

# Reaction norm variation between and within populations of two rare plant species, *Vicia pisiformis* and *V. dumetorum* (Fabaceae)

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A split-family design with progenies grown across a steep temperature gradient was used to examine the patterns of reaction norm variation in two locally rare, thermophilous plant species, *Vicia pisiformis* and *V. dumetorum*. We predicted (i) a negative association between the amount of genetic variation and the magnitude of response across temperatures; (ii) broader ecological tolerance and higher levels of genetic variation for reaction norm parameters in the broadly adapted *V. dumetorum* than in the ecologically restricted *V. pisiformis*; and (iii) higher performance across environments for central populations than for geographically marginal populations. Patterns of variation in 10 vegetative characters, including measures of overall plant size, provided no evidence of a trade-off between plasticity and genetic variation. Our data indicate greater performance across temperatures and more divergent genotypes in *V. dumetorum* than in *V. pisiformis*. Central populations of *V. pisiformis* performed better than conspecific populations from the marginal (northern) regions.

**Keywords:** genetic variation, genotype × environment interaction, phenotypic plasticity, rarity, *Vicia dumetorum*, *Vicia pisiformis*.

## Introduction

Phenotypic plasticity, or the ability of an organism to modify its phenotype in response to changes in the environment, represents an important aspect of the reaction norm. It has been suggested that reaction norms can be changed by selection (Bradshaw, 1965; Schlichting & Levin, 1984; Via & Lande, 1985; Sultan, 1987) and that phenotypic plasticity and genetic variation represent alternative modes of adaptation in plants and other organisms in heterogeneous environments (Marshall & Jain, 1968). According to the latter idea, one would expect genetically variable species or populations to be less plastic than those with low levels of heritable variation. Yet despite numerous attempts to test this hypothesis, there is little empirical evidence of an inverse relationship between plasticity and genetic variation (Marshall & Jain, 1968; Scheiner & Goodnight, 1984; Schlichting & Levin, 1984; Taylor & Aarssen, 1988; MacDonald & Chinnappa, 1989; but see Cook & Johnson, 1968; Silander, 1985).

A related idea, termed the ‘ecology hypothesis’ by Schlichting & Levin (1984), predicts that the pattern of selection on plasticity differs from one habitat to another, leading to habitat-correlated variation in the reaction norm. Accordingly, one would expect greater diversity in reaction norm parameters in widespread and/or broadly adapted species than in rare species with narrow ecological amplitudes. However, although isozyme diversity tends to increase with the geographical range (Loveless & Hamrick, 1984), there have been few attempts to examine whether rarity is associated with low variation of traits directly related to fitness (Widén & Andersson, 1993; Ouborg & Van Treuren, 1995), including phenotypic plasticity (Andersson & Widén, 1993). Genetic differences in plasticity can be visualized as reaction norm diagrams and quantified as genotype–environment interactions (analysis of variance) or as the genetic correlation between the same character measured in two distinct environments (Schlichting & Levin, 1984; Via & Lande, 1985; Via, 1987).

Rabinowitz (1981) classified rare plant species into seven categories according to local population

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size, geographical range and habitat specificity. For example, *Vicia pisiformis* and *V. dumetorum* occur in large parts of Europe but are locally rare in the northern (marginal) areas, where climatic factors have restricted their expansion. Both species require high summer temperatures (Ellenberg *et al.*, 1991), but *V. dumetorum* occurs in a wider range of habitats than *V. pisiformis* (see below) and may therefore be considered as a commoner species (Rabinowitz, 1981). However, only genetic data can reveal whether these species owe their rarity to a lack of quantitative genetic variation, narrow ecological tolerance or historical factors (Kruckeberg & Rabinowitz, 1985).

