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Phosphorus and micronutrient dynamics during gymnosperm and angiosperm litters decomposition in temperate cold forest from Eastern Canada

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ABSTRACT

Molybdenum (Mo) and phosphorus (P) limitation and co-limitation of asymbiotic dinitrogen (N_2) fixation has been reported in many ecosystems, from tropical to boreal. However, the mechanisms leading to these limitations remain elusive. In cold temperate forests Mo and P limitation of asymbiotic N_2 fixation has been observed in gymnosperm litter but not in angiosperm litter suggesting an important role of the vegetative cover. In gymnosperm litters, P and Mo limitation is characterized by a strongly seasonality; P limitation was observed early in the growing season while Mo limitation appears midway in the growing season. This discrepancy between gymnosperm and angiosperm litters and the strong seasonality suggest that the quality of the litter and decomposition dynamics play an important role in the emergence of Mo and P limitation in gymnosperm litters from cold temperate ecosystems. While the dynamics of macronutrients (i.e. C, N) during decomposition are well documented, our understanding of micronutrient (i.e. trace metals) dynamics during litter decomposition remains limited. Here, we measured nutrient concentrations (P, Mo and others) during litter decomposition in various angiosperm and gymnosperm litters and their combinations (2 and 4 species) using litter bags. Results showed that angiosperm litter achieves higher nutrient concentrations (P and metals) than gymnosperm litter. The concentration of most elements increased in both litter types over a 6-month period of decomposition (Al, Co, Cu, Fe, Mn, V, Ti, and Zn), with the exception of P and Mg which decreased over time. During decomposition, the concentration of Mo increased by ~300% in angiosperm litter but decreased by ~50% in gymnosperm litter. Together, these results suggest that the litter can concentrate metals from the surrounding environment (i.e. soil and atmospheric deposition) except for Mo in gymnosperm litter. Litter quality (nutrient concentration) and nutrient dynamics during litter decomposition likely play an important role in P and Mo limitation of asymbiotic N_2 fixation.

1. Introduction

Biological nitrogen (N) fixation is a major source of newly bioavailable N in unmanaged ecosystems (Cleveland et al., 1999; Galloway et al., 2004). In recent years, asymbiotic N fixation (ANF) has attracted interest in the scientific community for its potential importance to the N budget, especially in high latitude ecosystems where cyanobacteria associated with feather moss have been shown to significantly contribute to N inputs (DeLuca et al., 2002; Gundale and Wardle, 2012). Although recent efforts have attempted to better integrate ANF into conceptual models of the N cycle (Reed et al., 2011), these efforts are hindered by a lack of knowledge concerning the factors controlling ANF activity in natural habitats.

The effect of abiotic properties (e.g. temperature, humidity) and phosphorus (P) availability on biological N fixation is well documented (Zielke et al., 2002; Hicks et al., 2003; Vitousek and Howarth, 1991; Vitousek and Farrington, 1997; Mills et al., 2004). The availability of molybdenum (Mo), an essential metal cofactor of the enzyme nitrogenase that is responsible for the reduction of atmospheric N_2 into bioavailable ammonium, has been reported to limit ANF in various environments from tropical to cold temperate ecosystems (Silvester, 1989; Barron et al., 2009; Wurzberger et al., 2012; Jean et al., 2013). Jean et al. (2013) recently reported that vegetation type (gymnosperm vs. angiosperm) in a cold temperate forest can affect N fixation via the emergence of Mo and P limitations; Mo and P limitation is more likely to emerge in gymnosperm litter than angiosperm litter. Furthermore, the emergence of P and Mo limitation varies across seasons; P limitation of ANF in gymnosperm litters was observed in the early stage of the growing season, while Mo limitation was observed in mid-season. Neither P nor Mo were limiting to ANF at the end of the growing season

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(Jean et al., 2013). The processes leading to the observed seasonality in nutrient limitation of ANF remain unclear. However, since both microbial activity and litter decomposition also have a strong seasonal variability in temperate and boreal ecosystems that likely affects nutrient dynamics and thus nutrient limitations, these might be related to nutrient limitation of ANF.

Leaf litter is of great ecological importance as a source of nutrients in soils (Aber et al., 1990; Kuzyakov and Domanski, 2000). The annual fall of fresh litter contributes up to 60–70% of N and up to 75–95% of P supply to living organisms (Cole and Rapp, 1980; Nordén, 1994). The amount of organic matter and nutrients that return to the soil through litter decomposition is key to the biogeochemistry of forest ecosystem (Camirand et al., 1983; Liski and Westman, 1995; Giesler et al., 1998; Groffman et al., 2006; Baribault et al., 2010). While the role of leaf litter in the cycling of major nutrients such as C, N and P has been intensively investigated (Berg, 1986; Berg and Staaf, 1987; Laskowski et al., 1995), data on the dynamics of micronutrients during litter decomposition are scarce in comparison.

The main objective of this work was to better characterize nutrient dynamics during litter decomposition with a specific interest for essential elements for ANF, i.e. P and Mo, in different tree litters. We measured biomass loss and nutrient (P, metals) dynamics during litter decomposition in leaf litters of different species of gymnosperm and angiosperm trees. This field experiment was conducted in Southern Quebec in 2012 using litter bags.

