

REPORT

Local adaptation enhances performance of common plant species

J. Joshi,^{1,*} B. Schmid,¹
M. C. Caldeira,²
P. G. Dimitrakopoulos,³ J. Good,⁴
R. Harris,⁴ A. Hector,⁵
K. Huss-Danell,⁶ A. Jumpponen,^{6,†}
A. Minns,⁵ C. P. H. Mulder,^{6,‡}
J. S. Pereira,² A. Prinz,⁷
M. Scherer-Lorenzen,^{7,§}
A.-S. D. Siamantziouras,³
A. C. Terry,^{8,¶} A. Y. Troumbis³
and J. H. Lawton⁵

*Correspondence: Institute of
Evolutionary and Ecological
Sciences, University of Leiden,
PO Box 9516, NL-2300 RA
Leiden, The Netherlands.
E-mail: joshi@uwinst.unizh.ch

Abstract

Geographic variation can lead to the evolution of different local varieties, even in widespread forage plants. We investigated the performance of common forage plants in relation to their genetic diversity and local adaptation at a continental scale using reciprocal transplants at eight field sites across Europe over a 2-year period. The overall performance of the three test species, *Trifolium pratense*, *Dactylis glomerata*, *Plantago lanceolata*, was generally highest for plants replanted at their home site and declined with increasing transplanting distance. The three species differed in the fitness components responsible for the increased overall performance and selection advantage at home sites. In addition to the effects of local adaptation, the majority of measured traits in all three species also showed ecotypic variation. However, no single ecotype of any species was able to outperform the locally adapted strains and do best at all sites, highlighting the importance of maintaining these plant genetic resources.

Keywords

Dactylis glomerata, fitness, genetic diversity, phenotypic variation, *Plantago lanceolata*, population differentiation, spatial variation, stability, transplant, *Trifolium pratense*.

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INTRODUCTION

Common plant species with wide distributions, such as crops, ideal weeds (Baker 1974) and invasive plants (Drake *et al.* 1989) may perform well in a wide range of environmental conditions. However, the costs of carrying adaptations to all possible environments (DeWitt *et al.* 1998) could make it impossible for individual genotypes to perform well across the full range of conditions. Instead, common plant species are often characterized by both phenotypic plasticity and large genetic variation (Bradshaw 1984; Bazzaz 1986),

and the successful occupation of many sites may be explained by the occurrence of many genotypes specialized to particular environmental conditions rather than by the existence of a single general-purpose genotype (Van Tienderen 1990).

Because many globally widespread, invasive species are common constituents of European grassland communities and agriculturally important forage plants, we wished to determine the extent to which the success of these species is related to local specialization of populations from different geographical regions, i.e. based on genetic differentiation and adaptation within species to particular environmental

¹Institut für Umweltwissenschaften, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland.

²Departamento de Engenharia Florestal, Universidade Técnica de Lisboa, Tapada da Ajuda, Lisboa, PT-1349-017, Portugal.

³Biodiversity Conservation Laboratory, Department of Environmental Studies, University of the Aegean, Karadoni 17, Mytilene, Lesbos, GR-811 00, Greece.

⁴Department of Zoology and Animal Ecology, University College Cork, Lee Maltins, Prospect Row, Cork, Ireland.

⁵Natural Environment Research Council (NERC) Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire, SL5 7PY, U.K.

⁶Crop Science Section, Department of Agricultural Research for Northern Sweden, Box 4097, Swedish University of Agricultural Sciences, Umeå, SE-90403, Sweden.

⁷Max-Planck Institute for Biogeochemistry, PO Box 10 01 64, D-07701 Jena, Germany.

⁸Department of Animal and Plant Sciences, University of Sheffield, South Yorkshire, S10 2TN, U.K.

[†]Present address: Division of Biology, 125 Ackert Hall, Kansas State University, Manhattan, KS 66506, U.S.A.

[‡]Present address: Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, U.S.A.

[§]Present address: Department of Environmental Science, University of Bradford, West Yorkshire, BD7 1DP, U.K.

