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The importance of local processes to landscape patterns of grassland vegetation diversity

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Abstract This study aimed to determine the importance of local processes to variation in plant species diversity by comparing soil fertility/diversity relationships across and within different environments. Vegetation diversity and soil fertility were measured in four different grassland communities in southern North Island, New Zealand. Vegetation species richness, Shannon diversity (H') and evenness (J') were significantly negatively related to the concentration of most plant nutrients in the soil, only phosphorus being not significantly related. Across-environment diversity/fertility relationships generally agreed with within-environment relationships. We suggest that local-scale processes, influenced by the availability of nutrients, are the key determinants of landscape patterns of vegetation diversity in grassland communities.

Keywords soil fertility; managed grasslands; scale; New Zealand

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INTRODUCTION

Gradients of environmental variables that directly impact on plant growth or resource availability have been associated with recurring patterns of species richness (see Pausas & Austin (2001) for review). Soil fertility has been identified as a key factor regulating plant community structure and, although theories on the mechanisms differ (Thompson 1987; Tilman 1987), numerous field and laboratory studies have found a negative relationship between soil fertility and plant species richness (Goldberg & Miller 1990; Tilman et al. 1994; Wedin & Tilman 1996; Leps 1999; Roem & Berendse 2000).

Perspectives on community structure regulation differ fundamentally on the basis of scale (Huston 1999). Small scale (local) perspectives emphasise the importance of local processes such as competition, facilitation or herbivory between proximate organisms (Tilman 1982; Pimm 1991). These biotic interactions are expected to regulate or limit the number of species found in any one location. Alternatively, under a larger-scale regional perspective (i.e., regions between geographical barriers such as oceans or mountain ranges), species isolation, speciation and extinction control the regional species pool, and local species richness is expected to be a predictable fraction of the regional richness (Schluter & Ricklefs 1993; Caley & Schluter 1997).

Recent evidence supports the importance of regional processes in controlling global species diversity (Rosenzweig 1995), but at smaller spatial scales local processes are assumed to have greater importance (Huston 1999). Conceptually, biotic (e.g., competition, facilitation) and environmental (e.g., resource stress, disturbance) filters determine local species composition from wider regional species pools (Zobel 1997; Diaz et al. 1998; Fridley 2001).

Local processes must be examined at the appropriate spatial scale (Huston 1999). Huston suggested that the spatial scale at which variation in diversity has traditionally been measured is not the same at which diversity-determining processes actually operate. Scales of measurement classified as "local" are often so large and environmentally heterogeneous that they reflect an aggregation of many different localities, obscuring local environment-diversity relationships. In grasslands, large herbivores generate heterogeneity through their grazing behaviour (Parsons et al. 2000), and also through their urine and faeces, by concentrating nutrients in patches (Steinauer & Collins 1995).

This experiment aimed to determine the importance of fertility as a diversity-influencing factor in four grassland communities inherently differing in diversity, fertility, topography, and grazing management. This was achieved by determining if diversity/soil fertility relationships observed across differing environments (i.e., landscape scale relationships) were consistent with those observed within management regimes (i.e., local scale relationships).

METHODS

Site and treatment

On 10–11 February 1998 eight experimental sites were established in the Manawatu region of New Zealand. Two replicate sites were established at each of four different management regimes (MR) operating at AgResearch Grasslands research farms, Ballantrae (hill-country) and Aorangi (lowland). Management regime details are given in Table 1 (refer to Lambert et al. (2000) for full management history of the experimental sites at Ballantrae Hill-country Research Farm). Management regimes were applied to many paddocks within a farm.

Each experimental site was divided into three blocks and within each block a species-poor and a species-rich sampling location (approximately 2 × 2 m) was identified, giving a total of 48 sampling locations. Visual decision rules were used to identify species-rich and species-poor areas, as previous research had determined that certain species were strongly correlated with the species richness of a local area (Nicholas 1999). At Aorangi, low predicted species richness (PSR) areas were identified as being dominated by *Lolium perenne* L. and at Ballantrae, high PSR areas were associated with the indigenous *Nertera setulosa* Hook.f. and *Centella* species.

The Ballantrae sites were based on sedimentary soils derived from sandstone, siltstone, and mudstones, mainly yellow-brown earths with intergrades to yellow-grey earths (Lambert et al. 2000).

