The plant community as a niche bioassay: Environmental correlates of local variation in Gypsophila fastigiata

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THE PLANT COMMUNITY AS A NICHE BIOASSAY: ENVIRONMENTAL CORRELATES OF LOCAL VARIATION IN *GYPSOPHILA FASTIGIATA*

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(1) Quantitative plant community composition was used as a bioassay of niche in a study of fine-scale niche differentiation in the perennial herb *Gypsophila fastigiata* on the Baltic island of Öland.

(2) Canonical correspondence analysis was used to investigate the relationship between genetic (allozyme) and phenotypic (seed morphological) variation and niche variation.

(3) There were significant correlations between electrophoretic variation at the *PGI-2* locus and fine-scale gradients of compositional change in the limestone grassland plant communities occupied by *G. fastigiata*. In contrast, variation at the *AAT-3* and *IDH* loci and in seed phenotype showed no significant correlations with plant community composition.

(4) The bioassay approach to niche description integrates the interacting abiotic and biotic components of niche and provides a practical means of quantifying the realized niche of individuals in natural plant populations. This approach to niche description should have wide potential applications in studies which attempt to explain the extent to which genetic variation in natural populations can be related to niche variation.

INTRODUCTION

There is an increasing awareness of the need to conserve genetic resources in rare and decreasing species (e.g. Schonewald-Cox *et al.* 1983; Lande 1988). If conservation strategy is to function in practice, it is important to understand how genetic variation is maintained in natural—as well as in experimental and theoretical—populations. Historical and demographic processes that influence population size and isolation, and thus the likelihood of gene flow on different spatial and temporal scales, must play a dominant role in determining the amounts and partitioning of genetic variability within decreasing plant species (Lande & Barrowclough 1987). Habitat variation may also play a role in the temporal and spatial dynamics of genetic variation in natural populations. Theory predicts that genetic diversity may be maintained within populations or species by microhabitat selection (e.g. Powell & Taylor 1979). The niche-variation model of Van Valen (1965) is an explicit formulation of the classic tenet that species with broad niches should vary more than species with narrow niches (Stebbins 1942; Mayr 1945) and that the ecological amplitude or 'potential' of a species is related to the degree of variability within the species. However, tests of the niche-variation hypothesis in natural populations are celebrated for having produced conflicting results which variously support or reject the model (e.g. Rothstein 1973; Patterson 1983 and references therein). Differences in the definition of the term 'niche' (Hutchinson 1957; Green 1971; Whittaker, Levin & Root 1973) must, in part, be responsible for these conflicting results. The concept of niche is multidimensional (Hutchinson 1957; Colwell & Futuyma 1971; Whittaker *et al.* 1973) and

embraces interacting biotic and abiotic components and their interactions: "the 'structure' of the [niche] hyperspace is inseparable from the community of which this structure is an abstraction" (Whittaker *et al.* 1973). The lack of overall niche descriptors has hindered the development of niche differentiation studies in natural populations. In particular, studies of perennial plant species in closed vegetation require niche descriptors which can handle interacting biotic (cf. Turkington & Harper 1979) as well as abiotic components of niche.

Most work on niche variation has been carried out on animals (see Austin 1985), yet the sedentary nature of plants should simplify the task of niche circumscription and description. Experimental work on niche variation in plants includes the demonstration of fitness differences between enzyme genotypes along a moisture gradient (Zangerl & Bazzaz 1984). Although experiments with simple abiotic habitat gradients may provide evidence for niche differentiation, there is also a need to consider variation in the context of realized niche space within natural plant communities and habitats (e.g. Turkington & Aarssen 1984; Aarssen & Turkington 1985; Mazzoni & Gouyon 1985; Nevo *et al.* 1986; Nevo, Beiles & Krugman 1988a, b).

