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Genetic analysis of ecologically relevant morphological variability in *Plantago lanceolata* L.

5. Diallel analysis of two natural populations*

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Summary. Morphological variability was studied in two populations of *Plantago lanceolata* using diallel analysis. In each population, reciprocal crosses between all possible pairs of ten plants were made. In the greenhouse, six members of each family were grown and many characters were measured. Using the model of Cockerham and Weir, the contributions of the different genetic variance components were calculated. From earlier papers it was postulated in advance to what extent and by which effect the characters in both populations were genetically determined. The populations had been differentiated for life history and morphological characters, and varied also in the relative contribution of genetic components to variability. In the Merrevliet (Me) population, where strong biotic selection was assumed, low levels of additive-genetic variability were present and the relative dominance appeared to be high. The contrasting population, Westduinen (Wd), which is abiotically controlled and shows strong environmental variability, possessed higher levels of additive-genetic variability and lower levels of relative dominance. It is possible that differential natural selection has diminished additive-genetic variability to different extents in both populations: plasticity and environmental heterogeneity prevented the loss of additive-genetic variability in Wd, whereas in the stable population, Me, natural selection had the opportunity of not only changing the means of the characters but also of diminishing additive-genetic variability to a great extent.

Key words: Diallel analysis – *Plantago lanceolata* – Morphological variability – Population differentiation – Maternal effects

Introduction

Considerable ecotypic variation has been demonstrated in the self-incompatible wind-pollinated species *Plantago lanceolata*. The ecotypes are associated with the height of the vegetation in which the species occurs (Van der Toorn and Ten Hove 1982). *P. lanceolata* from high and dense vegetation is characterized by erect plants with a small leaf angle and long broad leaves, while in short vegetation, such as grazed pastures, low prostrate plants occur. The genetic basis of these ecotypic differences was confirmed by Wolff and Van Delden (1987) in a greenhouse and a garden experiment. Transplant experiments of different *P. lanceolata* ecotypes showed lower survival in the alien transplantation sites (Van der Toorn et al. 1984; Van Groenendael 1985 a). Wolff (1988 b) confirmed these findings by demonstrating natural selection in an F_2 generation of a cross between two ecotypes. Bidirectional selection for leaf angle, a character that is highly discriminating for the hayfield and pasture ecotypes of *P. lanceolata,* gave rapid and considerable response (Wolff and Van Delden 1989), while several genetic correlations were found.

In the present study a further analysis was made of the genetic variation of ecologically relevant characters in *P. lanceolata*. Fisher's Fundamental Theorem of Natural Selection (Fisher 1930, 1958) addresses the impact of natural selection of genetic variability. One implication is that strong directional selection for a specific character leads to loss of additive-genetic variability for that character, unless it is prevented by unfavorable genetic correlations with other characters related to fitness (Charlesworth 1984; Loeschcke 1987; Schaal and Leverich 1987). Favorable correlations are those combinations of characters that are generally found and that are supposed to give rise to higher fitness in a habitat. Strong directional

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selection should further lead to the evolution of dominance of the allele favored by selection (Fisher 1930; Lawrence 1984). The purpose of this study is to test these predictions in natural populations of *P. lanceolata.*

For this purpose two populations, growing in two contrasting habitats, were compared. Both populations had been studied in earlier experiments in which the habitat, the demography, and morphological characteristics of the populations were compared (Van Groenendael 1985a, 1986; Van der Toorn et al. 1984; Wolff and Van Delden 1987). The Merrevliet (Me) population is from a very wet hayfield, mown once a year in the beginning of July. It is situated on a medieval river bed, now completely filled in. The vegetation is dense, relatively tall, and uniform. Plant numbers and plant performance are mainly under biotic control, in particular by strong competition for light (van Groenendael 1985a). The second population, Westduinen (Wd), is from a dry dune grassland lightly grazed by cattle for centuries. This habitat is relatively heterogeneous both in space and time due to irregular severe droughts in summer, which lead to large fluctuations in numbers of plants (Van Damme and Van Delden 1984). Because of grazing and relatively now nutrient levels, the vegetation is open and low (Van Groenendael 1985a). Plant numbers and growth are mainly under abiotic control. Differential natural selection in the two habitats resulted in considerable differences in the morphology and demography of *P. lanceolata* (Van Groenendael 1985a; Wolff and Van Delden 1987).

