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Long-term nitrogen and phosphorus enrichment alters vegetation species composition and reduces carbon storage in upland soil

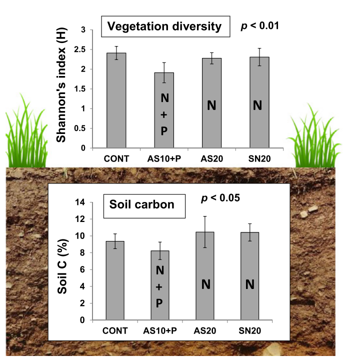
William A.V. Stiles [a,*], Edwin C. Rowe [b], Peter Dennis [a]

[a] Institute of Biological, Environmental and Rural Sciences, Penglais Campus, Aberystwyth University, Wales SY23 3DD, United Kingdom
[b] Centre for Ecology & Hydrology, Bangor, Environment Centre Wales, Bangor LL57 2UP, United Kingdom

HIGHLIGHTS

- Under simulated N pollution, plant diversity was reduced by the addition of P.
- Differences were observed for vegetation species and biomass after P addition.
- N addition increased soil C and N whereas N + P addition reduced soil C and N.
- P limitation can limit ecosystem productivity in situations of chronic N pollution.

GRAPHICAL ABSTRACT



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ABSTRACT

Reactive nitrogen (N) deposition can affect ecosystem processes, particularly in oligotrophic upland habitats. Phosphorus (P) addition has been proposed to reduce the effects of N enrichment on N leaching and acidification, since P limitation can reduce biomass production and consequent sequestration of reactive N. However, biodiversity is often reduced in more productive ecosystems and P limitation may protect against this effect. Responses to P availability in instances of high N deposition are poorly understood. This study investigated the ecosystem response to alleviation of P limitation, using a long-term nutrient addition experiment (1996–2012) three years after ceasing N inputs and 15 years after a single P application. Substantial differences were observed in the structure and composition of vegetation species and above-ground vegetation biomass. Vegetation height was greater in the N + P addition treatments (+38% cf. control), with increased cryptogam cover (+47%), whereas N addition increased graminoid species cover (+68%). Vegetation diversity was significantly reduced by the addition of P (−21%), indicating that P limitation is likely to be an important mechanism that limits biodiversity loss in upland habitats exposed to chronic N deposition. Significant differences in soil C and N contents were also observed between treatments. Relative to control, the addition of N increased soil C (+11%) and N (+11%) pool sizes, whereas the addition of N and P reduced soil C (−12%) and N (−13%) pool sizes. This demonstrated the importance of P availability for upland ecosystem processes, and highlights the long-term effects of P addition on vegetation species composition and C storage. Thus, the addition of P cannot be endorsed as a method for reducing impacts of N deposition.
Capsule: Phosphorus limitation is a major mechanism governing ecosystem processes in situations of high atmospheric nitrogen deposition.

* Corresponding author.
E-mail address: wvs@aber.ac.uk (W.A.V. Stiles).

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1. Introduction

Reactive nitrogen (N) enrichment from anthropogenic sources is a significant threat to ecosystem processes and function in oligotrophic upland habitats (Jones and Power, 2012; Southon et al., 2013). Oligotrophic ecosystems are highly sensitive to changes in nutrient availability, where increases in reactive N can alter plant competitive interactions and ultimately species composition (Stevens et al., 2004, 2010; Maskell et al., 2010). Nitrogen enrichment may also impact upon vegetation through direct toxicity, increased soil acidity, and increased plant susceptibility to other environmental stresses (Bobbink et al., 2010). Globally, reactive N inputs from anthropogenic sources are projected to double in size from current levels by 2050 (Galloway et al., 2004; Phoenix et al., 2006). In Western Europe inputs of reactive N are reported to be in decline (Fowler et al., 2004), but from historically high levels. Nonetheless, a sizeable proportion (58%) of UK upland habitats of conservation importance are subject to N deposition rates in excess of the nutrient N critical load, with some areas receiving threefold the recommended limit (RoTAP, 2012). Increases in reactive N availability in conventionally N limited environments, can cause a shift from N limitation to phosphorus (P) limitation (Crowley et al., 2012; Peñuelas et al., 2013; Rowe et al., 2014). Ecosystems which are P limited may be unable to sequester reactive N inputs if P limitation restricts vegetation biomass production, which could result in N saturation and therefore N leaching (Emmett et al., 1995; Britton and Fisher, 2007). However, by constraining ecosystem productivity in this way, P availability may limit some of the impacts of increasing N enrichment on biodiversity (Olde Venterink, 2011; Ceulemans et al., 2014).

