

# Do plant species with different growth strategies vary in their ability to compete with soil microbes for chemical forms of nitrogen?

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## Abstract

We used dual labelled stable isotope (<sup>13</sup>C and <sup>15</sup>N) techniques to examine how grassland plant species with different growth strategies vary in their ability to compete with soil microbes for different chemical forms of nitrogen (N), both inorganic and organic. We also tested whether some plant species might avoid competition by preferentially using different chemical forms of N than microbes. This was tested in a pot experiment where monocultures of five co-existing grassland species, namely the grasses *Agrostis capillaris*, *Anthoxanthum odoratum*, *Nardus stricta*, *Deschampsia flexuosa* and the herb *Rumex acetosella*, were grown in field soil from an acid semi-natural temperate grassland. Our data show that grassland plant species with different growth strategies are able to compete effectively with soil microbes for most N forms presented to them, including inorganic N and amino acids of varying complexity. Contrary to what has been found in strongly N limited ecosystems, we did not detect any differential uptake of N on the basis of chemical form, other than that shoot tissue of fast-growing plant species was more enriched in <sup>15</sup>N from ammonium-nitrate and glycine, than from more complex amino acids. Shoot tissue of slow-growing species was equally enriched in <sup>15</sup>N from all these N forms. However, all species tested, least preferred the most complex amino acid phenylalanine, which was preferentially used by soil microbes. We also found that while fast-growing plants took up more of the added N forms than slow-growing species, this variation was not related to differences in the ability of plants to compete with microbes for N forms, as hypothesised. On the contrary, we detected no difference in microbial biomass or microbial uptake of <sup>15</sup>N between fast and slow-growing plant species, suggesting that plant traits that regulate nutrient capture, as opposed to plant species-specific interactions with soil microbes, are the main factor controlling variation in uptake of N by grassland plant species. Overall, our data provide insights into the interactions between plants and soil microbes that influence plant nitrogen use in grassland ecosystems.

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## 1. Introduction

There is a growing awareness that the uptake of organic nitrogen (N) by plants constitutes a critical component of the terrestrial N cycle (Schimel and Bennett, 2004; Jones et al., 2005). While it has been known for some time that plants have the capacity to uptake organic N from soil, in the form of amino acids, it is still unclear how important this pathway of N acquisition is compared to the uptake of N from microbial mineralization (Schimel and

Bennett, 2004; Jones et al., 2005). Despite this, there is now ample evidence that direct uptake of organic nitrogen, in the form of amino acids, represents a substantial fraction of total plant N uptake in a number of terrestrial ecosystems, especially those that are strongly N limited, such as arctic and alpine tundra (Kielland, 1994; Schimel and Chapin, 1996; Raab et al., 1999; Henry and Jefferies, 2003; Nordin et al., 2004), boreal (Näsholm et al., 1998; Nordin et al., 2001) and temperate forest (Finzi and Berthrong, 2005), and low productivity temperate grassland (Streeter et al., 2000; Bardgett et al., 2003; Weigelt et al., 2003, 2005; Harrison et al., 2007).

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Plant species-specific differences in uptake of different chemical forms of N, both organic and inorganic, have also been shown to occur in strongly N limited ecosystems. For example, different species of plants of arctic tundra have been shown to differ in terms of timing, depth and chemical form of N uptake (McKane et al., 2002). Similarly, co-existing plant species of alpine meadows are reported to differ in their ability to take up different forms of soil N (Miller and Bowman, 2002, 2003). It has been argued that this form of partitioning of N, where individual species are differentiated in their use of a limited range of chemical forms of N, might provide a mechanism for plants to efficiently partition a limited soil N pool, thereby facilitating species coexistence and the maintenance of plant diversity (McKane et al., 2002; Reynolds et al., 2003; Miller and Bowman, 2003; Bardgett, 2005). Whether this form of species-specific partitioning of the soil N pool occurs in temperate situations, where rates of N turnover are generally faster (Schimel and Bennett, 2004), is less clear: Pot experiments of individual grassland plant species grown in field soil reveal species-level differences in preferences for different forms of N (Weigelt et al., 2005), suggesting that these species have fundamental niches based on chemical form of N. Also, a  $^{15}\text{N}$ -labelling study of a range of grasslands in Germany showed that different plant functional groups relied on different N pools to meet their N demands, suggesting that N uptake patterns across functional groups are driven by different fundamental niches for chemical forms of N (Kahmen et al., 2006). In contrast,  $^{15}\text{N}$ -labelling studies in British grasslands showed that while co-existing grassland species varied in uptake rates of different chemical forms of N, they all had a similar preference profile across N forms, in that all species preferentially took up simple N forms, such as inorganic N, over more complex amino acids (Harrison et al., 2007). Collectively, these studies suggest that while plant species and functional groups of grassland have fundamental niches based on chemical forms of N (Weigelt et al., 2005; Kahmen et al., 2006), these are not always realised in nature when co-existing species compete for N (Harrison et al., 2007).

