Determining the important environmental variables controlling plant species community composition in mesotrophic grasslands in the UK

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Abstract

Question:

Location: Ten mesotrophic grassland sites of high conservation value in southern England.

Methods: In 1998 and 1999 species cover in between 10-20 randomly selected 1m^2 quadrats were assessed at each site, at each quadrat degree of waterlogging (SEV, metre.weeks), soil Olsen extractable phosphorus (P) and soil pH were measured. Variation Partitioning was used to separate site and soil effects, and HOF modelling was used to produce response curves for the major species on each of the soil gradients. These gradients were coenoclines derived from partial canonical correspondence analysis (pCCA).

Results: Variation partitioning identified site as the most important environmental variable (23%), with 19% accounted for by climate and only 10% accounted for by soil. However, when shared variation was removed the effects of site and soil were reduced to 13% and 5%, respectively; effects of geographical location and local climate were negligible. Of the soil variables, degree of waterlogging was most important, followed by pH and soil phosphorus. The species responses to each of these soil environmental factors could be separated into four types on each gradient. Most species were abundant where the quadrats had a low degree of waterlogging, low soil phosphorus and intermediate pH.

Conclusions: Site-based factors were more important than the three soils variables, which were assumed to be directly or indirectly associated with productivity. This implies that each site has unique properties, as yet undefined, that are more important than the measured soil variables. The three soil factors (W, P, pH) were, however, still significant and the groups of the most common species, based on significant response curves, can be used as a first approximation of indicators of environmental conditions in UK mesotrophic grasslands for conservation purposes, for example targeting restoration efforts or interpreting changes in environmental conditions.

Key words: Variation partitioning, HOF modelling, species response curves, realized niche, environmental gradients.

Nomenclature: Stace (1997)

Abbreviations: CCA = Canonical Correspondence Analysis; DCA = Detrended Correspondence Analysis; VP = Variation Partitioning; P = soil Olsen available phosphorus (µg P g^{-1}); W = degree of waterlogging (SEV in m.weeks).

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Introduction

In most of Europe unimproved, semi-natural grassland communities have a high conservation value (Duffey et al. 1974; Bakker 1989) and many are protected by conservation designation (Anon. 1995a,b). These grasslands are plagio-climax communities and their composition, and hence conservation value, is controlled by a series of environmental factors that impinge on any given site in combination with any applied management. The species composition and diversity of grassland plant communities is conditioned by a number of interacting environmental factors, for example, the local species pool, historic as well as present management (Wells et al. 1976; Gustavsson et al. 2007; Klimek et al. 2007), and site-specific conditions, i.e. water regime and soil physico-chemical properties (Ejrnæs & Bruun 2000; Critchley et al. 2002a; Havlová et al. 2004; Marini et al. 2007). Grace (1999) codified these processes into a conceptual model which suggested that the important drivers of species density were (1) spatial heterogeneity and species pool which influenced colonization, (2) community biomass, and (3) the disturbance regime which included natural events like floods, fires, herbivory and human activities, management like grazing, mowing or cultivation. The role of disturbance, especially cutting and grazing, in controlling grassland species diversity and composition has been shown empirically (Smith et al. 2000; Smith & Rushton 1994). Clearly, all of these factors interact within a given site to control the observed species composition. An important goal, therefore, for conservation biology must be to determine the relative importance of the various factors that control plant biodiversity (Corney et al. 2006).

In this paper the relative importance of site factors relative to factors that can be viewed as surrogate measures of productivity will be quantified for an important vegetation type from a conservation viewpoint: species-rich mesotrophic grassland in lowland, southern England (Rodwell 1992). During the 20th century over 98% of the area of these grasslands has been lost mainly to agricultural use, through ploughing, re-seeding and fertilizing (Anon. 2001). The remnants left in the UK (now <15,000 ha) are generally subject to conservation management; usually a hay crop is taken followed by aftermath grazing. They are developed on soils that often remain waterlogged for considerable periods as they are subject to periodic inundation. Soils tend to be mesotrophic to nutrient-rich with a pH range from moderately acidic (4.5) to circum-neutral (6.5-7.0). The important environmental variables likely to influence productivity are therefore, the water regime and soil fertility.

Productivity is one of the key factors put forward to explain species diversity, and often the relationship between species richness and productivity gradient is often presumed to have the shape of humped-back or unimodal curve (Grime 1979; Huston 1979; Tilman 1982). Mittelbach et al. (2001) in a major review stressed the difficulty in making direct measurements of productivity, and in most studies indirect or surrogate measures, i.e. correlated variables such as peak plant biomass, rainfall, and evapotranspiration, have been used. Two major reviews (Grace 1999; Mittelbach et al. 2001) have shown unimodal responses in the majority of cases, although positive relationships have also been detected. Janssens et al. (1998) argued, that the same relationship can be expected between gradient of soil fertility, because the community biomass is directly influenced by its productivity which depends on the availability of soil nutrients. In their study of a wide range of European grasslands, they found a unimodal relationship between maximal species density and two of the major soil nutrients, P and K.

On any gradient the overall species density will reflect the combined responses of individual species to that gradient, essentially the realized species niche, described ‘as the position and shape of species response’ showed as species abundance on the resource gradient (Austin et al. 1990). Therefore, modelling the response of species (realized species niche) along gradients should provide important information for determining community responses, which will in turn inform conservation management. These response curves have been modelled as symmetric Gaussian relationships (Begon et al. 1996). However, Huisman et al. (1993) proposed that alternative non-unimodal and skewed relationships were possible, and Oksanen & Minchin (2002) have tested their existence and exaplined it by changing environmental stress could cause skewed or result in non-unimodal responses. In their study of vascular plants on altitudinal gradients, skewed curves were found for 20% of species and in a subsequent study 29% of species produced skewed responses (Lawesson & Oksanen 2002). Few attempts have been made to fit such skewed relationships along surrogate productivity gradients.

Here, we use mesotrophic grasslands in the UK as a model system to address some of these issues. This dataset was particualrly suitable for this analysis because of the detailed asseement of the water regime at each sampling position. First, we attempt to quantify the relative importance of a range of environmental variables in determining plant species composition in these grasslands (site factors versus variables that control productivity, e.g. water regime and soil variables), and second we describe the realized niches of species on gradients described by the soil variables that reflect productivity.

Methods

Study sites and sampling methods

Ten sites were chosen with a representative cover of the mesotrophic grassland communities found in southern England (Table 1). Detailed field sampling methods are provided in Gilbert (2000). Briefly, at each of the 10 sites between 10 and 25 sampling positions were located randomly (194 in total) in either 1998 or 1999. At each location the cover (%) of each species of vascular plant and bryophytes in a 1 m^2 quadrat was recorded. A Dutch auger was used to take four cores (0–15 cm depth) from the corners of each quadrat, which were then mixed together to produce a bulked quadrat sample. These soil samples were then air-dried, ground to pass a 2 mm sieve and both available P (µg $P.g^{-1}$ extracted using Olsen's reagent) and pH measured in water (MAFF 1986). Degree of waterlogging (SEV in metre.weeks, integrated over 5-years, full description in Silvertown et al. 2001) was calculated for each quadrat as the degree to which the water table at each site was above a threshold soil depth during the growing season (March–September). Climate data (30 year annual averages for maximum and minimum temperature (^{o}C), days of air frost, days of rainfall over 1 mm, hours of sunshine and total rainfall) were derived from nearest meteorological recording station.

