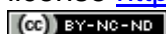


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1 **Long term nitrogen and phosphorus enrichment alters vegetation species**
2 **composition and reduces carbon storage in upland soil**
3

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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.

Keywords: nitrogen deposition; phosphorus limitation; mosses; vascular plants; soil carbon

INTRODUCTION

Reactive nitrogen (N) enrichment from anthropogenic sources is a significant threat to ecosystem processes and function in oligotrophic upland habitats (Jones & 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 & 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 & 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 & 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.

METHODS

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 metres 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 1.5 sheep ha⁻¹). Grazing effect was not considered as a factor in this current study since sufficient time was deemed to have lapsed to allow vegetation re-growth, but the randomised blocks were distributed evenly among the original grazing-treatment paddocks i.e. with three blocks per paddock.

VEGETATION ANALYSIS

All vegetation data were collected in June 2015. Vegetation covers were recorded visually with the Domin scale, subsequently transformed to percentage cover for statistical analysis (Currall 1987). All plants and bryophytes were identified to species level. Vegetation height was the average of five measurements taken using a sward stick (Dennis et al. 2005). Plant strategy functional signatures were calculated for each study plot (Hunt et al. 2004) to determine the effect of changes within the vegetation community to levels of competition, stress and environmental disturbance (Grime 1974). Environmental indicator values (Ellenberg, 1992) adjusted for British vascular plants (Hill et al. 2004) and bryophytes (Hill et al. 2007) were also calculated from the vegetation survey data, without cover-weighting. Ellenberg scores indicate habitat characteristics by utilising known values of plant species preference/tolerance for nutrient level, acidity, moisture and light, which relate to plant realised niches (Hill et al. 1999). Vegetation species diversity was calculated for each treatment plot with the Shannon diversity index, H (Equation 1).

$$H = -\sum_{i=1}^S (P_i \times \ln P_i) \quad (\text{Eq 1})$$

(Eq. 1)

where s = total number of species and P_i is the abundance (proportional cover) of species i

SOIL ANALYSIS

Soil samples were collected in June 2015 from five locations within each treatment plot, using a 20 mm diameter soil corer up to a depth of 30 cm, and bulked together. The samples were air dried and passed through a 2 mm sieve. Soil pH was measured with a Hydrus 400 meter (Fisherbrand, Leicestershire, UK) in a slurry of 10 g fresh soil in 25 mL water. Total N and C were measured by the Dumas combustion method using an elemental analyser (Vario MAX Cube – Elementar Analysensysteme, Hanau, Germany).

STATISTICAL ANALYSIS

Prior to analysis all data were tested for normality and homoscedasticity, and Log ($x+1$) transformed where necessary. Analysis of variance was used to assess relationships between response variables for vegetation (height, species richness and diversity), soil variables (total C, total N, C:N and pH) and the four experimental treatments. When differences between treatments were detected ($p < 0.05$), post-hoc tests were conducted using LSD pairwise comparisons. For analysis of vegetation cover between treatments, species were grouped into functional types (graminoid, cryptogam (bryophyte and lichen), dwarf shrubs and forbs). These data did not conform to parametric test assumptions so a Kruskal–Wallis test was used for analysis. Differences in the composition and abundance of vegetation species between treatments were investigated using Principal Component Analysis (PCA). The first and second principal components were also compared using one-way ANOVA, with LSD pairwise comparisons used to further investigate individual relationships. All univariate statistical analyses were conducted with SPSS 21.0 (IBM SPSS Statistics for Windows, 2012), and PCA was undertaken using Multi-Variate Statistical Package (MVSP version 3.2 - Kovach Computing Services, Anglesey, Wales).

RESULTS

Vegetation was considerably taller in AS10+P than either control or N-only treatments ($p < 0.001$), but N-form treatments (AS20 and SN20) did not increase height relative to the control (Table 1). Species richness did not differ overall, but a response for forb richness ($p < 0.05$) was observed by analysing plant functional types (PFT) independently, with fewer forb species in control plots (0.67 on average) compared to the two N form treatments, AS20 and SN20 (1.67 on average for both) (Table 1). Species diversity was different between treatments (Table 1) with lower vegetation species diversity recorded for the N + P (AS10+P) treatment than either control or N-form treatments (AS20 and SN20) ($p < 0.01$). No difference in Shannon diversity was observed between control and N-form treatments.

Table 1. Mean ($n = 6 \pm$ standard deviation) response of vegetation variables to experimental N and P addition treatments 19 years after commencement and three years after cessation. F values are displayed for one-way ANOVAs, H values for Kruskal-Wallis tests.

