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Nitrogen and phosphorus co-limitation and grazing moderate nitrogen impacts on plant growth and nutrient cycling in sand dune grassland

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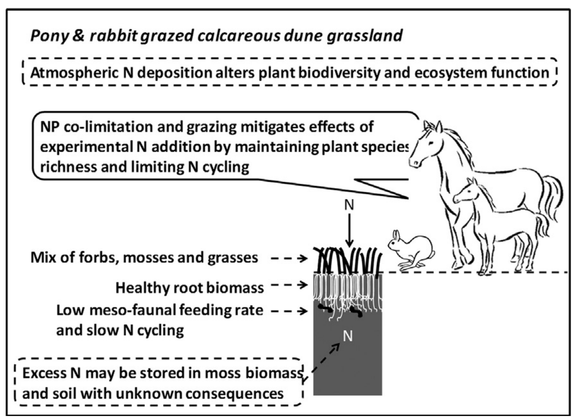
HIGHLIGHTS

- Nutrient addition and grazing were manipulated in species-rich dune grassland.
- NP co-limitation can moderate impacts of nitrogen at and above the critical load.
- Grazing management de-coupled N and P cycling

GRAPHICAL ABSTRACT



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ABSTRACT

Atmospheric nitrogen (N) deposition alters plant biodiversity and ecosystem function in grasslands worldwide. This study examines the impact of 6 years of nutrient addition and grazing management on a sand dune grassland. Results indicate that co-limitation of N and phosphorus (P) moderates the impact of realistic rates of N addition (7.5, 15 kg N ha^1 $year^{-1}$). Combined NP addition (15 kg N + 10 kg P ha^{-1} $year^{-1}$) was the only nutrient treatment to differ significantly from the control, with greater above-ground biomass (mainly moss), and enhanced N and P mineralisation rates. Grazing management altered plant functional group composition, reduced above-ground biomass and meso-faunal feeding rates, and decoupled N and P mineralisation. There were no synergistic effects of grazing and N treatment. Although NP co-limitation apparently prevents adverse impacts of N deposition above the critical load, excess N is likely to be stored in moss biomass and soil, with unknown future consequences.

Capsule: This study shows that at realistic levels of N addition, NP co-limitation in a dune grassland appears to prevent adverse impacts of N on plant growth and nutrient cycling.

1. Introduction

Atmospheric nitrogen (N) deposition is an increasing global problem with clear consequences for grassland ecosystem function (Bobbink et al., 2010; Phoenix et al., 2012). The world's N cycle is now largely controlled

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by human activity (Galloway et al., 2004) with two main sources of N: ammonia from agriculture and nitrogen oxides from fossil fuel combustion (RoTAP, 2012). Nutrient enrichment via N deposition is threatening the diversity of species rich grasslands that are diverse precisely because of their low nutrient soil status (Bobbink and Willems, 1987; Stevens et al., 2011; Field et al., 2014; Jones et al., 2014). In addition to plant composition change, N addition can also alter plant available N, nutrient cycling and soil pH (Phoenix et al., 2012) leading to further changes in ecosystem functioning. Phosphorus (P) limitation is common in many semi-natural grassland soils, especially calcareous grasslands (Willems et al., 1993; Carroll et al., 2003; Vitousek et al., 2010) where P availability is partly determined by soil pH, forming complexes with calcium at high pH (Kooijman and Besse, 2002). As a result, plant growth may be limited by P supply (Jeffrey and Pigott, 1973; Morecroft et al., 1994; van den Berg et al., 2005), thereby reducing some of the negative impacts of N deposition mediated through above-ground competition for light (Ten Harkel and van der Meulen, 1996; Vitousek et al., 2010).

In addition to soil nutrient status the maintenance of species-rich grasslands often depends on the activity of grazing animals (Ten Harkel and van der Meulen, 1996). Grazing management of low productivity grasslands, either for food production or conservation, maintains high plant diversity and influences both plant composition and nutrient cycling (Ford et al., 2012a), potentially interacting with the effects of N addition (Bardgett and Leemans, 1995). Grazers such as ponies, sheep, cattle and rabbits can reduce the dominance of tall grasses and maintain a short sward of species rich forbs (Bakker, 2003; Ford et al., 2012a; Millett and Edmondson, 2013; van Dijk, 1992). Decomposition and nutrient cycling may also be altered by grazing management. Classic theory suggests that grazed land will be dominated by faster bacterial nutrient cycling and un-grazed grassland by slower fungal cycling (McNaughton et al., 1997; Bardgett et al., 1998) due to altered plant litter quality. However, this is not always the case, with both net nitrification and N mineralisation rates lower in grazed than in un-grazed coastal grassland (Ford et al., 2012a, 2013). Nutrient cycling is important as it determines plant available N, a limiting factor for plant primary productivity (Bardgett et al., 2011), mediated by grassland decomposition rate. Soil organic matter decomposition can be measured by mineralisation assays and by the biological activity of soil meso-faunal decomposers using bait lamina (Ford et al., 2012b) and is likely to be enhanced by N addition treatments in grass-dominated habitats due to enhanced litter quality and palatability (Gong et al., 2015). There is a theoretical contrast apparent between the impact of enhanced N additions, expected to increase N cycling rates, and grazing which might increase or decrease N cycling, depending on which theory you subscribe to. Therefore, grazing could either exacerbate or moderate effects of N deposition on nutrient cycling.