Data analysis

The soil variables (W, P, pH) were examined using Box and whisker in STATISTICA 7.1 (StatSoft Inc. 2004). Differences between sites were tested using the non-parametric Kruskal-Wallis test because of the non-normal distribution of all variables. The mean unweighted Ellenberg indicator values (corrected for the British flora, Hill et al. 1999) for moisture (F), light (L), nutrients (N) and reaction (R) were calculated for each quadrat based on species cover data using JUICE v. 6.4 (Tichý 2002).

Most multivariate analyses were performed using VEGAN (Oksanen 2005) implemented in R (v. 2.6, R Development Core Team 2004) on $\log_e(x+1)$ transformed data. Species occurring in only one plot were excluded. A full description of preliminary data analysis is available in Kalusová (2008). Four environmental datasets were defined; (1) comprised two surrogate variables, the Site name which reflecting the effects of the local species pool, management history and current site management; (2) Geographical location (Easting, Northing) as a crude measure of site climatic conditions; (3) Climate variables, and (4) the three measured soil variables (W, P, pH). As sampling was done over two years, sampling year was included as a covariable in all ordinations to remove variability caused by inter-annual changes in conditions and sampling.

An exploratory DCA produced a gradient length 5.52 for axis 1 so the unimodal model (CCA) was adopted thereafter (ter Braak & Šmilauer 2005). To give an insight into the relationship between species composition and the main environmental gradients Spearman rank correlations were calculated between the DCA scores (axes 1 and 2) and the three soil variables and the weighted quadrat Ellenberg indicator values.

VP based on CCA (ter Braak & Šmilauer 2005) was then used to assess the relative importance of the environmental variables in explaining species composition. The variation explained by predefined subsets of environmental variables (Site, Geographic location and Soil), and the shared variation between them, was calculated (e.g. Borcard et al. 1992; Økland & Eilertsen 1994; Marrs & Le Duc 2000; Corney et al. 2006). VP was subsequently applied to the three soil variables (W, P, pH) with all other variables removed as covariables. Significance of all analyses was tested using a Monte-Carlo test (999 permutations) with randomization restricted within Site.

Modelling species responses to soil gradients

A coenocline was derived for each of the soil variables using CCA; i.e. axis 1 represented the soil variable on its own with all of the other significant variables removed. The use of such complex gradients derived from ordination is appropriate for estimation of realized plant niche characteristics (Lawesson & Oksanen 2002; Økland 1992; Austin et al. 1990). The responses of the 32 most frequent species (present in more than 35 quadrats, ~20%) were then modelled along the coenoclines using the HOF modelling approach (Huisman et al. 1993). Although Gaussian response curves (Lawesson & Oksanen 2002), Beta response functions and Generalized Additive Models (Oksanen & Minchin 2002) can also be used, their applicability has been previously criticized, and HOF modelling has been suggested as an adequate substitution (Lawesson & Oksanen 2002). The HOF procedure fits five models in a hierarchical sequence and assesses whether the response is monotonic or plateau-like, unimodal or skewed against a null model (Huisman et al. 1993). Here the HOF models were fitted using GRAVY (Oksanen 2004), a Gaussian error distribution and the AIC statistic were used for model selection. The models for species were also compared using ΔD, i.e. the difference between the deviances of the null model and the one selected. The species niche optima and probability of occurrence, tolerances and niche width of species along all coenoclines were estimated for the unimodal and skewed models (Lawesson & Oksanen 2002).

Results

There was significant between-site variation in the soil variables, using the Kruskal-Wallis test: W ($H=106.4$; $P<0.001$; $n=187$), P ($H=89.5$; $P<0.001$; $n=187$) and soil pH ($H=127.3$; $p=0.001$; $n=187$). The most waterlogged sites were Berney Marshes (mean 5.43 m.weeks), Wet Moor (4.64 m.weeks) and East Harnham (3.57 m.weeks) and the least waterlogged were Stonygillfoot (0.44 m.weeks), Portholme (2.08 m. weeks) and Cricklade (1.68 m.weeks). Soil P was greatest at Upton Ham (mean=14.0 μg P. g^{-1}), Berney Marshes (11.6 μg P. g^{-1}) and Cricklade (14.6 μg P. g^{-1}), whereas Moorlinch (2.4 μg P. g^{-1}) and Stonygillfoot (5.2 μg P. g^{-1}) were much lower. Soil pH ranged from relatively neutral (mean=pH 6.2–7.0) at East Harnham, Cricklade and Portholme, to more acidic sites at Southlake, Berney Marshes and Upton Ham (pH 4.91–5.05).

Indirect gradient analysis (DCA)

The DCA biplot (Figure 1) illustrated two major gradients. Axis 1 is positively associated with waterlogging, with species typical for drier soils (*Anemone nemorosa*, *Euphrasia confusa*, *Trisetum flavescens*, *Ajuga reptans*, *Conopodium majus*, *Hypochaeris radicata)* at the negative end and species of wetter soils *(Bolboschoenus maritimus*, *Ranunculus sceleratus*, *Azolla filiculoides*, *Atriplex prostrata*, *Potentilla anserina*, *Alopecurus geniculatus)* at the positive end. Axis 2 was more complex being associated with pH at the positive end and P as well as Easting and Northing at the negative end. The site factor had a significant but small effect on both axes. There were significant positive correlations between waterlogging and Ellenberg F-values with a weaker positive relationship with N-values (Table 2). Similarly, P was significantly correlated with Ellenberg N-values but showed weaker positive correlations with Ellenberg R- and F-values. Soil pH had a significant negative but weak relationship with Ellenberg N-values but no relationship with R-values.

Variation partitioning and direct gradient analyses (Table 3)

The VP analysis explained 28.5% of the total variation in the dataset. Site explained the greatest amount of variation in the dataset with climate second. Soil was the third most important and Geographic location explained the least. However, when the variation that was shared between Site, Climate and Geographical location was removed, Climate accounted for less variation than the constrained variables, and Geographical location was non-significant. The Soils subset explained 10% of the variation but when Site variation was removed only 5% was explained by soil factors alone. Of the soil variables the greatest proportion of variation was explained by W, followed by P and then pH. When variation due to each soil variable on its own was calculated, W remained most important, pH was intermediate and P accounted for the least.

The biplot from the pCCA where all soil variables were included (Figure 2a) but Site was removed as a covariable showed a strong positive relationship between W and P and axis 1; W had a slight negative relationship with axis 2 and P had a slight positive one. Soil pH was correlated positively with axis 2. Accordingly, the pCCA analyses were re-done for each soil variable separately with the influence of the other two soil variables and Site removed as covariables (Figure 2b,c,d).

For W, the greatest degree of waterlogging was found at the negative end of axis 1 where the following species were present *Drepanocladus aduncus*, *Galium palustre*, *Myosotis laxa*, *Lysimachia nummularia*, *Lotus pedunculatus* or *Carex rostrata*, all species typical for *moist* grasslands (with Ellenberg F-values > 7) and a lesser degree of waterlogging were found at the positive end, species such as *Ranunculus sardous*, *Poa humilis*, *Carex flacca* or *Cirsium dissectum* (Ellenberg F-values < 8).

For P, the gradient was found from species such as *Veronica beccabunga*, *Myosotis scorpioides*, *Galium uliginosum*, *Carex acutiformis*, *Iris pseudacorus* or *Azolla filiculoides* (with Ellenberg N-values > 4) through to *Drepanocladus aduncus*, *Dactylorhiza praetermissa*, *Briza media*, *Equisetum palustre* or *Bellis perennis* (Ellenberg N-values < 4).

pH had the shortest of the three soil gradients. *Myosotis scorpidioides*, *Iris pseudacorus*, *Veronica beccabunga*, *Rumex conglomeratus* (Ellenberg R-value < 7) were found at the acidic end of gradient and *Juncus subnodulosus*, *Juncus inflexus*, *Carex distans*, *Achillea ptarmica* and *Bellis perennis* (with Ellenberg R > 5) were found at the opposite end on more neutral soils.

