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Dependence of ombrotrophic peat nitrogen on phosphorus and climate

Hannah Toberman[1,2], Edward Tipping[2], John F Boyle[1], Rachel C Helliwell[3], Allan Lilly[3], Peter A Henrys[2]

[1] *School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP*

[2] *Centre for Ecology and Hydrology, Lancaster Environment Centre, Lancaster, LA1 4AP*

[3] *The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, Scotland, UK*

Correspondence to: Professor Edward Tipping
Centre for Ecology and Hydrology
Lancaster LA1 4AP
United Kingdom
et@ceh.ac.uk

ABSTRACT

Nitrogen (N) is a key, possibly limiting, nutrient in ombrotrophic peat ecosystems, and enrichment by pollutant N in atmospheric deposition (N_{dep}, g m^{-2} a^{-1}) is of concern with regard to peatland damage. We collated data on the N content of surface (depth ≤ 25 cm, mean 15 cm) ombrotrophic peat (N_{sp}) for 215 sites in the UK and 62 other sites around the world, including boreal, temperate and tropical locations (wider global data), and found N_{sp} to range from 0.5 % to 4%. We examined the dependences of N_{sp} on surface peat phosphorus (P) content (P_{sp}), mean annual precipitation (MAP), mean annual temperature (MAT) and N_{dep}. Linear regression on individual independent variables showed highly significant ($p < 0.001$) correlations of N_{sp} with P_{sp} ($r^2 = 0.23$) and MAP ($r^2 = 0.14$), and significant ($p < 0.01$) but weaker correlations with MAT ($r^2 = 0.03$) and N_{dep} ($r^2 = 0.03$). A multiple regression model using log-transformed values explained 36% of the variance of the UK data, 84% of the variance of the wider global data, and 47% of the variance of the combined data, all with high significance ($p < 0.001$). In all three cases, most of the variance was explained by P_{sp} and MAP, but in view of a positive correlation between MAP and MAT for many of the sites, a role for MAT in controlling N_{sp} cannot be ruled out. There is little evidence for an effect of N_{dep} on N_{sp}. The results point to a key role of P in N fixation, and thereby C fixation, in ombrotrophic peats.

Key words:

peat; ombrotrophic; nitrogen; phosphorus; climate; nitrogen deposition; global; nutrient cycling

INTRODUCTION

The role of nitrogen (N) in peatland ecosystem dynamics has received much recent attention, primarily due to concern about the effects of anthropogenically-driven elevated atmospheric N deposition (N_{dep}) on carbon sequestration (Turunen et al. 2004; Bragazza et al. 2006; Wu et al. 2014;) and biodiversity (Berendse et al. 2001; Chapman et al. 2003; Limpens et al. 2011). Ombrotrophic peats can have a range of N contents; for example in northern peatlands the range is 0.2% to 3% (Loisel et al. 2014). Such variation likely has implications for carbon fixation, peat functioning and sensitivity to increased N inputs.

Peat N contents depend upon inputs from N fixation and atmospheric deposition, and losses by burial into the anaerobic catotelm, leaching, erosion and microbial processing including denitrification. Data compiled by Loisel et al. (2014) imply an average long-term (i.e. thousands of years) burial rate of N in northern peatlands of the order of 0.5 g m^{-2} a^{-1}. Since N_{dep} values of this magnitude are a phenomenon of only the last half-century (Vitousek et al., 1997; Fowler et al., 2004), this accumulation is due almost entirely to inputs by N fixation, which must also account for losses by processes other than burial. Nitrogen fixation rates of the required magnitude, or even greater, have indeed been reported for ombrotrophic bogs (Martin and Holding, 1978; Hemond 1983; Vile et al., 2014).