Reactive N deposition can be categorised as either reduced (NH_x) or oxidised (NO_y) N. Reduced forms (e.g., NH_3, NH_4^+) predominantly arise from agricultural activities such as livestock production and fertiliser addition, whereas oxidized forms (i.e. NO_3^-, HNO_3, N_2O) are primarily emitted from transport and industrial sources (Bobbink et al., 2010; Stevens et al., 2011). In soil, NO_y binds weakly to soil particles and is readily leached (Sparks, 2003). Ammonium ions have a longer residence time than NO_y, since they bind strongly to soil cation exchange sites (Rowell, 1994). Nitrogen retention is therefore dependent on the NO_y/NH_x ratio in soil and thus on factors governing nitrification such as aeration and pH. Nutrient pollution in the form of P deposition from anthropogenic activities receives less attention than N deposition, but is a potential risk from the spread of mineral aerosols of dust from P fertilizer usage onto natural ecosystems (Ceulemans et al., 2014; Tipping et al., 2014). The addition of P has been suggested as a method to negate the effects of N enrichment (Armitage et al., 2012; Blanes et al., 2012), but this management strategy may release productivity from P limitation, with negative consequences for biodiversity. Phosphorus has low mobility in soil (Nye and Tinker, 1977) and is strongly adsorbed onto particle surfaces, resulting in long residence times (Rowell, 1994) and therefore long-term influence on ecosystem function. The legacy effect of N and P enrichment in upland systems has been under-investigated. A decline in N deposition rate results in reductions in observed impacts over time (Edmondson et al., 2013), which suggests the potential for some level of recovery.

The availability of both N and P can alter vegetation species composition (Avolio et al., 2014), with increases in bryophyte cover observed after P addition (Gordon et al., 2001) and increases in graminoid cover observed after N addition (Field et al., 2014). This can impact the size and structure of the soil microbial pool (Fanin et al., 2015) and affect key soil processes such as carbon (C) turnover (Kaspari et al., 2008; Schimel and Schaeffer, 2012). Changes in vegetation species composition modifies plant-soil interactions, which alters soil characteristics such as the size of C and N pools (Quin et al., 2014; Ward et al., 2014). Changes to plant-soil feedbacks can also affect soil organisms through the alteration of root exudation patterns and C allocation, and via modification of plant litter input quality (Bardgett et al., 1998).

Experimental trials into ecosystem responses to N and P enrichment have shown mixed responses with regard to decomposition rate and C storage. Mack et al. (2004) found that nutrient enrichment in arctic tundra systems resulted in stimulation of both plant production and decomposition, but had a larger effect on decomposition, therefore resulting in an overall net loss of C. For blanket bog, increased *Sphagnum* spp. growth aided by improved N assimilation facilitated by P availability, resulted in greater C sequestration (Limpens et al., 2004). For grasslands, soil C has been shown to decrease with N and P inputs (Scott et al., 2015), to be unaffected by multi-nutrient inputs (N, P, potassium and magnesium) but to increase with N alone (Fornara et al., 2013), and to increase with either N or P addition when released from limitation (He et al., 2013). Nitrogen and P were also shown to positively interact with P addition reducing N leaching through increased biomass assimilation (Scott et al., 2015). The combined roles of N and P availability in modifying rates of organic matter decomposition are clearly complex and need further investigation.

The aim of this study was to assess the long-term impact of N and P addition on upland vegetation structure and species composition, soil chemistry and the size of soil C and N pools, and to assess the role of P availability as a factor controlling productivity. This was done using a long-term nutrient addition experiment (1996–2012), three years after cessation of N addition and 15 years after a single P application. P was originally added to plots to test the hypothesis that N impacts would be greater in non-P limited systems (Emmett et al., 2007) and this treatment offered an opportunity to further investigate the long-term ecosystem response to increased P availability and concurrent effects on nutrient limitation. We hypothesised that differences in nutrient availabilities from long-term addition would result in: 1) altered vegetation species composition, with greater graminoid species cover found in N addition treatments and greater cryptogam species cover with P addition; 2) reduced soil C and N contents where P was added, due to increased turnover in soil organic matter after release from P limitation, and potentially also to changes in vegetation composition; and 3) reduced vegetation diversity in treatments where P was added as a consequence of higher productivity. By testing these hypotheses we aim to provide insight into the role of P availability over the long term, as a factor governing ecosystem productivity, particularly in situations of high N enrichment, and assess the addition of P as a management strategy to alleviate the impacts of N deposition in upland systems.

2. Methods

2.1. Experimental design

The original experiment was established at Pen y Garn, Pwllpeiran (52° 37′ N, 3° 76′ W), mid-Wales, on a transition between NVC U4 *Festuca ovina - Agrostis capillaris* grassland and H18 *Vaccinium myrtillus - Deschampsia flexuosa* heath on shallow ferric stagnopodzol soil, to investigate whether site specific critical loads of N should be moderated to account for the different forms and N deposited and the grazing intensity on site (Emmett et al., 2007; Phoenix et al., 2012). The site is within an altitude range of 500–600 m a.s.l., with an annual rainfall rate of 1512 mm (UK Meteorological Office, n.d.) and a background N deposition rate of 22 kg N ha^{-1} yr^{-1} (Emmett et al., 2007). Nitrogen was added fortnightly between 1996 and 2012 in a randomised block design, of four 3 × 3 m plots which were replicated six times. The treatments consisted of a control (CONT, no addition), ammonium sulphate at 10 kg N ha^{-1} yr^{-1} + sodium dihydrogen orthophosphate at 20 kg P ha^{-1} yr^{-1} (AS10 + P), ammonium sulphate at 20 kg N ha^{-1} yr^{-1} (AS20) and sodium nitrate at 20 kg N ha^{-1} yr^{-1} (SN20). Phosphorus was added once in 2000 to the AS10 + P treatments to test whether the impact of N would be greater in non-P limited systems. The original experiment incorporated sheep grazing as a factor; sheep were present between 1990 and 2007 at two levels (1.0 sheep ha^{-1} and