Response of individual species to soil gradients

The HOF models selected and the amount of Deviance explained are presented in E-Appendix I (species abbreviations E-Appendix II). With one exception (*Cardamine pratensis*) all species showed a significant relationship to at least one of the soil variables. For W and P most of the responses (53 % and 63 % respectively) were unimodal or skewed models (IV, V). In both cases the symmetric model IV was more common. In contrast, for pH 68 % of species had a non-unimodal response (i.e. a decreasing/increasing response up to an asymptote) or a null response.

Response to waterlogging (Figure 3)

More species showed a greater abundance at the drier end of the W gradient. The species could be grouped on the basis of their response to waterlogging into four general types of response:

(a) Species that increase with W (*Agrostis stolonifera*, *Carex disticha*, *Carex nigra*, *Calliergonella cuspidata*);

(b) Species that showed an unimodal response, peaking near the drier end of the W gradient (*Rumex acetosa*, *Holcus lanatus*, *Ranunculus acris*, *Cerastium fontanum*, *Anthoxanthum odoratum*, *Trifolium pratense*, *Cynosurus cristatus*, *Lolium perenne*);

(c) Species that showed an unimodal response, peaking near the middle of the W gradient (*Trifolium repens*, *Poa trivialis*, *Alopecurus geniculatus*, *Senecio aquaticus*, *Deschampsia cespitosa*);

(d) Species that showed a decrease with W (*Alopecurus pratensis*, *Sanguisorba officinalis*, *Leontodon autumnalis*, *Hordeum secalinum*, *Centaurea nigra*, *Bromus racemosus*, *Filipendula ulmaria*, *Taraxacum* sect. *vulgaria*, *Plantago lanceolata*, *Festuca rubra*)

Poa trivialis, *Trifolium repens*, *Anthoxanthum odoratum* and *Senecio aquaticus* had the largest niche width on the W gradient and *Sanguisorba officinalis*, *Deschampsia cespitosa* and *Hordeum secalinum* had the narrowest (Figure 4). From the species which had either a unimodal or skewed response two groups were distinguished (Figure 4): with *Deschampsia cespitosa*, *Alopecurus geniculatus*, *Senecio aquaticus*) having their optima at higher W values than *Rumex acetosa*, *Holcus lanatus*, *Ranunculus acris*, *Cerastium fontanum*, *Anthoxanthum odoratum*, *Trifolium pretense*, *Cynosurus cristatus*, *Lolium perenne*, *Trifolium repens*, *Poa trivialis*, *Alopecurus pratensis*, *Sanguisorba officinalis*, *Leontodon autumnalis*, *Hordeum secalinum*. There was, however, substantial overlap in tolerance range between the groups.

Response to soil phosphorus (Figure 5)

More species showed a greater abundance at the low end of the gradient with five showing a positive response to soil P. The widest niche was observed for *Lolium perenne*, *Trifolium repens*, *Cynosurus cristatus* and *Taraxacum* sect. *vulgaria* and the smallest were found with *Centaurea nigra*, *Carex disticha* and *Calliergonella cuspidata*. There was, however, very little difference in tolerance intervals for all of the species with a unimodal or skewed distribution except for *Pedicularis palustris* which was associated at greater soil P concentrations than all other species. (E-Appendix III, Kalusová 2008). The species could be grouped on the basis of their response to soil P into four general types of responses:

(a) Species that decreased with P (*Trifolium pratense*, *Senecio aquaticus*, *Cerastium fontanum*, *Ranunculus acris*, *Sanguisorba officinalis*);

(b) Species that showed an unimodal response, peaking at the low-mid point of the P gradient (*Bromus racemosus*, *Festuca pratensis*, *Filipendula ulmaria*, *Rumex acetosa*, *Trifolium repens*, *Festuca rubra*, *Lolium perenne*, *Anthoxanthum odoratum*, *Holcus lanatus*, *Taraxacum* sect. *vulgaria*, *Cynosurus cristatus*, *Carex nigra*, *Plantago lanceolata*, *Calliergonella cuspidata*, *Leontodon autumnalis*, *Centaurea nigra*, *Carex disticha*);

(c) One species that showed an unimodal response, peaking near the high end of the P gradient (*Hordeum secalinum*);

(d) Species that showed an increase with P (*Deschampsia cespitosa*, *Pedicularis palustris*, *Poa trivialis*, *Alopecurus geniculatus*, *Glyceria fluitans*).

Response to soil pH (Figure 6)

The species with the widest niche on the pH gradient were *Lolium perenne*, *Alopecurus pratensis*, *Poa trivialis* and *Anthoxanthum odoratum*, whereas the narrowest niche was found for *Ranunculus acris*, *Sanguisorba officinalis* and *Alopecurus geniculatus*. There was again only very little difference in tolerance intervals for all of the species with a unimodal or skewed distributions (E-Appendix IV, Kalusová, 2008). The species could be grouped on the basis of their response to pH into three general types of responses:

(a) Species that increased with pH (*Carex distans*, *Taraxacum* sect. *Vulgaria*, *Senecio aquaticus*, *Hordeum secalinum*, *Leontodon autumnalis*);

(b) Species that showed an unimodal response. Within this group the species could be further sub-divided into those that peaked around the mid-point of the gradient (*Poa trivialis*, *Deschampsia* *cespitosa*, *Anthoxanthum odoratum, Calliergonella cuspidata*, *Ranunculus repens*, *Agrostis stolonifera*, *Ranunculus acris*, *Alopecurus pratensis*, *Lolium perenne*), and those that peaked nearer to the acid end of the pH gradient (*Sanguisorba officinalis*, *Alopecurus geniculatus*);

(c) Species that showed an decrease with pH (*Filipendula ulmaria*, *Rumex acetosa*, *Glyceria fluitans*)

Discussion

The relative importance of environmental variables in determining species composition

A major finding of this study has been the identification and quantification of the relative roles of site-based factors and productivity as determinants of species richness. Whilst there is general agreement that site factors, usually assumed to be dependent on the local species pool, are important (Grace & Pugesek 1997; Grace 1999; 2001; Loreau *et al*. 2001) there have been few attempts to assess their relative significance: Grace & Pugesek (1997) being an exception. Here, we used VP (*sensu* Borcard et al. 1992; Marrs & Le Duc 2000; Økland 1999, 2000; Økland & Eilertsen 1994; Corney et al. 2006), to quantify the relative contributions of macro-site factors (a crude composite variable which combined information on the local species pool, historical management, current local management practices, site moisture regime, and local climate) and other environmental factors controlling production. The year of sampling was always included as a covariable because sampling was spread over two years, and it is quite possible that there is a seasonal effect induced as a result of differential species performance in the different years, or sampling error. As the sampling was done by the same experienced team in both years it is unlikely that the latter is a major error. The most important drivers of species composition in these mesotrophic grasslands were the site-based variables (Site; Geographical variables - Easting, Northing) which accounted for 23% and 7% of the variation respectively, That local climatic factors expressed here crudely as annual means and the geographical variables reflecting location were subsumed within Site implying that Site accounted for all variaiton associated with local climatic responses also. This result was expected but it is useful to have it confirmed. Soil variables (W, P, R) explained much less of the variation (10 %), W was the most important variable followed by P and pH.