One of the complications in determining species-level uptake of different N forms from soil is the extent that individual plant species experience competition from soil microbes for N, which greatly influences the availability of soil N to plants at the individual plant level (Kaye and Hart, 1997). In fertile situations, such as temperate grasslands, plant roots are considered to be poor competitors against microbes for amino acids in soil (Hodge et al., 1999; Owen and Jones, 2001). This view is supported by in situ  $^{15}\text{N}$  labelling studies in grassland, which show that soil microbes take up a greater proportion of  $^{15}\text{N}$ -labelled amino acid added to soil than do plants (Bardgett et al., 2003; Harrison et al., 2007). Likewise, pot experiments show that microbes compete more effectively than plant roots for  $^{15}\text{N}$ -labelled amino acids and inorganic N, and that the intensity of microbial competition for this N is

enhanced by stimulation of microbial biomass, leading to reductions in plant growth (Dunn et al., 2006). Coupled with this is the potential for plants themselves to modify the extent that they are subject to microbial competition for N at the species level, by modifying the size and structure of their associated soil microbial community: It is well established that different plant species of grassland can select for specific microbial communities by altering the quantity and quality of resources entering the soil (Bardgett et al., 1999; Wardle et al., 1999; Porazinska et al., 2003; Innes et al., 2004; Wardle et al., 2004; Bartelt-Ryser et al., 2005; Bardgett, 2005). Therefore, it is plausible that selection for microbial communities at the plant species level will alter microbial sink strength for N, thereby altering plant N availability.

The aim of this study was to examine how plant species of temperate grassland vary in their ability to compete with soil microbes for different chemical forms of N, both inorganic and organic. We also tested whether some plant species might actually avoid microbial competition by preferentially using those chemical forms of N that are less favoured by microbes. These objectives were tested in a pot experiment where monocultures of five co-existing grassland species, namely the grasses *Agrostis capillaris*, *Anthoxanthum odoratum*, *Nardus stricta*, *Deschampsia flexuosa* and the herb *Rumex acetosella*, were grown in field soil from an acid, unfertilised and semi-natural temperate grassland (Bardgett et al., 2001). After seven weeks growth, each plant species was presented with a mixture of four, increasingly complex forms of N: ammonium-nitrate, and the amino acids glycine, serine and phenylalanine. The use of dual labelled ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) stable isotope approaches (Streeter et al., 2000) allowed us to detect variability in plant-microbial uptake of the different N forms at the species level. The plant species used cover the range of growth strategies found in British grassland: *D. flexuosa* and *N. stricta* are slow-growing, stress-tolerator grasses, whereas *R. acetosella*, *A. capillaris* and *A. odoratum* are fast-growing, competitive species (Grime and Hunt, 1975). Our prediction was that fast-growing species will select for a soil microbial community that does not compete effectively with roots for different N forms, thereby allowing these species to maintain high rates of N uptake, irrespective of N form. In contrast, we predict that slower-growing grasses will select for a soil microbial community that competes effectively for N forms, especially more simple forms, thereby reducing the availability of N for plant uptake (Weigelt et al., 2005).

## 2. Materials and methods

### 2.1. Experimental setup

Five common grassland species (*A. capillaris*, *A. odoratum*, *N. stricta*, *D. flexuosa* and the herb *R. acetosella*), which typically coexist in acidic, agriculturally unimproved grassland (UK National Vegetation Classification U4a;

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