Table 1 Management regime (MR) characteristics.

	Management regime			
	1	2	3	4
Location[1]	Ballantrae	Ballantrae	Aorangi	Ballantrae
Soil fertility[2]	Low-low	Medium-medium	High-medium	Medium-high
Vegetation history[3]	Resident	Resident	Resident	Improved[4]
Major herbivore	Sheep	Sheep	Beef bulls	Beef bulls
Grazing type[5]	Continuous	Rotational	Rotational	Rotational
Stocking rate (ssu)[6]	10	16	16	16

[1] Ballantrae: 40°20′S, 175°50′E, 125–350 m a.s.l.; Aorangi: 40°29′S, 175°41′E, 25 m a.s.l.

[2] Rating based on published soil analyses for Ballantrae (Lambert et al. 2000) and Aorangi (Rijkse & Daly 1972) and the analyses performed for this experiment, expressed as: general soil nutrient index – soil phosphorus concentration. Annual applications of 13 kg P ha^{-1} to MR1, 46 kg P ha^{-1} to MR2 and MR4, 15 kg P ha^{-1} to MR3; 1250 and 2500 kg ha^{-1} of ground limestone to MR2 and MR4 in 1975 and 1979, respectively.

[3] Ballantrae, without fertiliser since 1950, was under low intensity continuous sheep grazing and dominated by low-fertility tolerant grasses (*Agrostis capillaris* L., *Anthoxanthum odoratum* L., and *Cynosurus cristatus* L.). In 1974 *Trifolium repens* L., *Trifolium pratense* L., *Trifolium subterraneum* L., and *Lotus pedunculatus* Cav. seed was broadcast over all Ballantrae sites. Aorangi was under permanent pasture (dominated by *L. perenne* and *T. repens*) for at least 10 years prior to this experiment.

[4] Herbicide (Glyphosate™) applied to MR4 in autumn 1993 at 720 g ha^{-1} to suppress the existing vegetation then lime coated *Dactylis glomerata* L. cv. ‘Grasslands Wana’ seed was broadcast from the air at 12 kg ha^{-1}. An annual application of 150 kg di-ammonium phosphate ha^{-1} was initiated at this time.

[5] Continuous = animals permanently on site. Rotational = higher instantaneous stocking rate for short periods (1–2 days) at intervals from 20 to 80 days.

[6] 1 ssu ha^{-1} $year^{-1}$ (sheep stock unit) = 1 breeding ewe with a lamb to weaning; 1 breeding cow = 6 ssu.

The Aorangi sites were based on an alluvial soil (Kairanga silt loam) (Rijkse & Daly 1972). The average annual rainfall at Ballantrae was 1.2 m and average daily soil temperature (0.1 m depth) ranged from 7°C (winter) to 16°C (summer). Average annual rainfall at Aorangi was 0.9 m and soil temperature ranged from 7 to 18°C.

A 0.5-m^2 exclusion cage representing a plot was placed within each low and high diversity area to prevent grazing. At two sampling dates, 23 March 1998 and 25 May 1998, the vegetation within the exclusion cages was clipped down to the same height as the surrounding vegetation. A subsample from the clipped vegetation was separated into individual species; material was then dried (24 h at 80°C) and weighed.

Soil samples for fertility analysis were taken at all sites on 12 February 1998. Four 0.025 m diameter by 0.075 m deep cores were removed from each sampling location from within the exclosure cages. Cores from the same PSR group were bulked across blocks for each experimental site, giving a total of 16 samples. The soil samples were analysed for pH, organic carbon content, and major element (Ca, K, P, Mg, Na, N, S) content by the Soil Fertility Service, AgResearch Ruakura, Hamilton, New Zealand.

Data analysis

Individual species biomass data was used to determine species richness and calculate indices of the distribution of individuals among species (Shannon diversity index H' and evenness of diversity J') (Magurran 1988):

$$H' = \sum_{i=1}^{k} p_i(\text{In}\, p_i) \tag{1}$$

$$J' = \frac{H'}{\text{In}\, k} \tag{2}$$

where k = number of species and p_i = the proportion of individuals (i.e., tillers or growing points) belonging to species i. p_i is estimated using

$$\frac{n_i}{N};$$

where n_i = number or biomass of individuals of species i and N = total number or biomass of individuals.