These results agree with Grace's (1999) suggestion of importance assigned to site-base factors as drivers of species diversity and productivity. The Site variable is a surrogate one covering a very large number of potential variables, for example variations in the local species pool at each site, different management histories and differing current management. Thus, site is a very crude variable, and merely highlights that much more detailed research is needed to identify the important environmental drivers and to quantify influence. Nevertheless, soil variables were still of importance, so a detailed study of these was made.

Although this study included grasslands that broadly covered the core of British lowland neutral or mesotrophic grasslands (Rodwell 1992), some communities were not included, specifically MG1 and MG2. MG1, the *Arrhenatherum elatius* grassland occurs where the mowing management is absent or grazing is irregular, and it is often found on lowland road verges and railway embankments. MG2, the *Arrhenatherum elatius-Filipendula ulmaria* community is a tall-herb grassland with tussock grasses and tall dicotyledons and tends to be found in the uplands of the northern England. Most of the other mesotrophic grassland communities (MG9, MG11, MG12) are species-poor swards, usually have dominanted by species adapted to unsuitable conditions (Rodwell 1992), and have limited conservation importance. Thus, although most of the communities of major conservation importance have been included here an expanded survey is required for an assessment of the entire mesotrophic grassland resource. However, it provides a first approximation of the response to these UK plant communities to some of the important variables likely to influence species composition.

Responses to soil variables

Of all the soil variables, W was the most important determinant of plant community composition in these mesotrophic grasslands (Rodwell 1992; Wallace et al. 2002). A strong significant correlation was found between the Ellenberg indicator value for moisture (F, modified for the UK by Hill et al. 1999), and the measured degree of waterlogging, confirming that these modified Ellenberg values are useful indirect indicators of water regime (Wallace et al. 2002). The positive correlation between Ellenberg values for light (L) and waterlogging (W) can be explained by the fact that at the wet end of moisture gradient there are permanently waterlogged soils where only open, species-poor vegetation is found because of these extreme wet conditions. The wet conditions found in these grasslands are, however, not just important for maintaining plant populations; they provide suitable conditions for other conservation targets, e.g. breeding wading birds (Lyons & Ausden 2005).

Species composition was also affected by soil available P but its influence was not completely independent from W: when their shared variability was removed pH became even more important. P, on its own, had a relatively minor role in determining species composition. However, P is a limiting nutrient for most plant species and can significantly influence vegetation (DiTomasso & Aarsen 1989; Janssens et al. 1998; Critchley et al. 2002a, b). However, is difficult to separate the effects of P from N and other plant nutrients. For example, it has been suggested that the role of P in controlling vegetation composition is through interactions (ratio) with soil N and K concentrations (Bobbink 1991; Roem & Berendse 2000). Unfortunately in this study no measurements of soil available N or K were made, and we do not have enough information for to determine the potential complex role of P as one of the drivers of grassland species composition.

The highest values of soil available P were recorded on sites which were seasonally flooded (Wallace et al. 2002); this can be inferred from the positive relationship between soil P and waterlogging degree in the DCA. Presumably this reflects increased P deposition in alluvial silt containing washed out P from fertilisers used on upstream arable land and from sewage water treatment plants (Lawson pers. comm.). In addition, the higher proportion of soil P in waterlogged soils can also be maintained by chemical reactions when the soils are under anoxic reducing conditions (Olila & Reddy 1997). The zonation of vegetation in the mesotrophic meadows is likely to be linked to both waterlogging and the inevitable nutrient addition that occurs during inundation. The species-poor communities occur often in depressions, where water remains the longest time and the largest proportion of sediments are deposited (Rodwell 1992).

The strong positive correlation between Ellenberg N values, which reflects soil fertility or biomass production (Schaffers & Sýkora 2000) with P and W is probably the result of biomass increase in swards with an increase P availability though inundation and a reduction in loss through decomposition in the waterlogged soils. Both processes lead to a dominance of more competitive species and a greater biomass production.

Here, soil pH had a lesser effect than W and P which contrasts with Critchley (2002a), who reported pH as the main factor separating different communities and sub-communities of improved or unimproved mesotrophic grasslands. This apparent discrepancy might be because of the communities sampled. Here, the pH range was much greater (pH 4.5–7.0), whereas Critchley's study also included improved grasslands, where soil pH might have been increased by liming. No relationship was found between Ellenberg R value and soil pH, but a significant relationship was found with soil P. These results agree with those from the long-term Rengen Grassland Experiment in Germany where Ellenberg R values were significantly increased by P fertilizer addition (Chytrý et al. 2009). As Ellenberg R values have been considered better related to the total amount of calcium present rather than to soil pH per se (Schaffers & Sýkora 2000), perhaps a relationship with pH should not be expected.

Niche investigation and its application

In this study, complex coenocline derived from pCCA ordination was used for modelling species responses and for obtaining measure of species niche in relation to three soil variables (W, P, pH). This coenocline represents 'floristic-environment gradient' (Heikkinen 1996) assessing not only the position of species to the single environmental variable, but also interactions between species in given dataset. Use of complex gradients derived from ordination is more appropriate for estimation of plant niche characteristic (Lawesson & Oksanen 2002; Økland 1992). Models of species niches are necessary for description of the role of environment and competition in determining community composition (Austin et al. 1990). The main value of this approach is that the response of a given variable can be estimated, once all other interactions with other environmental variables have been removed (as covariables). The coenocline was, therefore, derived from the site scores from the pCCA with all interacting variables defined as conditional or covariables. The species response curves and estimates of niche parameters for modelling of species niche on gradient of single soil variable were then estimated using the HOF procedure (Huisman et al. 1993). The disadvantage of this approach is that the accurate values of soil variables for parameters as species optima cannot be obtained in comparison with using measured values as a gradient.

Four groups of species were distinguished according to their position and response for each of the three soil gradients. This could have a potential application for the predicting change in species composition if there is a change in management regime. This can also be easier way for initial phases of targeting sites under potential threat of changes in environmental conditions, when field observation based on species composition can substitute expensive and time-consuming repeated measuring. Knowledge of species preferences can be useful in choosing target communities for restoration schemes, and the choice of seed mixtures (Gilbert et al. 2003).

Species responses to soil gradients

The majority of species were more abundant on the drier part of the waterlogging gradient, suggesting that extreme conditions of waterlogging (anoxic conditions, toxicity of Fe and Mn) restrict the occurrence and performance of species from very wet sites. Only those species with specific adaptation to waterlogging, for example through the creation of internal air-space tissues, the ability to exclude toxins from roots by their oxidation because of radial loss of oxygen or enzymatic oxidation, and ability to respire anaerobically (Etherington 1975) can prosper. The species able to withstand waterlogged conditions include (a) those with high optima on the W-axis *Deschampsia cespitosa*, *Alopecurus geniculatus*, *Senecio aquaticus*, and (b) species with increasing abundance on the W gradient *Agrostis stolonifera*, *Carex disticha*, *Carex nigra*, *Calliergonella cuspidata*. It should be noted that mesotrophic grasslands tend to occur from moist to wet conditions and so dry grasslands or meadows on strictly free-draining soils were not included in this study. Thus, the overall response of these species to water was not determined, merely the response to degree of waterlogging. Thus further studies are needed to cover a range of water regimes from extreme drought through to substantial waterlogging.

Although P was of lesser importance than W, the same pattern of species responses was found on the P gradient. Most species were more abundant at low P, almost certainly because of reduced inter-specific competition. This conforms to the general view that species diversity is increased at low soil fertility (Marrs 1993). The competitive grasses *Deschampsia cespitosa*, *Poa trivialis*, *Alopecurus geniculatus* and *Glyceria fluitans* showed a positive response to available P, and these species probably exclude other species on the more fertile soils. These species could be also use as indicators of high P availability in mesotrophic grasslands.