[¶]Present address: Institute for Biodiversity, Zeppelin Werftgelände 31, D-88045 Friedrichshafen, Germany.

conditions. On small scales, environmental variation can occur through different edaphic or biotic conditions and, on large scales, through different climatic conditions (Clausen *et al.* 1940; Schmid 1985; Weber & Schmid 1998; Bell *et al.* 2000). To assess the contribution of environmental and genetic variation and their interaction to phenotypic variation and performance over small scales, e.g. metres to kilometres, reciprocal replant–transplant experiments have often been used (Langlet 1971; Bradshaw 1984; Schmid 1985; Linhart & Grant 1996; Briggs & Walters 1997). If environments with contrasting selection pressures, such as different management regimes or soil conditions, are compared in reciprocal replant–transplant experiments, significant home vs. away advantages may reflect local specialization by genetic adaptation (Bradshaw 1984; Linhart & Grant 1996). Indeed, local adaptation in different life-history stages over short distances has been observed in many of these experiments (e.g. Smith & Bradshaw 1979; Antonovics & Primack 1982; McGraw & Antonovics 1983; Bennington & McGraw 1995; Kindell *et al.* 1996; Prock & Körner 1996; Nagy & Rice 1997; Gauthier *et al.* 1998). We extended this replant–transplant experimental approach to a European scale by repeating the same experiment at eight field sites simultaneously, hypothesizing that climatic distances or other correlates of geographical distances between sites (Table 1) would exert selection pressures large enough to lead to local specialization by adaptation to conditions at home sites. Further, because the distances between sites represented a considerable range, we were able to test not only whether home strains had an advantage over away strains, but also whether selection against away strains increased with distance. To enhance the generality of the study, the transplant experiments were replicated for three common species belonging to three plant functional groups (Körner 1993), and the overall performance of each species was estimated by studying the whole life-cycle combined with a matrix-model approach.

MATERIALS AND METHODS

Reciprocal transplant experiment

We selected three abundant, mainly outbreeding perennial species, each representative of a major plant functional group in grassland ecosystems (Hector *et al.* 1999): the N-fixing legume, *Trifolium pratense* L. (red clover), the grass, *Dactylis glomerata* L. (orchard grass, cocksfoot), and the non-leguminous forb, *Plantago lanceolata* L. (ribwort plantain). All three species are native to Europe and occur as invasive species and important forage plants also in other parts of the world (Beddows 1959; Cavers *et al.* 1980; Taylor & Quesenberry 1996). In summer and autumn 1996, seeds were collected randomly as mixed seed samples from at least

20 spaced (> 2 m) individuals per species at each of eight sites (Table 1, Hector *et al.* 1999) on old-grown, extensively managed grasslands or, where this was not possible, at hedgerows and roadside verges. Seeds of *T. pratense* at the Greek site and *P. lanceolata* at the Swedish site could not be collected because these species did not occur there.

All seed samples were sent to the first author, who sorted them and sent random samples of all strains to the coauthors at the other field sites. At the beginning of the 1997 growing season, seeds were germinated and the seedlings grown for 3 weeks in a glasshouse at each of the eight sites. After their initial size had been recorded, seedlings that had at least one leaf (excluding cotyledons) were replanted to their original sites (“replants”) or reciprocally transplanted to the other European sites (“transplants”).

At each field site (see Hector *et al.* 1999 for climatic and geographical details of each site), five plots (180 × 75 cm) were established (due to poor germination of seeds, only three plots were established in Ireland), each of which contained 44 plants (two individuals per strain and species; eight *D. glomerata* strains, seven *T. pratense* strains, seven *P. lanceolata* strains) planted randomly in rows at 15 cm intervals.

Plots were weeded, but they were not protected from herbivory or pathogen attack. Growth, reproduction and survival of each individual at each site were monitored for two consecutive years (1997–98), with the exception of the Irish site (plants were monitored for 1 year only) and the Greek site (plants were monitored for one field season, harvested, resown and replanted, and again monitored for 1 year in accordance with the growth pattern of most species in the annual grasslands at this site; the data of the two generations were pooled and included in analyses of environmental and genetic effects on individual life-history characters after correcting for the time effect). At all sites, seedlings that died during the first 2 weeks after transplanting were replaced after recording mortality. After each season, all plots were mown to 5 cm. The following measurements were recorded each year (early, mid and late season): survival; length of the longest leaf or ramet per individual; number of tillers, ramets or leaves; number of inflorescences; and length or diameter of the longest inflorescence.