The present study explores the use of quantitative plant community composition as a bioassay of niche that provides a cumulative record of the local environment experienced by plant individuals during their life-span. The use of plant community composition as a niche descriptor builds on the use of gradient analysis in community ecology, whereby ordination techniques are used to reduce the dimensionality of patterns of species variation among series of vegetation samples (Gauch 1982). The response curves of the individual species along the ordination axes reflect the species' reactions to composite, underlying abiotic and biotic habitat gradients. The 'cross-section' through the different species' abundance curves at a given point on an ordination axis provides a sensitive characterization of local microhabitat. The niches of individual plants can thus be described by their scores on the axes of an ordination based on quantitative samples from the plant communities in their immediate surroundings.

This paper presents results from a study of *Gypsophila fastigiata* L. (Caryophyllaceae), a perennial, insect-pollinated herb growing in species-rich steppe grassland (see Bengtsson *et al.* 1988) on the Baltic island of Öland (Sweden). The study used quantitative plant community composition as a niche descriptor. The technique of canonical correspondence analysis (Ter Braak 1986, 1987a) was used to reduce the dimensionality of variation in plant community composition and to investigate if there were correlations between fine-scale niche variation and either phenotypic (seed morphological) or genetic (allozyme) variation in *G. fastigiata*.

G. fastigiata has a disjunct distribution in northern Europe and the USSR and there is considerable variation in population size, isolation and habitat both within and between regional metapopulations (Prentice 1986; Prentice & White 1988; Bengtsson *et al.* 1988). On Öland, there is both between-site variation in plant community composition and pronounced fine-scale spatial variation within sites (Bengtsson *et al.* 1988). Palaeoecological evidence indicates that *Gypsophila fastigiata* was more widespread in its overall geographic distribution during the Late Weichselian and early Flandrian (Berglund 1966) and also that the extent of the steppe grassland in which *G. fastigiata* grows on Öland has fluctuated considerably since deglaciation (Königsson 1968). These changes in habitat availability are expected to have influenced the population structure of *G. fastigiata*. Yet gene flow among populations on a historical time-scale appears to have been sufficient to replenish local variation after episodes of population contraction: levels of within-site

allelic diversity are not correlated with estimates of present-day population size or isolation (Prentice & White 1988).

METHODS

Field sampling and data handling

Seven *Gypsophila fastigiata* sites were sampled along a 60-km transect on the Baltic island of Öland (*c.* 56°–57°N, *c.* 16°–17°E). Within each site, individuals of *G. fastigiata* were selected for sampling using a stratified routine (cf. Noon 1981) based on a grid with a frame size of 7 m × 7 m. The 7-m sampling mesh was chosen so that it was considerably coarser than the scale of the local vegetation mosaic. Seeds were sampled from the most central individual within each grid frame. The number of individuals sampled at each site was determined by the spatial extent of the 'populations'. The maximum extent of the sampling grid was limited to 49 m × 49 m in the two most spatially extensive populations; the other five populations occupied smaller areas and are thus represented by a smaller number of sampled individuals. Sampling on a standard scale ensured that the range of within-site variation in plant community composition and the levels of within-site genetic or phenotypic diversity were not confounded by spatial differences in sampling intensity. Seed samples were collected from a total of 160 individuals. Site names, abbreviations and the number of individuals sampled at each site are as follows: Odensflisor (ON, 7 and OS, 10), Tornrör (TN, 23 and TS, 23), Gynge Alvar (GY, 45), Grönhögen (VE, 49) and Stora Muren (MU, 3).

The niche of each sampled individual was characterized by data on the cover/abundance of the associated vascular plant species (using a modified Braun–Blanquet scale (Mueller-Dombois & Ellenberg 1974)) in a 1-m × 1-m quadrat centred on the target *G. fastigiata* individual. Data were also collected on the total vegetation cover (percentage ground-area covered by vegetation) and on the respective percentage covers of vascular plants, bryophytes and lichens in each quadrat. Finally, each plot was characterized by a series of measures of species diversity (cf. Peet 1974). A total of 117 vascular plant species was present in the quadrats. All the site data were collected during a three-week period in June–July 1984.