Whereas N can be acquired by fixation from the atmosphere, P cannot, and this may be significant because P is required for N fixation both as a constituent of the responsible organisms and through the ATP energy-transferring function (Sprent and Raven 1985; Elser et al. 2007; Augusto et al. 2013; Batterman et al. 2013; Reed et al. 2013; Vitousek et al. 2013). Although in most soils, the supply of P is primarily from mineral weathering, this is not the case for ombrotrophic peat, which by definition receives most or all of its inputs from the atmosphere in rain, dust, biological debris from other ecosystems, and the activities of insects, birds and mammals (Rydin and Jeglum 2013; Tipping et al. 2014). Therefore P acquisition is likely a major determinant of variations amongst peats with respect to nutrition, including N fixation. Indeed, the role of P as a limiting factor of biomass growth and functioning in peatlands has been clearly demonstrated (Fritz et al. 2012; Larmola et al. 2013; Hill et al. 2014). Whilst there have been no studies looking specifically at P effects on biological N fixation in peatlands, the findings that P additions increase both peatland plant N uptake (Limpens et al. 2004) and microbial N processing (White and Reddy 2000) illustrate the importance of P in peatland N cycling.

Given the influences of ambient temperature and moisture regimes on biological N cycling (Rustad et al. 2001; Houlton et al. 2008; Ollivier et al. 2011), it is likely that climate also affects N acquisition by peats. Positive effects of temperature on the N dynamics of peat bogs (Weedon et al. 2012) and on biological N fixation by bryophytic symbionts (Houlton et al. 2008; Lindo et al. 2013) have been demonstrated. Moisture has also been shown to be important for feathermoss-associated N fixation (Gundale et al. 2009; Jackson et al. 2011).

To obtain a wider picture of the possible controlling effects of P and climate on the variation of the N content of ombrotrophic peats, we conducted a meta-analysis of data for a total of 277 sites across boreal, temperate and tropical regions.

METHODS

We defined three data sets as follows (Table 1): UK-only, wider global (all data except UK), combined (all data). The data were divided between UK and wider global sites because of the much greater number of UK data (see Results). Values for surface peat total N concentrations (N_{sp}) and surface peat total P concentrations (P_{sp}) measured simultaneously at the same ombrotrophic peatland sites were collated from both published literature and previously unpublished data (Table S1). The previously unpublished data were for UK sites from the Centre for Ecology and Hydrology (A F Harrison pers. comm.), Scottish Soils Database (Hudson *et al*. 2012), and for Finnish sites from the University of Helsinki (R Laiho, pers. comm.). In total our database comprises data from 277 ombrotrophic peatland sites including 215 from the UK, 14 from other temperate localities, 14 from boreal regions and 34 from the tropics (see Table S1 and Figure 1). 'Surface' peat was defined as peat sampled from starting depths of 0-10 cm from the surface down to a maximum of 25 cm from the surface. The mean sample depth was 15 cm. Analytical methods for measurements of N_{sp} and P_{sp} for each data source are summarised in Table S1. All peat samples had a C concentration ≥ 40%, the mean C concentration across all sites being 51%. We assume that both N and P in these organic rich soils are overwhelmingly in organic forms. None of the sites considered have been afforested or fertilised. For the UK, however, some sites may have been subjected to variable intensities of drainage.

Values for mean annual precipitation (MAP, m), mean annual temperature (MAT, ^{o}C), and total annual N deposition (N_{dep}, g m^{-2} a^{-1}) were collated for each site (Table S1). For the UK sites, MAP and MAT are 1970-2000 means from the UK Meteorological Office, and N_{dep} data are 2006-2008 means derived by the CBED model (Smith et al. 2000). For sites not in the UK, MAP and MAT are either values reported in each publication, or 1930-1960 means from the global data set of Cramer and Leemans (2001), with months summed or averaged to give annual values. For all non-UK sites, N_{dep} data are modelled values for 1993 (Dentener 2006).

