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The role of soil phosphorus sorption characteristics in the functioning and stability of lowland heath ecosystems

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Abstract Previous research indicates that transition between lowland heath and scrub ecosystems depends upon soil phosphorus (P) sorption capacity (PSC). Experimental work found a positive relationship between P availability and tree invasion but the relationship between PSC, P availability and scrub invasion is poorly understood making it difficult to clearly link landscape invasion patterns with small-scale experimental findings. Using a combination of descriptive and experimental studies we re-examined the relationship between PSC and tree invasion and investigated the hypothesis that PSC is a key determinant of P retention and therefore the P available to scrub colonists. In a statistical model fitted to soil data from three regions soil organic matter (SOM) content explained most of the variation in available P but PSC also accounted for a significant portion of the variance. Additional models suggest that soil P saturation and the proportion of available P in water desorbable form, both indicators of leaching losses, are strongly dependent on PSC. These findings are supported by experimental results; there was greater retention of added P, in plant available form, on high PSC soils and low PSC soils saturated at lower levels of addition. When synthesized with existing data, these results demonstrate that the relationship between PSC and P availability operates via a variety of mechanisms and at several spatio-temporal scales. PSC may for instance, influence post-disturbance SOM accumulation rates. Therefore PSC, by controlling P-availability and ecosystem development, may control the propensity of a site to either heath or scrub.

Keywords Heathland · Leaching · Disturbance · Ecosystem state · Transition · Invasion

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Introduction

Changes in nutrient availability are known to provoke transitions between ecosystem states in many ecosystems e.g. grasslands, coral reefs and lakes (Petraitis and Latham 1999; Scheffer et al. 2001). Most research in this field has focused upon anthropogenic nutrient inputs but regional differences and autogenic processes also generate variation in nutrient supply rates (e.g. Morris and Boerner 1998; Wardle et al. 2004). Such natural differences may also influence the likelihood of transition and significantly affect community structure and ecosystem function.

The persistence of European lowland heath is threatened by successional change to scrub and grassland (Aerts and Heil 1993; Rose et al. 1999). Although not always intrinsically nutrient poor, lowland heaths have a low phosphorus (P) and nitrogen (N) bio-availability resulting from nutrient sequestration in organic compartments and slow mineralization rates (Gimingham et al. 1979; Berendse et al. 1989). Heathland persistence may be a consequence of this oligotrophy because experimental studies demonstrate that changes in productivity and species abundance, including grasses (Aerts and Berendse 1988), invading trees (Manning et al. 2005), lichens, bryophytes (Helsper et al. 1983) and herbivorous beetles (Brunstig and Heil 1985) occur when nutrients are added. Similar changes in unmanipulated heaths may be driven by disturbances, autogenic nutrient accumulation, positive feedbacks in supply driven by invading species, or by a combination of these factors (Berendse 1990; Mitchell et al. 1999).

Although most work on heathland nutrient dynamics has focused upon the role of N (e.g. Van Vuuren et al. 1992) the potential importance of P was indicated by Chapman et al. (1989a, b), who related major ecosystem properties to P sorption capacity (PSC). The simulation model of Chapman et al. (1989a) suggested that PSC could, by determining P retention, drive growth and soil organic matter (SOM) accumulation rates. These variables are in turn, believed to affect the speed of transition between growth phases of the dwarf shrub vegetation cycle (*sensu* Watt 1947) (Chapman and Clarke 1980), fire outbreak frequency and N mineralization rates (Berendse 1990).

A survey of heaths in Southern England found that soil PSC displayed strong regional variation but that most sites could be categorized into three types that coincided with major areas of UK heath (Chapman et al. 1989b). This indicates that P retention and availability, and therefore heathland ecosystem dynamics, may differ greatly between regions. Field experiments have found that P availability determines *Betula* seedling colonization in a wide range of heathland conditions (Manning et al. 2004, 2005), the moment of transition between heath and scrub ecosystem states (Hester et al. 1991a, b; Mitchell et al. 1999). If P availability is determined by PSC then the likelihood of transition between heath and scrub may differ between regions. This deduction is supported by the observations of Chapman et al. (1989b) who identified a correlation between the likelihood of scrub invasion and PSC and suggested an arbitrary threshold for tree invasion where soil PSC is >700 μg P g^{-1} and where traditional management had ceased. Beyond this, the relationship between PSC and invasion was not explicitly defined.

Although Chapman et al. (1989a, b) suggest that PSC plays a crucial role in heathland dynamics their conclusions are grounded on correlative patterns (Chapman et al. 1989b) and a simulation model with many assumed parameters and relationships (Chapman et al. 1989a). There is also an implicit, but unproven, assumption in their research that PSC influences productivity and scrub invasion by affecting the P availability. Finally, Chapman et al. (1989b) implied that greater invasion of disturbed sites (Manning et al. 2005) could be related to soil disturbance bringing high PSC soils to the surface and raising P availability. This idea has not been tested experimentally.