Seed morphological data

Data on variation in the seed phenotypes of the wild-sampled individuals were obtained with the help of automated image acquisition and shape description routines. Seed shape was characterized by a suite of eight characters, including both conventional metric and differential chain-code descriptors (White, Prentice & Verwijst 1988; White & Prentice 1988). The seed morphological data used in the present analyses consisted of the scores of individuals on the five significant axes in a canonical variates analysis (CVA) in which the 160 individual plants were the pre-defined groups (each individual being represented by two to five seeds, with a total of 513 seeds being included in the analyses).

Enzyme-electrophoretic data

Progeny derived from seed from the wild-sampled individuals were grown in cultivation in a randomized block under non-competitive conditions. One randomly selected member of the progeny from each wild-sampled individual was screened for enzyme variation. Enzyme electrophoresis was carried out on fresh leaf material using standard starch-gel techniques (Soltis *et al.* 1983). The use of cultivated material in the

present survey was dictated by the fact that electrophoresis of frozen leaf material from *G. fastigiata* gave poor and unreliable results, suggesting modification of enzymes during sample storage (H. C. Prentice, unpublished data). A total of 143 plants was screened for variation at three polymorphic loci [aminoaspartate transferase (*AAT-3*, three alleles), isocitrate dehydrogenase (*IDH*, two alleles) and phosphoglucoisomerase (*PGI-2*, four alleles)]. Locus designation for the *AAT* enzyme system differs from that used by Prentice & White (1988): *AAT-3* in the present survey is equivalent to Prentice & White's *AAT-2*. Alleles were numbered according to decreasing anodal mobility with the fastest allele designated as 1. Band patterns at these three loci were invariant within individuals throughout the year and variation is interpretable in terms of allozymes at loci coding for dimeric enzymes (Gottlieb 1981): a limited number of crosses carried out for other purposes (H. C. Prentice, unpublished data) confirm this interpretation in the cases of *AAT-3* and *PGI-2*. Allelic diversities (H) were estimated according to Nei (1973, 1975).

Canonical correspondence analysis

Canonical correspondence analysis (CCA) (Ter Braak 1986, 1988; Ter Braak & Prentice 1988) is a method of multivariate direct gradient analysis in which gradients of community composition are directly related to variation in a set of 'external' variables. Ordination axes (representing gradients of change in community composition) are extracted as in unembellished correspondence analysis, but with the additional constraint that the axes are linear combinations of pre-defined external variables which have been scored for each sample. The species are assumed to have unimodal response surfaces with respect to linear combinations of the external variables (Ter Braak 1986; Ter Braak & Prentice 1988). The external variables of interest are usually habitat factors (e.g. Ter Braak 1986; Cramer & Hytteborn 1987; Fängström & Willén 1987), but CCA can also be used to analyse the relationship between variation in other types of external variables (such as genetic or phenotypic characters) and variation in community composition. In the resulting ordination diagram the centroids (weighted averages) of categorical external variables can be represented as points and continuous variables as arrows. The number of constrained (canonical) axes cannot exceed the number of external variables. In a CCA with few external variables, residual variation in plant community composition (i.e. variation not accounted for by the constrained axes) is taken up by subsequent, unconstrained axes. A variant of CCA known as 'partial CCA' can be used to remove the effects of 'covariables'—variables 'the effects of which are not the prime object of study' (Ter Braak & Prentice 1988).

A Monte Carlo permutation test (Hope 1968; Ter Braak 1987b) can be used to test the extent to which variation in community composition is significantly related to variation in external data.

CCA and environmental correlates of variation in G. fastigiata

Quantitative plant community composition was directly related to phenotypic or genetic variation in *G. fastigiata* in four CCAs. External variables and numbers of canonical (constrained) axes in the separate analyses are summarized in Table 1. Between-site effects were removed during the analyses by using the 'partial' variant of CCA and treating site-membership as a set of dummy covariables (Ter Braak 1987b).