RESULTS

The collated data cover appreciable ranges of N_{sp}, P_{sp}, MAP, MAT and N_{dep} (Table 1). The values of N_{sp} vary by a factor of 7 and those of P_{sp} by a factor of 19, while the NP ratio ranges from 6 to 138. The mapped data (Figure 1) show that the wider global data come from a broad range of locations, although remote peatland localities such as northern Canada and Russia are under-represented. From Table S1 it can be seen that tropical and UK locations have the highest values of N_{sp}, while NP ratios are lowest for non-UK temperate and boreal sites, and highest for tropical sites, with UK sites in between. Values of MAP and MAT were not significantly correlated for the UK sites, but for the wider global set we found a strong positive correlation which can be parameterised as MAP = 0.49 $e^{0.077\ MAT}$ ($r^2 = 0.96$, $p < 0.001$), and for the combined data set the relationship is MAP = 0.93 $e^{0.053\ MAT}$ ($r^2 = 0.53$, $p < 0.001$). For neither the UK nor the wider global data set was N_{dep} correlated to MAP or MAT.

Regression analysis of the relationships of N_{sp} to individual potential driving variables for the combined data set revealed highly significant ($p < 0.001$) positive correlations with P_{sp} and MAP, and significant ($p < 0.01$) positive correlations with MAT and N_{dep} (Figure 2). However, none of the relationships explained very much of the variation in N_{sp} ($r^2 \leq 0.23$). The NP ratio varied positively and significantly with both MAT ($r^2 = 0.10$, $p < 0.001$) and MAP ($r^2 = 0.11$, $p < 0.001$).

Because increased N_{dep} is a fairly recent phenomenon, and most prevalent in temperate regions, we also conducted a separate analysis of the observations made after 2000 for temperate sites only (n = 68). This increased the value of r^2 from 0.03 for the combined dataset (n = 277) to 0.07, but the significance was lower ($p < 0.05$). Furthermore, we found that neither UK N_{sp} nor the UK NP ratio in surface ombrotrophic peat increased with time between 1963 and 2009.

We applied the following multiple regression model to the data;

$$\log N_{sp} = c1 \times \log P_{sp} + c2 \times \log MAP + c3 \times \log (MAT+10) + c4 \times \log N_{dep} + c5 \qquad (1)$$

We used log-transformed data to meet the requirements for a normal distribution of the residuals, and added 10 to the MAT values to make them all positive. Because of the imbalance in the spatial distribution of the data, in particular the large number of UK sites, we conducted separate multiple regression analyses of relationships between N_{sp} and the drivers for UK sites only, wider global data, and combined data. The overall picture was the same in each case, with highly significant dependences on P_{sp} and MAP and weaker ones on MAT and N_{dep} (Table 2, Figure 3). Furthermore, the values of the coefficients c1 and c2 were similar for the three data sets, whereas c3 and c4 were variable, and only in two cases are their values significant. The model explained 36%, 84% and 47%

of the N_{sp} variance in the UK, wider global, and combined data sets respectively. The standard errors in log N_{sp} (0.12, 0.09, 0.13) were less diverse than the r^2 values.

A simplified model using only P_{sp} and MAP explained 29%, 84% and 44% of the variances in the UK, wider global, and combined data sets respectively, with standard errors of 0.12, 0.09 and 0.13 (Table S2). If MAT was used with P_{sp}, the fits were poorer although still highly significant ($p < 0.001$), explaining 27%, 76% and 31% of the variances, with standard errors of 0.12, 0.11 and 0.15 (Table S3).

DISCUSSION

The results show that ombrotrophic peat N_{sp} depends strongly upon P_{sp} and MAP. The results of the multiple regression analyses are consistent with a multiplicative effect, which can be expressed as;

$$N_{sp} = k \ P_{sp}^{c1} \ MAP^{c2} \quad (2)$$

with values of *k*, *c1* and *c2* of 3.9. 0.35 and 0.44 respectively (Table S2). Because *c1* and *c2* are both less than one, N_{sp} is most sensitive to P_{sp} and MAP when the two drivers have low values, and the relative response decreases as they get larger (Figure S1). The dependence on P_{sp} is consistent with the need for this element in N fixation (see Introduction), and raises the question as to whether ombrotrophic peats might be P-limited. Indeed P has been found to limit Sphagnum growth at sites receiving high N deposition (Aerts et al. 1992; Gunnarsson and Rydin 2000; Bragazza et al. 2004) and increased investment in P acquisition via phosphatase activity has been observed with peatland N additions (Phuyal *et al.*, 2008).