Van Groenendael (1985b) expected from a sensitivity analysis that the Wd population is under stronger selection pressure and will, therefore, contain less genetic variability. We, however, advocate a different opinion in view of the high plasticity and environmental heterogeneity in the Wd population. Wolff and Van Delden (1987) showed that the Wd population had the highest environmental sensitivity when greenhouse and garden results were compared for four *P. lanceolata* populations, including the Me population. High plasticity appeared to be an important character for survival in Wd but not in Me (Van Groenendael 1985b; Wolff and Van Delden 1987). It was evident from a reciprocal transplantation experiment in Wd and a hayfield (Heteren, closely resembling Me) that surviving plants in Wd were clustered but were randomly dispersed over the plot in the hayfield (Wolff 1988b). This indicates a high environmental heterogeneity in the Wd population that strongly determines plant survival and growth. We consider the high mortality in the Wd population not as genotype-specific selection, but as an environmentally determined, high risk of death.

We, therefore, expected the effect of selection on additive-genetic variability to be much stronger in Me than in Wd. In other words, additive-genetic variability in the Wd population would be hidden partly by plasticity (Stearns 1980) and high environmental variability (Wolff 1988b). Another supposition was low additive-genetic variability for flowering date in the Me population, because selection had occurred for early flowering in this hayfield. We expected a relatively high maternal effect to be present in both populations for seed weight, as Alexander and Wulff (1985) showed a strong maternal temperature effect on seed and seed characteristics in *Plantago lanceolata.*

We chose to unravel the different genetic components of variability and to establish interpopulation differences by means of a diallel analysis, for which several variant methods are available (e.g., Cockerham and Weir 1977; Pooni et al. 1984). The diallel design allows the partitioning of genetic variability into additive and dominance components, and also the separation of a reciprocal (or maternal, plasmon) component from the nuclear component. Natural populations of plant species have been studied with the aid of diallel analyses as, e.g., *Lolium perenne* (Hayward and Breese 1968), *Papaver dubium* (Lawrence 1965), and *Anthoxanthum odoratum* (Antonovics and Schmitt 1986). Diallel analysis has also been applied in animal species, e.g., in studying behavior components in the *Drosophila virilis* group (Hoikkala and Lumme 1987), showing large dominance components and small additive components of variability for characters related to fitness. Mitchell-Olds and Rutledge (1986) stated, however, that a heritability of zero can almost never be reached, as heritabilities and genetic correlations are strongly environmentally influenced and selection may change over time. This especially refers to the more variable habitats. Schaal (1984) found that in plants maternal effects were, in many cases, restricted to seed and seedling characteristics, where in animals maternal influences were found to be present over a longer period (Van Sanford and Matzinger 1982). Using diallel analyses, Hayward and Breese (1968) showed that in *Lolium perenne,* a highly vegetatively reproducing species, variability at the plasmon level was more important than additive-genetic variability.

In the present study, diallel analyses were used to measure the relative contribution of the different genetic components to the genetic variability in two contrasting populations, and to test whether the hypotheses concerning the effect of natural selection on genetic variability, the loss of additive-genetic variability, and the evolution of dominance effects could be confirmed.

Materials and methods

Ten flowering, adult plants were sampled both in the Me and Wd population. Each genotype was reciprocally crossed with the other nine genotypes from the same population, resulting in 90 full-sib families for each population. Selfed families were not obtained, as the species is self-incompatible and enforced selfing would lead to too many aberrant forms (Van Damme 1983). In this way two diallels, without selfs, each resulting from ten genotypes were available. All crosses gave healthy seeds; no complete incompatibility or male sterility appeared to be present. Six members of each full-sib family were grown in a computer-controlled greenhouse. A light regime of 16 h daylight and 8 h darkness was partly mediated by additional light. Temperature and humidity were controlled over the whole period.