(i) Partial CCA constrained by seed phenotypes. Individual scores on five axes from a canonical variates analysis were used as the external variables to constrain the vegetation axes extracted by CCA.

(ii) Partial CCA constrained by allele presence/absence. The presence or absence of alleles in progeny individuals was used as external data in three separate CCAs (one for each of the enzyme loci *AAT-3*, *IDH* and *PGI-2*).

Estimates of species diversity and vegetation cover were related passively to the scores on the canonical axes from the CCAs using Pearson correlation coefficients (with two-tailed significance tests).

The Monte Carlo permutation test was used to assess the levels of significance of relationships between constraining external variables (allozymes or seed shape) and the gradients of change in plant community composition extracted by CCA. The external variables were randomly re-assigned to the vegetation samples within sites (restricted permutation test). The data were then re-analysed in this way 999 times to test the null hypothesis that plant community composition was unrelated to the external variables. Significance probabilities of the null hypothesis are given both for the first axis eigenvalues and for the overall 'trace' (sum) of the eigenvalues for the constrained (canonical) axes (see Ter Braak 1987b).

For comparison, we also carried out a conventional DCA [detrended correspondence analysis (Hill & Gauch 1980; Peet *et al.* 1988)] of the trends in plant community composition, using detrending by polynomials as recommended by Ter Braak & Prentice (1988). The 'partial' variant of DCA (Ter Braak & Prentice 1988) was used in this analysis to remove between-site variation in community composition in the same way as in the constrained analyses. Four DCA axes were extracted and subjected to standard correlation analysis with the CCA axis scores.

The CCA and DCA analyses were carried out using the program CANOCO (Ter Braak 1987b). Diversity statistics were calculated using the program DIVCLUS (R. Leemans, unpublished) and the correlation analyses were carried out using SPSS (1986).

RESULTS

It was not possible to extract CCA axes that showed significant correlations between the seed phenotypes of *G. fastigiata* individuals and the plant communities from their immediate surroundings. Nor was there any significant relation between the variation at the *AAT* and *IDH* enzyme loci in cultivated individuals and variation in their maternal habitats (Table 1).

In contrast, CCA revealed significant correlations between variation at the *PGI-2* locus in cultivated individuals and fine-scale gradients of plant community composition in their maternal habitats. The results of the CCA analysis based on *PGI* allelic variation are shown in Table 2 and in Fig. 1. The ordination of the vegetation samples was constrained so that the first three axes were linear combinations of presence/absence values for the three common *PGI* alleles (see Table 1). The ordination diagram in Fig. 1 shows the locations of the vegetation samples that characterize the niches of *G. fastigiata* individuals in ordination space. Centroids for the presence of alleles in the individuals corresponding to the vegetation samples are also shown. Allele 1 is separated from alleles 2 and 3 on the first axis. Alleles 2 and 3 are separated from each other on the third axis and, to a lesser extent, on the second axis. Despite the fact that the CCA presented in Fig. 1 was constrained by the presence/absence of alleles in individuals, there is a tendency for homozygous individuals to be associated with the vegetation samples that occupy the extremes of variation in three-dimensional space, while heterozygotes are associated with more intermediate vegetation samples.

TABLE 1. External variables and numbers of constrained (canonical) axes in four (partial) canonical correspondence analyses based on seed morphology and the presence/absence of alleles at three enzyme loci in *Gypsophila fastigiata*. A total of four axes was extracted in each of the analyses: 160 *G. fastigiata* individuals and their associated vegetation samples were included in the seed analyses and 143 in each of the enzyme analyses.

Type of analysis	External variables	Number of canonical axes*
Seed phenotype	Scores on five CVA axes	4
Allele presence/ absence		
AAT-3†	alleles 1 & 2	2
IDH	alleles 1 & 2	2
PGI-2†	alleles 1, 2 & 3	3

* Variation in plant community composition not accounted for by the constrained axes is taken up by subsequent, unconstrained, axes.