Previous work on *V. pisiformis* (Black *et al.*, 1995) has revealed genetic variation for biomass and fecundity, and differences between populations in their phenotypic response to different temperatures, contrasting with the low genetic variation revealed with random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP) (rDNA) (Gustafsson & Gustafsson, 1994). In the study presented here, we quantified genetic variation and phenotypic plasticity in a wide range of vegetative traits in *V. pisiformis* and *V. dumetorum* over a broader range of temperature conditions. Our aims were to investigate the relationship between amounts of genetic variation and phenotypic plasticity, to test the supposition that *V. dumetorum* is more tolerant to changes in temperature or that this species shows higher levels of heritable or plastic variation than *V. pisiformis*, and to determine whether central and marginal populations differ in their response to temperature.

## Materials and methods

### Species description

*Vicia pisiformis* and *V. dumetorum* (Fabaceae) are diploid, herbaceous plants capable of limited vegetative reproduction. Both species are self-fertile (unpublished) and pollinated by bumble bees, honey bees and small solitary bees (Hanelt & Mettin, 1989). *Vicia pisiformis* and *V. dumetorum* occur in large parts of Europe with a centre of distribution in Germany and the Czech Republic. *Vicia pisiformis* has about 30 localities in Sweden and Norway, and *V. dumetorum* is known from about 25 localities in Sweden. The northern (marginal) sites are geographically isolated with fewer than 300 (*V. pisiformis*) or 2000 (*V. dumetorum*) shoots per locality. Most populations have been small and isolated over the past 200 years. *Vicia pisiformis* and *V. dumetorum*

are classified as 'vulnerable' and 'care-demanding', respectively, on the Swedish list of threatened plant species (Aronsson *et al.*, 1995).

*Vicia pisiformis* and *V. dumetorum* are thermophilous (Ellenberg *et al.*, 1991), but differ in their breadth of adaptation, at least in the northern regions. *Vicia dumetorum* occurs in a variety of natural and anthropogenic habitats, e.g. conifer and deciduous forests, edge-zones between forest and open land, gardens, road verges and ruderal sites (Gustafsson, 1992), whereas *V. pisiformis* is restricted to natural sites exposed to sunlight, e.g. south-facing slopes in deciduous forests (Gustafsson, 1991). The latter species has disappeared from many localities in Sweden as a result of increased competition from surrounding vegetation attributable to spontaneous closing of forests and plantation with conifers (Gustafsson, 1991).

### Experimental procedures

Seeds were collected from five to nine (mostly seven) maternal plants in each of 13 populations representing marginal (Sweden and Norway) and central (Germany and Czech Republic) localities of both species (see Table 1 for geographical locations). To minimize the risk of repeated sampling within clones, seeds were collected from plants separated by at least 3 m. The seeds were pooled across pods and kept separate by maternal parent (hereafter 'family'). Average seed weight for each family was determined by weighing a bulked seed sample of

**Table 1** Geographical location of populations of *Vicia pisiformis* and *V. dumetorum* used in the present study

Population	Location	Latitude (north)	Longitude (east)
<i>V. pisiformis</i>			
Borgehall	Sweden	58°30'	13°40'
Rudu	Sweden	57°50'	14°18'
Björkåsholm	Norway	59°47'	10°30'
Sjöstrand	Norway	59°47'	10°29'
Chlum	Czech Republic	50°23'	14°55'
Unětický'	Czech Republic	50°08'	14°19'
<i>V. dumetorum</i>			
Tullinge	Sweden	59°13'	17°52'
Krokek	Sweden	58°39'	16°26'
Kristinelund	Sweden	55°54'	14°01'
Ho. Junkershausen	Germany	50°21'	10°21'
Hart	Germany	49°50'	10°04'
Chlum	Czech Republic	50°23'	14°55'
Průhonice	Czech Republic	50°00'	14°34'

11–20 seeds per family, with the exception of the Unéticky' population, in which each bulk sample consisted of 18–40 seeds.