This study aimed to assess the impact of realistic N addition and grazing management on plant functional type, above and below-ground biomass and nutrient cycling in a species-rich sand dune grassland of circum-neutral pH. The experiment fulfils three key criteria which many N deposition experiments fail to meet (Phoenix et al., 2012): i) long time scales — here N addition treatments were applied for 6 years prior to the measurements currently presented; ii) realistic N loadings (7.5–15 kg N ha^{-1} $year^{-1}$) on top of a relatively low background N level of 11 kg N ha^{-1} $year^{-1}$ (Jones et al., 2013); iii) frequent applications of N–N addition treatments were applied once a month at realistic solute concentrations. We propose the following three hypotheses: 1) the impact of N addition on plant composition and plant biomass and nutrient cycling in sand dune grasslands will be moderated by soil P limitation; 2) grazing management will alter ecosystem characteristics, with the removal of large herbivores leading to a shift towards increased grass cover, fewer forbs, greater above-ground biomass and faster nutrient cycling; and 3) there will be an interaction of grazing and nitrogen, with grazing management moderating N impacts on plant biomass and nutrient cycling.

2. Materials and methods

2.1. Study site and experimental design

Fixed sand dune grasslands are species rich, low-productivity semi-natural grasslands, and a European designated Annex 1 habitat. Newborough Warren is a calcareous coastal sand dune grassland, located in NW Wales (53° 8′ 59″ N, 4° 21′ 1″ W), noted for its high biodiversity and designated as a National Nature Reserve, Site of Special Scientific Interest and Special Area of Conservation (Natura 2000 site) under the EC Habitats and Species Directive 1992. The 389 ha site is managed by Natural Resources Wales (NRW) and grazed by ponies (*Equus ferus caballus*; 0.2 ha^{-1}), cattle (*Bos Taurus*; 0.05 ha^{-1}) and rabbits (*Oryctolagus cuniculus*; 45 ha^{-1}), to maximise plant diversity (Maddock, 2008; Plassmann et al., 2009). Grazed vegetation is characteristic of UK National Vegetation Classification (NVC) plant communities: *Carex arenaria–Festuca ovina–Agrostis capillaris* dune grassland (SD12) and *Festuca rubra–Galium verum* fixed dune grassland (SD8) (Rodwell, 2000). In 2003, three replicate experimental blocks, each containing three 10 × 10 m experimental units: one fully grazed unit (unfenced), one rabbit grazed unit (fenced with 10 × 10 cm mesh to exclude large grazers) and one un-grazed unit (fenced with 10 × 10 cm mesh and an additional 2.7 × 3.7 cm mesh buried 20 cm underground to prevent rabbit access) were set up as described by Plassmann et al. (2009). Small mammals such as field voles (*Microtus agrestis*) and invertebrate herbivores were assumed to be present within all experimental units. Fully grazed units are denoted as PR (pony and rabbit grazed); rabbit grazed units as R and un-grazed units as U. Two years prior to the measurements in this study, the rabbit population was drastically reduced by an outbreak of viral haemorrhagic disease. Without large grazers accessing these experimental plots to keep the sward short, when the rabbit population recovered the following year they did not return to these plots, preferring to remain in the shorter turf of the fully-grazed areas. Thus, the rabbit grazed treatment was (rabbit) grazed for 4 years, and then un-grazed for 2 years. It therefore represents a sward in transition, retaining some un-grazed characteristics (high sward height), but with residual characteristics of rabbit activity (altered nutrient cycling).

Within each grazing experimental unit five different nutrient treatments were applied: watered control (Control), low N treatment of 7.5 kg N ha^{-1} $year^{-1}$ (Low N), high N treatment of 15 kg N ha^{-1} $year^{-1}$ (High N), P treatment of 10 kg P ha^{-} $year^{-1}$ (P) and high NP treatment of 15 kg N ha^{-1} $year^{-1}$ and 10 kg P ha^{-1} $year^{-1}$ (High NP). All treatment plots measured 2 × 2 m and were located at least 1.5 m from the fence line and 0.75 m from each other to minimise edge effects. N was evenly applied over each treatment plot as ammonium nitrate, made up to 5 L with deionised water, once a month from June 2003 onwards. The watered control received 5 L of deionised water per month. Low and High N treatments started in 2003, the High NP treatment in 2004 and the P-only addition plot (P) later in the experiment, in early spring 2009, prior to the growing season.

2.2. Plant biomass and functional group

Six years after the start of the experiment, vegetation, including standing dead material, was harvested from two 25 × 25 cm squares for each nitrogen treatment, cut to ground level in autumn at the end of the growing season. Vegetation was then stored at 4 °C and subsequently sorted into functional groups (forbs, graminoids, bryophytes and lichens). Vegetation was dried at 65 °C in a fan oven for 24 h to give a measure of above ground or 'shoot' biomass. At the same time, root biomass was sampled by extracting two 50 cm deep soil cores of 5 cm diameter per treatment plot using plastic corers. These cores were divided into three depth zones: 0–15, 15–30 and 30–50 cm, soil removed via washing and roots dried at 65 °C for 24 h to give an indication of root biomass.