POTENTILLA ERECTA IN TWO CONTRASTING HABITATS-A MULTIVARIATE APPROACH

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SUMMARY

Transplant and seedling material of *Potentilla erecta* from three Scottish sites, two from the south and one from the far north, were grown from contrasting, adjoining habitats at each, dominated either by *Molinia* (little grazed) or *Festuca* (grazed by sheep); 10 variates were recorded. Canonical analysis of the data confirmed and strengthened the conclusion previously reached (Watson, 1969) that the contrasting habitats had evolved contrasting ecotypes. It was tentatively concluded that the habitat difference and a north-to-south difference of 200 miles were about equally effective in differentiating ecotypes.

1. INTRODUCTION

WATSON (1969) studied transplants and seedlings of *P. erecta* from three sites in southern Scotland (Loch o' the Lowes, Smidhopeburn and Wanlockhead) and one in the extreme north of Scotland (Ben Hope). At each site there were adjoining habitats dominated either by *Molinia* or by *Festuca*, in some cases with a very clear boundary, in others more of a mosaic. The single variate, plant diameter, was used to show that transplants from the Molinietum (M) were significantly bigger than those from the Festucetum (P, for pasture), that this difference, though diminished, could be confirmed in the seedlings (except from the Ben Hope site) and that the transplants from different sites were not significantly different in size. While observing the plots it was obvious which of the two habitats the transplants came from, yet the size measurement showed a large overlap. As several other variates were recorded, a multivariate analysis was tried to see whether it would give a clearer picture.

2. Methods

The variates used were: 1. Plant diameter (cm); 2. Length of longest stem (cm); 3. Length of first internode (cm); 4. Internode number; 5. Leaf length (mm); 6. Leaf breadth (mm); 7. Number of leaf teeth; 8. Severity of mildew (visual score); 9. Time to flowering in half-weeks, the first plants to flower scoring zero; 10. Erectness (visual score). The statistical method used was canonical analysis (multiple discriminant functions). The plots were laid out, so far as the classification by sites and habitats is concerned, in randomised comlete blocks (Watson *loc. cit.*), with separate trial areas used for seedlings and transplants. There were unequal numbers in the different groups; this does not bias the canonical variates, though it obviously affects the precision of estimates of their means. The computer program was based on the algorithm given by Seal (1964), which scales the eigen vectors (discriminant functions) to give unit variance within groups. A preliminary test showed that the within-group dispersion matrix for transplants was very significantly different from that for seedlings and so it was necessary to analyse the two kinds of material separately. The Wanlockhead material was excluded for technical reasons (a second collection of seed had been necessary and the seedlings were much younger than those from the other sites).

3. Results

Both transplants and seedlings have been analysed as two groups (one from each habitat) and as six groups, classified by habitat and site. The tables of means and the between- and within-group matrices of sums of

TABLE 1
Discriminant functions (eigen vectors) for two groups, classified by habitat only, of
(a) transplants and (b) seedlings

(a) i ranspiants										
Variate*:	1	2	3	4	5	6	7	8	9	10
Vector:	0.60	0.73 0	·13 0	·11 –	0.03	-0.07	0.20	-0.09	0.30	0.65
Eigen value 1.80	6, $\chi^2 20$)3·3, d.f.	10							
Transplants		P		Μ						
Number		101	10	03						
Mean		6.445		9.120						
Misclassificatio	on	9	•3%							
(b) Seedlings										
Variate:	1	2	3	4	5	6	7	8	9	10
Vector:	0.35	-0.13	5 0.23	0.00	0.42	-0.20	0.04	0.30	0.68	0.73
Eigen value 0.99	7, χ^2 10)9·3, d.f.	10							
Seedlings		P		М						
Number		118		47						
Mean		5.027		7.225						
Misclassificatio	n	1	3.6%							
		* See	text fo	r descrit	otion o	f variates				

square and products are too bulky to reproduce here but can be supplied on request (to J. L. F.). To give an idea of the discriminatory importance of the different variates, the eigen vectors are given here as for standardised variates.