After scarification and imbibition in water, the seeds were quickly dipped in Vitaflow 6 per cent to eliminate fungus infections. The seeds were sown in pots with a mixture of perlite, vermiculite, sand and gravel, and the pots were placed in a phytotron (20°C, 24 h light). After the development of the first leaf, seedlings were planted in mineral wool 'Grodan' and incubated at 18°C for 16 h light and at 12°C for 8 h darkness for 2–3 weeks. The initial length of each plant (LENG) was measured, and pots with equal-sized plants were placed in the same block, in order to obtain uniform blocks, before transfer to growth chambers representing the following temperature regimes: 12°C/7°C, 17°C/12°C, 22°C/17°C and 27°C/22°C (day/night temperature). This gradient spans the full range between the high summer temperatures in the central parts of the range to the lower summer temperatures prevailing in the northern parts. Each of the 13 populations was represented by one plant in each of 14 blocks within each temperature treatment, resulting in a total of 728 plants (13 populations × four treatments × 14 plants). Each family was represented by one to three (mostly two) offspring per temperature regime. The plants were grown in transparent plastic tubes to simplify harvest and to minimize competition. The plants were watered with a nutrient solution according to their size, i.e. plants in warmer treatments were given nutrient more frequently than plants in cooler treatments, a procedure that prevented stress symptoms seen in previous experiments (unpublished). The relative air humidity was 75 per cent at all temperature regimes.

All plants were harvested after approximately 6 weeks when the plants in the 27°C/22°C treatment had reached the height of the plastic tubes (170 cm). Each plant was scored for the variables in Table 2. Traits reflecting growth rate and overall plant performance (SHOOT, MLENG, DWTOT) are directly related to flower production and may therefore be under positive selection irrespective of growth conditions, whereas the other characters (ratios and leaf variables) may be selectively neutral or subject to more complex patterns of selection. Some of the variables are likely to be redundant, but each is expected to provide at least some information not revealed by the other traits. The dry weight of root and above ground material was recorded after drying for 40 h at 70°C. Analysis of residuals showed that all traits were approximately normally distributed, except for DWSHO, which was log-transformed.

#### Statistical analyses

Nested, factorial analysis of variance was conducted for each variable using type III sum of squares (PROC GLM; SAS, 1989) with treatment and species considered as fixed effects and population (nested within species) and family (nested within population) as random effects. Preliminary analyses revealed nonsignificant effects of block and initial length (covariate), so these factors were excluded from the final analyses. Analyses of the full data set were based on the following statistical model (referred to as 'model 1'): trait = treatment + species + population + treatment × species + treatment × population + error, whereas separate analyses for each species included 'family' and 'family × treat-

**Table 2** Character abbreviation and description of vegetative traits measured in *Vicia dumetorum* and *V. pisiformis*

Character	Description (unit, type of transformation)
SHOOT	Number of basal shoots $\geq 10$ cm
MLENG	Length of main shoot (cm)
DWAR	Dry weight ratio above ground/root material
DWTOT	Total dry weight (g)
DWSHO	Dry weight/shoot (g, log-transformed)
DWNODE	Dry weight/node (g)
NODESHO	Number of nodes/shoot
BRANODE	Number of branches $\geq 10$ cm/node
LEAFL	Length of leaflet closest to stem at sixth node (mm)
LEAFS	Ratio leaf length/leaf width at widest point on leaflet closest to stem at sixth node

ment' as additional factors ('model 2'). The approximate error term for each *F*-test was synthesized with the Satterthwaite approximation using the TEST option in the RANDOM statement of PROC GLM (SAS, 1989). The fraction of variance accounted for by each of the random factors was calculated as the ratio of the variance component to the sum of all components. Estimates of the variance components were obtained using the REML option in PROC VARCOMP (SAS, 1989), and the standard errors of the relative components were found using the Delta technique (Bulmer, 1980).

To quantify the elevation of the reaction norm for each population, we averaged the treatment means for each character, whereas the amount of response (i.e. the slope of the reaction norm) was quantified as the coefficient of variation of treatment means (CV = standard deviation/mean). We also calculated the product-moment correlation coefficient (*r*) between the mean of each population in the most extreme environments (12°C/7°C, 27°C/22°C) to test whether increased adaptation to low temperatures has been achieved at the expense of decreased adaptation to high temperatures, i.e. whether genetically

based trade-offs within the reaction norm have prevented the species from exploiting a wider range of temperature environments. Such trade-offs are indicated if *r* is negative for characters directly related to fitness (Via, 1987).