The aim of this research was to test these assumptions and formulate a clear conceptual bridge between the experimental findings of Manning et al. (2004, 2005) and the landscape-scale patterns described by Chapman et al. (1989b). This was achieved by reanalyzing the Chapman et al. (1989b) data to generate a detailed and quantitative model of the relationship between PSC and scrub invasion, describing the soil properties of sites differing in their soil P characteristics and investigating changes in P characteristics with soil depth. We hypothesized that PSC increases with soil depth as result of leached Fe and Al compounds. Additionally, statistical models which describe the relationships between soil characteristics, including P availability and PSC, were formed. These descriptive studies were supported by experimental work in which P addition and disturbance treatments were applied to the experimental sites of Manning et al. (2004, 2005). We hypothesized that greater proportions of added P would be retained, in a plant-available form, on high PSC sites, and that disturbance would bring higher PSC soils to the surface, increasing available P. We synthesize our results with existing knowledge to form a model of how PSC controls the functioning and stability of lowland heath ecosystems which integrates with the framework of ecosystem state transitions described by Scheffer and Carpenter (2003) and Suding et al. (2004a).

Methods

Reanalysis

We reanalyzed data from the appendix of Chapman et al. (1989b) to generate a statistical model describing the likelihood of invasion. These data describe the grazing regime, tree invasion history (assessed using historic aerial photographs), PSC, isotopically exchangeable P (IEP), acetic acid extractable P (AEP), SOM content and pH of 68 sites in the south of England. IEP measurement relies upon the constancy of the sorption–desorption process to measure sorbed P by quantifying the proportion of an added $^{32}PO_4$ label that remains in solution when incubated (for 24 h) with a soil sample. Soil samples were taken from areas of uninvaded heath, and for sites classified as invaded, from uninvaded areas adjacent to the scrub. As there was no tree invasion on any persistently grazed sites their estimated probability of invasion was zero and they were excluded from the analysis. The remaining, ungrazed, sites (n=50) were classified as being invaded (1) or not (0). The general linear model (GLM) procedure of S+ 6 for Windows (Anonymous 2001) was used, specifying binomial errors and a logit link. The procedure for model selection followed that described by Crawley (2002) and Manning et al. (2004) in that all variables were tested as descriptors of the binomial variable and systematically deleted using likelihood ratio tests until a ''minimum adequate'' model (MAM) was reached. The MAM has the smallest minimal residual deviance (analogous to r^2) possible, with the constraint of all parameters being statistically significant. Once the MAM was fitted, the relative contribution of each explanatory variable was obtained by deleting it from the model and measuring the change in explained deviance over the total deviance. This value is expressed as deviance change on deletion (%DCD). DCD values for main effects include the effect of removing any interaction terms containing the main effect.

Soil sampling and chemical analysis

We selected three heath sites in Southern England with similar vegetation type (the M16c of the National Vegetation Classification (Rodwell 1992), topography (flat), soil type (humus-iron podsol), proximity to mature *Betula* but expected differences in PSC. The first, at Arne, Dorset (UK National grid ref. SY976894) was thought to possess Dorset Type sorption characteristics (PSC ≤ 100 μg P g^{-1}) (*sensu* Chapman et al. 1989b). The other two sites were believed to have the New Forest type (PSC c.1500 μg P g^{-1}). The first site, at Denny wood, New Forest (SU340062), has a history of free ranging grazing while the others: Arne and Horsell Common, Surrey (TQ014598) have seen little management in the last 50 years. The management histories and experiments conducted at these sites are fully described by Manning et al. (2004, 2005).

Samples were taken, in November 1999, on a regular sampling grid that provided maximum coverage of the study sites. These occupied areas of 41 × 8 m at the Surrey and New Forest sites and 78 × 11 m in Dorset. Thirty samples were taken at the New Forest and Surrey sites, 72 at the Dorset site. About 15 cm deep soil cores were taken with a 20 mm diameter cylindrical soil borer and divided into two depths: 0–5 cm and 5–15 cm. The top 5 cm typically included L (litter), F (decomposing organic) and H (completely humified organic matter) layers. The 5–15 cm portion contained A (humic dark sand) and Ea (grey sand) layers. The Bh (iron pan) layer was infrequently observed. All samples were analyzed for pH, water content and SOM content according to standard methods (Allen 1989).

Acidified ammonium oxalate extractable P (P_{ox}) was used to measure long-term available P. The combined mix of ammonium oxalate and oxalic acid dissolves non-crystalline oxides of Fe and Al (Wang et al. 1991). P_{ox} may also include organic P that is exchangeable with inorganic fractions over longer time periods making it more comparable with the combined fractions, except residual P, of the Hedley P test (Hedley et al. 1982) than the P desorbed by resins, Fe oxide strips and short-term IEP measures such as that used by Chapman et al. (1989b). 100% of P_{ox} is thought to be desorbable in sandy soils within 100–400 days (Lookman et al. 1995). P_{ox} has been found to be a good predictor of long-term available P in weathered soils (Guo and Yost 1999) and has been used as a measure of sorbed P in acidic grassland soils (Pote et al. 1996). P_{ox} was estimated for all samples of the 0–5 cm depth, and for the 15 samples that were used in PSC analysis (see below) for the 5–15 cm depth. This was done according to the method of Pote et al. (1996); 2 g of soil was extracted in 40 ml of 0.2 M, pH3 ammonium oxalate, the extract was then filtered, ashed, re-dissolved and analyzed colorimetrically.