2. Materials and methods

2.1. Experimental design

The experiment was conducted as part of the International Diversity Experiment Network with Trees (IDENT, Tobner et al., 2013) linked to TreeDivNet, at McGill University. The Canadian experimental site used in this study is localized at Sainte-Anne-de-Bellevue, Québec, Canada (45.5°N, 73.9°W,) and was established in spring 2009 on ~0.6 ha of a former high-input agricultural site in sandy soil. Details of the experimental design and the physical environment can be found in Tobner et al. (2013) and Jewell et al. (2015) and IDENT website http://www.treedivnet.ugent.be/ExpIDENT.html. The experiment was performed using fiberglass mesh (2 mm) litter bags (15 cm × 15 cm). Each block consisted of 12 monoculture communities (7 type of gymnosperm litters and 5 types of angiosperm litters), 14 two-species mixture, and 10 four-species mixtures (Sup. inf. Tables S1 and S2). Gymnosperm species were; *Abies balsamea* (ABBA), *Larix laricina* (LALA), *Picea glauca* (PIGL), *Picea rubens* (PIRU), *Pinus resinosa* (PIRE), *Pinus strobus* (PIST), and *Thuja occidentalis* (THOC). Angisoperm species were; *Acer rubrum* (ACRU), *Acer saccharum* (ACSA), *Betula alleghaniensis* (BEAL), *Betula papyrifera* (BEPA), and *Quercus rubra* (QURU). Each 4 m × 4 m plot, established from one year-old saplings in spring 2009 on previously agricultural land, contained 64 trees of a single species or 2-species and 4-species mixtures. Leaf metal contents and chemistry can be affected by senescence due to reallocation and changes in metal bindings (Buchanan-Wollaston, 1997). In order to be representative of the litter material decomposed on the forest floor, angiosperm leaves were collected during the peak period of leaf senescence (October). For sampling consistency, gymnosperm leaves were also collected in October. Litter was collected from litter traps placed beneath trees of each species growing in the vicinity of, but not within, the experimental plots and collected within a few days of leaf fall. Litter was collected during the autumn of 2011, air dried and then maintained a 4 °C until placement in the litter bags. Each bag contained an equal dry mass of 2.0 g regardless of the number of species included. Litter was not shredded prior to placing it in the litterbags but was cut when necessary to obtain the correct mass. The litterbags had a mesh size of 2 mm and so allowed entry of all macrofauna less that this size, including earthworms. In each block, four identical litterbags to be destructively harvested at four different (28, 59, 124, 184 days after incubation) dates were placed in each tree community with the corresponding species combination directly onto the soil surface. At the beginning of the present experiment (spring 2012), individuals (averaged by species) had been growing for four years on site, were 5 years old (planted at one-year old), and varied in height from 1.32 m (*Picea glauca*) to 4.14 m (*Betula papyrifera*). Upon collection of the litter bags, the remaining litter was first gently washed to remove soil and then immediately dried at 60 °C for 3 days to prevent further decomposition and weighted.

2.2. Elemental analysis

Dried samples were reduced into powder in liquid N, using a mortar and pestle. 100 mg of sample was placed in the digestion tubes (15 ml Digitubes, SCP SCIENCE) with 2 ml of concentrated nitric acid (trace metal grade) and digested at 65 °C for 4 h using a digester plate (DigiPREP Jr digester, SCP SCIENCE, Baie d'Urfé, Canada). After a cooling step, 500 μl of H_2O_2 was added, followed by a second cycle of 4 h at 65 °C. The solution was collected, diluted (MilliQ water) and analyzed for its elemental concentration with an Inductively Coupled Plasma-Mass Spectrometer (ICP-MS, XSeries 2, Thermo scientific). The elements analyzed were; aluminum (Al), cobalt (Co), cupper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), molybdenum (Mo), phosphorus (P), titanium (Ti), vanadium (V) and zinc (Zn). Data are presented as elemental concentration (g of element/g of litter) and as loss index.

Loss index equation:

$$\text{Loss index} = (1-(\text{g element at tx}/\text{g element at t0}))$$

with tx referring to the time of harvest (x = 28, 59, 124, 184 days after incubation).

2.3. Statistical analysis

We first compared the responses of monoculture and mixture litters using a two-way ANOVA, Tukey test ($p < 0.05$, Simplot, Systat Software Inc.). Second, using only the monoculture litters, and based on our expectations described in the introduction, we first classified the litter of each species as either gymnosperm or angiosperm; this defined the first categorical factor with two levels. A second categorical factor coded each particular monoculture (i.e. a single tree species and its litter in litterbags). This second factor was therefore nested within the first factor since a particular species only produced one type of litter. The litter in each litterbag was also classified by collection date (0, 28, 59, 124, 184 days); "collection date" was treated as a categorical factor rather than a continuous variable because any relationship between elemental composition of the litter and age would not be linear. We focused on three important elements for nitrogen fixation (Mg, P, and Mo). Using the concentration of each element separately as a dependent variable, we then performed a three-way analysis of variance in which monoculture type was nested within litter type, followed by Tukey's post hoc test to detect which levels within each factor were significantly different from one another. These statistical analyses were performed using the R statistical language 3.1.0 (www.r-project.org/). Normality and homoscedasticity of residuals were evaluated graphically. Significance was declared at the traditional level of 0.05.

3. Results and discussion

No significant difference was observed between monoculture and mixture of litter. Similarly, according to two-way-analysis of the monoculture litters, we observed no significant differences between species of the same type of litter (gymnosperm and angiosperm) with respect to either biomass or element concentrations (Figs. 1 and 2). In contrast, differences between gymnosperm and angiosperm litters were clear,