## Results

### *Phenotypic plasticity and genetic differences in the overall mean*

The main effect of treatment was significant in all cases, with the exception of SHOOT (*V. pisiformis*) and LEAFS (both species; Table 3). Judging by the reaction norms (Fig. 1), most characters showed a positive response to increasing temperature. The average amount of response (CV) was highest for DWAR and BRANODE and lowest for LEAFL and LEAFS, but differed little between species (Table 4).

*Vicia dumetorum* was characterized by higher mean values for SHOOT, MLENG, DWAR, BRANODE and LEAFS, whereas *V. pisiformis* had higher means for DWNODE and LEAFL (Fig. 1, Tables 4 and 5). Separate analyses for each species

**Table 3** Results of nested, factorial analysis of variance of 10 vegetative traits in *Vicia pisiformis* and *V. dumetorum*

Character	Treatment	Population	Family (population)	Treatment × population	Treatment × family (population)
<i>V. pisiformis</i>	(3)	(5)	(36)	(15)	(99)
SHOOT	0.764	6.376**	0.915	1.789*	0.996
MLENG	526.676***	6.076*	0.993	0.620	0.967
DWAR	74.331***	3.977*	1.111	5.967***	0.970
DWTOT	62.413***	4.747**	1.710*	1.976*	0.922
DWSHO	235.770***	2.084	1.124	0.567	0.988
DWNODE	127.383***	1.745	1.026	0.499	1.099
NODESHO	93.749***	1.192	1.000	1.420	1.110
BRANODE	5.640**	2.263	0.826	0.875	1.204
LEAFL	5.851**	4.597*	1.056	1.648	0.976
LEAFS	1.008	2.099	1.157	2.028*	1.285
<i>V. dumetorum</i>	(3)	(6)	(43)	(18)	(124)
SHOOT	23.110***	2.436*	2.101***	2.224**	1.135
MLENG	551.289***	2.123	1.273	1.027	1.017
DWAR	79.211***	2.553	1.579*	5.232***	1.154
DWTOT	62.819***	1.613	2.039**	2.701***	1.344*
DWSHO	76.642***	1.779	1.037	3.396***	1.404*
DWNODE	41.184***	2.987*	1.550*	3.288***	0.949
NODESHO	28.055***	1.511	1.061	6.257***	1.530**
BRANODE	29.368***	2.316	1.735**	4.983***	0.898
LEAFL	16.384***	6.141**	1.047	1.317	1.486**
LEAFS	0.775	4.339**	1.391	0.847	1.026