PSC estimates were taken from five random samples selected from both depth categories at each site and used in soil P sorption isotherm analysis. Two gram of air-dry soil were incubated in an orbital incubator at 10°C for 24 h at 100 rev min^{-1} with 40 ml of standard phosphate solution at 10 concentrations (0, 5, 10, 20, 30, 40, 60, 70, 100 and 150 mg P l^{-1} in 0.02 M KCl). Three drops of chloroform (to inhibit microbial activity) were also added. After settling for 1 h at 10°C the supernatant was removed, filtered through a 0.45 μm cellulose nitrate membrane filter and analyzed colorimetrically. P sorption was calculated as amount initially in solution minus amount remaining. The amount of P currently sorbed to the soil (P_{ox}) was added to all sorption estimates. This method closely conformed to that of Chapman et al. (1989b), the only major difference being division into two depth categories. Description of soil P sorption characteristics was achieved by fitting statistical models to data describing the amount of P sorption (x) across the range of soil solution concentrations (c). P sorption is described by the Langmuir equation, a two-component model based on the assumption of low and high-energy sorption surfaces (Eq. 1) (Barrow 1978).

$$x = \frac{a_1 x m_1 c}{(1 + a_1 c)} + \frac{a_2 x m_2 c}{(1 + a_2 c)} \qquad (1)$$

Each component of the Langmuir equation contains two key parameters: a, which describes the soil phosphate affinity of each surface (a_1 and a_2), and xm which represents the maximum amount of P that can be sorbed onto each surface, and when summed for the two surfaces (xm_1 and xm_2) represents PSC. A modified version of the Langmuir two-surface equation, in which the second surface is represented by a constant, may also be used. Both variants of the Langmuir equation were fitted to the data. Curve fitting was performed using the S+ 6 for Windows non-linear least-squares procedure, with the model possessing the minimum r^2 being selected. This procedure found our sorption data to be best described by the Langmuir 1 surface + constant model.

Because the energy of P sorption declines as x approaches PSC, P saturation has been found to be a good estimator of leaching losses (Pote et al. 1996). The degree of soil P saturation ($\%P_{sat}$) was calculated using a modified form of the molar ratio method used by Lookman et al. (1995) and Pote et al. (1996) in which P_{sat} is the proportion of PSC represented by P_{ox}. The fraction of P_{ox} that is water desorbable (%WDP) represents solution or weakly sorbed P. This fraction is the most available to plants but also the most likely to be leached (Lookman et al. 1995). %WDP was calculated as the percentage of P_{ox} in a water desorbable form (WDP), when WDP is that measured in the 0 mg P l^{-1} concentration of the sorption isotherm.

Statistical modelling of soil P properties

GLM's describing P_{ox}, P_{sat} and %WDP were formulated using the P-sorption isotherm sample data (n=30) and the MAM procedure described above. However, the identity of the link functions and error distributions differed between models depending on the data's structure. Variables used as descriptors were: SOM, pH, PSC, Langmuir a, and site and depth categories. In all model fitting the PSC variable was log *e* transformed as P sorption theory (Barrow 1978) would suggest that the relationship between PSC and P_{ox}, P_{sat} and %WDP is unlikely to be linear.

Experimental P addition and disturbance

At each site three (Surrey and New Forest), or four (Dorset), plots of 50 × 50 cm were placed in a checkered arrangement within larger 1 × 2 m plots, randomly allocated within each block of the larger experiments. At the Dorset site there were four P addition levels and two disturbance levels in factorial combination in, four experimental blocks. Two replicates per block, gave a total of eight replicates per treatment combination (*n*=64). At the Surrey and New Forest sites three P addition levels and two disturbance levels in factorial combination in three experimental blocks, with two replicates per block gave six replicates per treatment combination (*n*=36).

Disturbance was applied manually in June 1999 by striking and turning the ground with a mattock for 150 s m^{-2}. This aimed to produce a non-specific form of disturbance that simulated the soil disruption and plant death common to many heathland disturbances (e.g. burning, trampling by humans and grazing animals and beetle outbreaks), and which are associated with scrub invasion. Most vegetation was destroyed and the top 100 mm of soil was disrupted. P was applied in pulses of triple super-phosphate in which each pulse was equivalent to that released in the burning of a 30 year old Dorset heath (Chapman 1967) in which 5% of P had been lost in smoke (Allen 1964); 17.6 kg ha^{-1}. The treatment levels used were control, 1, 2 and 3 additions at the Dorset site and control, 1 and 3 additions at the Surrey and New Forest sites. The first P addition was in July 1999, the 2nd January 2000, and the 3rd June 2000.

Soil cores were taken with a 15 cm diameter cylindrical borer from the central area of the 50 cm^2 plots in November 2000 and 0–5 cm soil was analyzed for P_{ox} according to the method described above. Data were analyzed using the ANOVA procedure of S+ 6 for Windows, specifying Tukeys HSD with a significance threshold of $P < 0.05$ as the post-hoc test for the comparison of means. Variance was standardized through log *e* transformation.

Results

Reanalysis

The MAM fitted to the Chapman et al. (1989b) data contained two significant variables: log *e* PSC, which had a positive relationship with the probability of invasion and IEP, which displayed a negative relationship and explained no deviance in the absence of the PSC variable (Table 1).

Examination of the fitted model, when IEP is held constant at 20, reveals that the probability of tree invasion rises from 0.2 to 0.7 between PSC of 375 and 1050 (Fig. 1). The probability of invasion where PSC = 700 is 0.49.