A positive response to P was shown mainly by grasses, but also by *Pedicularis palustris* (high optimum and tolerance). *Pedicularis palustris* belongs to a group of root hemi-parasites in the *Scrophulariacae*, which parasitize grasses (Press & Graves 1995), thus its mineral nutrition is mainly obtained from host plant and is not directly dependent on soil nutrient content. The abundance of *Pedicularis palustris* at high concentrations of available P might reflect an indirect effect, i.e. an increased availability of suitable host species in the sward rather the soil available P itself. Its value as an indicator of high P is, therefore, disputable.

As the majority of response curves for both soil variables were unimodal symmetric or skewed, it can be concluded, that a major part of their gradients was evaluated in the study and entire niches of chosen species for mesotrophic grasslands were described. Soil pH on the other hand had a very short gradient and there were a large number of non-unimodal species responses. This may have been brought about by site selection which excluded communities at the extremes of soil pH. However, selected groups of species could be used for indicating pH changes within these mesotrophic grasslands, for example those species with decreasing responses *Filipendula ulmaria*, *Rumex acetosa* and *Glyceria fluitans* may be useful as indirect indicators of acid conditions or acidification.

Relevance for conservation management

The most important result from this paper has been the clear identification that site-based factors are the most important environmental variables controlling species community composition in these mesotrophic grasslands, and these are much greater than variables directly associated with productivity. Of course at this point we do not know which of the myriad of interacting factors that are most important on any site, but they must include differences in the local species pool, historic as well as present management (Wells et al. 1976; Gustavsson et al. 2007; Klimek et al. 2007), and site-specific conditions, i.e. water regime and soil physico-chemical properties and soil microbial properties (Balátová-Tuláčková 1966, 1968; Ejrnæs & Bruun 2000; Critchley et al. 2002a; Havlová et al. 2004; Marini et al. 2007). Of particular note has been the recent discovery by Gustavsson et al. (2007) that historic management signatures remain evident for centuries, and being more important than some recent management practices (Marrs 2008). In spite of this, the soil factors (W, P, pH) were also significant in affecting community composition, and the most common species found in these grasslands were grouped into response types along each of these environemtnal gradients. These, groups, therefore, can be used as a first approximation of environmental indicators of environmental conditions in UK mesotrophic grasslands for conservation purposes.

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Table 1. Description of the mesotrophic grassland communities found at each site; (a) site locations, number of quadrats sampled and the NVC mesotrophic grassland communities found at each site, and (b) a brief description of the NVC communities detected (after Rodwell 1992, 2000; Rodwell et al. 2000). NVC communities were fitted using TABLEFIT (Hill 1996).

(a)

Site	Grid reference	Year sampled	Number of quadrats sampled	Main vegetation type	NVC Mesotrophic grassland communities ascribed to quadrat data
Berney Marshes	TG465055	1998	20	*Lolio-Potentillion*	MG13
Cricklade	SU096958	1998	20	*Alopecurion*	MG4, 5, 7c, OV28
East Harnham	SU151289	1999	10	*Calthion*	MG8
Moorlinch	ST393362	1999	25	*Calthion*	MG8[1], Ag/Cx
Portholme	TL238708	1999	20	*Alopecurion*	MG4, OV28
Southlake	ST364301	1998	19	*Alopecurion/Calthion*	MG7c, Ag/Cx,
Stonygillfoot	NY926263	1999	11	*Polygono-Trisetion*	MG3, 8
Tadham	ST416455	1998	24	*Cynosurion/Calthion*	MG5[2], 8[1], OV28
Upton Ham	SO860400	1999	25	*Alopecurion*	MG4, 7c, OV28
Wet Moor	ST435245	1999	20	*Calthion*	Ag/Cx

(b)

NVC Community	Brief description
MG3	*Anthoxanthum odoratum–Geranium sylvaticum* grassland: Northern hay meadow
MG4	*Alopecurus pratensis–Sanguisorba officinalis* grassland: Flood meadow
MG5	*Cynosurus cristatus–Centaurea nigra* grassland: Old hay meadow
MG6	*Lolium perenne–Cynosurus cristatus* grassland: Ordinary pasture
MG7c	*Lolium perenne-Alopecurus pratensis-Festruca pratensis* grassland leys
MG8	*Cynosurus cristatus–Caltha palustris* grassland: Water meadow
MG13	*Agrostis stolonifera–Alopecurus geniculatus* grassland: Inundation grassland
OV 28	*Agrostis stolonifera-Ranunculus repens* community
Ag/Cx	*Agrostis stolononifera- Carex nigra* community

[1] similar to *Ranunculo-Senecionetum* (Schaminée et al. 1996)
[2] similar to *Cynosurion* (O'Sullivan 1968)
[3]Ag/Cx, *Agrostis stolonifera – Carex nigra* community (Rodwell et al. 2000).

Table 2. Spearman rank correlation coefficients of (1) measured soil variables: W is waterlogging (m.weeks), P is Olsen phosphorus (µg P. g^{-1}), pH and (2) DCA axes scores and Ellenberg indicator values. Significance: *** P<0.001; * P<0.05; n.s. non significant.

Contrast	Spearman r_s	Signif.	Contrast	Spearman r_s	Signif.
P & Light	0.116	n.s.	DCA1 & Light	0.307	***
P & Moisture	0.149	*	DCA1 & Moisture	0.728	***
P & Reaction	0.394	***	DCA1 & Reaction	0.220	**
P & Nutrients	0.567	***	DCA1 & Nutrients	0.538	***
pH & Light	0.027	n.s.	DCA2 & Light	-0.088	n.s.
pH & Moisture	-0.112	n.s.	DCA2 & Moisture	0.296	***
pH & Reaction	0.084	n.s.	DCA2 & Reaction	-0.557	***
pH & Nutrients	-0.281	***	DCA2 & Nutrients	-0.659	***
W & Light	0.269	***			
W & Moisture	0.663	***			
W & Reaction	0.089	n.s.			
W & Nutrients	0.365	***			

Table 3. The relative contributions of three sets of environmental variables in explaining species composition in Variation Partitioning. Total Inertia (TI) is value of constrained inertia in the CCA; Var the variation explained by the variable set as a % of TI; Pseudo-F is value of a Monte-Carlo test with 999 permutations. Significance: *** P<0.001; n.s. non significant; n.c.= not calculable, i.e. variation accounted for by variable < variation accounted for by covariables.

Groups / Variables	Including variability shared with other groups, Conditional variable=Time			Excluding variability shared with other groups		
	Inertia	Variation (%)	Pseudo-F	Inertia	Variation (%)	Pseudo-F
Total	6.3219					
All (Site, Geog, Soil)	1.8004	28.48	4.053***			
Site	1.4533	22.99	4.545***	0.7986	12.63	3.082***
Geography (Northing, Easting)	0.4424	7.00	4.558***	0.0139	0.22	0.377 n.s.
Climate (Temperature, Sunshine, Rainfall, Frost)	1.1750	18.59	4.628***	n.c.	0	n.c.
Soil (P, W, pH)	0.6364	10.07	4.524***	0.3331	5.27	2.999***
P	0.1733	2.74	3.411***	0.0635	0.97	1.714***
W	0.3438	5.44	6.965***	0.1166	1.84	3.150***
pH	0.1569	2.48	3.080***	0.0916	1.45	2.474***