Vegetation diversity and composition data were analysed as a factorial design by analysis of variance (ANOVA) using SAS® Release 8.01 (SAS Institute 1999). Replicates were treated as nested within MR. Differences between main effect means were determined by calculating Tukey test statistics for pair-wise comparisons (Zar 1996) and differences between means within MR were determined using the SLICE option of the LSMEANS statement within SAS®.

The soil nutrient data indicated that sampling sites low or high in any given nutrient were generally low or high in all nutrients and therefore well suited to dimensionality reduction by multivariate statistics. A general soil nutrient index was derived from Axis 1 component scores of a principal component analysis (PCA) of the soil nutrient data.

Regression analysis was used to examine the relationships between soil fertility and diversity indices. For the comparison between vegetation diversity and soil fertility, the vegetation data from the same predicted species richness group were combined to obtain diversity indices.

RESULTS

Diversity and composition

The number of species within the 0.5 m^2 sampling areas ranged from 3 to 11. On average, the lowland rotationally grazed vegetation (MR3) contained significantly ($P < 0.001$) fewer species than the other management regimes (8.3, 7.4, 4.7, and 7.4 species for MR1, 2, 3, and 4, respectively). Sampling locations predicted to have a higher number of species did contain more species (1.3, 0.6, 0.7, and 3.8 more species in high PSR areas for MR1, 2, 3, and 4, respectively), and were also more diverse as measured by H' and J' indices ($P < 0.01$ for MR by PSR effect sliced by MR for species richness, H' and J'). There were no significant differences in species richness, diversity, and evenness between sampling times.

MR1 vegetation was dominated by *Agrostis capillaris* L. and other low-fertility tolerant grasses (Table 2). In MR2 the contribution from *A. capillaris* had decreased and *L. perenne* substantially increased. Non-legume dicotyledonous species abundance was greatest in the sheep-grazed vegetation (MR1 and 2). Lowland vegetation (MR3) was dominated by *Lolium perenne* and legume species (predominantly *Trifolium repens* L.), whereas a previous *Dactylis glomerata* establishment experiment (Barker et al. 1999), resulted in *D. glomerata* comprising nearly half of MR4 vegetation. Legumes and *L. perenne* were the other notable contributors to MR4 vegetation.

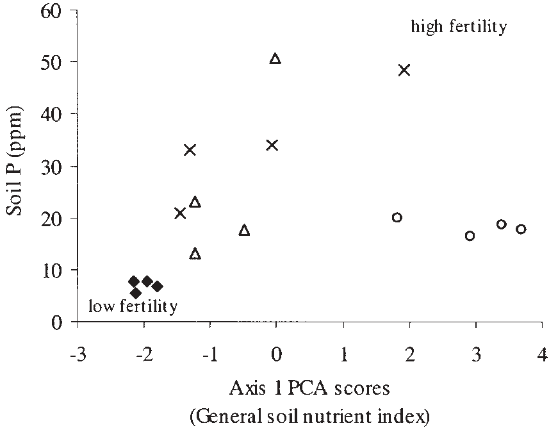

Fig. 1 Axis 1 component scores from the principal components analysis (PCA) of the soil nutrient data compared with soil phosphorus concentration for the four management regimes (MR). Symbols: MR1, ◆; MR2, ○; MR3, △; MR4, ×.

Soil properties

The soil of MR1 was of generally lower fertility than the other management regimes, particularly in calcium and phosphorus (Table 3). MR2 sampling sites had similar values as MR1 sites for magnesium, potassium, sodium, and slope, but considerably more soil phosphorus and calcium. MR3 soil was characterised by flat topography, moderate levels of phosphorus, and high levels of calcium, potassium, magnesium, sodium, sulphur, and total nitrogen (Table 3). The calcium content of MR3 soil was particularly high. Sampling locations within MR4 were of steep topography, had high soil phosphorus content, higher calcium contents than MR1 and MR2, but slightly lower levels of organic matter and total nitrogen. The only soil property not to show any appreciable difference between MR was pH.

Principal component analysis of the soil nutrient data revealed that all soil nutrients (except P) were significantly and highly positively correlated with Axis 1 (Pearson correlation coefficient, $r > 0.75$, $P < 0.001$), which explained 61% of the variance. Accordingly, Axis 1 principal component scores represent a general fertility index; higher component scores indicate higher fertility (Fig. 1). Phosphorus was the only nutrient to be significantly correlated with Axis 2 (which accounted for 19% of the total variation). Therefore, actual soil phosphorus contents, instead of Axis 2 component scores, were used when making comparisons with vegetation diversity measures.