	CONT	AS10+P	AS20	SN20	F/H
Height (cm)	10.33 ^b ± 2.91	14.28 ^a ± 3.55	8.06 ^b ± 1.67	7.54 ^b ± 1.29	$F=8.83^{***}$
Species diversity	2.41 ^b ± 0.17	1.91 ^a ± 0.26	2.28 ^b ± 0.14	2.31 ^b ± 0.22	$F=6.94^{**}$
Species richness	17.67 ± 2.73	15.33 ± 1.50	17.83 ± 2.04	17.83 ± 1.47	$F=2.24$
Graminoid richness	5.17 ± 0.98	5.00 ± 1.67	4.50 ± 1.05	4.83 ± 0.75	$F=0.36$
Cryptogam richness	7.17 ± 2.48	6.17 ± 1.60	6.50 ± 1.64	7.17 ± 1.47	$F=0.44$
Dwarf shrub richness	2.67 ± 1.37	1.83 ± 0.75	3.50 ± 1.05	2.83 ± 0.75	$F=2.75$
Forb richness	0.67 ^a ± 0.82	1.17 ± 0.41	1.67 ^b ± 0.82	1.67 ^b ± 0.52	$F=3.11^*$
Graminoid cover (%)	45.93 ± 6.77	34.25 ± 23.34	73.18 ± 29.75	81.24 ± 17.66	$H=6.62^{**}$
Cryptogam cover (%)	54.18 ± 17.27	79.55 ± 21.97	34.19 ± 17.48	35.58 ± 16.69	$H=7.89^{**}$
Dwarf shrub cover (%)	14.87 ± 7.89	8.77 ± 4.02	17.47 ± 11.28	10.14 ± 5.61	$H=3.33$
Forb cover (%)	2.90 ± 3.55	2.97 ± 1.75	3.78 ± 3.93	5.83 ± 2.40	$H=3.90$
Leaf chlorophyll	18.66 ± 1.01	19.78 ± 3.69	17.56 ± 1.78	18.58 ± 2.58	$F=0.81$
Ellenberg Fertility:					
All species	1.98 ± 0.20	2.17 ± 0.23	1.98 ± 0.18	1.96 ± 0.10	$F=0.96$
Vascular plants	1.93 ^b ± 0.23	2.27 ^a ± 0.22	2.09 ± 0.14	1.98 ^b ± 0.14	$F=3.85^*$
Cryptogams	2.01 ± 0.22	2.07 ± 0.34	1.86 ± 0.32	1.95 ± 0.13	$F=0.67$

Bold indicates significant results, $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. CONT = control; AS10+P = ammonium sulphate at 10 kg N ha⁻¹ yr⁻¹ + phosphorus at 20 kg P ha⁻¹ yr⁻¹; AS20 = ammonium sulphate at 20 kg N ha⁻¹ yr⁻¹; SN20 = sodium nitrate at 20 kg N ha⁻¹ yr⁻¹. The lowercase letters indicate significant differences ($p < 0.05$) due to the treatments.

The PFT composition response varied between treatments. Graminoid species cover was higher in the two N form treatments, AS20 and SN20 (Table 1) compared to the control and N + P (AS10+P) treatments. Cryptogam species cover was higher (Table 1) in the N + P (AS10+P) treatment compared to control or either N form treatment (AS20 or SN20).

PCA analysis revealed differences in vegetation species composition, with plots clustering strongly between treatments. The first two axes explained 63.32% of the total variation of the species composition. Differences were observed between treatments for axis 1 ($F_{3,20} = 14.056$, $p < 0.001$, Figure 1), where the value of the first principal component for AS10+P (N + P) was greater than either the control or N form treatments (AS20 or SN20). Control plots also had higher values for the first principal component than either AS20 or SN20 treatments. No difference was observed between AS20 and SN20, thus any effects from different N forms on vegetation species composition were not evident three years after the last application.