Because of restricted capacity, the plants from both populations could not be grown at the same time. The Me population was grown in the beginning of the summer and harvested after 12 weeks. The Wd population was grown in late summer and the experiment ended after 13 weeks. Comparisons of ratios of variances, heritabilities, and mean relative dominance were comparable among experiments. This was shown by comparing heritabilities of two separate experiments with full sibs: the heritabilities found were in general in the same range (Wolff and Van Delden 1987).

The seeds were germinated in petri dishes on wet filter paper, after which they were grown in pots in the greenhouse. Germination was recorded, and seeds that did not germinate spontaneously were dissected at the root-tip end to force germination. In the Wd population one plant died during the growth period, and in the Me population 60 plants, kept on two trays, were severely damaged. These plants were not used in further analyses. During growth of the plants, cotyledon length (at the three-leaf stage) and leaf angle (angle between third and fourth leaf, at the eight-leaf stage) were measured. Flowering date was recorded as the day after germination on which the first stamens were visible. At harvest time the following characters were measured: number of rosettes, number of leaves, length of the longest leaf, width of the widest leaf, number of scapes, length of the longest scape, and length of the spike belonging to this scape. The above-ground biomass was separated in leaf material (leaf weight) and in scapes and spikes (generative weight). For weight determination the material was dried at 80 °C for several days. The weight of the leaves and the generative organs as well as the weight of the dry ripe seeds were determined. From these data reproductive effort [ratio generative weight/(generative + leaf weight)] and seeds/(mm spike) were calculated.

All calculations were done on untransformed data as well as on transformed data in such a way as to give the best approximation to a normal distribution. Since the outcome of the calculations was not dramatically different between both sets and led to identical conclusions, the set with untransformed data was used in this paper. Ouadratic analysis after the methods of Cockerham and Weir (1977) were carried out for partitioning the variance into nuclear and reciprocal effects. The following effects could be separated: (i) nuclear: this effect is often called the general combining ability (GCA) and represents one-half of the additive-genetic variance (V_A), as *P. lanceolata* is an outcrossing species; (ii) nuclear specific: this effect is often called specific combining ability (SCA), meaning nuclear effects specific to a particular cross; it represents one-fourth of the nonadditive or the dominance genetic variance (V_D); (iii) reciprocal: this effect includes maternal or paternal effects of a genotype; paternal and maternal effects can be separated in this model (using the method of symmetrical products), but cannot be tested for significance; (iiii) reciprocal specific: this effect is caused by interactions of nuclear effects of the zygote and reciprocal effects of the parents.

The analysis requires a balanced design, a problem given the unexpected loss of some Me plants. To restore the balanced design the first four, randomly numbered members of each family, which were not on the two trays, were used. In the case of the scape and spike length in the Wd population, five members per family could be used and two parents were totally omitted, because those plants did not flower or started flowering too late. For this reason, seed weight and number of seeds/mm spike could not be analyzed in the Wd population. The data of the missing plant in the Wd population were replaced by the means of the family. If data were missing in other cases (never more than five plants for any character), these data were replaced by the family mean.

Heritabilities were calculated as two times the ratio of nuclear variance to total variance. The relative dominance genetic variance was calculated as V_D/V_A, in which is V_D is four times the nuclear specific component and V_A is two times the nuclear effects.

To get a variance measure of heritabilities and relative dominance variance the data were jackknifed, leaving out one genotype at a time (Sokal and Rohlf 1981). In this way, a mean and variance were derived to test the differene between populations. When zeros or infinite numbers were present in the jackknife procedure, calculation of a mean and variance was not possible.