The fecundity (m) was estimated as the average total number of inflorescences per plant collection of the same origin and species (defined hereafter as “strains”) per site and per season, and the survival probability (p) was estimated from survival data for each strain per site and season. The effective fecundities for the first and second seasons (F) were calculated as $F = p \times m$. As a fitness-related estimate during the period of the experiment, dominant eigenvalues obtained from Leslie matrices were calculated for each set of plants of the same origin and planting site for two field seasons (Charlesworth 1994). Dominant eigenvalues correspond to the finite rate of

Table 1 Climatic similarity and geographical distance between sites. In bold type, climatic similarity coefficients (%) derived from Euclidean distances between sites using mean January and July temperatures and mean annual precipitation (see Hector *et al.* 1999) as axes; in normal type, geographical distances between sites (km). Sites are ordered according to similarity as far as possible.

Strain	Site							
	Silwood (U.K.)	Sheffield (U.K.)	Germany	Switzerland	Ireland	Sweden	Greece	Portugal
Silwood (U.K.)	—	235	917	714	560	1798	2458	1542
Sheffield (U.K.)	98	—	1060	917	498	1679	2625	1703
Germany	98	94	—	370	1441	1655	1590	2024
Switzerland	81	90	80	—	1244	1929	1750	1655
Ireland	73	86	66	95	—	2113	2989	1435
Sweden	86	80	93	69	50	—	2762	3322
Greece	70	71	69	57	42	36	—	3048
Portugal	72	70	71	50	34	39	99	—

population increase (λ): if an individual never flowers, it does not contribute to population growth ($\lambda = 0$). Using the finite rate of population increase as a measure of plant performance or fitness, we calculated selection coefficients for each strain i relative to the best strain at a particular planting site as $s_i = 1 - (\lambda_i/\lambda_{\max})$ (McGraw & Antonovics 1983). A selection coefficient of zero indicates that a strain is the most successful one of that species at that site, while a coefficient of unity indicates complete selection against a strain. However, estimates of λ and s are conservative as a population that survived vegetatively only (and might have thus flowered in the third year) is considered a population that has $\lambda = 0$ and $s = 1$. The Greek and the Irish site were excluded from the analyses of λ and s .

Statistical analysis

Data from each field site were centrally collected, collated in a Microsoft Access-97 database and analysed with Genstat 5 (Payne *et al.* 1993). Individual life-history traits were analysed separately by repeated measures analyses (Table 2; data on average survivorship per species, strain and site for each year are reported in Joshi 2000). This was preferred over a multivariate approach combining all the traits but for each census separately. Correlations among the individual life-history traits varied over time, but were rarely larger than $r = 0.5$. The variation in overall fitness was analysed using the selection coefficient.

We used generalized linear models (McCullagh & Nelder 1989; Crawley 1993) to calculate summary analyses of variance and deviance (survivorship data) tables. Analyses of variance tables are obtained for continuous variables by specifying a linear link function and a normal distribution for the errors. For survivorship data, the appropriate link function is a complementary log–log link, the corresponding error distribution the binomial distribution and the summary table an analysis of deviance table (Candy 1986; Egli & Schmid 2001). First, we fitted

full models with all factors and interactions and then obtained the final model sequences by backward elimination of terms with $F < 2$ (Green & Tukey 1960; Crawley 1993).

The following terms were fitted in the regressions (for explanations, see next paragraph): site, plot, strain and the site \times strain interaction, which was subsequently decomposed into home vs. away and distance contrasts and the remaining variation. The direction of the contrasts distinguished adaptation from maladaptation (adaptation: home > away or near > far). The factors “site” and “strain” were regarded as fixed factors because we were interested in their interaction with each other (decomposed into the fixed home and distance effects), and in their interactions with species in the analysis for selection indices (Table 4, see later). Individual and time terms (split into linear, quadratic and residual terms), together with their interactions with the other terms, were included in the analysis of repeated measures. Significance tests were based on F tests (analysis of variance) or quasi- F tests (analysis of deviance; see also Meyer & Schmid 1999; Egli & Schmid 2001). Dependent variables were transformed prior to the analysis where necessary to meet the assumptions of homoscedasticity and normality.

Environmental (“site”) or genetic (“strain”) main effects in the statistical analyses represent the general superiority of plants growing at, or originating from, particular sites, respectively. Interaction effects indicate that different strains respond differently at different sites. When comparing the rankings of strains at each site, “home strains” having a high performance and all or most “away strains” having lower performance can be interpreted as local specialization or, more liberally, as local adaptation to conditions prevailing at the home site (Bradshaw 1984). In the site \times strain matrix (Table 3), ordered according to increasing distance (see Table 1), a home effect is shown on the main diagonal, whereas a distance effect is reflected by continuous change of values away from the main diagonal.