† The allozyme data included single (heterozygote) occurrences of rare alleles at the *AAT-3* and *PGI-2* loci: these rare alleles were not included as external variables and hence did not contribute to the constraint of the vegetation axes.

The Monte Carlo permutation test on the trace statistic ($P < 0{\cdot}01$) provides strong evidence that the null hypothesis of no correlation between variation in plant community composition and the presence/absence of *PGI-2* alleles can be rejected. All three canonical axes (Table 2) show correlations between *PGI* alleles and vegetation composition. However, despite the fact that there is a significant correlation between variation at *PGI-2* and variation in plant community composition, the eigenvalues for the three constrained

TABLE 2. Eigenvalues for constrained (external variables = allele presence/absence at the *PGI-2* locus: see Table 1) and unconstrained analyses of vegetation data. The trace is the sum of all canonical eigenvalues. Both analyses used the 'partial' variant of CCA and excluded site effects by treating site membership as a categorical covariable.

Analysis	Eigenvalues				
	trace	1	2	3	4
CCA constrained by presence/ absence of alleles 1, 2, 3 at *PGI-2* (axis 4 unconstrained)	0·090**	0·036	0·030	0·024	0·172
Unconstrained vegetation ordination (DCA)	—	0·195	0·119	0·110	0·096

** $P < 0{\cdot}01$ using the Monte Carlo permutation test.

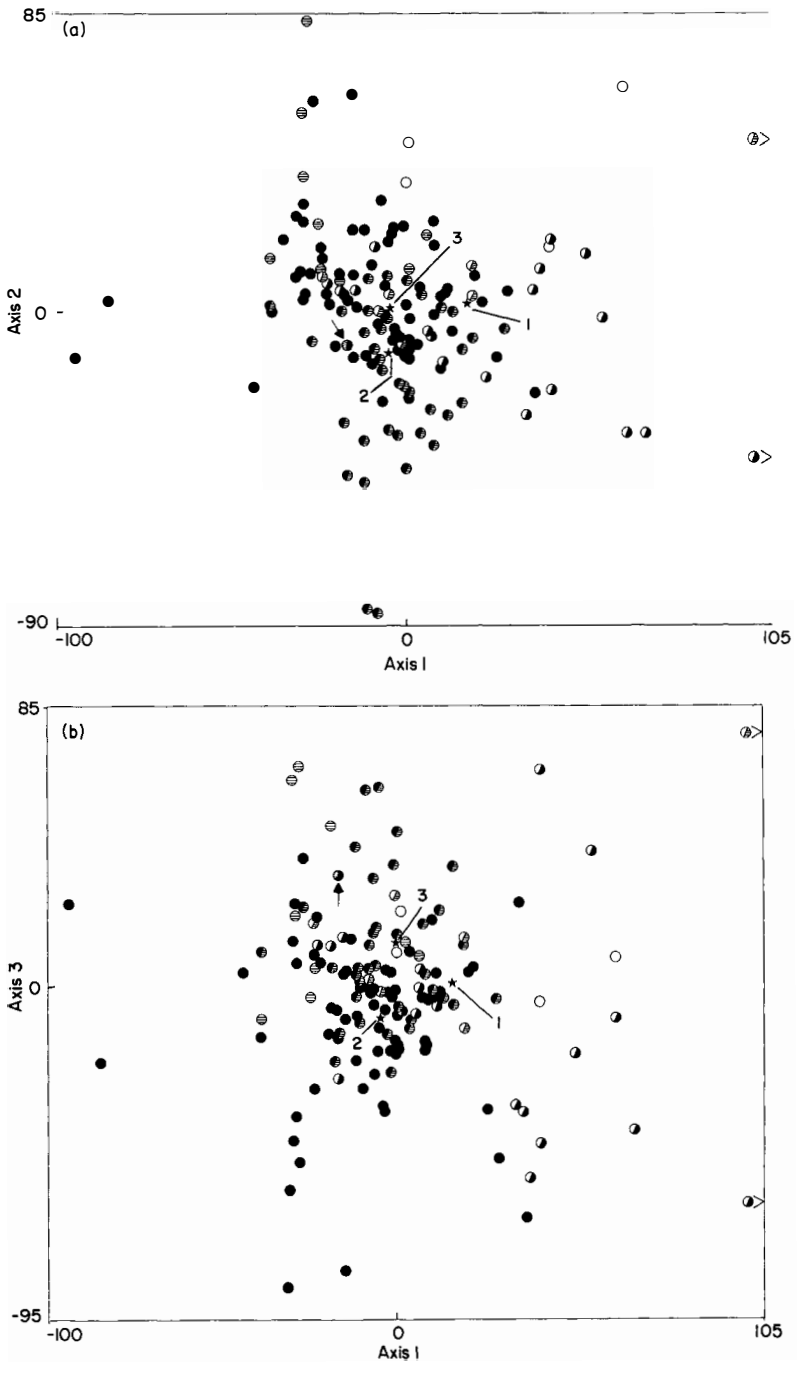

FIG. 1. Plots of (a) axis 1 against axis 2 and (b) axis 1 against axis 3 (scale = × 100) in a canonical correspondence analysis of vegetation data constrained by variation at the *PGI-2* locus (presence/absence of alleles 1, 2 and 3) for 143 individuals of *Gypsophila fastigiata*. Centroids for the alleles are indicated by stars. Homozygous individuals are represented by undivided symbols, heterozygotes by diagonally divided symbols. Allele 1 = white, allele 2 = black, allele 3 = hatched. A fourth allele (allele 1b, represented by dotted shading and indicated by an arrow) is present only once in a heterozygote: this allele did not contribute to the constraint of the axes (see Table 1). Outliers are indicated by the symbol >.

TABLE 3. Correlations between CCA (constrained by *PGI-2* allele presence/absence) and DCA (unconstrained) axis scores ($n = 161$).