Both temperature and moisture are likely to affect N accumulation, either through N fixation or by affecting other biogeochemical processes in peats (see Introduction). It also seems possible that the MAP effect arises from seasonal variation, with disruption of N cycling processes occurring during times of moisture deficiency - for example, during periods of low temperature and precipitation in boreal winters and periods of low rainfall in temperate summers. Although significant temperature effects appear when only P_{sp} and MAT are used as explanatory variables (Table S3), stronger relationships are found with MAP as the second explanatory variable (Table S2), and when both MAP and MAT are included in the multiple regression model, the former is selected as the more explanatory (Table 2). Interpretation here is confounded by the correlation between MAP and MAT, especially in the wider global data set. However, with the UK data set this correlation is not seen, and it may be significant that this is the one instance where both MAP and MAT are significant predictors (Table 2). Therefore we cannot rule out a separate dependence on MAT of N_{sp}, and it may be that our data are insufficient to draw it out. Nonetheless, it is quite clear that climate exerts a strong effect on the N content of ombrotrophic peats. Furthermore, the positive correlations of peat NP ratio to MAT and MAP suggest that in warmer, wetter regions, proportionally more N is incorporated into surface peat per unit P than in colder, drier regions, which suggests a greater efficiency of P utilisation for N acquisition where climatic conditions favour biological activity.

Our results show that N_{sp} does not depend strongly on N_{dep}, even when data are selected to make a fairer comparison by considering only samples collected over a constrained time period, or in a restricted climate zone. There are significant positive responses, but the relationships explain little variation in the data. Although there is evidence that current N deposition influences the N concentration of *Sphagnum* moss (Bragazza et al. 2005), because elevated N_{dep} is a recent occurrence, there probably has not been sufficient time for it to affect N_{sp} as considered here, most of which has instead accumulated via N fixation. Furthermore, it is known that, at least in forest ecosystems, N_{dep} down-regulates N fixation (DeLuca et al., 2008), and this will tend to cancel any effects of deposition.

The wider global data set is explained very well by equation (2), but not so well the UK data, in terms of r^2, and this may partly be a statistical artefact because the wider global data are more evenly spread. The SE values (Tables 2, S2, S3) in predicted N_{sp} are not so different among the three data sets considered, although it is still true that the SE values for the UK-only and combined data sets are higher than that for the wider global set. Whilst to our knowledge the sites included in our analysis were all subject to minimal human disturbance, current and past management practices such as drainage, grazing and burning may have affected their nutrient status (Ramschunder et al. 2009; Jauhiainen et al. 2012; Andersen et al. 2013). This is particularly the case for the UK with its long history of upland management for livestock and grouse rearing (JNCC 2011), and site specific variations in land-management practices may therefore have contributed to the weaker correlation between surface peat N and surface peat P concentrations and climate for the UK sites. Other factors which might account for the unexplained variance in the data include plant type, the effects of atmospherically-deposited contaminants (sulphur, heavy metals, persistent organic pollutants), and the availability of other nutrients.

The great current interest in the role of peatlands in regional and global carbon cycles has resulted in the publication of major reviews (e.g. Limpens et al. 2008; Lindsay 2010; Yu 2012), and the development of sophisticated models (Frolking et al. 2010; Heinemeyer et al. 2010), but only recently has attention has been focused on the role of nutrients and nutrient stoichiometry in carbon fixation (Wu and Blodau 2013; Wang et al. 2014, 2015). As noted by Vile et al. (2014), ombrotrophic peats are highly efficient at fixing C, having net primary production values typically of several hundred g m^{-2} a^{-1} despite their low nutrient status. This is due to the low nutrient contents of their vegetation and high nutrient use efficiency (Small 1972; Wang et al 2014).

