



## Hemiparasitic litter additions alter gross nitrogen turnover in temperate semi-natural grassland soils



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### ABSTRACT

Hemiparasitic plants accumulate nutrients in their leaves and therefore produce high-quality litter with faster decomposition and nutrient release rates compared to non-parasitic litter. Higher levels of plant-available nitrogen (N) in the presence of hemiparasitic plants have been attributed to this 'litter effect', but effects on N dynamics in the soil remain unstudied. We tested the hypothesis that litter of *Rhinanthus angustifolius* and *Pedicularis sylvatica* increases N transformation rates in the soil more than non-parasitic litter of a species mix from the same communities. We expected the litter effect to be higher in the oligotrophic *Pedicularis* soil compared to the mesotrophic *Rhinanthus* soil. Gross N transformation rates were quantified using a <sup>15</sup>N tracing modeling approach. Differentially <sup>15</sup>N labeled NH<sub>4</sub>Cl + KNO<sub>3</sub> was added to two soils with three treatments (control, soil amended with non-parasitic litter, soil amended with *Rhinanthus* or *Pedicularis* litter) in a laboratory incubation experiment. The concentration and <sup>15</sup>N enrichment of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> in the soil were measured at six time points within one or two weeks (depending on the soil) after label addition. Hemiparasitic litter addition increased the overall cycling of N more compared to the addition of non-parasitic litter. Relative to the non-parasitic litter, addition of *Rhinanthus* litter increased the net flux from organic N to NH<sub>4</sub><sup>+</sup> by 61% and net (autotrophic) nitrification by 80%. Addition of *Pedicularis* litter increased the net flux from organic N to NH<sub>4</sub><sup>+</sup> by 28% relative to addition of non-parasitic litter, while there was no effect on nitrification. Surprisingly, gross mineralization of organic N to NH<sub>4</sub><sup>+</sup> decreased with litter addition for the *Rhinanthus* soil (control soil > non-parasitic litter > *Rhinanthus* litter), while it increased with litter addition in the *Pedicularis* soil (control soil < non-parasitic litter < *Pedicularis* litter). Our results support the hypothesis that litter from hemiparasitic plants increases soil N availability more than non-parasitic litter, but contradicts the expectation that the hemiparasitic litter effect would be more pronounced in an oligotrophic as compared to a mesotrophic system. This litter-induced augmentation in soil fertility provides – in addition to the parasitic suppression of hosts – a second potentially important pathway by which hemiparasitic plants impact on plant community composition. However, future research on P and K return via hemiparasitic litter should be considered.

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### 1. Introduction

The net effect of hemiparasitic plants on plant community structure and diversity results from both parasitism and litter

pathways (Press, 1998; Spasojevic and Suding, 2011). The parasitism pathway refers to direct negative effects of hemiparasitic plants on host species and indirect positive effects on non-host species. Most parasitic plants are generalists, but show high levels of host preference (Press and Phoenix, 2005). Therefore, parasitism changes the competitive relations between preferred and non-preferred hosts in the vegetation with possible effects on diversity (Gibson and Watkinson, 1991; Matthies, 1996; Press et al.,

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1999). For example, the decrease of total, graminoid and legume biomass in grasslands infected with *Rhinanthus* spp. is thought to alter the species composition in favor of non-leguminous forbs and to increase the local diversity (Ameloot et al., 2005; Davies et al., 1997; Gibson and Watkinson, 1991). The litter pathway operates via effects on nutrient cycling. Hemiparasitic plants accumulate nutrients in their tissues, which is thought, in part, to be a result of their high transpiration rates (Gauslaa, 1990; Gauslaa and Odasz, 1990; Pate, 1995; Phoenix and Press, 2005) and therefore produce litter with high decomposability (Press, 1998; Press et al., 1999; Quested et al., 2003a, 2002; Seel and Press, 1993). There is limited evidence that hemiparasites can increase the amount of nitrogen (N) inputs to the soil (March and Watson, 2010; Quested et al., 2003a), increase net N mineralization (Bardgett et al., 2006), increase the amount of plant-available N (Ameloot et al., 2008), and enhance plant growth (Quested et al., 2003b). In grassland ecosystems, this increase in plant-available N (and likely other nutrients) potentially increases graminoid biomass and therefore might decrease diversity and change community composition as generally observed in nutrient addition experiments (De Schrijver et al., 2011; Hejman et al., 2007; Silvertown et al., 2006). All together, parasitism is expected to decrease productivity and to impact on diversity, either positively or negatively, depending on host preference, while litter effects may increase productivity and have weaker impacts on diversity (Spasojevic and Suding, 2011).

While the impact of hemiparasites on community structure is well-studied (see the reviews of Ameloot et al., 2005; Press and Phoenix, 2005), studies looking at the litter pathway are scarcer. Press (1998) suggested that litter effects of hemiparasites should be investigated both in field and microcosm, through simple species manipulation experiments, coupled to litter and tracer studies. Quested et al. (2005, 2003a,b, 2002) used litter in field and mesocosm experiments and found that litter of the sub-arctic *Bartsia alpina* increased N inputs to the soil, released N faster than co-occurring, non-parasitic species and enhanced plant growth more than litter of non-parasitic species. March and Watson (2007, 2010) found that the mistletoe *Amyema miquelii* increased both litterfall and annual litter N ( $\times 1.65$ ), phosphorus (P,  $\times 3$ ) and potassium (K,  $\times 8.5$ ) returns in temperate eucalypt forest. Ameloot et al. (2008) measured  $^{15}\text{N}$  abundance in the vegetation four months after a  $^{15}\text{N}$  tracer was added to the soil of plots with and without *Rhinanthus minor*. A lower  $^{15}\text{N}$  enrichment in the vegetation of parasitized plots indicated that the added tracer was more diluted by  $^{14}\text{N}$  from the soil solution, suggesting higher N availability in the presence of *R. minor*. The authors discussed several possible reasons for this increase in N availability, of which one is hemiparasitic litter input. In an observational study, Spasojevic and Suding (2011) associated *Castilleja occidentalis* presence with higher productivity and foliar N concentrations in co-occurring species in alpine tundra. Based on decomposition trials, in which *C. occidentalis* (alone and in mixtures) lost N much faster compared to the tested non-parasitic species, Spasojevic and Suding (2011) speculated that litter effects outweigh parasitism effects. However, the authors found no higher soil inorganic N pool associated with *C. occidentalis*. They concluded that future research should examine N cycling in more detail.