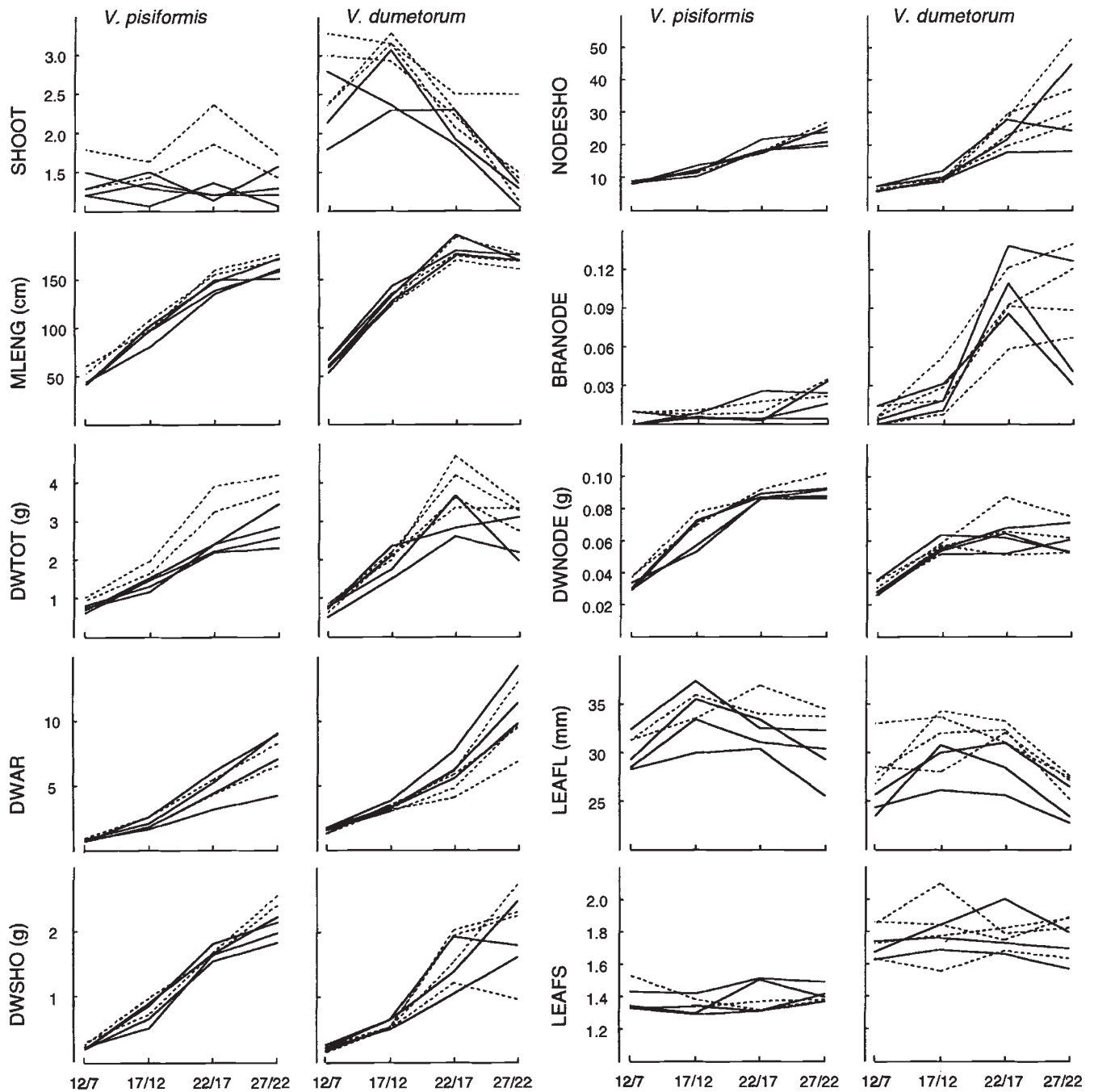
Values are *F*-ratios (degrees of freedom in brackets).

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ .

revealed significant between-population variation for half of the characters in both species (Table 3), and the variance attributed to population accounted for 0–19 per cent of the variation in *V. pisiformis* and for 3–14 per cent of the variation in *V. dumetorum* (Table 6). Although central populations of *V. pisiformis* performed better across environments (larger

means for SHOOT, MLENG and DWTOT) than populations in marginal areas, there was no clear regional pattern in *V. dumetorum* (Fig. 1).

Families within populations of *V. pisiformis* differed significantly only for DWTOT, whereas populations of *V. dumetorum* showed a significant between-family component for SHOOT, DWAR, and



**Fig. 1** Norms of reaction of growth traits in populations of *Vicia pisiformis* and *V. dumetorum* to four temperature treatments. Marginal populations are indicated by straight lines and central populations by dotted lines.

DWTOT, DWNODE and BRANODE (Table 3; see also Table 6).

#### Genetic variation in response

*Vicia pisiformis* and *V. dumetorum* differed significantly in their response to temperature for most characters (Table 5). For instance, there was a tendency for some characters (e.g. SHOOT, MLENG and DWTOT) to reach a maximum value at lower temperatures in *V. dumetorum* than in *V. pisiformis* (Fig. 1).