RESULTS

Environmental ("site") and genetic ("strain") main effects, as well as strain \times site effects for life-history characters, were large in all three plant species in separate repeated measures analyses (Table 2). Significant environmentally induced variation occurred in the number and size of modules (leaves, tillers, ramets, spikes) and in survival (Table 2). We found ecotypic, genetic differentiation among strains in the majority of the measured characters but, importantly, no strain of any species performed best at the majority or even at all sites (Table 3). In the case of *D. glomerata* and *T. pratense*, limits to adaptation seemed to be reached at the most northern (Sweden) and southern (Portugal) planting sites, where some strains did not survive to reproduction (Table 3).

Large amounts of strain \times environment interactions were explained by the home vs. away and distance contrasts that remained constant or even increased with time (Table 2). The fitness components responsible for the increased total fitness and increased selection advantage at home and nearby sites (see Table 2) differed among the three species. In *D. glomerata*, local adaptation was most clearly expressed in vegetative and reproductive characters, as well as in survival, and became more visible over time.

Plants of home strains were larger than away strains (14.13 tillers vs. 9.55 tillers; 32% longer leaves), produced 20% more inflorescences that were also larger (5.03 cm compared with 3.33 cm) and showed a significantly higher survival probability (+9.3%) in the second year of the experiment. In *T. pratense*, reproductive characters, such as inflorescence size and, to a lesser degree, number of inflorescences, were larger in home strains than in strains from more distant sites (twice as many inflorescences and, on average, 13% larger inflorescences in home plants), whereas, in *P. lanceolata*, in addition to reproductive characters, such as inflorescence number and size, vegetative traits, such as leaf length, were also enhanced in local strains (Table 2).

Significant home and distance effects, as well as significant main effects of strain and planting sites, were also observed in the combined analysis of the selection index for the three species together (Table 4). Averaged over the three species, selection pressure was strongest at the most southern and northern planting sites, with an average selection index of 0.50 (Portugal) and 0.42 (Sweden), respectively. Averaged over planting sites, selection was strongest against northern strains of the three species (plants originating from Sweden, Ireland and Sheffield, U.K.).

Table 2 Environmental and genetic effects on plant life-history characters. Table entries are *P* values from repeated analyses of deviance (survival) and variance (morphological traits). These included further factors not listed in the table ("time", "plot", "individual"). Arrows denote the direction of significant (bold; $P < 0.05$) and marginally significant ($P < 0.1$) home and distance effects (\uparrow , home > away or near > far; \downarrow , away > home or far > near).

			Site × Strain interaction				
	Site	Strain	Home	Distance	Residual of site × strain	Time × home	Time × distance
(a) <i>Dactylis glomerata</i>							
Survival (total)	<0.0001	<0.0001	0.99	0.0253↑	0.56	0.0006↑	0.55
Max. leaf length	<0.0001	<0.0001	0.0060↑	0.44	0.0016	0.84	0.67
Tiller number	<0.0001	<0.0001	0.0016↑	0.0158↑	0.0270	0.0201↑	0.42
Inflorescence no.	<0.0001	0.0248	0.0108↑	0.81	<0.0001	0.0092↑	0.41
Inflorescence length	<0.0001	<0.0001	0.37	0.93	<0.0001	0.21	0.55
(b) <i>Trifolium pratense</i>							
Survival (total)	<0.0001	0.13	0.54	0.69	0.73	0.34	0.88
Max. ramet length	<0.0001	<0.0001	0.23	0.67	<0.0001	0.16	0.0880
Ramet number	<0.0001	0.0079	0.61	0.13	<0.0001	0.43	0.11
Inflorescence no.	<0.0001	<0.0001	0.0664(↑)	0.70	<0.0001	0.69	0.97
Inflorescence diameter	0.0002	0.89	0.0283↑	0.0009↑	0.38	0.59	0.30
(c) <i>Plantago lanceolata</i>							
Survival (total)	<0.0001	0.0002	0.11	0.81	0.0004	0.14	0.0444
Max. leaf length	<0.0001	<0.0001	0.0343↑	0.64	<0.0001	0.12	0.0251
Leaf number	<0.0001	<0.0001	0.0559(↓)	0.32	<0.0001	0.0366↑	0.90
Inflorescence no.	<0.0001	0.0038	0.0430↑	0.0091↑	<0.0001	0.52	0.67
Inflorescence length	0.19	0.0034	0.0269↑	0.54	0.0134	0.41	0.29

Table 3 Selection coefficients (derived from the finite rate of population increase) for strains of *Dactylis glomerata* (a), *Trifolium pratense* (b) and *Plantago lanceolata* (c), transplanted/replanted into away and home sites on a European scale. A selection coefficient of zero indicates that a strain of a given species is the most successful at a particular site with a selection advantage over all other strains at that site.