Relationships between soil fertility and diversity

When comparisons were made across all MR, vegetation species richness, Shannon diversity (H') and evenness (J') were significantly and negatively related to the general soil fertility index at both March and May sampling dates (Fig. 2A–F). That is, communities growing from soil poor in nutrients tended to have higher species richness, higher H' and higher J' values than those from nutrient-rich soil. By contrast, phosphorus, the only soil nutrient not incorporated in the general fertility index, was not significantly related to any of the three diversity measures (Fig. 3A–F).

Soil fertility index and diversity comparisons made within MR were largely consistent with those made across all MR. That is, when the soil fertility index and vegetation diversity of adjacent low and high PSR areas were compared, there was general agreement with the trends observed across all MR (Fig. 2). The arrows linking low and high PSR pairs

Table 2 Composition (% of live biomass) of vegetation under four management regimes (MR, Table 1) (averaged across seasons and predicted species richness (PSR) areas). Expressed as a percentage of live biomass (±SEM). Species abbreviations: Aca, *Agrostis capillaris*; Dgl, *Dactylis glomerata*; Hla, *Holcus lanatus*; Lpe, *Lolium perenne*. Legumes = Predominantly *Trifolium repens* but also some *Lotus pedunculatus* Cav., *Trifolium dubium* Sibthorp and *Trifolium subterraneum* L. Dead matter expressed as percentage of total biomass.

MR	Aca	Dgl	Hla	Lpe	Legumes	Other grass	Non-legume dicots	Dead matter
1	46 (±3)	0.6	8 (±1)	9 (±1)	5 (±1)	23 (±2)	8 (±2)	16 (±2)
2	28 (±3)	0.0	7 (±2)	37 (±4)	6 (±1)	17 (±2)	6 (±2)	13 (±2)
3	11 (±2)	0.0	1 (±0.5)	65 (±4)	15 (±2)	7 (±2)	0.3 (±0.1)	13 (±1)
4	9 (±2)	47 (±5)	6 (±1)	16 (±2)	16 (±2)	4 (±1)	2 (±0.6)	16 (±2)