Table 1 Relationship between soil phosphorus properties and invasion success. Minimum adequate model (MAM, binomial error, logit link) describing the relationship between the natural logarithm of heathland soil log *e* phosphorus sorption capacity (PSC), isotopically exchangeable phosphorus (IEP) and the probability of tree invasion

	Coefficient	Standard error of coefficient	DCD[a]	*P* (*T*-test)
Intercept	–13.12	4.73		
IEP (μg P g^{-1})	–0.05	0.03	8.5%	<0.05
Log *e* PSC (μg P g^{-1})	2.13	0.78	41.5%	<0.001

The coefficients given are those from the right hand side of this regression model. Explained deviance = 41.5%, residual d.f. = 47

[a]DCD = deviance change when deleted from MAM. Deleted terms: ACP, pH, SOM

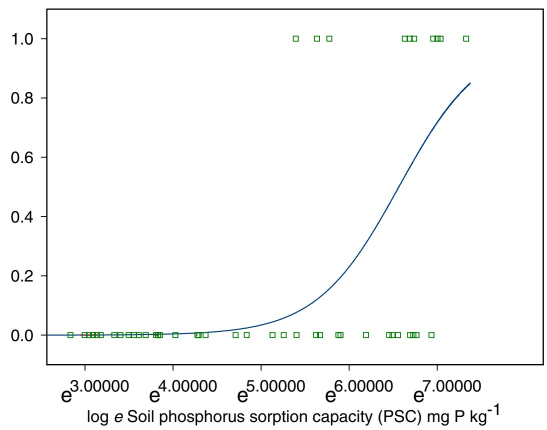

Fig. 1 Relationship between soil phosphorus sorption capacity (PSC) and the probability of tree invasion on heathlands. The fitted logistic regression model is presented in Table 1. Isotopically exchangeable P was held constant at 20 mg P kg^{-1}. Square points represent the original data of Chapman et al. (1989b)

Soil P characteristics

Soil of all three sites had similar properties for pH and water content, and to a lesser extent SOM content, P availability and Langmuir *a* (Table 2), but not PSC, which varied greatly between sites and depths (Fig. 2a).

PSC values concurred with the regional types described by Chapman et al. (1989b). The Dorset soils had PSC that were slightly higher than the regional ''type'' but not atypical. Soil PSC from 0–5 cm at the Surrey and New Forest sites was slightly below that expected especially in the 5–15 cm depth at the Surrey site.

Values for %WDP and P_{sat} correlated fairly closely (Pearson's r=0.70), and like PSC varied greatly between sites and depths (Fig. 2b, c). %WDP and P_{sat} were highest at the Dorset site, lowest at the New Forest and were generally higher in the 0–5 cm depth. High variability in all variables indicated small-scale spatial heterogeneity in soil P properties.

Relationships between soil P properties

The model describing available-P (P_{ox}) explained 84.1% of the variance, was of standard multiple linear regression form, and contained three descriptor variables, SOM, pH, log *e* PSC, and an interaction term (Table 3). Deletion tests reveal that most of the explained deviance was unique to each descriptor. Exploration of the fitted relationship suggest that increases in PSC from 50 and 500 μg P g^{-1} have strong effects on P_{ox} (Fig. 3a). However, the most important descriptor was SOM ($P<0.001$, DCD = 43.4%), which displayed a positive relationship with P_{ox} (Fig. 3b). log *e* PSC displayed a positive relationship with P_{ox} ($P<0.05$, DCD = 8.63%) that is likely to represent a direct effect on phosphate retention. The third significant descriptor in the model, pH, had a positive relationship with P_{ox} ($P<0.01$, DCD = 8.4%) but interacted antagonistically with SOM ($P<0.05$, DCD = 4.4%). The relationship between pH and P_{ox} is negative over the typical range of heath conditions, with the exception of low SOM soils (Fig. 3b).

Phosphorus saturation (%P_{sat}) was explained by a regression model which accounted for 95.2% of the deviance. This model had Poisson errors and a log link function and contained two interacting variables that were also included in the P_{ox} model, log *e* PSC and SOM (Table 4). The most important descriptor was log *e* PSC ($P<0.001$, DCD = 73.2%). SOM accounted for less deviance ($P<0.001$, DCD = 29.3%) and, like PSC, displayed a positive relationship with saturation. The interaction term ($P<0.01$, DCD = 2.0%)

Table 2 Soil properties of three experimental heathland sitesNumbers in parentheses represent ±1SE

Site and depth	pH	Soil organic matter content (% dry mass)	P_{ox} (μg P g^{-1})	Langmuir *a* sorption affinity parameter
Dorset 0–5 cm	3.99 (0.04)	52.75 (6.91)	92.50 (17.10)	0.048 (0.014)
Dorset 50–15 cm	4.07 (0.04)	14.56 (3.23)	21.86 (5.34)	0.038 (0.015)
Surrey 0–5 cm	3.91 (0.03)	37.97 (4.76)	88.92 (10.84)	0.011 (0.002)
Surrey 50–15 cm	4.11 (0.06)	3.94 (0.77)	16.47 (3.45)	0.038 (0.009)
New Forest 0–5 cm	4.04 (0.06)	47.29 (3.77)	68.61 (12.33)	0.013 (0.002)
New Forest 50–15 cm	4.04 (0.05)	9.98 (1.32)	30.93 (5.42)	0.031 (0.013)