The single eigen vectors for transplants and for seedlings classified only by habitat are given in table 1. The within-group variance being unity, half the difference between means is a unit normal deviate (Hope, 1968), leading to an estimate of 9 per cent as the probability of misclassifying an individual transplant belonging to one or other of these types and 14 per cent for an individual seedling.

With classification into six groups there are five possible eigen values and vectors. For the transplants only the first two eigen values were significant; for the seedlings the third was also significant at the 5 per cent level but it only accounted for $5 \cdot 5$ per cent of the total variance and will not be considered further. The eigen values and vectors are given in table 2 and the canonical variates in table 3. Fig. 1 shows the plot of the two canonical variates for transplants (with the sign of the second variate reversed) and fig. 2 for seedlings.

To understand the very different weights given to the observed variate "time to flowering" in discriminating among transplants and among seedlings, information is needed on the variate itself. This is given in table 4.

	Transp vect	olants ors	Seedlings vectors		
Variate	1	2	1	2	
1	0.20	0.61	0.09	0.70	
2	0.79	-0.50	0.21	0.47	
3	0.10	0.17	0.22	0.17	
4	0.08	-0.36	0.00	0.23	
5	0.08	-0.31	0.77	-0.94	
6	-0.13	0.58	- 0.36	0.38	
7	-0.25	0.06	-0.06	0.14	
8	-0.13	0.61	0.05	0.11	
9	0.34	0.44	0.46	0.94	
10	-0.01	-0.01	0.94	0.34	
Eigen value	2.109	0.229	1.634	0.307	
% of total	83.6	9.1	74.3	13.9	
χ^2	295.8	74.6	231.4	80.3	
d.f.	50	36	50	36	

Eigen values and vectors for transplants and seedlings, classified in six groups, by habitat and site

TABLE 2

Analyses of variance of this attribute showed that the effects of habitat, site and their interaction were each significant in the seedling material but none was significant in the transplant material. This was so in spite of a much greater error variance for seedlings (12.97) than for transplants (1.80).

TABLE 3 Mean canonical variates for transplants and seedlings, classified in six groups, by habitat and site

			Trans	splants	Seedlings		
Site	*	No.	1	2	No.	1	2
LL	Р	26	6.886	-3.591	85	4.209	0.717
	Μ	35	9.476	- 4.101	17	6.033	1.750
SB	Р	59	6.325	- 3.362	23	3.768	1.316
	Μ	36	9.445	-3.317	10	6.370	2.296
BH	Р	16	7.656	-2.648	10	6.217	0.970
	\mathbf{M}	32	9.441	-2.641	20	7.449	0.174

* Abbreviations as for table 4

4. DISCUSSION

The multivariate approach confirms and greatly strengthens the conclusion reached in the previous paper, that the contrasting habitats at a site are occupied by contrasting types of P. *erecta*. It agrees much more closely with the observer's experience, that plots of transplants could always be assigned to the correct habitat by inspection. With a random sample of nplants, all from the same habitat, the method of using a discriminant



FIG. 1.—Transplant material classified by site and habitat (cf. table 3). The first canonical variate is represented on the horizontal axis and the second on the vertical axis. Points represent the group means and the radii show the 90 per cent confidence limits $(1.645/\sqrt{n})$. + = Pasture, X = Molinietum. BH = Ben Hope, LL = Loch o' the Lowes. SB = Smidhopeburn.



FIG. 2.—Seedling material classified by site and habitat (cf. table 3). Conventions and symbols as in fig. 1.

function closest to an experienced observer's judgment would probably be to apply the vector to the means of the sample. The effect would be to multiply the unit normal deviate by n^{\ddagger} ; *e.g.* with four plants, it would be multiplied by 2 and a misclassification rate of 9 per cent would be reduced to 0.4 per cent. This is not strictly applicable to the experimental material, since the plants in a plot were not a random sample, but it is probably not far wrong to say that a misclassification rate around 10 per cent for individuals would be reduced by an order of magnitude for groups of four. Other strategies for discriminating might be even more effective.