Variance component correlations between characters were calculated from variance and covariance components for the different effects.

Results

From the relative germination rate of the seeds, it appeared that germination rate was strongly maternally determined, and also that some maternal-paternal genotype interaction was present (data not presented). The mean and CV of the various characters measured in both populations, obtained in two separate experiments, are given in Table 1. The genetic variance components are shown as a percentage of total variance (Table 2). Nuclear general (additive) variance components were significant for all but one character (cotyledon length) in the Wd population and for all but two characters (cotyledon length and leaf width) in the Me population. Eight char-

Table 1. Means and coefficients of variation (bracketed) of two populations of *Plantago lanceolata* measured in the greenhouse in two separate experiments

Character	Population			
	Westduinen		Merrevliet	
Cotyledon length (mm)	37.5	(22)	50.9	(19)
Leaf angle (degrees)	97.8	(34)	50.4	(35)
Flowering date (days)	60.4	(27)	42.3	(21)
Number of rosettes	5.1	(56)	3.8	(58)
Number of leaves	51.5	(36)	33.2	(37)
Leaf length (mm)	267	(21)	280	(19)
Leaf width (mm)	29.9	(18)	27.8	(17)
Number of scapes	8.6	(64)	7.5	(40)
Scape length (mm)	501	(17)	551	(14)
Spike length (mm)	41.4	(27)	35.8	(22)
Leaf weight (g)	4.19	(43)	3.83	(42)
Generative weight (g)	2.29	(62)	2.90	(38)
Reproductive effort	0.361	(62)	0.440	(38)
Seed weight (mg)	1.40	(19)	1.98	(16)
Seeds/mm spike	3.01	(34)	2.80	(30)

Table 2. Results from the analysis of variance for the different effects on several characters shown as the percent variance (%V) accounted for by each effect, and the significance of the effect

Effect	Pop.	Cotyl. length		Leaf angle		Flowering date		No. of rosettes		No. of leaves	
		%V	Sign	%V	Sign	%V	Sign	%V	Sign	%V	Sign
Nuclear	Wd	8	NS	6	*	26	***	11	***	9	**
	Me	6	NS	8	***	12	***	13	***	9	***
Nucl.spec	WD	–	NS	3	NS	2	NS	1	NS	–	NS
	Me	7	NS	–	NS	13	**	7	*	9	**
Recipr.	WD	24	***	4	NS	–	NS	–	NS	–	NS
	Me	10	*	–	NS	–	NS	–	NS	1	NS
Rec.spec.	Wd	9	**	3	NS	6	*	2	NS	7	*
	Me	17	***	9	*	4	NS	1	NS	–	NS
Environm.	Wd	59		84		66		86		84	
	Me	60		83		71		79		81	

Effect	Pop.	Leaf length		Leaf width		No. of scapes		Scape length		Spike length	
		%V	Sign	%V	Sign	%V	Sign	%V	Sign	%V	Sign
Nuclear	Wd	10	**	22	***	22	***	11	*	14	**
	Me	6	**	1	NS	26	***	6	*	12	***
Nucl.spec.	Wd	–	NS	2	NS	1	NS	–	NS	6	NS
	Me	3	NS	10	*	8	*	1	NS	–	NS
Recipr.	Wd	6	*	–	NS	–	NS	10	*	2	NS
	Me	–	NS	4	NS	–	NS	2	NS	4	NS
Rec.spec.	Wd	2	NS	8	*	–	NS	15	**	4	NS
	Me	–	NS	–	NS	5	NS	–	NS	5	NS
Environm.	Wd	82		68		77		64		74	
	Me	91		85		61		91		79	