However, accumulating peats have to combat the loss of nutrients by burial in the catotelm, and while peatland plants may actively hold nutrients in the top layers of peat bogs (Malmer 1998) perhaps by mycorrhizal uptake (Wang et al. 2014), they still bury a good deal of N (Loisel et al. 2014), which necessitates high rates of N fixation. Indeed, the N fixation rates of 1 to 3 gN m^{-2} a^{-1} reported for bogs by Martin and Holding (1978), Hemond (1983) and Vile et al. (2014) are comparable to the highest rates estimated for different global ecosystems by Cleveland et al. (1999). Our results strongly suggest that a key factor in the ability of peatlands to carry out N fixation, and thereby C fixation, is P availability, with important modification by climatic conditions, especially precipitation. It seems especially important to understand how peatlands, especially remote ones, acquire P, and how this may have varied over time, given for example Holocene-scale variations in dust transfer (Cockerton et al. 2014) and recent anthropogenic enhancement of this flux (Neff et al. 2008). The incorporation of N and P cycling into models of peat growth is a pressing need.

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SUPPLEMENTARY INFORMATION

Table S1	Surface peat N and P database
Table S2	Multiple regression analysis results P_{sp} and MAP only.
Table S3	Multiple regression analysis results P_{sp} and MAT only.
Figure S1	Predicted dependence of N_{sp} on P_{sp} at different MAP values (m yr^{-1})

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Table 1. Summary of data. See Table S1 for details.

Data source	n	time period	N_{sp} %	P_{sp} %	N:P	MAP m	MAT °C	N_{dep} g m^{-2} a^{-1}
UK[1]	215	1963-2009	0.5 - 3.6	0.01 - 0.19	11 - 138	0.8 - 2.8	2.7 - 10.8	0.4 - 3.0
Wider global[2]	62	1971-2012	0.5 - 2.9	0.02 - 0.15	6 - 85	0.4 - 4.0	-3.8 - 26.4	0.0 - 1.9
Combined	277	1963-2012	0.5 - 3.6	0.01 - 0.19	6 - 138	0.4 - 4.0	-3.8 - 26.4	0.0 - 3.0

[1] From: Scottish Soils Database; Emmett et al. 2007; Tipping et al. 2003; AF Harrison pers commun; Hayati and Proctor, 1991

[2] From: Minkkinen et al. 1999; Moore et al. 2008; Bragazza et al. 2005; Turetsky et al. 2000; Pakarinen and Gorham 1984; Richardson et al. 1978; Damman 1978; R Laiho pers commun; Keller et al. 2006; Bragazza and Gerdol 1999; Bragazza and Gerdol 2002; Clarkson et al. 2004a; Clarkson et al. 2004b; Bridgham et al. 1998; Hill et al. 2014; Cheesman et al. 2012; Page et al. 1999; Anderson 1983; Pajunen 1994

Table 2. Multiple regression analysis results; dependence of N_{sp} on P_{sp}, MAP, (MAT+10) and N_{dep} for log-transformed data; coefficients c1-c5 refer to equation (1)

	Variable Coefficient	P_{sp} c1	MAP c2	MAT+10 c3	Ndep c4	const c5	r^2	SE	p
UK	Value	0.30	0.35	0.89	-0.09	-0.52	0.36	0.12	1.6×10^{-19}
	SE	0.04	0.07	0.21	0.05	0.27			
	p	1.2×10^{-10}	2.9×10^{-7}	4.4×10^{-5}	0.057	0.055			
Wider global	Value	0.43	0.56	0.03	-0.02	0.51	0.84	0.09	8.2×10^{-22}
	SE	0.07	0.11	0.17	0.03	0.23			
	p	8.2×10^{-8}	2.2×10^{-6}	0.87	0.51	0.032			
Combined	Value	0.33	0.37	0.11	0.09	0.44	0.47	0.13	6.2×10^{-37}
	SE	0.04	0.06	0.10	0.02	0.12			
	p	2.0×10^{-14}	4.2×10^{-9}	0.30	6.0×10^{-5}	3.1×10^{-4}			

Figure captions

Figure 1. Map showing ombrotrophic peat sites. The numbers insider the symbols are the numbers of data for each country or region.