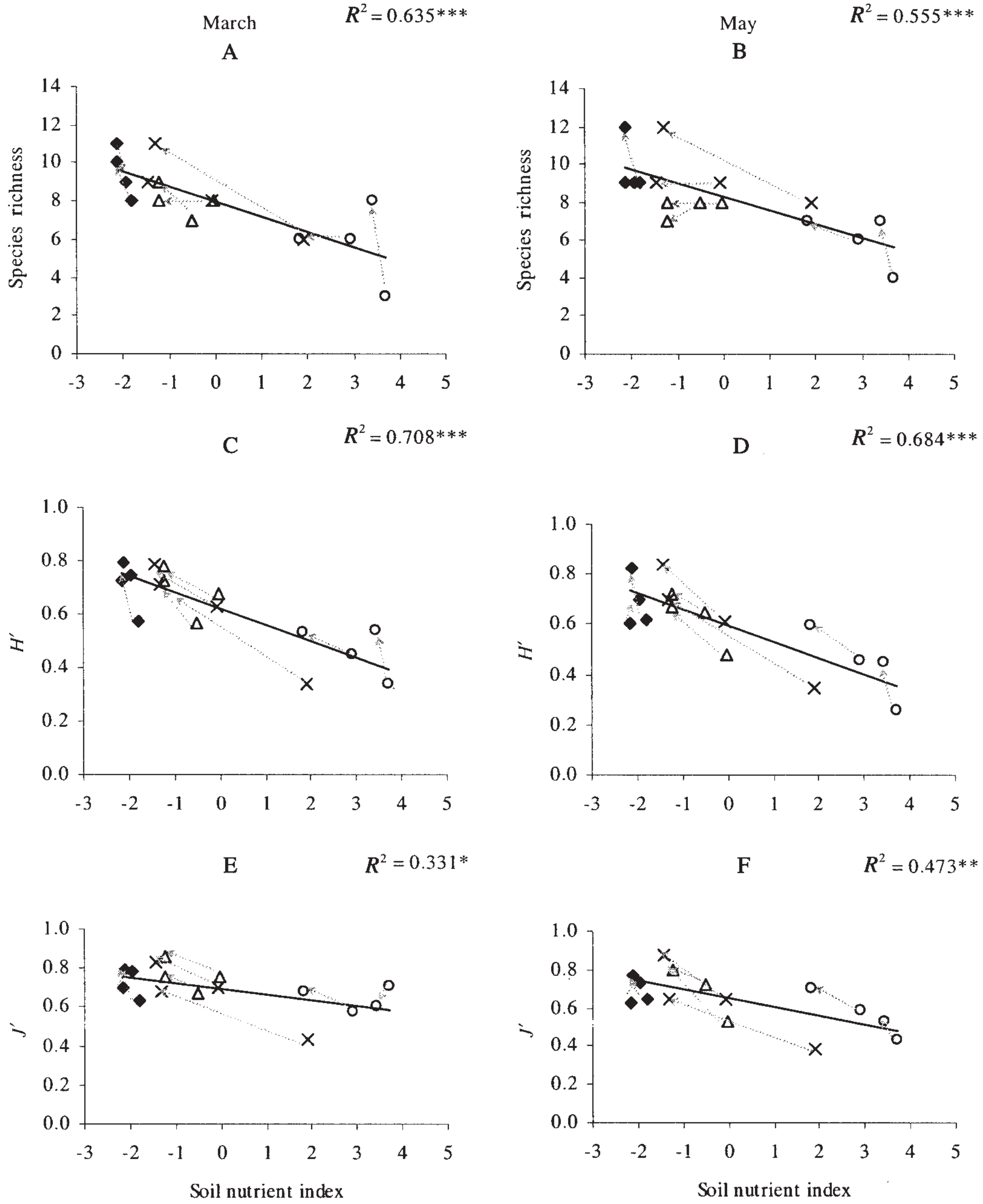

Fig. 2 Relationship between general soil nutrient index and measures of vegetation diversity–species richness, Shannon *H′* and evenness *J′* during March and May. General soil nutrient index was derived from Axis 1 component scores of a principal components analysis (PCA) of soil nutrient data (lower component scores equate to lower soil nutrient contents). Arrows originate from low predicted species richness (PSR) points and terminate at matching high PSR points. Symbols: MR1, ◆; MR2, ○; MR3, △; MR4, ×. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