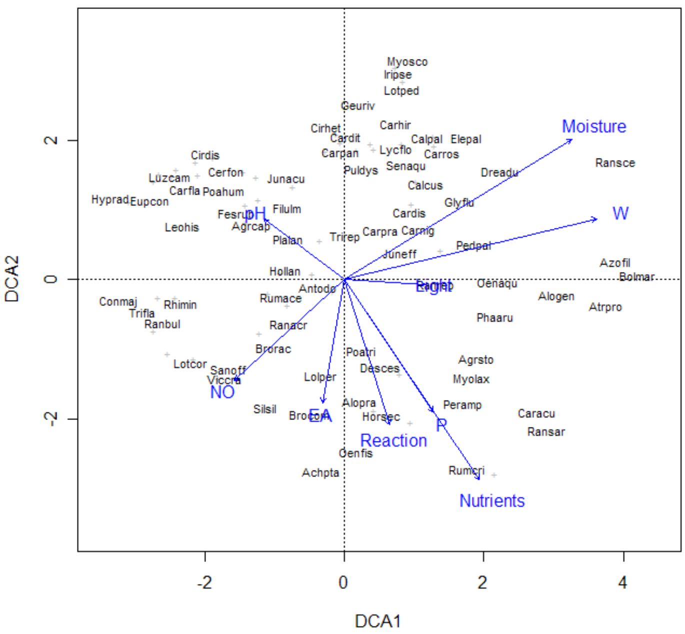

Fig. 1. DCA plot illustrating species position and relationship with the environmental variables. Species were drawn without overlap due to with priority of a higher abundance in the dataset. Abbreviations of species names can be found in E-Appendix II.

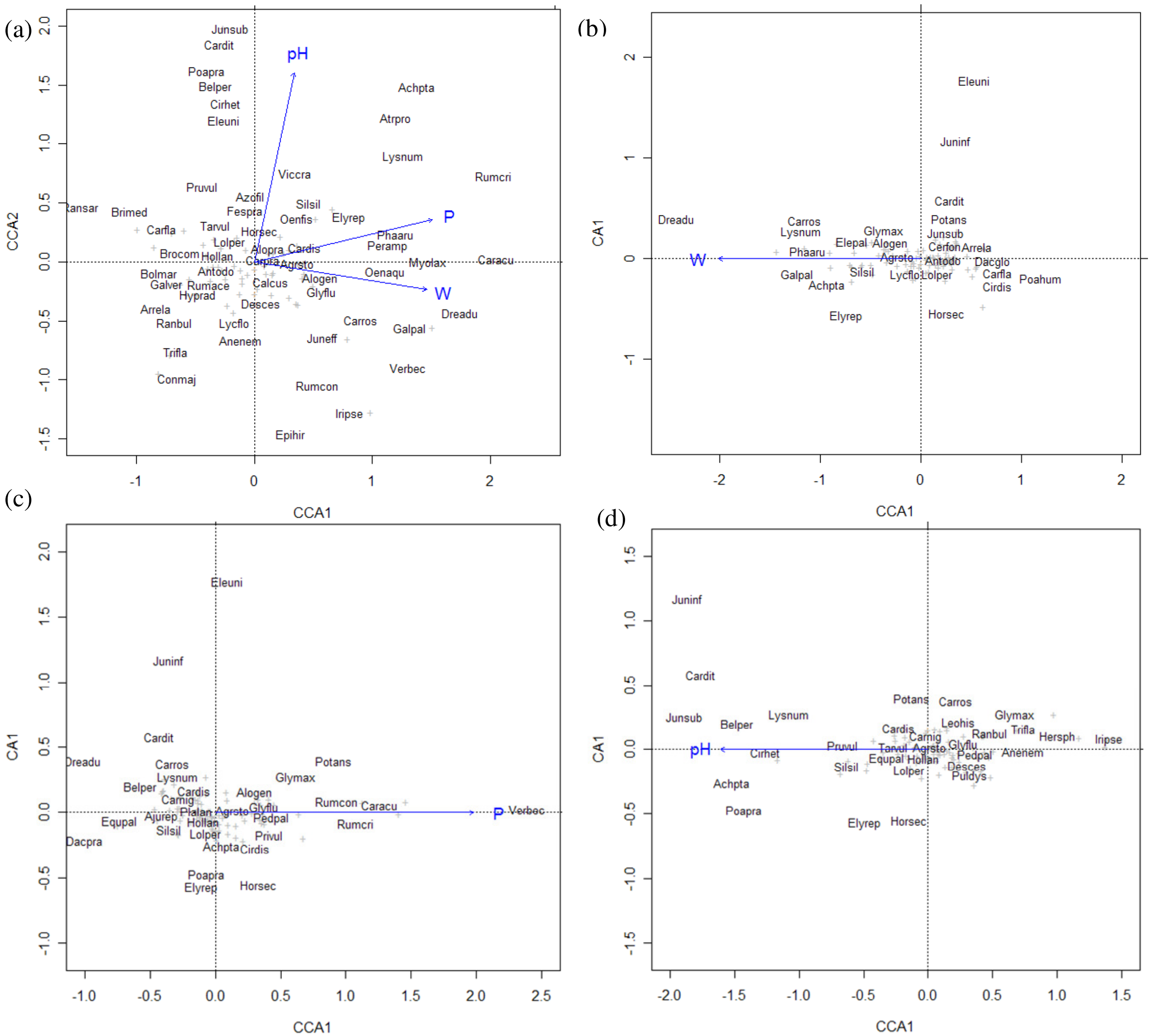
(a)
(b)
(c)
(d)
CCA1
CCA2
CA1
pH
P
W
Junsub
Cardit
Poapra
Belper
Cirhet
Eleuni
Achpta
Atrpro
Lysnum
Rumcri
Viccra
Pruvul
Azofil
Fespra
Silsil
Oenfis
Elyrep
Brimed
Carfla
Tarvul
Lolper
Horsec
Phaaru
Peramp
Brocom
Hollan
Alopra
Cardis
Agrsto
Myolax
Caracu
Bolmar
Antodo
Galver
Rumace
Hyprad
Calcus
Alogen
Glyflu
Oenaqu
Arrela
Desces
Dreadu
Ranbul
Lycflo
Carros
Galpal
Aneneм
Juneff
Trifla
Verbec
Conmaj
Rumcon
Iripse
Epihir
Juninf
Potans
Dreadu
Carros
Glymax
Elepal
Phaaru
Cerfon
Dacglo
Galpal
Achpta
Silsil
Lycflo
Cirdis
Poahum
Elyrep
Horsec
Belper
Carnig
Cardis
Plalan
Pedpal
Rumcon
Equpal
Ajurep
Rumcri
Privul
Dacpra
Poapra
Elyrep
Leohis
Ranbul
Trifla
Hersph
Iripse
Cirhet
Pruvul
Aneneм
Puldys

Fig. 2. pCCA biplots illustrating species composition of mesotrophic grasslands in relation to (a) three soil variables P is soil phosphorus (μg P. g^{-1}), W is waterlogging (m.weeks) and pH; (b) waterlogging W; (c) phosphorus P; (d) soil pH. Species were drawn without overlap with priority of a higher abundance in the dataset; abbreviations of species names can be found in E-Appendix II.