	DCA axis 1	DCA axis 2	DCA axis 3	DCA axis 4
CCA axis 1	0·49***	0·23**	0·29***	−0·17*
CCA axis 2	−0·22**	−0·10	−0·21**	−0·25***
CCA axis 3	0·16*	−0·33***	−0·33***	0·05
CCA axis 4	0·89***	0·46***	0·03	−0·02

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

axes indicate low *PGI*-related species turnover rates along the extracted gradients. The unconstrained DCA (Table 2) gave clearly higher eigenvalues than the constrained CCA, indicating that a major part of the total variation in plant community composition at these sites is not related to allelic variation at *PGI-2*. Correlation analysis between DCA and CCA axis scores (Table 3) showed that most of the total variation in community composition as expressed by DCA is accounted for by the fourth (unconstrained) CCA axis. Variation along the constrained CCA axes was only partly reflected in the DCA axes, confirming that the PGI-related gradients in vegetation composition are not congruent with the major trends in these grassland communities.

The *PGI*-related CCA axes are, however, significantly correlated with estimates of species diversity and vegetation cover. The first CCA axis is correlated with vascular plant cover ($P < 0·001$) and the third axis is correlated with the Shannon and 'reciprocal Simpson' alpha diversity measures ($P < 0·001$) (cf. Peet 1974). Presence of allele 1 is thus associated with relatively closed vegetation, and presence of allele 3 with relatively diverse plant communities.

Partitioning of allelic diversity among the seven sampled sites showed that 93% of the variation at *PGI-2* was contained within the sites ($G_{ST} = 0·071$, Table 4). Despite the low value of G_{ST}, allele frequencies at *PGI-2* do vary among the sites (Prentice 1986), as do overall habitat and vegetation composition. However, because site-membership effects were eliminated from the analyses (by using partial CCA), the correlation between variation at *PGI-2* and in plant community composition is not due to among-site differences in allele frequencies and vegetation. The removal of the among-site component of variation allowed the different sites to act as replicates in the investigation of finer-scale niche variation.