Effect	Pop.	Leaf weight		Gener. weight		Reprod. effort		Seed weight		Seeds/mm spike	
		%V	Sign	%V	Sign	%V	Sign	%V	Sign	%V	Sign
Nuclear	Wd	34	***	24	***	30	***				
	Me	14	***	18	***	20	***	8	**	15	***
Nucl.spec.	Wd	–	NS	5	NS	2	NS				
	Me	12	***	14	**	14	**	–	NS	–	NS
Recipr.	Wd	–	NS	–	NS	–	NS				
	Me	–	NS	2	NS	–	NS	–	NS	–	NS
Rec.spec.	Wd	7	**	7	**	6	NS				
	Me	–	NS	1	NS	1	NS	4	NS	17	***
Environm.	Wd	59		64		62					
	Me	74		65		65		88		68	

NS – not significant
* $P<0.05$;; ** $P<0.001$; *** $P<0.001$

acters showed a significant nuclear specific (dominance) component in the Me population, whereas no character had a significant dominance component in the Wd population. Reciprocal general (maternal) effects were only significant for cotyledon length in both populations and leaf length and scape length in the Wd population. For these cases, maternal and paternal effects were separated and expressed as percentages of the total variance. For cotyledon length these effects were in the Me population 8% and 1%, and in the Wd population 20% and 3%, respectively. In the Wd population, leaf length had maternal and paternal effects of 0% and 8% and scape length had 9% and 1%, respectively. Reciprocal specific effects were more often significant and present in both populations, e.g., cotyledon length and seeds/mm spike in the Me population.

Highly differing heritabilities (h^2) and relative dominance genetic variance (*rd*) were present for the different characters and for both populations (Table 3). Heritabilities were significant if the nuclear effect (additive-genetic component) was significantly different from zero (Table 2). The significance of the relative dominance variance was calculated using a t-test with the jackknifed variable, with H_0: relative dominance = 0. The Me population had overall lower heritabilities and larger relative dominance variance components than the Wd population (for Me 0.24 and 1.38; for Wd 0.35 and 0.37, respectively). The generalized difference between populations for heritabilities and relative dominance variance over all characters was tested using a Wilcoxon signed rank test (Sokal and Rohlf 1981). The Wd population had higher heritabilities than the Me population at the 1% significance level, and the Me population had higher relative dominance variance than the Wd population at the 5% significance level. Using a t-test of the jackknifed statistic it appeared that differences among populations of h^2 and *rd* of individual characters were significant in only a few cases (Table 3). The reason for this is likely the high variance, as is usual in these kinds of experiments. The heritability of leaf width was significantly higher at the 5% level in the Wd population, and the relative dominance of the reproductive effort was higher in the Me population at this level, whereas the heritability of leaf weight of Wd was higher than of Me at the 10% level. A reverse of this pattern is present, although not significant, for leaf angle.

Table 3. Heritabilities and relative dominance genetic variance components (*rd*), as calculated from the quadratic analysis, of both populations, as well as the significance of the difference between the populations. For further details on the significance testing, see text

Character	Population				Difference between populations	
	Wd		Me			
	h^2	*rd*	h^2	*rd*	h^2	*rd*
Cotyledon length	0.16	0.18	0.13	1.50	ns	nt
Leaf angle	0.11*	1.10	0.16***	0	ns	nt
Flowering date	0.53***	0.19	0.25***	1.44	ns	ns
No. of rosettes	0.23***	0.34	0.27***	1.05	ns	ns
No. of leaves	0.19***	0	0.18***	1.45	ns	nt
Leaf length	0.20**	0.30	0.12**	0.97	ns	nt
Leaf width	0.44***	0.42	0.02	4.99*	*	ns
No. of scapes	0.44***	0.31	0.52***	0.78*	ns	nt
Scape length	0.24*	0	0.13*	1.19	ns	nt
Spike length	0.29**	0.86	0.34***	0.70	ns	ns
Leaf weight	0.69***	0	0.27***	1.34*	ns$	nt
Generative wt.	0.47***	0.65	0.36***	1.25	ns	ns
Reproduct. eff.	0.57***	0.41	0.39***	1.26*	ns	*
Seed weight	–	–	0.17**	1.00		
Seeds/mm spike	–	–	0.38***	0		