(a) *Dactylis glomerata*

Strain	Site						Means \pm SE
	Silwood (U.K.)	Sheffield (U.K.)	Germany	Switzerland	Sweden	Portugal	
Silwood (U.K.)	0	0.225	0.198	0.221	1	0.528	0.36 \pm 0.32
Sheffield (U.K.)	0.451	0	0.391	0.362	0.548	1	0.46 \pm 0.30
Germany	0.285	0.104	0.347	0.281	1	0.704	0.45 \pm 0.30
Switzerland	0.605	0.231	0.278	0	1	0	0.35 \pm 0.35
Sweden	0.319	0.395	0.308	0.871	0	1	0.48 \pm 0.35
Portugal	0.276	0.491	0.444	0.537	1	0.310	0.51 \pm 0.24
Ireland	0.348	0.284	0.237	0.393	1	1	0.54 \pm 0.33
Greece	0.388	0.224	0	0.451	0.410	0.348	0.30 \pm 0.15
Means \pm SE	0.33 \pm 0.16	0.24 \pm 0.14	0.28 \pm 0.13	0.39 \pm 0.24	0.75 \pm 0.36	0.61 \pm 0.35	

(b) *Trifolium pratense*

Strain	Site						Means \pm SE
	Silwood (U.K.)	Sheffield (U.K.)	Germany	Switzerland	Sweden	Portugal	
Silwood (U.K.)	0.402	0	0.190	0.042	0	0.065	0.12 \pm 0.14
Sheffield (U.K.)	0.498	0.172	0.338	0.788	0.161	1	0.49 \pm 0.31
Germany	0.120	0.423	0	0.012	0.060	0.050	0.11 \pm 0.15
Switzerland	0.321	0.162	0.373	0	0.232	1	0.35 \pm 0.32
Sweden	0.784	0.436	0.885	0.687	0.201	1	0.67 \pm 0.27
Portugal	0	0.142	—	0.452	0.483	0	0.22 \pm 0.21
Ireland	0.824	0.759	0.395	0.415	0.783	1	0.70 \pm 0.22
Means \pm SE	0.42 \pm 0.29	0.30 \pm 0.24	0.36 \pm 0.27	0.34 \pm 0.31	0.27 \pm 0.25	0.59 \pm 0.48	

(c) *Plantago lanceolata*

Strain	Site						Means \pm SE
	Silwood (U.K.)	Sheffield (U.K.)	Germany	Switzerland	Sweden	Portugal	
Silwood (U.K.)	0.036	0.102	0.148	0.163	0.115	0	0.09 \pm 0.06
Sheffield (U.K.)	0.017	0.102	0.318	0.525	0.122	0.365	0.24 \pm 0.18
Germany	0	0.098	0.145	0	0	0.046	0.05 \pm 0.06
Switzerland	0.045	0	0	0.194	0.342	0.131	0.12 \pm 0.12
Portugal	0.340	0.160	0.187	0.267	0.306	0.178	0.24 \pm 0.07
Ireland	0.114	0.194	0.328	0.388	0.214	0.505	0.29 \pm 0.13
Greece	0.154	0.208	0.239	0.501	0.219	0.763	0.35 \pm 0.22
Means \pm SE	0.10 \pm 0.11	0.12 \pm 0.07	0.20 \pm 0.11	0.29 \pm 0.18	0.19 \pm 0.11	0.28 \pm 0.26	

The three species differed in their amount of environmental and genetic variation (significant species \times site and species \times strain interactions; Table 4). However, the home vs. away advantage and the decreasing selection advantage with distance were consistent over the three species (both the remainder of the site \times strain interaction term and the interactions of the

home and distance effects with species were small and non-significant; Table 4). We expected climatic factors to be the major cause of the distance effects. However, when climatic distance (see Table 1) was fitted first in the analysis of selection indices, it was not significant ($P > 0.27$) and it reduced the sum of squares of geographical distance by only 18%.

