



Nitrogen form and spatial pattern promote asynchrony in plant and soil responses to nitrogen inputs in a temperate grassland



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ABSTRACT

Homogeneous and patchy inputs of inorganic and organic nitrogen (N) are common in grazed grasslands, but little is known about the interactions between spatial pattern and form of N inputs for plant and soil processes. Understanding coupled plant and soil responses to heterogeneous N inputs is a critical step towards the improved prediction of field-scale ecosystem function. We compared impacts of uniform and patchy N addition on plant and soil properties using three N forms of increasing complexity (inorganic N; a simple amino acid, glycine; a complex protein, BSA) in an *in situ* grassland experiment. One month after N addition, patchy N treatments increased plant production but decreased biomass produced per gram nitrogen (a proxy of N use efficiency) compared with uniform N treatments. Contrary to expectations, plant production showed limited differences among N form treatments. However, microbial biomass and dissolved organic carbon showed significant N form \times pattern interactions, with strongest responses to patchy inputs of complex organic N. Irrespective of N form, plant responses to patchy N inputs occurred over a larger spatial area than soil microbe responses, consistent with optimal foraging by plant roots. Unlike plants, microbial responses to patchy N inputs were still observed after six months. Overall, our results indicate that patchy inputs of N promote the uncoupling of plant and soil properties, with greatest differences observed for complex organic N inputs. The spatial and temporal asynchrony between plant production and microbial biomass observed may have significant implications for the competitive balance of plants and soil microbes in space, as well as for plant–soil feedbacks involved with the regulation of biogeochemical cycling.

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1. Introduction

Nitrogen (N) inputs play a key role for primary productivity, plant community composition, soil microbial diversity and plant–soil interactions in grassland ecosystems (Tilman, 1987; Bardgett et al., 1999; Hodge et al., 2000a). However, a growing body of evidence suggests that grassland responses to N addition may depend not only on the quantity and form of N (organic and inorganic), but also on the spatial pattern of N (Hutchings et al., 2003; Maestre and Reynolds, 2006; Orwin et al., 2009). This is of particular interest for managed grasslands where both evenly-distributed and patchy inputs of N are common due to fertilizer management and grazer activity respectively.

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During grazing, up to 90% of ingested N from herbage is returned to the pasture in dung and urine patches which cover a small area but have high concentrations of N (equivalent to application rates of around 1000 kg N ha⁻¹ for dung patches, Haynes and Williams, 1993). Such spatial variation in the quantity of soil N has the potential to influence plant processes from the individual to the community level (Hutchings et al., 2003; García-Palacios et al., 2012). For example, root systems of individual plants may respond to local increases in soil N by the production of new lateral roots in N patches, increased growth of existing roots or plasticity in nutrient uptake kinetics, enhancing efficient capture of N (Campbell et al., 1991; Robinson, 1994; Hodge, 2006). Root foraging responses and improved nutrient capture by plants in heterogeneous N conditions may also modify plant population structure and enhance yield (Day et al., 2003a). In theory, species-differences in N foraging efficiency and/or N complementarity should enhance community-level production in heterogeneous conditions (Wijesinghe et al., 2005; Kahmen et al., 2006). In practice, evidence from field experiments on natural plant communities is lacking.

In contrast to the large number of studies addressing plant responses to patchy increases in soil N, very few studies have considered the impacts of soil heterogeneity on the plant–soil system as a whole (Day et al., 2003b; Maestre and Reynolds, 2006; but see Orwin et al., 2009). Soil N availability is a driver for microbial processes such as nitrification and denitrification in terrestrial ecosystems (Booth et al., 2005; Barnard et al., 2006), and recent work indicates that N inputs may also modify microbial community structure (Allison et al., 2008; Ramirez et al., 2012). In the absence of plants, soil respiration and microbial biomass have been shown to decrease under N addition (Ramirez et al., 2012). However, in the presence of plants, responses of microbial biomass to soil N enrichment are mixed (Hodge et al., 2000b; Allison et al., 2008; Treseder, 2008). Recent advances indicate that interactions at the above–belowground interface may provide important feedbacks regulating ecosystem processes and ecosystem N retention (de Vries and Bardgett, 2012). To date though, the effects of patchy increases in soil N on coupled plant–soil responses remain poorly understood.

Aside from modifying the quantity of soil N distributed across space, large herbivores alter the relative abundance of N forms in the soil via their animal returns (Augustine and Frank, 2001). The majority of N in urine is present as urea, which is rapidly hydrolysed to inorganic N (NH_4^+), whereas the bulk of N in large herbivore feces is in organic form (Haynes and Williams, 1993). Previous studies have shown that both plant species and microbial communities are capable of direct uptake of inorganic and organic N forms (Bardgett et al., 2003; Weigelt et al., 2005; Harrison et al., 2008; Näsholm et al., 2009). Work from pot and field experiments also suggests that plant and soil responses to homogeneous nutrient inputs may vary depending on whether inorganic or organic N is added (Dunn et al., 2006; Harrison et al., 2008). However, interactions between N form and spatial pattern are largely unknown. Ecosystem responses to heterogeneous N inputs could be modified by N form due to differences in diffusion, mineralization rates or availability for uptake between different N compounds (Hodge et al., 2000a; Jan et al., 2009). In addition, shifts in plant–soil competition for N over time (Hodge et al., 2000b) could promote variation in short- and long-term responses to patchy inorganic and organic inputs.