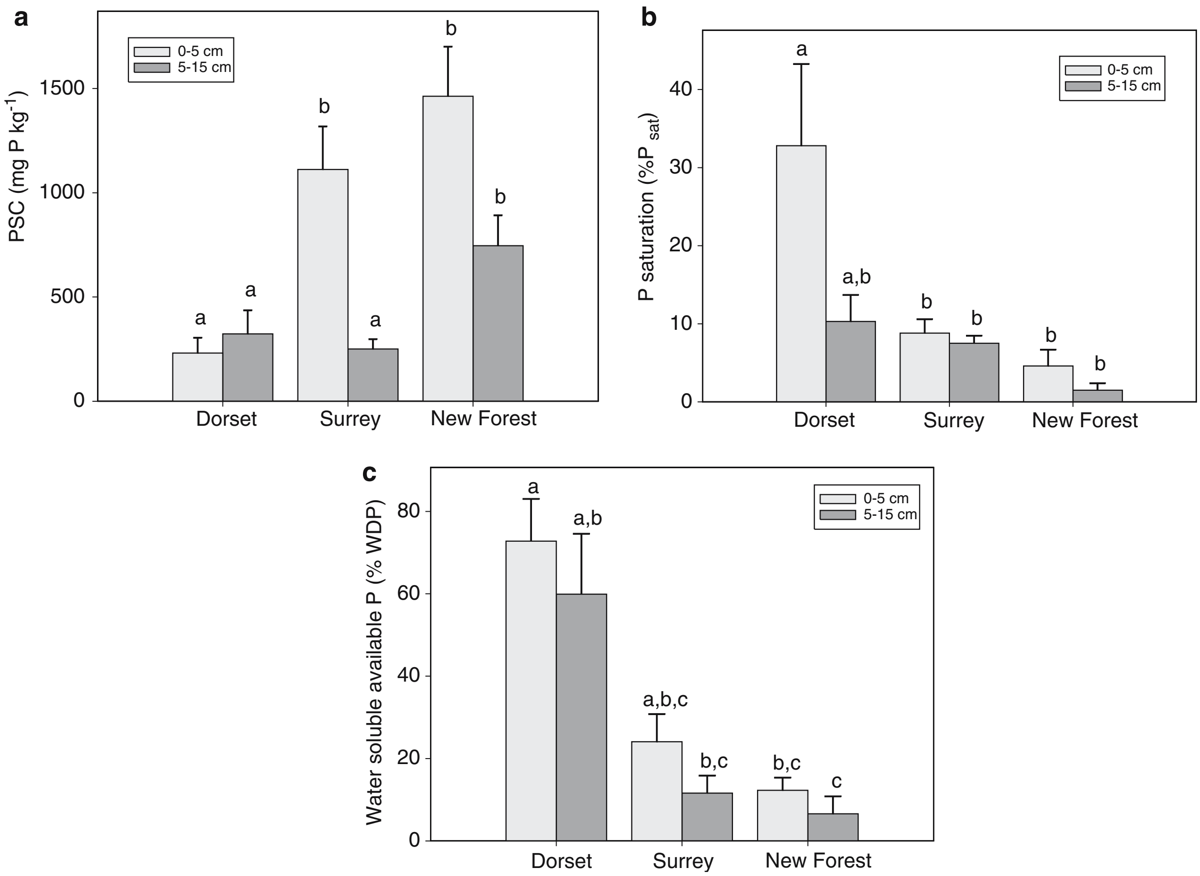

Fig. 2 Soil phosphorus properties of three experimental heathland sites: (**a**) Phosphorus sorption capacity (PSC), (**b**) P saturation (%P_{sat}) and (**c**) water-desorbable available P (%WDP). Error bars represent ±1SE. Prior to analysis data was log *e* transformed to correct for homogeneity of variance. It was then compared using Tukey post-hoc comparisons following a one way analysis of variance in which all six site × depth combinations were treated as separate factor levels. Common letters indicate that means were not significantly different at $P < 0.05$

suggests that saturation rises steeply when SOM is high and PSC is low (Fig. 4).

The model describing water desorbable phosphorus (%WDP) accounted for 92.5% of the deviance (Table 5) and contained two continuous predictors, log *e* PSC ($P < 0.001$, DCD = 19.2%) and SOM ($P < 0.05$, DCD = 2.0%), one categorical predictor, site ($P < 0.01$, DCD = 36.7%), and

Table 3 Statistical model describing long-term available phosphorus (P_{ox})

	Coefficient	Standard error of coefficient	DCD[a]	P (χ^2-test)
Intercept	4.17	0.87		
SOM content (% dry mass)	0.072	0.018	29.3%	< 0.0001
Log *e* (PSC (μg P g^{-1}))	–0.42	0.15	73.2%	< 0.0001
Log *e* PSC × SOM	–0.008	0.003	2.0%	< 0.01

The model (Gaussian error, identity link) describes the relationship between ammonium oxalate P (P_{ox}) and a number of soil properties including soil organic matter (SOM), pH and log *e* phosphorus sorption capacity (PSC). The coefficients given are those from the right hand side of this regression model. Explained deviance = 84.1%, residual d.f. = 23

[a]DCD = deviance change when deleted from MAM, deleted terms: Langmuir *a*, water content, site and depth categories