Data from *V. pisiformis* revealed a significant population  $\times$  treatment interaction for SHOOT,

**Table 4** Species means ( $\bar{X}$ ) and coefficients of variation (CV) across four temperatures (averaged over populations), and the correlation ( $r$ ) between population means in the two most extreme environments for 10 vegetative traits in *Vicia pisiformis* (*pis*) and *V. dumetorum* (*dum*)

Character	<i>pis</i> $\bar{X}$	<i>dum</i> $\bar{X}$	<i>pis</i> CV	<i>dum</i> CV	<i>pis</i> $r$	<i>dum</i> $r$
SHOOT	1.42	2.26	0.130	0.307	0.599	0.578
MLENG	114.48	135.72	0.467	0.399	0.696	0.451
DWAR	3.77	5.34	0.786	0.747	0.338	0.714
DWTOT	2.06	2.29	0.551	0.550	0.734	0.402
DWSHO	1.27	1.09	0.684	0.803	0.831	0.375
DWNODE	0.070	0.053	0.398	0.314	0.449	0.113
NODESHO	15.64	18.37	0.456	0.683	0.414	0.297
BRANODE	0.011	0.054	0.767	0.903	0.148	0.168
LEAFL	32.14	28.47	0.071	0.105	0.802	0.524
LEAFS	1.38	1.76	0.033	0.034	0.150	0.742

DWAR, DWTOT and LEAFS, whereas populations of *V. dumetorum* differed in response for all traits but MLENG, LEAFL and LEAFS (Table 3; see also Table 6). In *V. pisiformis*, central populations had a greater response to temperature (DWTOT) or a more distinct optimum temperature (SHOOT) than those in geographically marginal areas (Fig. 1). The average value for each population was positively correlated between the 12°C/7°C and 27°C/22°C regimes for all characters in both species (Table 4).

Maternal sibships in populations of *V. dumetorum* responded differently to temperature for DWTOT, DWSHO, NODESHO and LEAFL, whereas none of the traits was significantly affected by the family  $\times$  environment interaction in *V. pisiformis* (Table 3). Hence, the variance arising from family  $\times$  environment interaction was lower in *V. pisiformis* (0–5 per cent) than in *V. dumetorum* (0–18 per cent; Table 6).

#### Discussion

Average seed weight differed greatly between species and conspecific populations ( $P < 0.001$ , unpublished data), but seedling size had little effect on traits expressed later in the ontogeny, when initial plant height was entered as a covariate (data not shown). This finding agrees with studies showing that the maternal influence disappears at later stages (e.g. Ouborg & Van Treuren, 1995). In the following text, it is assumed that phenotypic differences between species, populations and families had a strong genetic component and that most characters are correlated with fitness. The latter assumption

**Table 5** Results of nested, factorial analysis of variance of 10 vegetative traits in *Vicia pisiformis* and *V. dumetorum*

Character	Source of variation				
	Treatment (3)	Species (1)	Population (species) (11)	Treatment $\times$ species (3)	Treatment $\times$ population (33)
SHOOT	14.885***	29.025***	3.959***	15.322***	2.104***
MLENG	1036.975***	37.078***	4.481***	18.282***	0.846
DWAR	153.090***	9.352**	3.272**	4.423*	5.191***
DWTOT	118.899***	0.962	4.456***	6.147**	2.360***
DWSHO	213.481***	4.530	1.909	0.910	1.969**
DWNODE	157.349***	35.925***	2.943**	12.304***	1.050
NODESHO	55.047***	2.998	1.469	4.690**	6.212***
BRANODE	29.976***	31.745***	2.561*	18.105***	3.419***
LEAFL	20.376***	9.003*	6.610***	1.572	1.528*
LEAFS	0.793	80.145***	4.879***	0.625	1.047

Values are  $F$ -ratios (degrees of freedom in brackets).

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ .