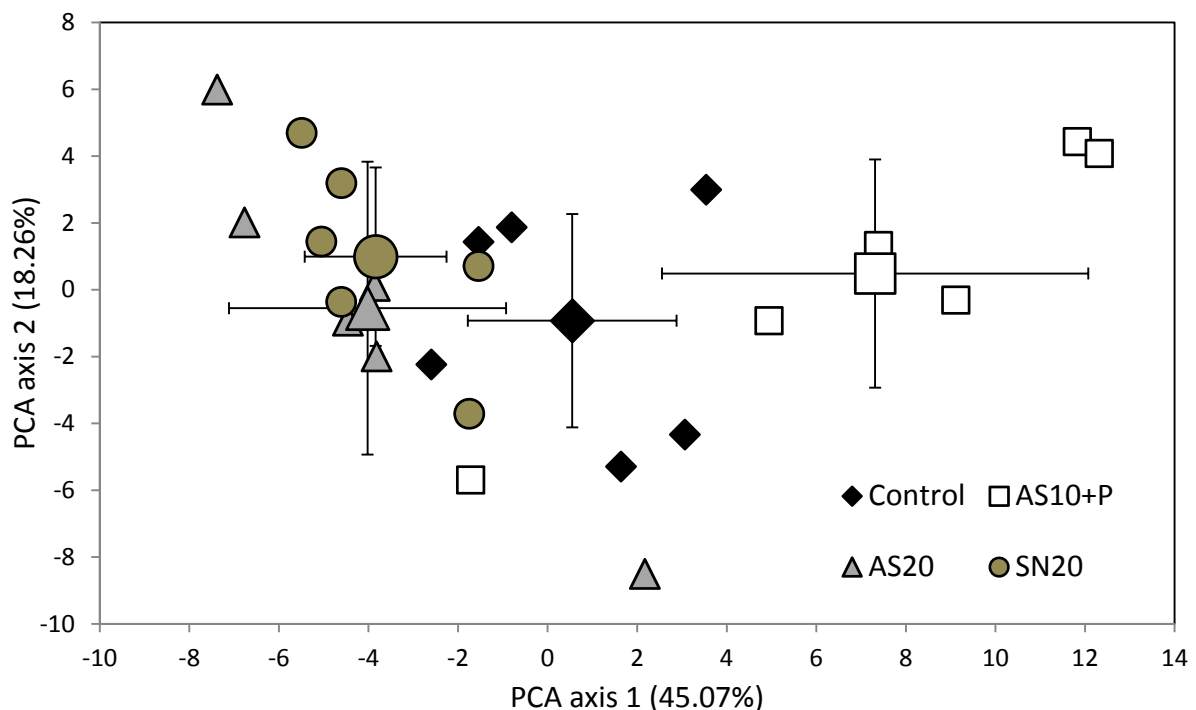


Figure 1. PCA of the vegetation species composition for the 24 treatment plots. CONT = control; AS10+P = ammonium sulphate at 10 kg N ha⁻¹ yr⁻¹ + phosphorus at 20 kg P ha⁻¹ yr⁻¹; AS20 = ammonium sulphate at 20 kg N ha⁻¹ yr⁻¹; SN20 = sodium nitrate at 20 kg N ha⁻¹ yr⁻¹. Error bars denote standard deviation.

No response was observed in Ellenberg fertility score for total vegetation species data, but when considered as separate groups for cryptogams and vascular plants (forbs, shrubs and graminoids), differences were observed for vascular plant species (Table 1). LSD pairwise comparisons revealed the difference to lie between N + P (AS10+P), and control and high nitrate treatment (SN20). No difference was recorded between the high ammonium (AS20) and the N + P treatments (AS10+P).

Table 2. Mean ($n = 6 \pm$ standard deviation) response of soil pH and total soil C and N to experimental N and P addition treatments 19 years after commencement and three years after cessation. $F_{3,20}$ values are derived from one-way ANOVAs

	CONT		AS10+P		AS20		SN20		<i>F</i>
pH	4.12	± 0.12	4.00	± 0.08	4.02	± 0.12	4.02	± 0.13	1.30
Soil C (%)	9.37	± 0.96	8.23 ^a	± 1.14	10.46 ^b	± 2.04	10.42 ^b	± 1.13	3.50*
Soil N (%)	0.58	± 0.07	0.50 ^a	± 0.06	0.64 ^b	± 0.11	0.65 ^b	± 0.09	3.76*
C:N	16.21	± 0.98	16.30	± 0.70	16.38	± 1.35	16.07	± 0.97	0.10

Bold indicates significant results, * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. CONT = control; AS10+P = ammonium sulphate at 10 kg N ha⁻¹ yr⁻¹ + phosphorus at 20 kg P ha⁻¹ yr⁻¹; AS20 = ammonium sulphate at 20 kg N ha⁻¹ yr⁻¹; SN20 = sodium nitrate at 20 kg N ha⁻¹ yr⁻¹. The lowercase letters indicate significant differences ($p < 0.05$) due to the treatments.