Table 4 Analysis of variance for selection index. The fitted terms were species (Species), experimental site (Site), the strains of different European origin (Strain), the site \times strain interaction decomposed into the contrast between home and away (Home) and the linear contrast of the geographical distance between sites (Distance). Sequential sum of squares was used to avoid adjusting contrast and interaction effects for terms marginal to them (see Nelder & Lane 1995).

Source of variation	d.f.	Sum of squares	Mean squares	<i>F</i>	<i>P</i>
Species	2	1.34694	0.67347	17.16	<0.001
Site	5	1.14271	0.22854	5.82	<0.001
Strain	7	1.73479	0.24783	6.31	<0.001
Home	1	0.70823	0.70823	18.04	<0.001
Distance	1	0.42222	0.42222	10.76	0.002
Residual site \times strain	33	1.48334	0.04495	1.14	0.323
Species \times site	10	1.30546	0.13055	3.33	0.002
Species \times strain	12	1.16859	0.09738	2.48	0.011
Species \times home	2	0.17299	0.08650	2.20	0.120
Species \times distance	2	0.01572	0.00786	0.20	0.819
Residual species \times site \times strain	55	2.15918	0.03926		

Stability analysis (Finlay & Wilkinson 1963; Jinks & Pooni 1984; Bell *et al.* 2000) showed that strains varied significantly in their selection index across sites within the three forage species investigated ($P < 0.01$ for species \times strain \times covariate interaction in the analysis of covariance; covariate is the x axis in Fig. 1 obtained by calculating site qualities from the mean selection indices for each species; home sites are indicated by arrows in Fig. 1). Remarkably, for *T. pratense* and *P. lanceolata*, there was a consistent pattern of strain stability in that those from Portugal, Germany and Silwood (U.K.) proved to be significantly less sensitive to selection than the remaining strains ($P < 0.001$ in analysis of variance with regression slopes as dependent variable).

DISCUSSION

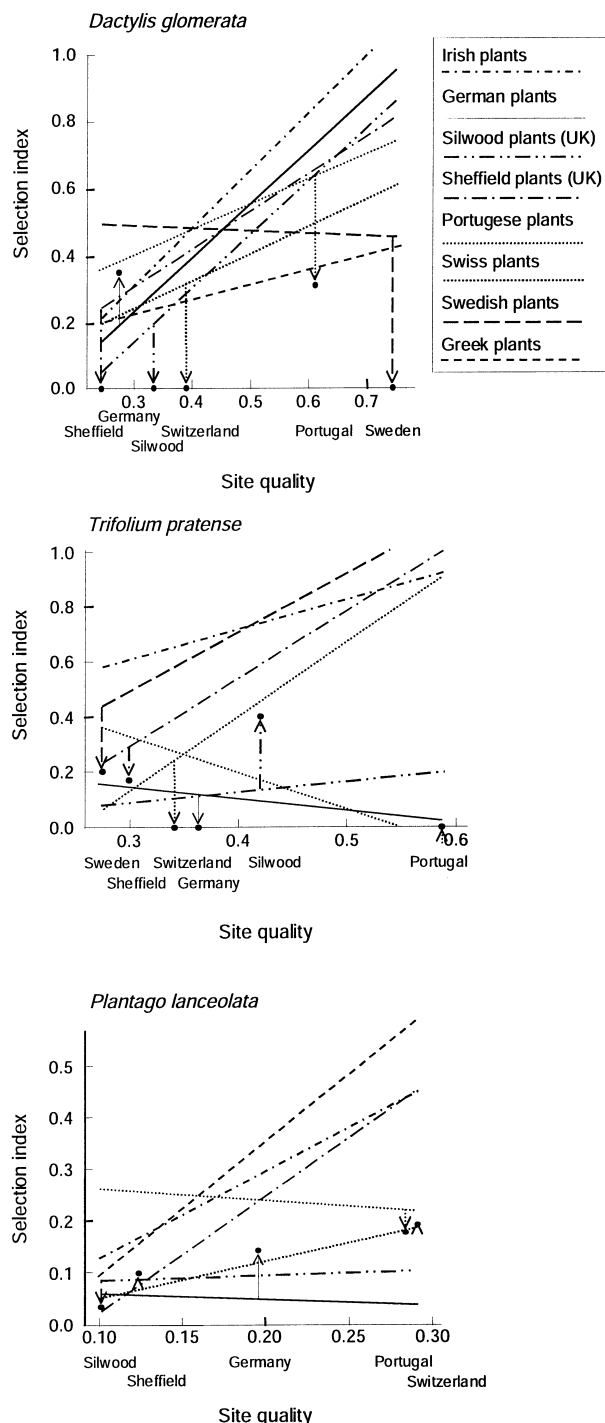
Over the three widespread and world-wide successful species, we found a consistent home vs. away advantage and a decreasing selection advantage with distance across Europe, suggesting that local specialization may be the rule in these species. Because the home and distance effects remained constant or even increased with time, it is unlikely that they reflected maternal carry-over effects (Schmid & Dolt 1994).