Here, we investigated plant and soil responses to N form and N application pattern using a factorial *in situ*, grassland experiment. We focus on impacts of uniform or patchy N addition on the soil–plant system in the short and longer term (one and six months respectively), using N forms of increasing complexity (inorganic N, simple amino acid, complex protein) to represent the range of N inputs that commonly occur in grasslands (Jones et al., 2004). We addressed four main hypotheses: (i) patchy N addition will enhance community-level plant production due to increased root biomass and nutrient-use efficiency; (ii) plant biomass will respond more strongly to inorganic compared with organic N forms, whereas carbon-limited microbial biomass will respond more strongly to organic N; (iii) plant and soil responses to patchy N addition will occur over a wider area within inorganic N plots compared to organic N plots, due to the higher mobility of inorganic N in soil; (iv) plant biomass responses to patchy N addition will occur over a wider area within plots compared to microbial biomass responses, due to plant root distribution and root foraging.

2. Material and methods

2.1. Study site

The study was conducted in a five-year old sown grassland located at INRA-Clermont-Ferrand, France (45°47' N, 03°05' E,

350 m a.s.l.). The climate is temperate with a mean annual precipitation of 575 mm and a mean annual temperature of 12.4 °C. The plant community is dominated by the grass *Dactylis glomerata*. Additional grass species include *Lolium perenne* and *Festuca rubra*. Other species include legumes (*Trifolium repens*, *Lotus corniculatus*) and forbs (*Taraxacum officinale*, *Achillea millefolium*). The soil type is silty clay loam (2.55% C, 0.23% N), with a $\text{pH}_{\text{H}_2\text{O}}$ of 7.8. Prior to this experiment, the site was mown three times a year and not fertilized.

2.2. Experimental design

In order to investigate the interactive effects of N form and N application pattern on plants and soil microbes, two spatial pattern treatments (homogeneous, HOM; heterogeneous, HET) were crossed with three N form treatments. The three N forms were ammonium nitrate (NH_4NO_3 , inorganic N, hereafter abbreviated as IN), glycine ($\text{C}_2\text{H}_5\text{NO}_2$, a simple amino acid, abbreviated as GLY), and bovine serum albumen (a model protein, abbreviated as BSA). These represent the range of N forms present in the soil soluble N pool of temperate grasslands; NH_4NO_3 is commonly applied in fertilized grasslands, GLY is the dominant amino acid in hydrolysed cow urine (Bathurst, 1952), and BSA was used to represent complex organic N forms with high molecular weight present in cow dung. BSA was used rather than cow dung itself to avoid possible confounding effects of other nutrients present in dung (e.g. phosphorous). In addition, a control treatment without N addition was established (total of seven N treatments \times 6 replicates = 42 plots).

In April 2012, 95 cm \times 95 cm experimental plots were established across the study site. The botanical composition of all plots was determined using the point quadrat method with 25 points recorded per plot. Principal components analysis was used to identify two classes of plots according to the relative abundance of grasses, legumes and forbs (data not shown). Plots were then assigned to experimental treatments such that each treatment included equal numbers of each vegetation class chosen at random (this ensured no significant difference between treatments in the relative abundance of species at the start of the experiment). Vegetation was cut to 5 cm on 23rd April, in line with local cutting practices. Immediately prior to N application, measurements of vegetation height indicated no significant difference between experimental plots (one-way ANOVA, $P > 0.05$).

All N treatments were established on 11th May 2012; N application was in liquid form, combined with a simulated small rainfall event (4 mm). In the homogeneous N treatments, dilute N solution was applied across the whole plot. In the heterogeneous N treatments, concentrated N solution was applied to the central 25 \times 25 cm patch of each plot (similar in size to cattle dung or urine patches) with distilled water alone applied to remainder of the plot. Total N and water addition were equal for all plots (N application equivalent to 50 kg N ha^{-1} , consistent with values of urea application and amino acid concentrations in grassland soil). Nitrogen loading in the central patch of the heterogeneous treatments (800 kg N ha^{-1}) was consistent with N from cattle excretion (Haynes and Williams, 1993). The control plots without N addition received water alone.

Plant communities were left to grow under natural rainfall conditions. Measurements of vegetation height were carried out at roughly ten-day intervals throughout the experimental period in the centre and 'edge' zone within all experimental plots (see description of within-plot zones below).

2.3. Harvests and analyses

Plants and soil were harvested at peak biomass (45 days after N addition) and again at the end of October (164 days after N

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