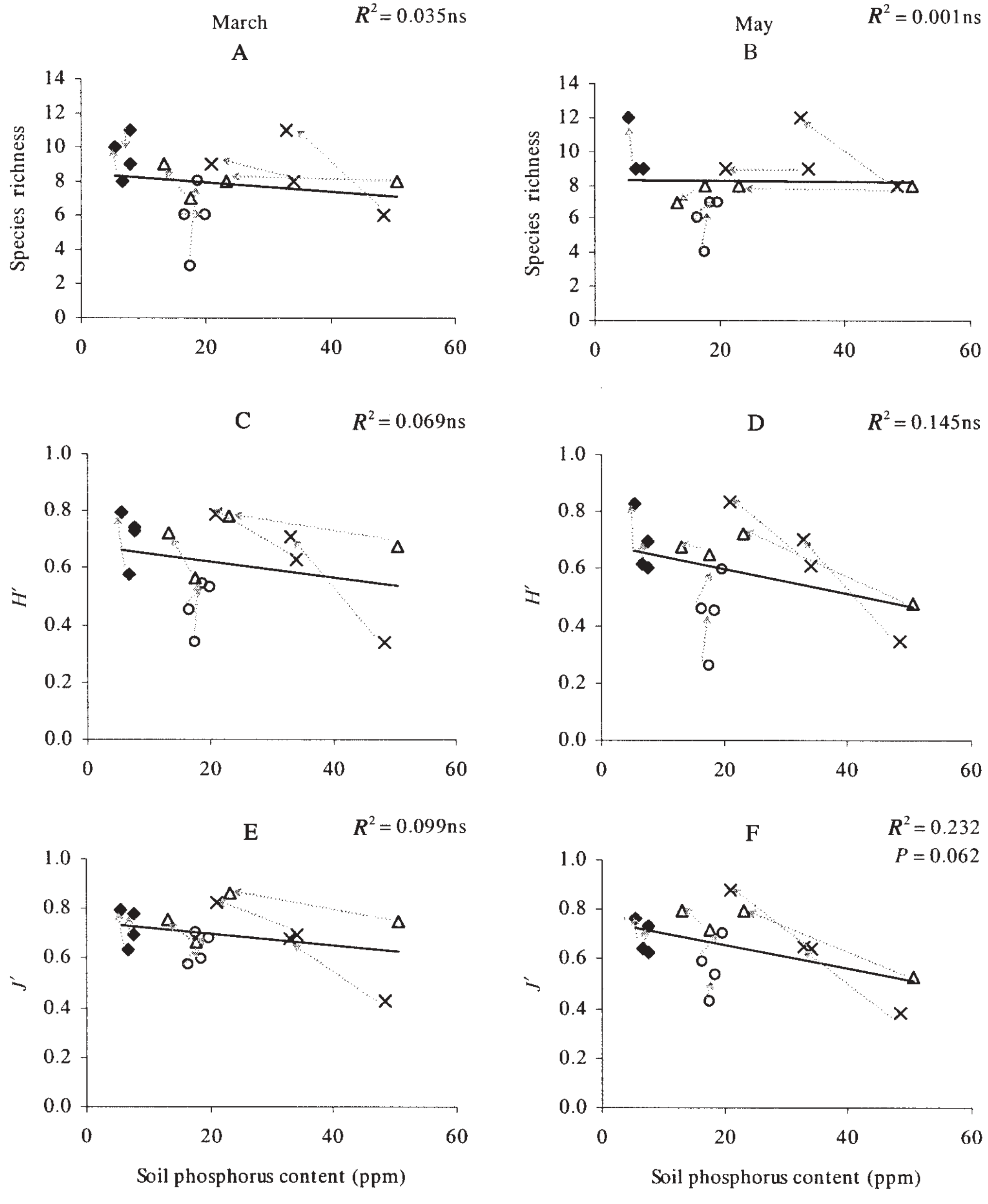

Fig. 3 Relationship between soil phosphorus (ppm) and measures of vegetation diversity–species richness, H' and J' during March and May. Arrows originate from low predicted species richness (PSR) points and terminate at matching high PSR points. See Fig. 2 for symbol descriptions. ns, $P > 0.05$.

for each MR tend to run the same direction as the overall relationship (arrows originate from the low PSR point and terminate at the corresponding high PSR point). This was particularly true when fertility was compared with the Shannon diversity index (Fig. 2C,D).

Similar comparisons between soil phosphorus concentration and diversity revealed greater variation in arrow direction (Fig. 3A–F). This was consistent with the lack of an overall relationship between soil P and vegetation diversity. The one exception was MR4, which provided evidence to

Table 3 Soil fertility and slope data. Expressed as the mean composite value of the two replicate sites within each management regime (MR) (±SEM); PSR, predicted species richness. Units of measure for soil elements are parts per million (ppm) for Ca, K, P, Mg, Na, S, and percent (%) for organic matter (OM) and total nitrogen (TN). Slope = degrees from horizontal.

MR	PSR	Ca	K	P	Mg	Na	S	pH	OM	TN	Slope
1	L	500 (±125)	160 (±40)	7 (±1)	128 (±13)	35 (±5)	5 (±0)	5.5 (±0)	10.2 (±1.2)	0.50 (±0.04)	9 (±2)
1	H	375 (±0)	180 (±20)	7 (±1)	110 (±10)	35 (±5)	6 (±0)	5.4 (±0)	10.8 (±0.9)	0.50 (±0.04)	8 (±1)
2	L	625 (±0)	320 (±20)	34 (±17)	128 (±3)	33 (±3)	8 (±1)	5.5 (±0.1)	10.6 (±0.6)	0.55 (±0.01)	8 (±1)
2	H	688 (±63)	190 (±50)	18 (±5)	118 (±3)	38 (±3)	8 (±0.5)	5.5 (±0.1)	9.8 (±0.5)	0.46 (±0.02)	12 (±2)
3	L	1188 (±63)	350 (±10)	17 (±1)	280 (±20)	53 (±3)	10 (±1)	5.6 (±0)	10.7 (±0)	0.62 (±0)	0 (±0)
3	H	1188 (±63)	360 (±140)	19 (±1)	248 (±3)	50 (±0)	9 (±2)	5.6 (±0.1)	9.5 (±0.2)	0.58 (±0.01)	0 (±0)
4	L	875 (±125)	300 (±40)	41 (±7)	160 (±10)	43 (±3)	10 (±3)	5.7 (±0.1)	9.4 (±0.1)	0.51 (±0)	17 (±3)
4	H	750 (±125)	120 (±0)	27 (±6)	145 (±0)	40 (±0)	6 (±0)	5.5 (±0.1)	8.3 (±0.5)	0.43 (±0.01)	23 (±2)