The niche of each individual of the target species (in this case *Gypsophila fastigiata*) is not likely to be due to spatial effects within sites because the mesh of the sampling grid was considerably coarser than the scale of the habitat mosaic (cf. Bengtsson *et al.* 1988). In addition, there were no significant differences between the numbers of heterozygous individuals observed at the different sites and the numbers of heterozygotes expected if the populations were in Hardy–Weinberg equilibrium (cf. Table 4). The lack of significant deviations from Hardy–Weinberg expectations within sites indicates an absence of pronounced allelic clumping on a scale larger than 7 m.

Screening electrophoretic variation on cultivated progeny excludes the possibility that correlations between enzyme variation and habitat variation are attributable to environmentally or age-induced modification of gene expression (e.g. Pedersen & Simonsen 1987). In an insect-pollinated species such as *G. fastigiata*, however, screening progeny for variation will reduce the chance of detecting significant correlations between environmental and genetic variation, because outcrossing will dilute the maternal

TABLE 4. Estimates of allelic diversity and observed heterozygosity at the *PGI-2* locus in samples from seven *Gypsophila fastigiata* localities on Öland.

Site	n	H_S	S.E.	H_O*
ON	8	0·33	0·144	0·38
OS	7	0·14	0·143	0·14
TN	16	0·55	0·031	0·50
TS	21	0·53	0·071	0·62
GY	43	0·51	0·043	0·40
VE	45	0·46	0·048	0·44
MU	3	0·00	0·000	0·00
H_T	0·497 (S.E. = 0·028)			
$\bar{H}_S$	0·462			
G_{ST}	0·071			

n = sample size, H_S = within-site allelic diversity (corrected for small sample size as in Prentice & White 1988), S.E. = jackknifed standard error for H_S (Prentice & White 1988), H_O = observed within-site heterozygosity (proportion of heterozygous individuals), H_T = total allelic diversity, $\bar{H}_S$ = mean within-site diversity (weighted by sample size), G_{ST} = the among-site component of total diversity ($H_T - \bar{H}_S/H_T$). Site abbreviations are given in the text.

* There were no significant deviations from Hardy–Weinberg expectations (χ^2 with one degree of freedom).

contribution to the progeny genotypes. Despite the diluting effect of outcrossing, the material investigated still showed a significant correlation between *PGI* variation in progeny and plant community composition in the maternal habitat.

DISCUSSION

CCA and niche characterization

In this study CCA was used to characterize variation in the realized niche of a perennial plant in a species-rich grassland habitat. The aim was not to correlate population variation directly with simple abiotic gradients. Instead plant community composition was used as a bioassay of niche that provides a cumulative record of the biotic and abiotic environment experienced by plant individuals during their life-time.

The niche of each individual of the target species (in this case *Gypsophila fastigiata*) is characterized by its scores on the CCA axes, each axis score representing a unique 'cross-section' of the abundance curves of the species that comprise the vegetation surrounding the target individuals. The abundance curves of the associated species along the CCA axes reflect not only those species' responses to soil and other abiotic parameters, but also to temporally cumulative competitive interactions among the species. Any infraspecific niche differentiation within the associated species is subsumed under their overall response curves. Although most previous applications of CCA (e.g. Cramer & Hytteborn 1987) have related habitat variation to species compositional data, the present study shows the potential of CCA as a tool in the exploration of the correlates of genetic and phenotypic variation in natural populations and habitats.

Variation at the PGI-2 *enzyme locus*

Allelic variation at *PGI-2* is significantly correlated with gradients of variation in plant community composition and with trends in species-diversity and vegetation-cover. The PGI-correlated gradients of species turnover are short, however, and account for a relatively low proportion of the total variation in plant community composition in the habitats occupied by *G. fastigiata*. Nor are the *PGI*-correlated gradients of species turnover congruent with the major trends of variation in plant community composition that are detected by a straightforward descriptive ordination. That there is a significant relationship between variation at *PGI-2* and niche, despite the imprecision of screening genetic variation in cultivated progeny rather than directly on maternal individuals, suggests that there should be a stronger correlation between maternal variation and plant community variation. The practical problems of field-sampling *G. fastigiata* for electrophoresis should be overcome and studies of maternal variation carried out.