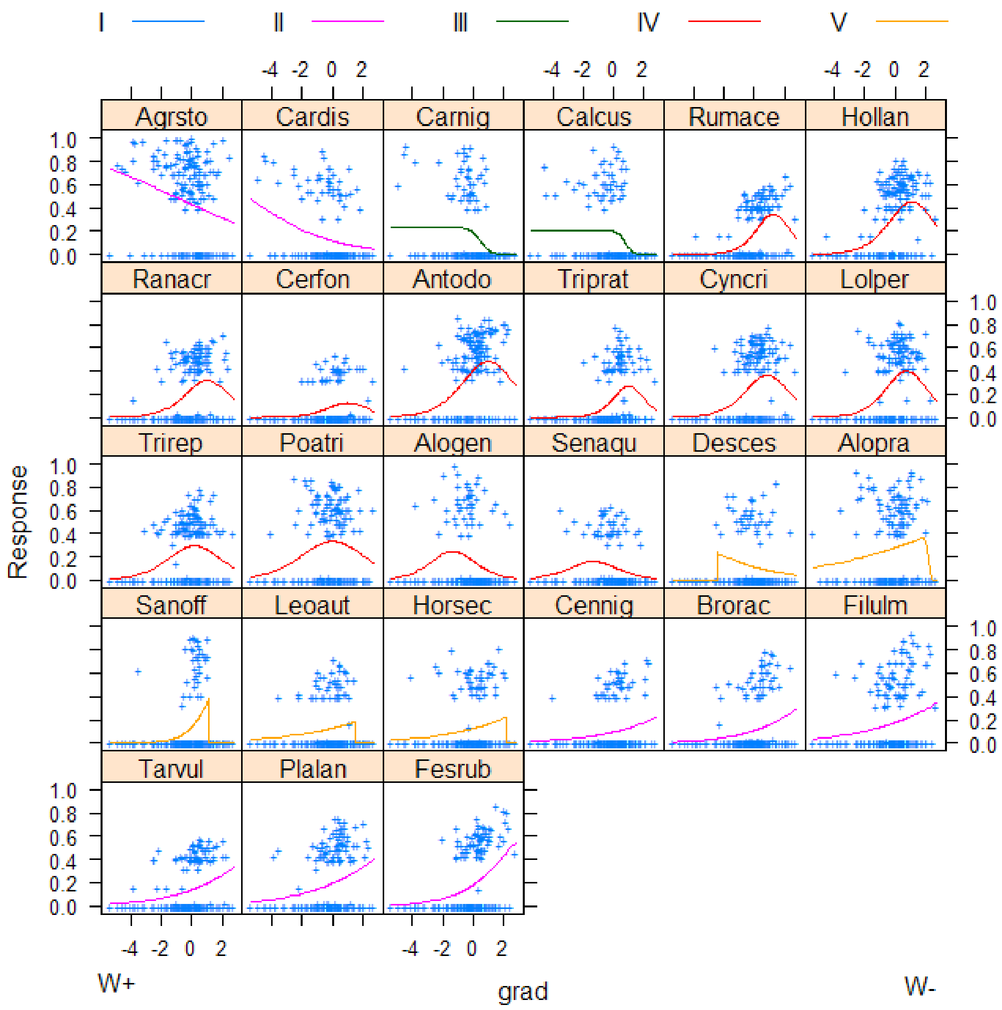

Fig. 3. Species response curves with respect to waterlogging (W) represented by site scores from constrained ordination (W is explanatory variable and all other environmental variables are removed as conditional); HOF models II, III, IV, V are shown. Abbreviations of species names are: Agrsto – *Agrostis stolonifera*, Cardis - *Carex disticha*, Carnig – *Carex nigra*, Calcus - *Calliergonella cuspidata*, Rumace – *Rumex acetosa*, Hollan – *Holcus lanatus*, Ranacr – *Ranunculus acris*, Cerfon – *Cerastium fontanum*, Antodo – *Anthoxanthum odoratum*, Tripra – *Trifolium pratense*, Cyncri – *Cynosurus cristatus*, Lolper – *Lolium perenne*, Trirep – *Trifolium repens*, Poatri – *Poa trivialis*, Alogen – *Alopecurus geniculatus*, Senaqu – *Senecio aquaticus*, Desce – *Deschampsia cespitosa*, Alopra – *Alopecurus pratensis*, Sanoff – *Sanquisorba officinalis*, Leoaut – *Leontodon autumnalis*, Horsec – *Hordeum secalinum*, Cennig – *Centaurea nigra*, Brorac – *Bromus racemosus*, Filulm – *Filipendula ulmaria*, Tarvul – *Taraxacum* sect. *vulgaria*, Plalan – *Plantago lanceolata*, Fesrub – *Festuca rubra*.

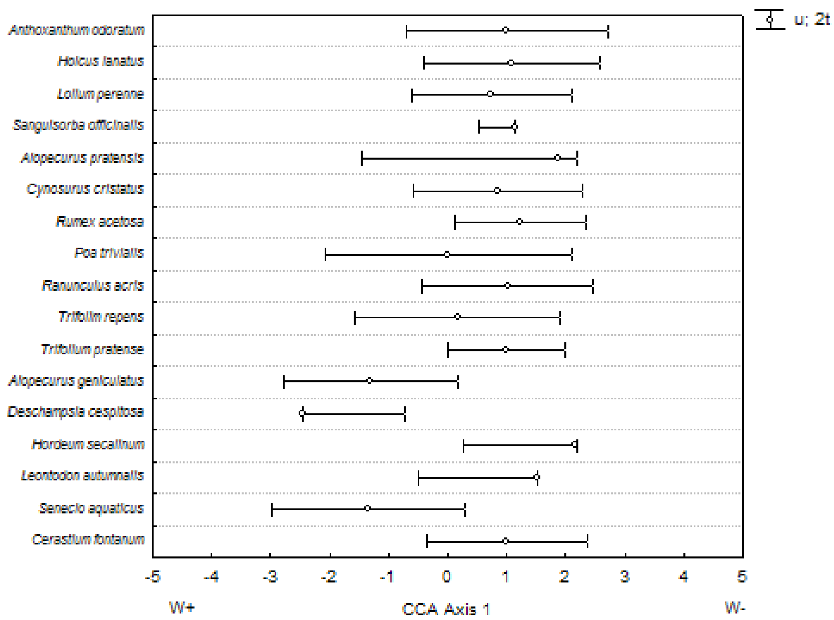

Figure 4. Tolerance intervals for species with unimodal symmetric or skewed response (IV and V HOF models) on gradient of waterlogging W (site scores from constrained pCCA ordination with W as explanatory variable and all other variables removed as conditional); location of optimum (u) and extent of tolerance for each species is shown; species are sort according to the decreasing height (top) value.