The much greater differences in time to flowering among seedlings than among transplants from different habitats at the same site accounts for the extra weight given to this variate in the analysis of the seedlings. The bigger differences are consistent with some degree of genetic isolation, caused by mismatched flowering, between adjoining habitats. This reinforces the caution sounded in the previous paper, that we do not know how much

Trans	plants			
Site		No.	Mean	P-M
$\mathbf{L}\mathbf{L}$	Р	26	2.615	-0.385 ± 0.347
	Μ	35	3.000	
	both	61	2.836 ± 0.263	
SB	Р	5 9	2.729	0·090 <u>+</u> 0·284
	Μ	36	2·6 39	
	both	95	2.695 ± 0.211	
BH	Р	16	2.875	0.813 ± 0.410
	Μ	32	2.062	
	both	48	2.333 ± 0.520	
Seedli	ings			
LL	Р	85	4.659	-3.341 ± 0.957
	М	17	8.000	
	both	102	5.216 ± 0.886	
SB	Р	23	6.130	-3.870 ± 1.634
	М	10	10.000	
	both	33	7.303 ± 1.655	
BH	Р	10	6.200	1.900 ± 1.395
	М	20	4.300	
	both	30	4.933 ± 1.736	
	Trans Site LL SB BH Seedl LL SB BH	Transplants Site LL P M both SB P M both BH P M both Seedlings LL P M SB P M both SB P M both SB P M both	$\begin{array}{c c c c c c c } Transplants & & No. \\ Site & No. \\ LL & P & 26 & & & \\ M & 35 & & & & \\ both & 61 & & & \\ SB & P & 59 & & & \\ M & 36 & & & & \\ both & 95 & & & \\ both & 95 & & & \\ BH & P & 16 & & & \\ M & 17 & & & & \\ Seedlings & & & & \\ Seedlings & & & & \\ LL & P & 85 & & \\ M & 17 & & & & \\ both & 102 & & \\ SB & P & 23 & & \\ M & 17 & & & \\ both & 102 & & \\ SB & P & 23 & & \\ M & 17 & & & \\ both & 102 & & \\ SB & P & 23 & & \\ BH & P & 10 & & \\ BH & P & 10 & & \\ M & 20 & & & \\ both & 30 & & \\ \end{array}$	$\begin{array}{c c c c c c } Transplants & No. Mean \\ Site No. Mean \\ LL P 26 2.615 & M 35 3.000 & both 61 2.836 \pm 0.263 & P 59 2.729 & M 36 2.639 & both 95 2.605 \pm 0.211 & P 16 2.875 & M 32 2.062 & both 95 2.062 & both 95 & 2.062 & both 48 2.333 \pm 0.520 & Seedlings & \\ LL P 85 4.659 & M 17 8.000 & both 102 5.216 \pm 0.886 & SB P 23 6.130 & M 10 & 10.000 & both 33 7.303 \pm 1.655 & BH P 10 6.200 & M 20 4.300 & both 30 & 4.933 \pm 1.736 & \\ \end{array}$

 TABLE 4

 Time to flowering (half-weeks) for (a) transplants and (b) seedlings

LL = Loch o' the Lowes. SB = Smidhopeburn. BH = Ben Hope.

genetical isolation there is between the habitats at the same site. The much smaller variances, both within and between groups, for transplants suggests that, in the wild, there is fairly stringent selection against extremes of earliness and lateness.

Canonical analysis maximises the variance between groups relative to that within groups. It does its best, so to speak, to bring out the genetic differences. The distances between points in figs. 1 and 2 (which are only slightly distorted generalised distances) might be taken as estimates, admittedly crude, of genetic distances between the groups. Fig. 2 shows that Ben Hope P seedlings are more distant from Loch o' the Lowes and Smidhopeburn P seedlings than from anything else and their closest genetical neighbours are the Loch o' the Lowes M seedlings. Even in the transplants, Ben Hope M is nearly as far from Loch o' the Lowes M as from Ben Hope P and the latter is nearly as far from Smidhopeburn P as from Ben Hope M. We tentatively conclude that the difference between a *Molinia*-dominated and a *Festuca*-dominated habitat is roughly as effective as a north-to-south difference of 200 miles in terms of selective forces. A study based more directly on genetic differences (e.g. isozyme frequencies) might of course give a different picture.

5. References

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