Studies on the correlates of genetic variation may provide valuable indirect support for microhabitat selection (Ennos 1983; Manly 1983). Demonstrating a correlation does not, however, indicate direct causation (Endler 1986). In the case of *G. fastigiata*, there is no evidence that variation at *PGI-2* is acting as anything other than a marker for variation at other linked loci or gene complexes which are themselves responding to local environmental variation. In a laboratory study of niche variation in *Amaranthus retroflexus*, Zangerl & Bazzaz (1984) demonstrated fitness differences between two homozygous *PGI* genotypes along an artificial moisture gradient. As well as discussing the possibility that the products of the *PGI* alleles themselves could be of selective importance under different degrees of oxygen availability, Zangerl & Bazzaz also discuss the role of *PGI* as a marker for variation at other loci. In the *Amaranthus* study, variation at *PGI* was correlated not only with physiological differences associated with germination response at different levels of oxygen availability but also with quantitative and reproductive characters 'the ecological value of which are more readily appreciated' (Zangerl & Bazzaz 1984).

Critical tests of the niche-variation hypothesis require both evidence of habitat-related fitness differences and demonstration of niche differentiation in natural communities. Experimental evidence for fitness differences between PGI genotypes is needed before any conclusions can be drawn about the role that microniche differentiation may play in the maintenance of local variation in *G. fastigiata*.

Variation in seed shape

Phenotypic variation in field populations can be divided into an environmental component as well as genetic and interactive components of variation (Falconer 1981). Studies of seed variation in natural populations have demonstrated environmental modification of seed size by maternal habitat (e.g. Winn 1985). The present study was based on variation in seed shape rather than seed size and, despite the expectation that phenotypic variation in wild-sampled seeds may show a relationship to maternal habitat, there was no significant correlation between seed variation in *G. fastigiata* and plant community composition. Seed shape in *G. fastigiata* appears to be less responsive to environmental modification during development than is seed size. Although seed size may vary within individuals during a single season (H. C. Prentice, unpublished observation), less than 3% of the total variation in seed shape in Öland *G. fastigiata* lies within individuals (Prentice & White 1988).

Seed weight and size may be related to maternal habitat as a result of environmental modification, but overall variation in seed morphology is more likely to be related to fine-scale gap characteristics at the time of germination than to variation in the plant community occupied by adult individuals (cf. Grubb 1986). The absence of any relationship between seed variation and variation in plant community composition suggests that a niche descriptor which integrates environmental variation over the life-span of the target individuals will not necessarily be appropriate for use in studies of variation in characters that belong to a particular life-phase component of niche. Variation in seed morphology which confers differential survivorship in the 'regeneration niche' (*sensu* Grubb 1977) may not be congruent with variation in the realized niche of adult plants.

The plant community as a niche bioassay

In the present study of *G. fastigiata* we have explored a methodology for the investigation of variation in realized niche in natural plant populations. The bioassay approach to niche description provides a practical means of integrating life-time variation in the biotic and abiotic environment of plant individuals. The ordination technique CCA allowed the extraction (from the complex variation in plant community composition) of niche dimensions which could be tested for relationships with genetic or phenotypic variation in *G. fastigiata*. This approach to niche description opens up new possibilities for testing the niche-variation hypothesis in perennial plants in species-rich vegetation.

The realized niche of an adult plant individual is a compound reflection of that individual's response to the surrounding biotic and abiotic environment during successive life-phase stages. Niche variation at different life-phase stages is not necessarily expected to be congruent, and different characters and character complexes may respond to selection in different life-phase niches. A niche descriptor that provides a cumulative record of microenvironmental variation across the life-span of target individuals is appropriate in studies of realized niche, but may not be appropriate in studies of niche variation at particular life-phase stages.

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