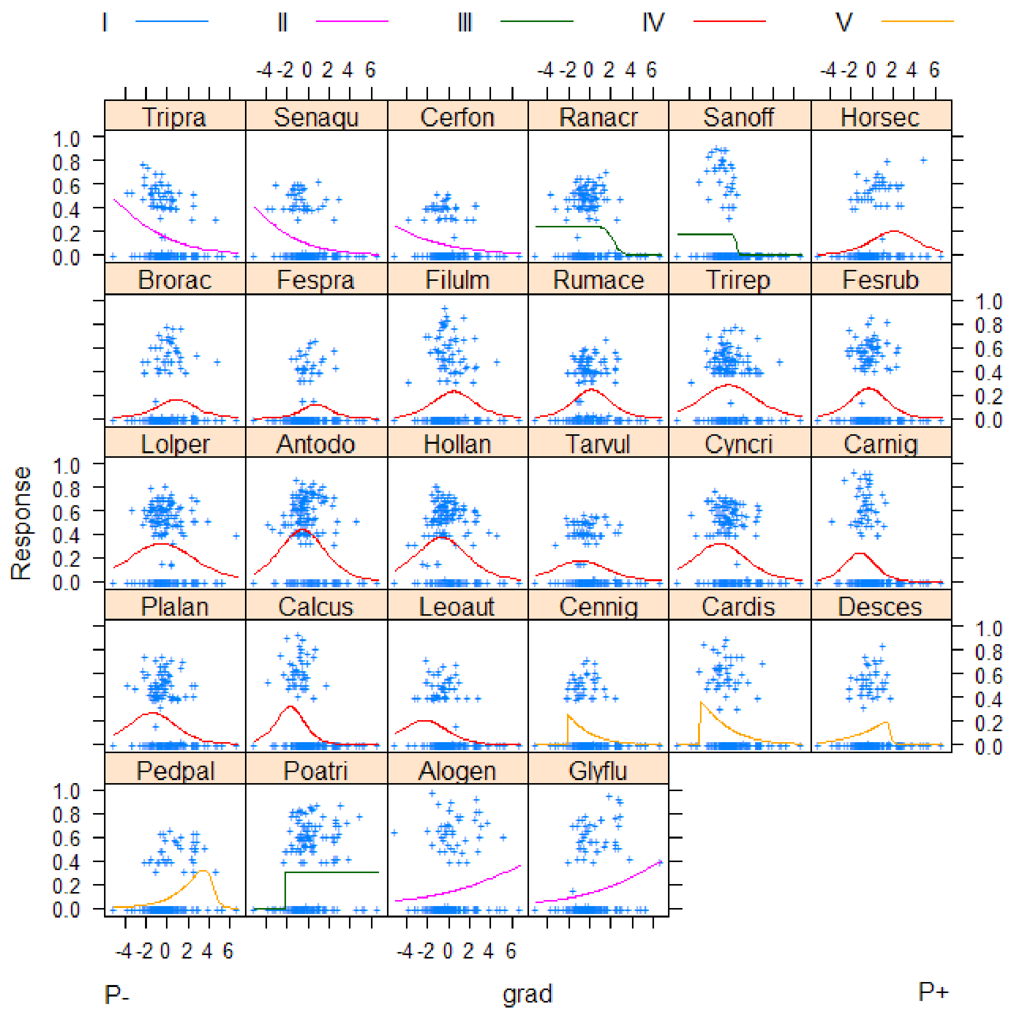

Fig. 5. Species response curves with respect to soil phosphorus (P) represented by site scores from constrained ordination (P is explanatory variable and all other environmental variables are removed as conditional); HOF models II, III, IV, V are shown. Abbreviations of species names are: Tripra – *Trifolium pratense*, Senaqu – *Senecio aquaticus*, Cerfon – *Cerastium fontanum*, Ranacr – *Ranunculus acris*, Sanoff – *Sanguisorba officinalis*, Horsec – *Hordeum secalinum*, Brorac – *Bromus racemosus*, Fespra – *Festuca pratensis*, Filulm – *Filipendula ulmaria*, Rumace – *Rumex acetosa*, Trirep – *Trifolium repens*, Fesrub – *Festuca rubra*, Lolper – *Lolium perenne*, Antodo – *Anthoxanthum odoratum*, Hollan – *Holcus lanatus*, Tarvul – *Taraxacum* sect. *vulgaria*, Cyncri – *Cynosurus cristatus*, Carnig – *Carex nigra*, Plalan – *Plantago lanceolata*, Calcus – *Calliergonella cuspidata*, Leoaut – *Leontodon autumnalis*, Cennig – *Centaurea nigra*, Cardis – *Carex disticha*, Desces – *Deschampsia cespitosa*, Pedpal – *Pedicularis palustris*, Poatri – *Poa trivialis*, Alogen – *Alopecurus geniculatus*, Glyflu – *Glyceria fluitans*.

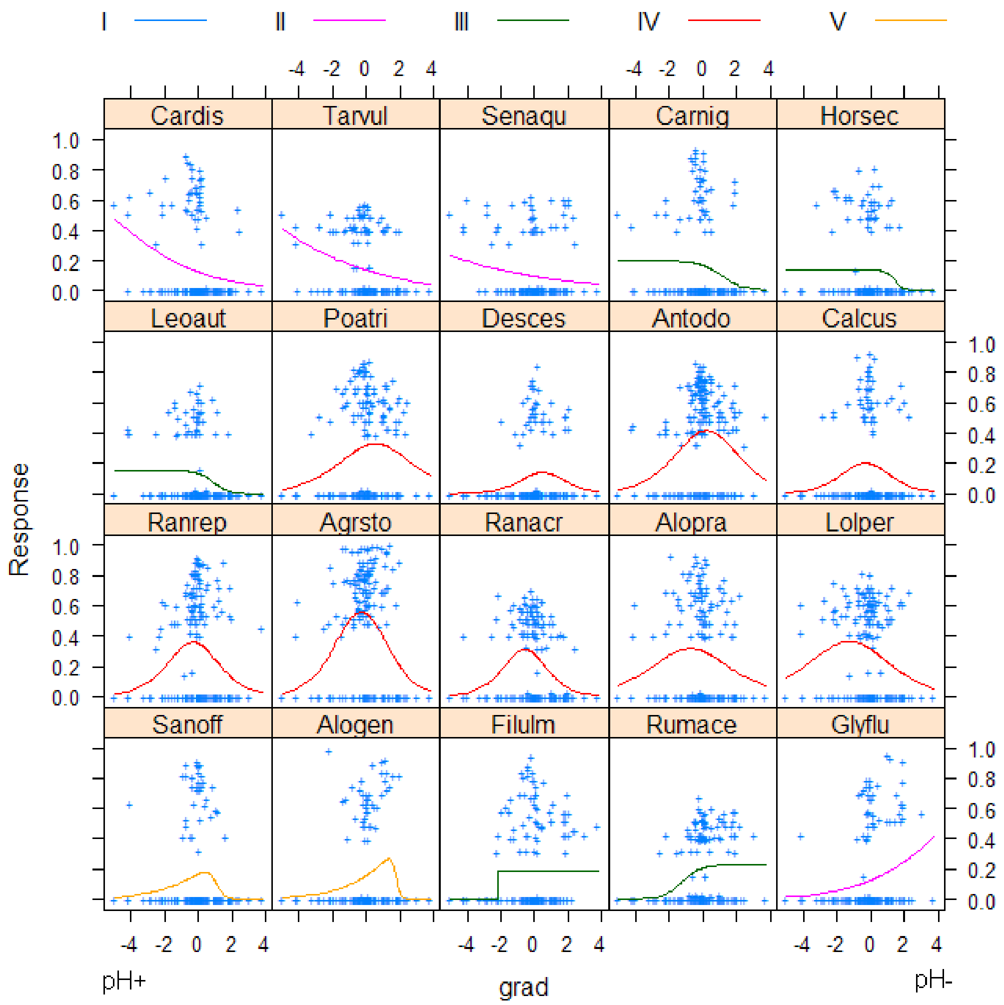

Fig. 6. Species response curves with respect to soil pH represented by site scores from constrained ordination (pH is explanatory variable and all other environmental variables are removed as conditional); HOF models II, III, IV, V are shown. Abbreviations of species names are: Cardis – *Carex distans*, Tarvul – *Taraxacum* sect. *vulgaria*, Senaqu – *Senecio aquaticus*, Horsec – *Hordeum secalinum*, Leoaut – *Leontodon autumnalis*, Poatri – *Poa trivialis*, Desces – *Deschampsia cespitosa*, Antodo – *Anthoxanthum odoratum*, Calcus – *Calliergonella cuspidata*, Ranrep – *Ranunculus repens*, Agrsto – *Agrostis stolonifera*, Ranacr – *Ranunculus acris*, Alopra – *Alopecurus pratensis*, Lolper – *Lolium perenne*, Sanoff – *Sanguisorba officinalis*, Alogen – *Alopecurus geniculatus*, Filulm – *Filipendula ulmaria*, Rumace – *Rumex acetosa*, Glyflu – *Glyceria fluitans*.