The possible evolutionary causes for the prevalence of local specialization in common European forage plants may include differential abiotic (edaphic, climatic) or biotic (mutualists, pathogens, herbivores) selection pressures exerted by natural or human forces. Phylogenetic history (gene flow, genetic drift, ancient selection), however, which is often used as an explanation in studies of molecular variation (Harwood & Amos 1999), may explain only a small part of recent local adaptation in fitness-related characters (Galloway & Fenster 2000). The significant decrease in the degree of adaptation with distance, observed for the first time in a comprehensive replant–transplant experiment, is consistent with the idea that environmental variance increases indefinitely with distance (Bell 1992) and points

to climatic factors as the major selection pressure. However, climatic distance only explained 18% of the variance of geographical distance in the analysis of selection indices. Thus, other factors, e.g. biotic influences such as the presence of specific mutualists, pathogens or herbivores, may have exerted even stronger selection pressures. Possible human influences include deliberate selection by breeding. Nevertheless, no super-varieties appear to have replaced the locally adapted strains, at least in the investigated species.

As local specialization seems to be the rule, plant breeding could try to take advantage of this. Thus, high-performance varieties may be developed for the specific environments in which they will be used. This is especially important where the environment itself cannot be improved by agricultural practices, for example in low-input agricultural systems. As restrictive and expensive seed certification procedures (Hardon 1999), as well as the application of the current system of intellectual property rights (Swanson & Göschl 2000), may threaten the maintenance of these plant genetic resources, our results suggest that agricultural policies should encourage the use and certification of local varieties and protect farmers' rights to grow these in accordance with the spirit of the Convention on Biological Diversity (United Nations Environment Programme 1992).

Improvement in the performance of local varieties could be one goal of selective breeding; another could be the development of plant material with low sensitivity to selection across localities (Jinks & Pooni 1984). This will be especially important if species have to adapt to new conditions in the light of global environmental change. Adaptive ecotypic differences and adaptive plasticity may be complementary rather than mutually exclusive ways to allow organisms to cope with environmental variation or to invade new habitats (Sultan 1995; DeWitt *et al.* 1998). Hence, the selection advantage of local or regional strains observed at their site or region of origin does not strictly imply that the individual strains were restricted to a narrow range of habitat in all three species. All three test species are



mainly outbreeding, morphologically variable, occur naturally in a broad range of habitats and are known to be successful invaders (Sagar & Harper 1964; Lumaret 1984; Grime *et al.* 1988). However, despite the wide range of these species, there seemed to be limits to evolutionary differentiation (Bradshaw 1991) on a continental scale.

Figure 1 Stability of different local strains of three common forage plants across eight European sites. The selection indices of the individual strains (y axis) are regressed against site quality, as measured by the mean selection index of all strains per site (x axis). A selection coefficient of zero indicates that a strain is the most successful at a given site, whereas a coefficient of unity indicates complete selection against a strain. Sites are ordered in the direction of increasing average selection coefficients from zero to unity (corresponding to decreasing site quality from left to right on the x axis). Regression slopes show the performance of each strain across all sites, and arrows link strains with their selection index at their home site (filled circles).

Averaged over the three species, selection pressure was strongest at the most northern and southern planting sites. Averaged over planting sites, however, selection was strongest against northern strains of the three species only. These strains may have paid the highest costs of adaptation. If species were analysed individually, there was a consistent pattern of strain stability for *T. pratense* and *P. lanceolata*, with individual strains from southern and mid-Europe being less sensitive to selection than the remaining strains. How this is related to differences in within-environment variation or in land-use practices across Europe is a question for future studies.

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BIOSKETCH

Jasmin Joshi's research interests include the importance of genetic diversity on local adaptation and the interrelationship between species diversity, ecosystem processes and community responses to disturbance. She is also involved in a project investigating the evolution of antiherbivory defences in invasive plants.

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