Here, we aimed at understanding better how hemiparasitic litter influences the bioavailability of N in the soil. Nitrogen bioavailability is primarily regulated by the depolymerization of N-containing organic compounds to monomers (e.g., amino acids), broadly available to both micro-organisms and plants. However, the main form of N taken up by plants likely varies depending on the N status of the soil (Schimel and Bennett, 2004). Except for extreme N-poor ecosystems, plants primarily use inorganic N, shifting from ammonium ( $\text{NH}_4^+$ ) to nitrate ( $\text{NO}_3^-$ ) with increasing N availability. As N mineralization and immobilization occur simultaneously in

the soil (Bottomley et al., 2012), net mineralization assays are inadequate for evaluating N supply rates and, hence, N bioavailability. Especially in N-limited soils, any produced inorganic N may immediately be immobilized by the plant or the microbial community due to the strong competition for available inorganic N in the soil matrix. To study the soil N cycle in detail, numerical models are the best available tool (Rütting et al., 2011). Combined with a robust technique for parameter optimization, they allow the estimation of several simultaneously occurring gross N transformations (Mary et al., 1998; Müller et al., 2007; Myrold and Tiedje, 1986). In addition, numerical models correct for re-mineralization of added  $^{15}\text{N}$ , which is not the case for analytical equations (Hart et al., 1994).

For this study, we selected two hemiparasitic species growing in ecosystem types with contrasting dynamics: *Rhinanthus angustifolius* C.C. GMEL growing in mesotrophic grasslands and *Pedicularis sylvatica* L. growing in oligotrophic heath-grassland (hereafter *Rhinanthus* and *Pedicularis*). Using a numerical data analysis based on a  $^{15}\text{N}$  tracing model (Müller et al., 2007), we compared N transformations in (i) control soil, (ii) soil amended with non-parasitic litter of a species mix and (iii) soil amended with hemiparasitic litter from the same communities. The first hypothesis we tested is that hemiparasitic litter addition increases gross soil N transformation rates more than addition of non-parasitic litter. Although plant uptake is excluded by the experimental design, increases in gross  $\text{NH}_4^+$  and  $\text{NO}_3^-$  forming process rates are expected to increase N bioavailability. The second hypothesis we tested is that the relative effect of hemiparasitic litter on gross soil N transformation rates is higher in the oligotrophic (nutrient-poor) *Pedicularis* soil compared to the mesotrophic (moderately nutrient-rich) *Rhinanthus* soil. In an oligotrophic soil, the impact of high-quality hemiparasitic litter on N cycling is expected to be large as N cycling is inherently slow. In a mesotrophic soil with faster N cycling, in contrast, the impact of hemiparasitic litter is expected to be less profound.

## 2. Materials and methods

### 2.1. Studied vegetation types

For both hemiparasites, a representative site was selected in the east of Flanders (northern Belgium). These were Doode Bemde ( $50^\circ 48' 57''\text{N}$ ,  $4^\circ 38' 54''\text{E}$ ) for *Rhinanthus* and Hooiput ( $51^\circ 18' 53''\text{N}$ ,  $5^\circ 7' 34''\text{E}$ ) for *Pedicularis* (hereafter Rhin-D and Pedi-H). The long term (1981–2010) mean annual precipitation in the region is 852 mm, and the mean annual temperature is  $10.5^\circ\text{C}$  (Royal Meteorological Institute of Belgium). The most important soil characteristics are listed in Table 1. Both sites are semi-natural grasslands located in nature reserves. The management consists of mowing once (Pedi-H) or twice (Rhin-D) a year. The vegetation at Rhin-D is particularly diverse with on average  $21 \pm 1$  species per  $0.25\text{ m}^2$ , whereas Pedi-H counts  $13 \pm 1$  species per  $0.25\text{ m}^2$ . Based on cover estimates, most important species at Rhin-D were *Juncus acutiflorus* EHRH. EX HOFFM. (21% average cover), *Lotus uliginosus* SCHKUHR (15%), *Anthoxanthum odoratum* agg. (12%), *Ranunculus acris* L. (9%) and *Lychnis flos-cuculi* L. (8%). At Pedi-H these were *Potentilla erecta* (L.) (20%), *Erica tetralix* L. (15%), *Polygala serpyllifolia* HOSÉ (14%), *Molinia caerulea* agg. (12%) and *Agrostis canina* L. (10%).

### 2.2. Litter collection

Withering *Rhinanthus* and *Pedicularis* plants were collected from both sites at the end of June 2010. Since the management is inherently connected to the presence of the hemiparasites, only the part of the plant that returns to the soil as litter under the management regime was used in our experiment: *Rhinanthus* leaves as

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