Differences among treatments were recorded for both soil C and soil N pools ($p < 0.05$, Table 2). For both pools, no treatment differed from control, however the addition of P resulted in smaller C and N pools in AS10+P treatment compared with the N form treatments (AS20 and SN20). No differences were recorded between treatments for soil pH or the C:N ratio.

DISCUSSION

VEGETATION RESPONSES TO NUTRIENT ADDITION TREATMENTS

Significant differences in vegetation characteristics were observed in this study when exposed to either N or N + P enrichment, which demonstrated the effect of P limitation in systems exposed to long term N enrichment as expected from the impact of N deposition (Crowley et al. 2012; Peñuelas et al. 2013).

Shifts in vegetation species composition were observed among treatments, which is consistent with previous research into effects of N and P additions (Gordon et al. 2001; Pilkington et al. 2007; Avolio et al. 2014). The PFT covers recorded supported our first hypothesis regarding vegetation species composition change, with greater graminoid species cover found in N treatments (AS20 and SN20) and greater cryptogam species cover with N + P (AS10+P) addition. Nitrogen enrichment has been shown to both decrease cryptogam cover (Arróniz-Crespo et al. 2008) and to increase graminoid cover (Field et al. 2014). Cryptogam sensitivity to N deposition is a result of tissue N build-up from high surface absorption capacity (Arróniz-Crespo et al. 2008). Phosphorus availability can alleviate this effect by increasing nitrate reductase activity via stimulation of photosynthesis and export of photosynthetic products from the chloroplast to the cytosol (Lambers et al. 1998; Gordon et al. 2001), which enhances N uptake allowing additional growth and reducing tissue N concentrations (Pilkington et al. 2007; Arróniz-Crespo et al. 2008). Thus, available P enhances cryptogam productivity and abundance (Gordon et al. 2001; Limpens et al. 2004) and the response of cryptogams to N deposition will vary with soil P status (Gordon et al. 2001). Any beneficial influence of P enrichment on cryptogam cover is expected to be highly species-specific however, with negative impacts from increased competition likely to affect slow-growing species (Arróniz-Crespo et al. 2008). This effect was observed in this study by the dominance of certain fast-growing species such as *Rhytidiadelphus loreus* in AS10+P plots. Contrary to some previous studies (Stevens et al. 2011), the addition of different N-forms was shown to have little long-term impact on vegetation species composition, presumably since soil mineral N at the site was mainly in reduced form in the poorly aerated, low pH soils. For both vegetation cover and composition the control treatment was intermediate in response between N + P and N-only treatments, but still significantly different from either of the N-form treatments (AS20 and SN20) or the N + P treatment (AS10+P).

The Shannon diversity of vegetation was lower in treatments in which N + P were added and supported the hypothesis regarding the influence of P limitation on vegetation biodiversity from factors such as increased productivity. Nitrogen enrichment is often considered detrimental for vegetation species diversity, but long term analysis has shown that the presence of other limiting factors such as P

availability may have greater influence than N availability alone (Hejman et al. 2007). Our results supported this idea and showed that the effects on species diversity of N addition alone were negligible, but with increasing P availability became more significant. The species richness of the vegetation was the same for all treatments but more forb species were found in both the N addition treatments compared to control. This is in contrast to the negative effects of N on forb diversity observed in a large UK wide survey (Stevens et al. 2006), and is presumably because responses to N are species-specific and are accepted to be variable (Henry et al. 2011; Stevens et al. 2012) and that species which are sensitive to N enrichment may have already disappeared at this location as a consequence of N deposition (Emmett et al. 2007). The taller vegetation height recorded in the N + P treatments was primarily driven by cryptogam species, which is consistent with other studies (Limpens et al. 2004; Pilkington et al. 2007). This demonstrates the productivity potential of some cryptogam species when released from P limitation in situations of high N enrichment (mechanism discussed above).

Ellenberg fertility scores were higher in the N + P (AS10+P) treatments than either control or nitrate (SN20), indicating higher levels of plant productivity (Wagner et al. 2007); an effect which is attributed to the long term influence of P in soil. No difference was observed with AS20. Grime's C-S-R functional signature analysis for vegetation composition showed no significant shift in prevailing plant strategy. Although treatments caused dramatic shifts in plant species composition, the prevailing strategy (C: competitor) remained stable, indicating overall high productivity at the site, presumably due to the high background rate of N deposition, and a continuing absence of disturbance.