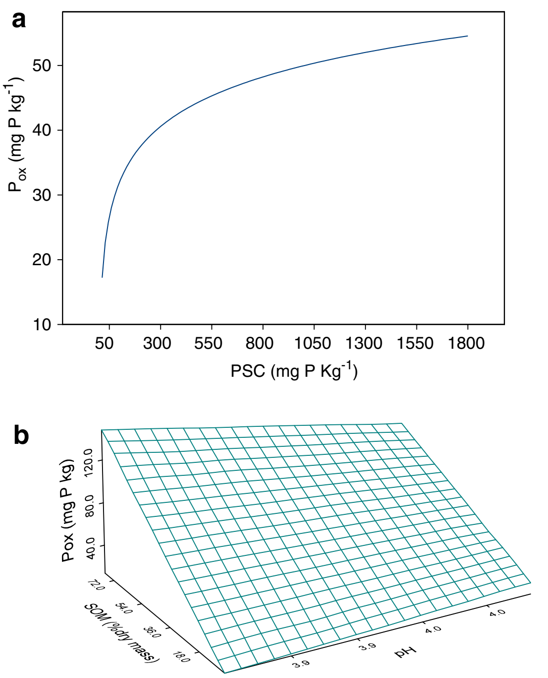

Fig. 3 Response of ammonium oxalate P (P_{ox}) to soil chemical properties in heathland soils. The relationship is taken from a fitted statistical model (Table 3). (**a**) Response of P_{ox} to phosphorus sorption capacity (PSC) when pH and soil organic matter content (SOM) are held constant at their mean values. (**b**) Response of P_{ox} to pH and SOM when PSC is held constant at its mean

an interaction term ($P < 0.001$, DCD = 15.1%) indicating that the relationship between %WDP and PSC was site-specific; low PSC soils at the Dorset and New Forest sites had proportionally more P_{ox} in readily desorbable or solution pools but the Surrey site displayed an opposing trend.

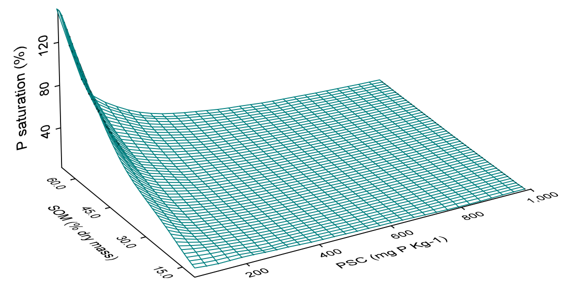

Fig. 4 Relationship between P saturation (%P_{sat}), soil organic matter content (SOM) and phosphorus sorption capacity (PSC) in heathland soils. The relationship is taken from a fitted statistical model (Table 4)

Experimental P-addition

A significant difference in the soil P_{ox} content of the Dorset site ($F = 4.95_{3,56}$, $P < 0.01$) (Fig. 5a) occurred between the control and high treatment level plots. There was no significant effect of disturbance. At the Surrey site, P addition significantly increased P_{ox} between high level plots and the other levels ($F = 13.4_{2,29}$, $P < 0.001$), but there was no effect of disturbance (Fig. 5b). At the New-Forest site both P addition ($F = 30.4_{2,30}$, $P < 0.001$) and disturbance treatments ($F = 5.8_{1,30}$, $P < 0.05$) had large significant effects on P_{ox}. The interaction term was not significant. Disturbance had a small effect size (r^2=0.06) compared to P addition (r^2=0.61) with all levels of P addition being significantly different to each other (Fig. 5c). Overall, the effect of P addition on topsoil P_{ox} was greater at the high PSC sites. This is supported by estimated values of P saturation achieved by dividing the P_{ox} of the undisturbed and three addition experimental soils by the mean

Table 4 Statistical model describing soil phosphorus saturation (%P_{sat})

	Coefficient	Standard error of coefficient	DCD[a]	P (F-test)
Intercept	–3222.13	275.08		
pH	72.81	67.99	8.4%	< 0.01
SOM content (% dry mass)	20.81	7.89	43.4%	< 0.0001
Log e (PSC (μg P g^{-1}))	7.80	2.54	8.6%	< 0.05
pH × SOM	–4.95	1.95	4.4%	< 0.05

The model (log link, Poisson error) describes the relationship between percentage saturation (%P_{sat}) and two soil properties: soil organic matter (SOM) and log e phosphorus sorption capacity (PSC). The coefficients given are those from the right hand side of this regression model. Explained deviance = 95.2%, residual d.f. = 24

[a]DCD = deviance change when deleted from MAM, Deleted terms: pH, Langmuir a, water content, site and depth categories