Figure 2. Relationships between surface peat %N (N_{sp}) and surface peat %P (P_{sp}), mean annual precipitation (MAP), mean annual temperature (MAT) and atmospheric N deposition (N_{dep}) for the combined dataset. Trend lines and r^2 are for linear regression ($n = 277$); the regressions are all significant, %P and MAP both $p < 0.001$, MAT and N_{dep} both $p < 0.01$.

Figure 3. Observed N_{sp} *vs*. values predicted from linear multiple regressions with P_{sp}, MAT, MAP and N_{dep} as independent variables. The 1:1 lines are shown. Numbers of data points are given in Table 1.

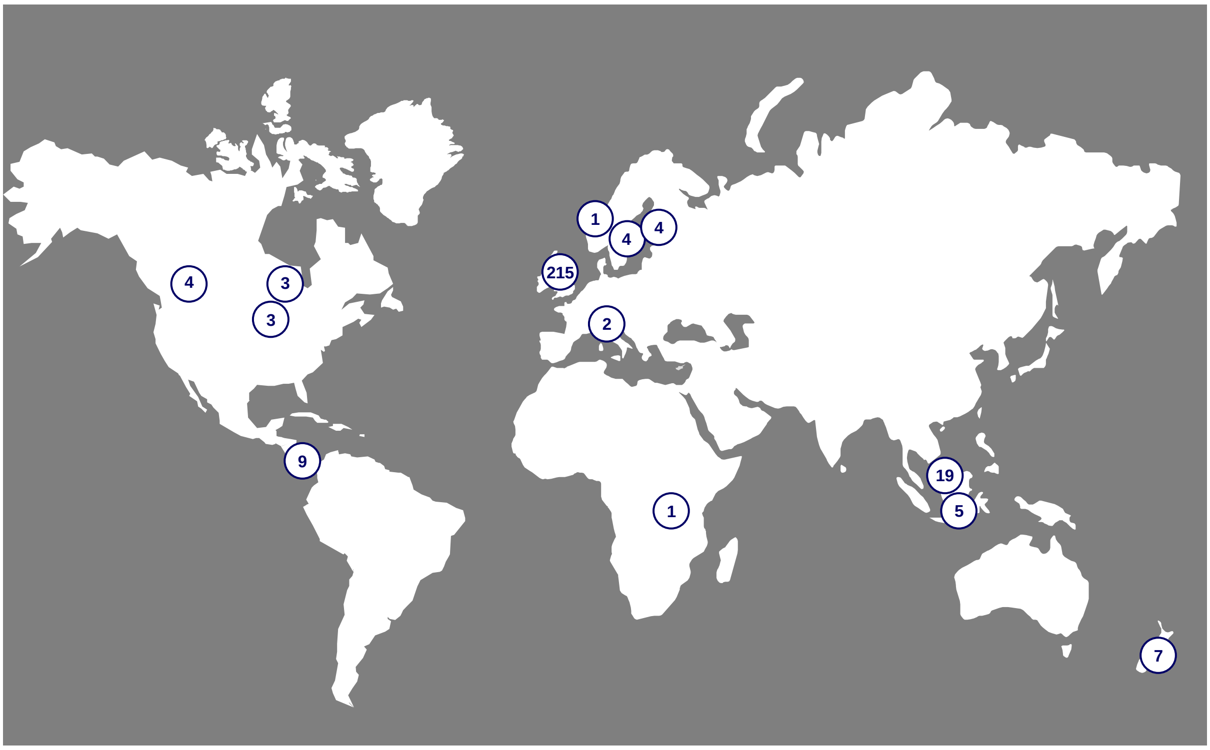

Figure 1

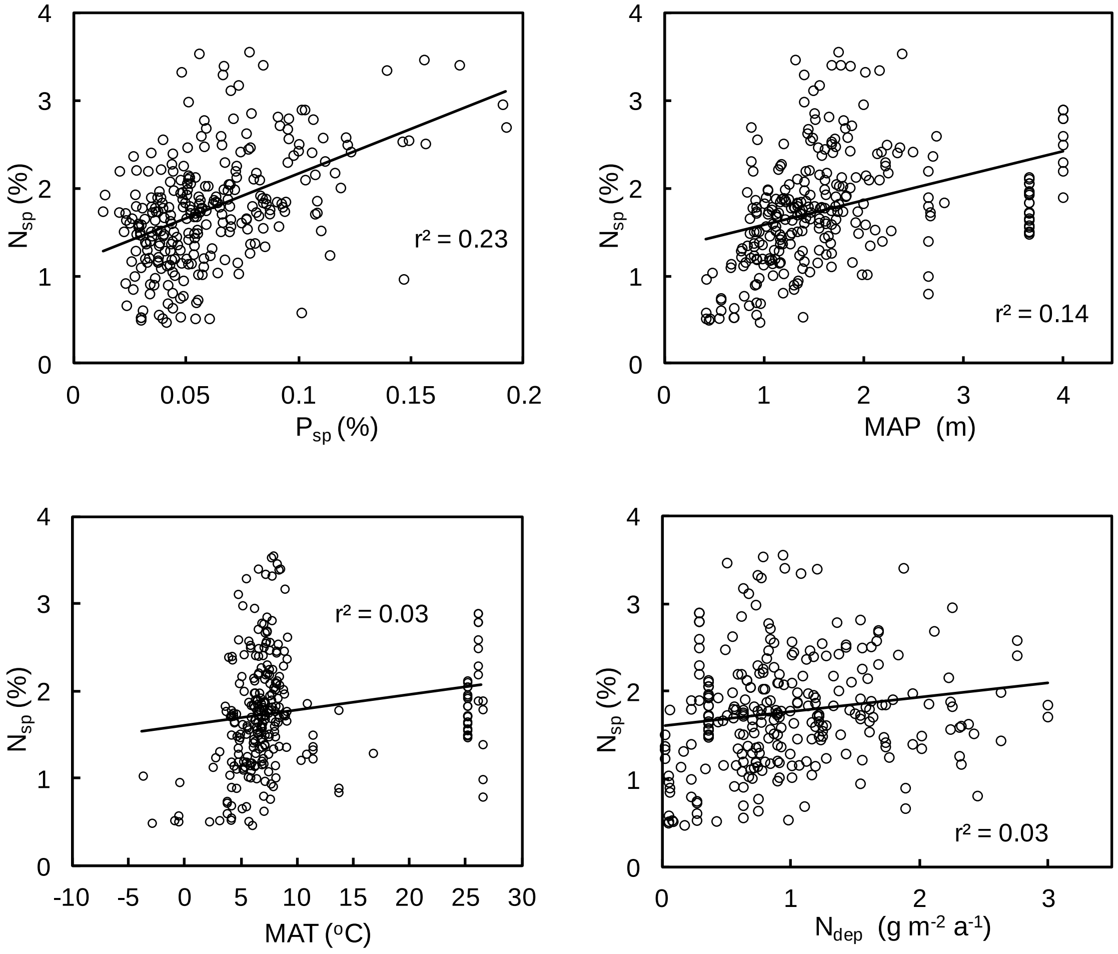
N_{sp} (%)
P_{sp} (%)
r² = 0.23
MAP (m)
r² = 0.14
MAT (°C)
r² = 0.03
N_{dep} (g m^{-2} a^{-1})
r² = 0.03
0
1
2
3
4
0.05
0.1
0.15
0.2
-10
-5
5
10
15
20
25
30