SOIL CHEMICAL RESPONSES TO NUTRIENT ADDITION TREATMENTS

The addition of N (AS20 and SN20) and N + P (AS10+P) in combination resulted in differences in soil C and N pool sizes, suggesting P limitation may have a large effect on below-ground ecosystem processes. The treatment with P added had smaller C and N pools compared to treatments with N alone, which is consistent with similar nutrient addition studies (Bradford et al. 2008; Scott et al. 2015) and supports the second hypothesis. The release from P limitation exerts a dual effect with regard to soil C cycling. The size of soil C pool is controlled by the rate of organic matter decomposition, which is

influenced by changes to vegetation species composition through the alteration of litter quality and quantity returned to the soil (Dorrepaal et al. 2005) and through the availability of nutrients, which stimulates soil microbial activity (Bragazza et al. 2006). The shifts in vegetation species composition towards greater cryptogam cover observed here resulted in vegetation cover with reduced root systems, therefore less direct input of organic matter into soil which is a principal vector for organic C sequestration (Freschet et al. 2013). In addition, roots with higher P tissue content are also potentially more susceptible to decomposition, resulting in faster C cycling rates (Smith et al. 2014). By contrast, He et al. (2013) found that N and P addition increased soil C pools through greater input of below-ground plant organic matter, which highlights the potentially variable response of different environments subject to prevailing vegetation composition.

The size of the N pool was also reduced in the current experiment by the addition of N + P compared to N alone. Increases in the rate of decomposition may augment the rate of N mineralisation by releasing N from storage in soil organic matter (Bragazza et al. 2013). Once mineralised, N can be readily leached or assimilated into biomass through plant uptake (Rowell 1994). Changes to vegetation species composition can affect the rates of N mineralisation, via cascading effects from above-ground to below-ground systems (Bragazza et al. 2012; Ward et al. 2014). Phosphorus availability enhances N uptake by increasing nitrate reductase activity, thus alleviating the negative effect of tissue N saturation by facilitating growth (Pilkington et al. 2007; Arróniz-Crespo et al. 2008). The smaller soil N pool observed in the N + P treatment may also be in part accredited to increased uptake and biomass assimilation, an effect corroborated by the largest vegetation biomass (measured as height) observed in the N + P addition treatment. Nitrogen pool sizes were similar between N only (AS20 and SN20) and control treatments, contrasting with surveys which have shown increases in soil N as a result of N inputs (Pilkington et al. 2005; Edmondson et al. 2010; Phoenix et al. 2012). This is potentially a consequence of background N deposition, which for this location is in the region of 22 -27 kg N ha⁻¹ yr⁻¹ (Emmett et al. 2007). This is above the critical load for this habitat (10 - 15 kg N ha⁻¹ yr⁻¹; APIS 2014), and this chronic enrichment is likely to have reduced the size of experimental response to added N. In addition, no effect of N form on total soil N was observed. Ammonium ions bind more strongly to soil than nitrate

ions and have a longer residence time, which can result in accumulation in soil (Stevens et al. 2011). No ammonium accumulation was observed in this study suggesting no inhibition of N transformation as predicted for NH_4 addition in low pH soil (Stevens et al. 2011). No difference in soil pH was observed between treatments. The addition of N was expected to increase soil acidity, following nitrification of ammonium or directly through nitrate leaching (Reuss & Johnson, 1986; Bobbink et al. 2010; Phoenix et al. 2012). The counter-ions would be expected to have opposite effects, with acidification by added sulphate and alkalisation by added sodium, but the net effect of these processes on pH appeared to be zero. The long-term nature of this existing experiment, including the rare opportunity to observe the effects of P addition on ecosystem processes over decadal timescales, make this a necessary study and effectively demonstrate the differential effect between nutrient availabilities and release from nutrient limitation.

CONCLUSION

Diversity, structure and composition of vegetation were significantly altered by the addition of P to ecosystems with enhanced N availability, with concomitant effects in below-ground systems. Soil C and N pool sizes were reduced by the addition of N and P in combination, via changes to the direct input of organic matter to soil, from vegetation species change towards the dominance of species with limited root systems, and through increased rates of decomposition facilitated by greater nutrient availability and higher nutrient content in soil organic matter. This demonstrates that P enrichment may reduce C storage potential in upland soils.

The persistent nature of P in soil means that the addition of P to upland ecosystems may result in changes in the above-ground and below-ground ecosystem characteristics over the long term. The results presented here demonstrate the nature and impact of P addition 15 years after addition, highlighting the long-term nature of change, thus providing essential insight for projects considering P addition as an amelioration measure.

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