$: 0.10 > P > 0.05
ns: $P > 0.05$, nt: not testable, – not measured
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Genetic correlations are only given for those pairs of characters where both characters had a significant additive component of variability and a significant additive component in the covariance analysis (Table 4). It appeared that correlations had, except for a single pair of characters, the same sign in both populations. The exception was the correlation of leaf angle and leaf weight, the correlation was not strong in either population, and being the only exception, it may have resulted by chance alone. The correlations found indicated that plants that flowered early had low vegetative growth and high gener-

Table 4. Genetic correlations, as calculated from variance and covariance components for the different effects; in the upper triangle the Wd population and in the lower triangle the Me population. No genetic correlations are given in those cases where an insignificant nuclear component was found in the analysis of variance or in the analysis of covariance (indicated by –)

Character	1	2	3	4	5	6	7	8	9	10	11	12	13
1 Leaf angle		–	–	–	–	−0.27	+0.10	−0.56	–	−0.23	–	–	
2 Flowering date	+0.20		+0.95	+0.99	+0.43	+0.57	−0.95	–	–	+0.90	−0.98	−0.99	
3 No. of rosettes	+0.34	+0.65		+1.0	–	+0.50	−0.88	−0.62	+0.25	+0.74	−0.96	+0.92	
4 No. of leaves	+0.60	+0.41	+0.93		–	+0.43	−0.95	–	+0.43	+0.75	−1.0	−0.95	
5 Leaf length	–	+0.63	+0.67	+0.55		+0.68	−0.54	–	–	+0.81	−0.39	−0.54	
6 Leaf width	–	–	–	–	–		−0.67	–	+0.50	+0.75	−0.58	−0.67	
7 No. of scapes	–	−0.88	−0.91	−0.72	−0.79	–		−0.22	–	−0.95	+0.98	+1.0	
8 Scape length	−0.95	+0.49	–	–	+0.77	–	−0.59		−0.52	–	–	–	
9 Spike length	–	+0.28	–	–	–	–	–	–		–	−0.18	−0.15	
10 Leaf weight	+0.34	+0.72	+0.87	+0.83	+0.16	–	−0.93	+0.46	–		−0.87	−0.94	
11 Gener. weight	−0.44	−0.90	−0.82	−0.70	−0.72	–	+0.96	–	–	−0.96		+0.98	
12 Reprod. effort	−0.39	−0.82	−0.86	−0.77	−0.76	–	+0.95	−0.39	–	−0.98	+1.0		
13 Seed weight	–	−0.97	+0.26	–	+0.69	–	−0.80	+0.52	+0.67	−0.77	–	+0.54	
14 Seeds/mm scape	−0.44	–	+0.23	–	–	–	–	−0.68	−0.91	−0.98	−0.89	−0.25	−0.40

ative growth and, in contrast, plants that flowered late had high vegetative growth and low generative growth.

Discussion

The quantitative genetic analyses applied to the present set of data reveal results that need to be biologically evaluated. The high reciprocal (general and specific) effects for germination and cotyledon length are in accord with expectation (Alexander and Wulff 1985; Weis et al. 1987). In this early life stage of the plants, the condition of the maternal parent is highly important as is the specific combination of the genotype of the maternal parent, paternal parent, and zygote. Mazer (1987) described the paternal and maternal interaction as a self-incompatibility reaction. Gamete or zygote selection has been described by Wolff (1987) as a cause of aberrant genotype ratios for two allozyme loci in an F_2 population of *P. lanceolata,* but they may also be responsible for quantitative differences such as cotyledon length and germination rate.