**Table 6** Relative variance components ( $\pm$ SE) for 10 vegetative traits in *Vicia pisiformis* and *V. dumetorum*

Character	Source of variation				
	Population	Family (population)	Treatment $\times$ population	Treatment $\times$ family	Error
<i>V. pisiformis</i>					
SHOOT	12.8 (7.0)	0	5.0 (1.4)	0	82.1 (6.4)
MLENG	6.1 (4.7)	0	0	0	93.9 (4.7)
DWAR	18.8 (13.4)	0.3 (1.9)	21.6 (4.6)	0	59.3 (9.2)
DWTOT	15.3 (10.2)	5.6 (3.6)	5.2 (3.8)	0	74.0 (9.6)
DWSHO	0.4 (1.5)	0.4 (3.2)	0	0	99.3 (3.1)
DWNODE	0	0.2 (2.8)	0	0	99.8 (2.8)
NODESHO	0.3 (2.1)	0	3.0 (3.8)	5.4 (7.2)	91.3 (7.4)
BRANODE	1.1 (1.9)	0	0	4.1 (7.8)	94.9 (7.9)
LEAFL	11.8 (7.9)	0	1.2 (2.8)	0	86.9 (8.0)
LEAFS	2.9 (4.4)	2.9 (3.7)	2.9 (3.8)	0	91.4 (5.9)
<i>V. dumetorum</i>					
SHOOT	6.4 (6.3)	11.6 (4.6)	7.5 (4.3)	5.4 (6.0)	69.2 (7.6)
MLENG	2.8 (2.9)	3.1 (3.6)	0	1.9 (7.1)	92.2 (7.2)
DWAR	10.8 (9.5)	6.1 (3.8)	19.2 (7.3)	4.3 (5.7)	59.6 (8.7)
DWTOT	5.9 (6.5)	10.7 (4.7)	10.0 (5.2)	11.1 (6.2)	62.3 (7.2)
DWSHO	14.2 (4.3)	0.4 (2.5)	14.2 (5.8)	11.4 (4.7)	59.7 (5.2)
DWNODE	13.2 (12.9)	6.6 (5.4)	13.2 (8.6)	0.7 (8.6)	66.2 (13.5)
NODESHO	4.2 (8.0)	1.0 (2.7)	29.7 (9.6)	13.6 (5.7)	51.4 (7.4)
BRANODE	8.6 (8.3)	5.1 (3.0)	17.7 (6.7)	0	68.6 (7.5)
LEAFL	13.8 (8.4)	1.5 (3.7)	3.4 (3.7)	18.0 (6.9)	63.4 (8.1)
LEAFS	5.8 (5.0)	4.6 (3.9)	0	0.3 (7.0)	89.2 (8.5)

seems reasonable for characters reflecting vegetative size and overall plant vigour, whereas the other traits have unknown relevance to fitness.

#### Genetic variation vs. phenotypic plasticity

The average effect of population and/or family was significant for a wide variety of traits, including vegetative size, leaf shape and the proportional allocation of biomass. About half of the traits were significantly variable at the between-population level in both species, whereas the between-family component reached significance for a greater number of characters in *V. dumetorum* (five) than in *V. pisiformis* (one). Populations and families also differed in their response to temperature, particularly in *V. dumetorum*. The presence of genetic variation at these levels shows that there is a potential for further evolutionary change in some characters. The significant level of genetic variation in *V. pisiformis* is particularly interesting in view of the low inter- and intrapopulation molecular variation in RAPD and RFLP (rDNA) markers found in a previous study (Gustafsson & Gustafsson, 1994). Heritable variation in fitness components has also been docu-

mented in other rare, threatened plants, including *Plantago cordata* (Meagher *et al.*, 1978) and *Senecio integrifolius* (Andersson & Widén, 1993; Widén & Andersson, 1993), suggesting that rarity may not always be associated with low genetic variance for ecologically important traits.

Almost all the characters were significantly affected by temperature, the amount of the response ranging from 3 per cent to 90 per cent when standardized by the grand mean (CV). The magnitude of response was similar in *V. pisiformis* and *V. dumetorum*, and there were no consistent differences in CV between categories of traits, except that leaf shape was phenotypically stable in both species.