Figure 2

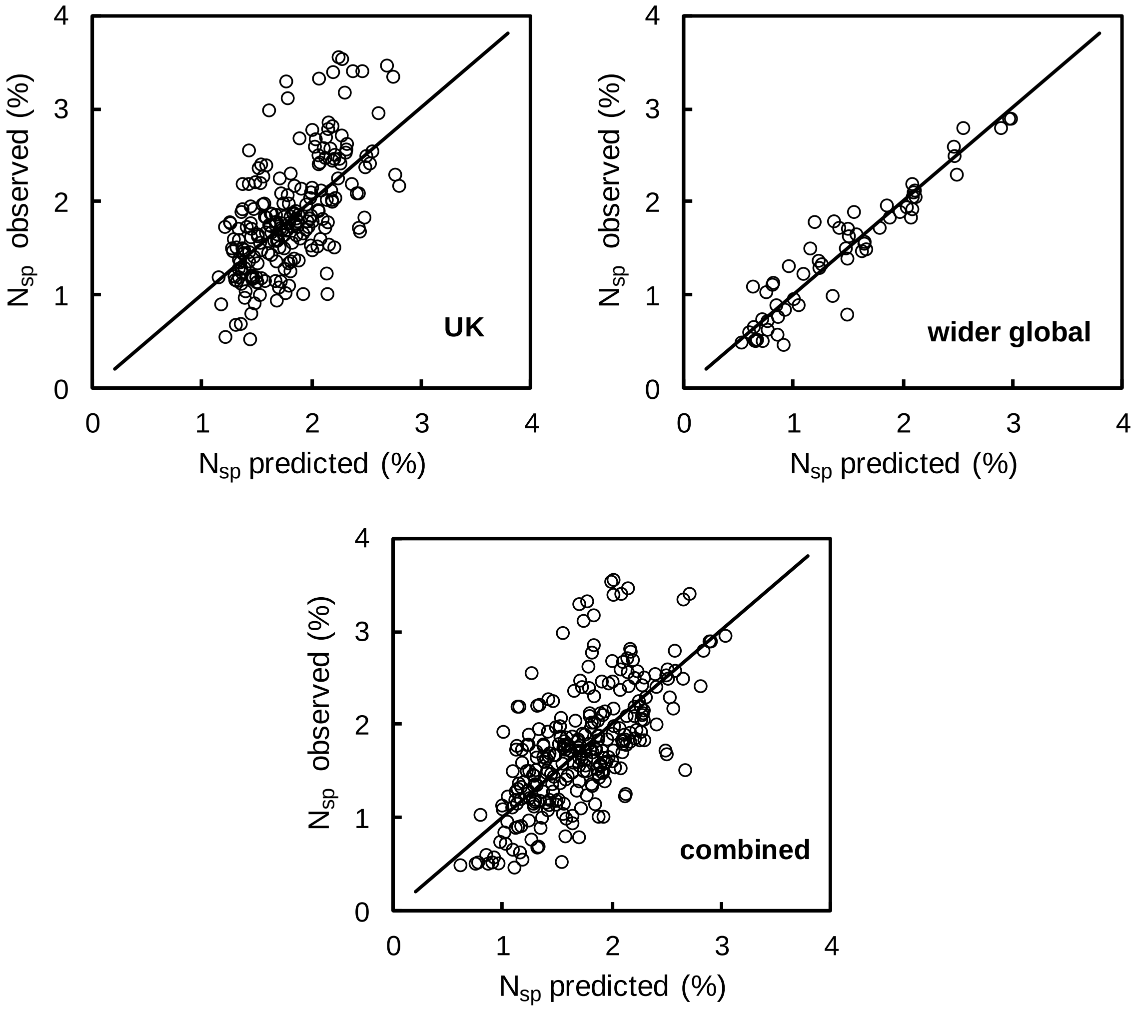

Figure 3