In the later life stages, nuclear effects are in most cases more important than reciprocal effects. Schmitt and Antonovics (1986) found an identical shift from reciprocal to nuclear effects in *Anthoxanthum odoratum.* The relatively large nuclear (general and specific) effects in *P. lanceolata* are in contrast to the relatively large contribution of reciprocal effects in *Lolium perenne* (Hayward and Breese 1968). This contrast is probably caused by the different reproductive systems of the two species: a strong dependence on generative reproduction by seed in *Plantago* versus vegetative reproduction in *Lolium.*

The differences between populations in the relative contributions of the genetic components to total variability and the differences in heritabilities and relative dominance genetic variance are as expected, given the strong selection through competition in the Me population versus the low effect of selection through the plasticity of the plants and the spatial and temporal heterogeneity in the Wd population. Averaged over all characters, the Me population has a higher heritability and a lower relative dominance than the Wd population. I suggest that natural selection has had a more pronounced effect on fitness characteristics such as flowering date and size characteristics in the more stable and biotically controlled Me population.

Leaf angle was the only character in the Wd population that had a high relative dominance variance component. In the Wd habitat those plants coincidentally growing in more favorable conditions have a higher fitness when possessing an extremely large leaf angle (thus prostrate leaves). Otherwise, leaves and scapes will be eaten immediately and no offspring will arise, or the plant may desiccate easily. In other words: strong directional selection has probably exhausted the additive-genetic variance for this character, resulting in the high dominance ratio.

The results of this study (large dominance components in Me and large additive components in Wd) seem to be at first glance in contrast to the results of Van Groenendael. Van Groenendael (1985b) used cloned plants and calculated *F* values from variance components of among-clone variability and total variability, in order to compare levels of genetic variability among populations. He observed only small differences between the populations – slightly lower *F* values (lower genetic variability) in the Wd population than in the Me population. The *F* values are an indication of the total genetic variability in the populations and are, therefore, the sum of additive and dominance variance components. In the present experiment the sum of these components is also approximately the same for both populations.

The similarity of the genetic correlations of both populations suggests the presence of species-specific correlations. It should be realized, however, that genetic correlations may be influenced by the environment (Law 1979; Silander 1985). In the present greenhouse experiment, specific nutrient limitations may have caused the correlations observed (Bradshaw 1984). In the natural situation of the Me population nutrients may not be limiting for growth but, on the other hand, light interception is probably limiting. As light limitation is strongly influenced by leaf length and leaf angle, this may lead to different correlations. The presence of specific genetic correlations may be of importance for the result of selection on a specific character: unfavorable associations of characters may prevent further evolution (Hegmann and Dingle 1982). In both populations the genetic correlations represent in some cases unfavorable associations of characters. In the Me population (a hayfield), the associations of early flowering, a low vegetative growth, and many short scapes are not favorable, considering the ecological needs in this habitat and the means generally found for these characters in similar habitats. In the pasture population, Wd, the possession of many rosettes is associated with long leaves and a low number of long scapes, which is not a favorable combination.

Differentiation of populations with respect to ecologically important morphological characters has been shown in many experiments (see, e.g., Venable 1984), and has also been observed for several *Plantago* species (Van Dijk and Van Delden 1981; Van Delden 1985; Wolff 1988a). Differences between populations for the relative contribution of the different genetic components, probably caused by effects of natural selection, plasticity, and environmental heterogeneity, have been shown in the present experiment. In the literature it is often stated that a species or a population has either a high level of genetic variability or a high plasticity (Scheiner and Goodnight 1984). It seems there is also another possibility. Plasticity uncouples the gene pool from the short-term selection pressures (Stearns 1980), and this may thus indicate both high plasticity and high genetic variability. In *Plantago* this may be the case in the population Wd of *P. lanceolata* and in the species *P. coronopus* as a whole (Wolff 1988 a).

Travis et al. (1987) state rightly that the conclusions considering selection in the past or present, as drawn from an experiment like the present one, should be confirmed by empirical studies. In our case, the earlier demographic work of Van Groenendael (1985 a, b) and the transplantation experiments of Van Groendael (1985 a) and Wolff (1988 b) were used as a starting point. From these results the important characters of each population were indicated, as well as the importance of environmental heterogeneity and plasticity, and this was confirmed in the present experiment.

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