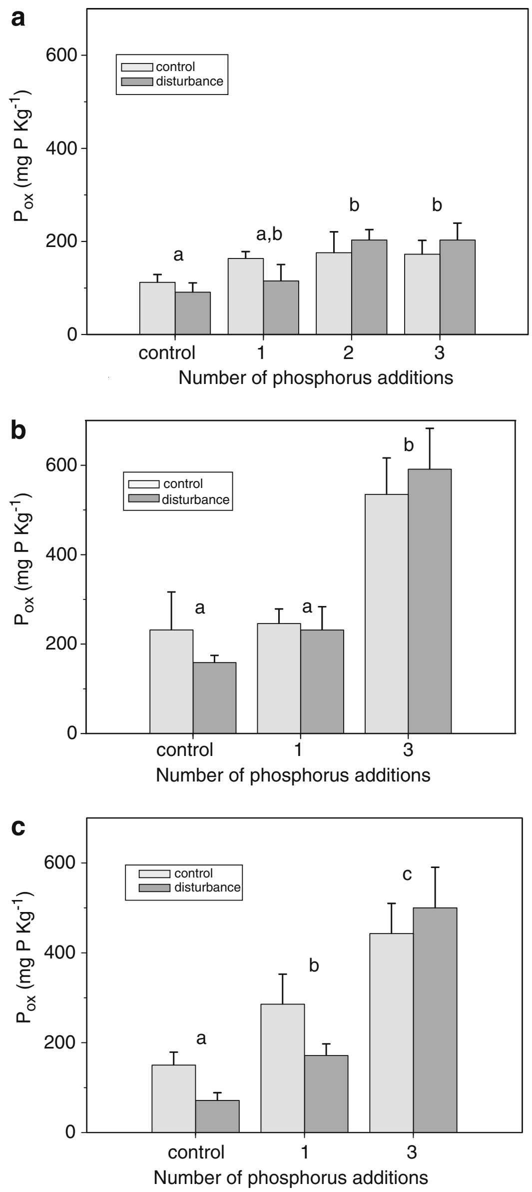

Fig. 5 (**a**–**c**) The effects of phosphorus addition and disturbance on ammonium oxalate extractable P (P_{ox}) at three heath sites with differing phosphorus sorption capacity (PSC). (**a**) Dorset (low PSC), (**b**) Surrey (high PSC) and (**c**) New Forest (high PSC). Error bars represent 1 standard error. Common letters indicates that means within P addition treatment were not significantly different at $P < 0.05$ (When compared using Tukey post-hoc comparisons after log *e* transformation to correct for homogeneity of variance)

PSC of the sites at the 0–5 cm depth. The Dorset site (PSC = 231 μg g^{-1}) reached a saturation of 75.3%, compared to 53.2% in the Surrey site (PSC = 1112 μg g^{-1}) and 30.3% at the New Forest site (PSC = 1463 μg g^{-1}).

Discussion

The reanalysis of the Chapman et al. (1989b) data clearly demonstrates that invasion is more likely where soil PSC is high. Because P availability controls *Betula* invasion, and both experimental and observational evidence indicates that high PSC soils retain more phosphate, resulting in greater plant availability it would seem apparent that there is a clear and simple relationship, mediated via available P, between PSC and invasion. However, IEP (in many ways a similar measure to P_{ox} although values are likely to be lower) explained no variance in invasion probability in the absence of the PSC variable, thus suggesting that a more complex model is required to explain the PSC-invasion relationship. Our studies of the patterns in soil properties, when synthesized with existing data, provide such a model, which we explain fully below.

The descriptive studies of soil properties concur with the findings of Chapman et al. (1989b) but add a description of how PSC varies across the soil profile and over short horizontal separation distances. Soil profile trends in PSC are likely to depend on the depth at which Fe and Al oxides are precipitated. Failure to observe higher PSC at greater soil depths is explained by the infrequent sampling of the iron pan. Fe and Al oxides are, however, also likely to be sorbed onto organic colloids in the topsoil (White 1980) thus explaining higher PSC at this depth in the Surrey and New Forest site soils. A dual peak in PSC across the profile implies that only extreme soil disturbances, e.g. ploughing, increase topsoil PSC and that turf stripping may reduce surface PSC, providing the iron pan is reasonably deep. Heterogeneity in PSC over short distances demonstrates that although much variation occurs at the regional scales (Chapman et al. 1989b) there is also small-scale heterogeneity that may influence local processes. Further study is required to fully understand the consequences of this variability.

Table 5 Statistical model describing water soluble available P (%WDP)

		Coefficient	Standard error of coefficient	DCD[a]	P (χ^2-test)
Intercept (Dorset site)		39.06	3.93		
Site	New Forest	–15.27	2.80	36.7%	< 0.0001
	Surrey	–40.15	4.41		
SOM content (% dry mass)		0.188	0.078	2.0%	< 0.05
Log e (PSC (μg P g^{-1}))		–0.045	0.007	19.2%	< 0.001
Log e PSC × Site	New Forest	0.019	0.004	15.1%	< 0.0001
	Surrey	0.064	0.010		

The model (identity link, Gaussian error) is site-specific and describes the relationship between the proportion of ammonium oxalate extractable P (P_{ox}) in water-soluble form (%WDP) and two descriptors, log e phosphorus sorption capacity (PSC) and soil organic matter (SOM). The coefficients given are those from the right hand side of this model which contains continuous (SOM, log e PSC) and factor variables (site). Explained deviance = 92.5%, residual d.f. = 21

[a]DCD = deviance change when deleted from MAM, deleted terms: Langmuir a, pH, soil water content, depth category

Numerous determinants were required to explain P_{ox}. The variable with the greatest explanatory power was SOM, which displayed a positive relationship that is likely to represent P mineralization but may also overlap with PSC as Fe and Al oxides sorb onto organic colloids. The relationship between pH and P_{ox} was complex but generally negative. Available P is thought to be reduced by low pH because of the formation of iron and aluminum phosphates. The P_{ox} method however, dissolves these, and so recognizes that the P remains soil bound and plant-available over long time periods. PSC was also found to affect P_{ox}. Though its effect was relatively small, compared to that of SOM, and probably resulted from greater retention, PSC effects on P availability over longer timescales are probably far greater. P retention may affect microbial N fixation rates, and ultimately the rate of SOM accumulation (Tate and Salcedo 1988). A second mechanism underlying this pattern is suggested by the simulation model of Chapman et al. (1989a), and the empirical studies of Chapman and Clarke (1980); greater P availability in high PSC soil enables faster plant growth and therefore, more rapid SOM accumulation. Study of different aged heath stands found that P content accumulates alongside SOM after burning (Chapman et al. 1975). Although the ratio between soil organic and inorganic P remains relatively constant with age (Chapman 1970) the organic horizon deepens during stand development resulting in increased inorganic P as the stand approaches the degenerate state.