If genetic variation and plasticity represent alternative adaptive strategies, there should be a negative association between these parameters (Marshall & Jain, 1968). However, even though *V. dumetorum* exhibited significant genetic variation and genotype  $\times$  environment interaction for a larger number of traits than *V. pisiformis*, we found no tendency for *V. dumetorum* to be less plastic than its congener, and there was no trade-off between genetic and environmental variation on a trait-by-trait basis. Thus, our results provide no evidence of a negative

relationship between phenotypic plasticity and genetic specialization, extending the results of other recent studies (Scheiner & Goodnight, 1984; Schlichting & Levin, 1984; Taylor & Aarssen, 1988; MacDonald & Chinnappa, 1989).

#### *Ecological breadth and reaction norm evolution*

Given that the average reaction norm can respond to selection, one would expect greater divergence in reaction norm parameters in the broadly adapted *V. dumetorum* than in the narrowly distributed *V. pisiformis*. This hypothesis is supported by our finding that populations of *V. dumetorum* were more divergent in their response to different temperatures than those of *V. pisiformis*. Furthermore, there appears to be a greater potential for reaction norm evolution in *V. dumetorum*, given the strong effect of family and family  $\times$  treatment in this species. The tendency for *V. dumetorum* to maintain a higher shoot production across temperature regimes (broad ecological tolerance) and the presence of more divergent genotypes in *V. dumetorum* may have enabled this species to extend its ecological range beyond that of *V. pisiformis*.

We found no negative genetic correlations between fitness measured in different environments. Vegetative characters directly related to flower production were positively correlated between the most extreme temperature regimes, suggesting that there was little change in the ranking of populations over environments and that significant population  $\times$  environment interactions largely reflect differences among populations in the magnitude of response. These results provide little support for the hypothesis that increased adaptation to one habitat sacrifices adaptation to another habitat (Via & Lande, 1985). Hence, genetically based trade-offs within the reaction norm may play a minor role in preventing *V. dumetorum* and *V. pisiformis* from exploiting a wider range of habitats (cf. Andersson & Widén, 1993).

#### *Marginal vs. central populations*

Inbreeding, genetic drift and restricted gene flow result in genetic erosion, particularly in geographically marginal populations (Soulé, 1973). Assuming that phenotypic plasticity (or broad ecological tolerance) represents an alternative to genetic variation as a mode of adaptation, one would expect genotypes from marginal populations to be more plastic and/or more broadly adapted than genotypes from central populations (Stewart & Nilsen, 1995). Data from *V. pisiformis* and *V. dumetorum* are not consist-

ent with this hypothesis: marginal populations did not exhibit greater phenotypic plasticity than central populations, and central populations generally had a greater overall performance than those from marginal sites, at least in *V. pisiformis*. As for the latter result, it is important to stress that the experimental conditions may have been more favourable to plants representing the central (southern) distribution, making it difficult to separate the effect of latitude and marginality on reaction norm parameters. Moreover, selection in marginal conditions may have reduced phenotypic plasticity to produce more specialized, better adapted populations, even though wide plasticity may have been important in the initial establishment of these populations.

#### *Concluding remarks*

The present study quantified genetic variation for mean performance and plasticity in marginal and central populations of two rare species. We tested the hypotheses that heritable variation and phenotypic plasticity represent alternative strategies, that the specialized *V. pisiformis* is less variable than the more broadly adapted *V. dumetorum* and that marginal (northern) populations are more plastic (or tolerant) than central populations. There was no trade-off between genetic variation and phenotypic plasticity, but our results indicate a tendency for *V. dumetorum* to perform better and to show higher levels of genetic variation than *V. pisiformis*, and a trend towards higher overall performance in central populations of *V. pisiformis*. Given the genetic variation in *V. pisiformis* (this study) and the apparent lack of molecular variation in this species (Gustafsson & Gustafsson, 1994), it remains to be seen whether such a discrepancy also occurs in *V. dumetorum*. Comparison of polygenic and molecular variation will be the subject of further studies.

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