suggest that sampling locations with higher soil P concentrations had lower H' and J' values.

DISCUSSION

After reviewing the literature, Pausas & Austin (2001) concluded that resource availability (e.g., nutrients, water, light) and other environmental variables that have an impact on growth but are not consumed by plants (e.g., temperature), primarily determine local scale patterns of plant diversity. The fertility/diversity relationships observed in our study concur with Pausas & Austin (2001). Measures of vegetation diversity and nutrient availability observed *across* habitats varying widely in disturbance intensity (animal density), disturbance mode (grazing species), slope, aspect, and inherent fertility were generally consistent with diversity/fertility relationships observed *within* habitats, where variation in the above factors was minimised. This consistency suggests that local-scale processes influenced by the availability of nutrients such as interspecific competition are highly important in determining larger scale patterns of vegetation diversity in these grassland communities.

There were no significant overall relationships between phosphorus content in the soil and our three measures of vegetation diversity (Fig. 3A–F). Fertilisation studies that observe decreasing species richness in fertilised plots often add phosphorus as part of multi-nutrient fertiliser (usually containing N, P, and K), and fail to determine relationships between vegetation characteristics and individual nutrients (Smith et al. 1996a,b; Leps 1999). Goldberg & Miller (1990) tested the hypothesis that resource quantity was more important than resource identity to species diversity. Instead of accepting the hypothesis, Goldberg & Miller (1990) found that resource identity was important. Higher soil nitrogen levels were associated with lower species diversity but soil phosphorus concentration had little impact on diversity. However, it is surprising that soil phosphorus concentration does not have an impact on processes that determine species richness as it is one of the three most important mineral elements determining plant growth (Salisbury & Ross 1992). Furthermore, in terms of this study, the phosphorus concentrations of the soils were within a range where a growth response from the vegetation would be expected (Sinclair et al. 1997; Morton et al. 1999).

Some researchers suggest that phosphorus content *per se* is of lesser importance than its supply rate relative to other nutrients (e.g., N). Roem & Berendse (2000) studied Netherlands grassland and heathland vegetation diversity in relation to changes in soil acidity and nutrient concentrations as a result of increased atmospheric deposition of sulphuric and nitrogenous compounds. In agreement with the results of this study, there was not a close association between soil concentrations of P and diversity. Rather grassland species diversity was more closely related to the ratios of N:P and N:K in plant tissues. Based on the "resource balance hypothesis" of Braakhekke & Hooftman (1999), Roem & Berendse (2000) argued that biomass nutrient concentrations reflect nutrient supply rates, and that balanced N:P and N:K supply ratios, critical to supporting high plant community diversity, were being disrupted by increased atmospheric nitrogen deposition and soil acidification. Further experimentation is required to determine if balanced nutrient supply ratios are equally important to the plant species diversity of grasslands not influenced by the environmental impacts of "acid rain". Such research may help to explain variation in the relationship between vegetation diversity and phosphorus concentration observed for our different management regimes (i.e., MR4 compared with MR1, 2, and 3).

The results of this experiment demonstrate that soil fertility is a key factor influencing plant species diversity in managed grasslands. Consequently, land managers can greatly influence species diversity via their decisions on fertiliser application. Increasing availability of nutrients such as N, K, Mg, S, and Ca through fertilisation will ultimately decrease plant species diversity. A consequence of the negative relationship between soil fertility and diversity is that the grassland species of the least diverse areas are the fastest growing (White et al. 2004) and the most nutrient rich. Therefore, in grasslands managed for animal production, there appear to be few reasons to promote high diversity at a specific locality. Rather the benefits of species diversity occur at larger scales where differences in species characteristics are matched to specific environmental conditions that vary over the entire managed area (White et al. 2004).

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