PSC appeared to be an important determinant of both leaching loss indicators: %WDP and P_{sat}, thus suggesting that P availability may appear deceptively high in low PSC soils when weak extractant methods are used and that P mineralized from SOM, or released in pulses following disturbances, is more likely to be retained on high PSC soils. The %WDP observations at the New Forest and Dorset sites are consistent with soil P sorption theory; as soils saturate, a process which occurs at lower solution P concentrations on low PSC soils, sorption energy declines (Barrow 1978) and so a larger proportion will be water-soluble. The relationship between SOM and %WDP may be attributed to recent mineralization of P from SOM. Converse findings at the Surrey site may be explained by its denser vegetation depleting WDP in the high PSC 0–5 cm soil. This explanation is consistent with the model of Chapman et al. (1989a), which predicted a negative correlation between leaching losses and vegetation development.

Further evidence for the greater P retention and availability of high PSC sites is provided by the experimental results. P_{ox} could be divided into two fractions; the first, measured, fraction was inorganic sorbed and solution P and partially stabilized organic P in the upper soil and the second was the sum of leached, complexed and plant-absorbed fractions. Despite this lack of resolution the conclusion remains that P retention was greater at the high PSC sites, while the low PSC Dorset soils saturated after a few additions. Disturbance did not have the hypothesized effect on P availability. With the exception of plots that had received recent fertilizer applications P availability was slightly lower in disturbed plots, and significantly so at the New Forest site. This may reflect lower plant uptake which over time results in leaching losses. Results of the descriptive studies indicate that the disturbance treatment failed to bring leached Fe and Al oxides to the surface. Therefore positive disturbance effects on invasion are more likely to represent reduced plant competition than altered PSC, at least where disturbance does not disrupt the high PSC iron pan.

The experimental results are particularly relevant to fire and heather beetle outbreaks as large quantities of P are released over short periods of time. These events may be more important in generating P limitation differences between heath sites than chronic leaching, which was found to be minor in a multi-site study (Schmidt et al. 2004). Because P availability can determine *Betula* invasion of heath (Manning et al. 2005) the results imply that PSC, by controlling P retention, may significantly impact upon the speed and composition of post-disturbance vegetation recovery.

A second explanation for the relationship between PSC and invasion is the aforementioned effect on SOM accumulation and vegetation development. In our P_{ox} model PSC increases over a range that coincides with the steep area of the relationship between P_{ox} and *Betula* seedling densities (Manning et al. 2005) and so may partly explain regional patterns of invasion. A larger effect may be mediated by SOM effects. Chapman et al. (1989a) predicted that high PSC heaths can accumulate far greater amounts of SOM, thus generating much larger differences in P-availability than direct PSC effects on sorption.

We provisionally conclude that soil PSC is responsible for a small, direct, effect on P availability at small scales but will, by affecting P retention (especially after disturbance events), plant growth and SOM accumulation, play an important role in affecting P availability at larger spatio-temporal scales, and thus explain the PSC-invasion relationship. Additional indirect effects may operate via vegetation structure, which could shift more rapidly towards the invasible degenerate state in high PSC regions. If all other influences are considered equal then faster ecosystem development will result in high PSC regions having a greater proportion of invasible heath and that burning will need to be applied more frequently.

This model is consistent with the state transition models of Scheffer and Carpenter (2003) and Suding et al. (2004a). If the heath state is perceived as the F_1 state, the *Betula* scrub state the F_2 state and the conditions axis a multivariate description of factors (including P availability and vegetation structure) influencing *Betula* recruitment (Manning et al. 2005) then PSC would appear to control the rate of movement of the system along the conditions axis (see Fig. 1 of Scheffer and Carpenter 2003). High PSC systems will not only move more quickly towards transition to scrub but, by having a greater SOM maximum also reach greater distances along this axis. Transition should be avoided by managers as hysteresis (the requirement for conditions to be returned to pre-transition values before the system returns to its original state) is present because *Betula* generate self-reinforcing environmental changes, e.g. to seed bank densities and nutrient availability (Mitchell et al. 1999). However, despite mechanistic consistency these relationships remain somewhat hypothetical; deeper understanding of the relationships between PSC, ecosystem development and the determinants of tree invasion is required before the relative importance of PSC, and its potential interaction with management regimes can be quantified.

Our results and synthesis suggest that PSC, which is primarily controlled by underlying geology (Chapman et al. 1989b), influences heathland properties and therefore invasion, via several mechanisms and may therefore determine the propensity of a given location to either the heath or scrub state. Although a similar dependency of ecosystem state on P supply and retention has been observed frequently in freshwater systems (e.g. McGowan et al. 2005), this is, to our knowledge, the first clear example of how regional differences in phosphorus availability can regulate state transitions in a terrestrial environment. Strong dependencies of long-term ecosystem development on underlying geology (Ewing 2002), vegetation shifts in synchrony with PSC changes in pedogenesis (Walker and Syers 1976; Carriera et al. 1997; Crews et al. 1995) and the dependency of exotic plant invasions on P-availability (e.g. Suding et al. 2004b; Leishman and Thomson 2005) all suggest that such a dependency may be commonplace in the Earths terrestrial ecosystems.

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