labelled and the pine was unlabelled and one in which the maize was unlabelled and the pine was ^{15}N-labelled. This resulted in eight different sets of mixture microcosms plus four sets of single litters, each with six replicates, giving in total 72 microcosms.

Table 1
Initial (day 0) and final (day 190) C and N concentrations and N:C ratio in the litters. Values for mixtures calculated from values for the constituent litters. Data are mean values, with standard deviation in brackets. Abbreviations: M+ fertilised maize, M− unfertilised maize, P+ fertilised pine, P− unfertilised pine.

Litter	C (%)		N (%)		N:C	
	Initial	Final	Initial	Final	Initial	Final
M+	51.4 (1.5)	37.4 (0.4)	3.2 (0.6)	3.8 (0.1)	0.062 (0.010)	0.101 (0.003)
M−	52.3 (0.6)	41.6 (0.2)	1.4 (0.2)	3.1 (0.1)	0.027 (0.003)	0.075 (0.004)
P+	54.2 (2.7)	45.0 (0.7)	2.3 (0.4)	2.5 (0.1)	0.042 (0.006)	0.056 (0.003)
P−	55.2 (1.6)	46.2 (0.5)	1.5 (0.2)	1.7 (0.0)	0.027 (0.003)	0.037 (0.001)
M+P+	52.8 (1.5)	41.4 (1.1)	2.7 (0.3)	2.9 (0.2)	0.052 (0.012)	0.071 (0.007)
M+P−	53.2 (1.1)	42.4 (0.7)	2.3 (0.3)	3.2 (0.1)	0.044 (0.011)	0.077 (0.004)
M−P+	53.2 (1.4)	42.5 (1.0)	1.8 (0.2)	2.9 (0.2)	0.034 (0.007)	0.068 (0.006)
M−P−	53.7 (0.9)	44.3 (1.0)	1.4 (0.1)	2.2 (0.2)	0.027 (0.005)	0.050 (0.003)

The pieces of leaves and needles were randomly arranged within the microcosms and the pieces were in loose contact with each other. The litter in each microcosm was rehydrated by adding distilled water up to approximately 60% of water-holding capacity for optimal microbial activity (Persson et al., 1999). Each microcosm was then inoculated with 1 mL of a suspension prepared from field-collected material. Fresh and partially decomposed litter was collected from the floor of a mixed deciduous–coniferous forest and mixed with approximately equal amounts of fresh litter and soil collected from the surface of an agricultural field, both located in Uppsala, Sweden. The inoculum was then prepared by mixing 20 g of the collected material with 1 L distilled water using a hand blender, and letting the suspension sediment for 5 min. The dry mass of the added suspension was 0.0037 g.

The microcosms were arranged in random order on shelves in a climate room and incubated in darkness at 25 °C for up to 190 days. To maintain the moisture content the microcosms were weighed 2–3 times a week and distilled water was added to the initial weight. Almost no free water was present in the microcosms. Correction for mass loss was made after the first destructive sampling, at day 119.

2.3. Gas sampling and analysis

Gas samples were taken 7, 28, 56, 84, 119, 153, and 190 days after the start of the experiment in order to estimate C losses during decomposition. The CO_2 evolution in the microcosms was estimated by removing the lids, leaving the microcosms open for several minutes to equilibrate with the CO_2 concentration in the room and replacing the initial lids with airtight lids with a rubber membrane. After 9–324 min (depending on expected respiration rate), one 12 mL sample from each microcosm was extracted with a syringe inserted through the rubber membrane and directly transferred to evacuated glass tubes (Labco Exetainer, Labco Limited, UK). The tubes were evacuated 2–3 days prior to sampling. The time between closing and sampling of microcosms was chosen such that the CO_2 concentration in the gas sample would be about 300 ppm above the background CO_2 concentration, i.e. about 700 ppm. Microcosms that were expected to have high respiration rates were therefore sampled after shorter times than microcosms that were expected to have low respiration rates. The time was adjusted according to the results from the previous sampling date. On each sampling occasion, 8–12 samples of the ambient air were taken at intervals covering the period of sampling of the microcosms to estimate the background CO_2 concentration.

The samples were analysed for CO_2 concentration and ^{13}C abundance within a week after sampling via extraction by an autosampler connected to a gas purification module (trace gas)

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