Theor Appl Genet (1991) 81:119–126

THEORETICAL AND APPLIED GENETICS

Analysis of allozyme variability in three *Plantago* species and a comparison to morphological variability *

K. Wolff

Department of Genetics, Center of Biological Sciences, Kerklaan 30, NL-9751 NN Haren, The Netherlands

Received January 10, 1990; Accepted July 13, 1990
Communicated by P.M.A. Tigerstedt

Summary. The level of electrophoretic variability in three *Plantago* species, *P. major, P. coronopus,* and *P. lanceolata,* was analyzed in relation to their breeding systems and compared with their morphological variability. From each species several populations were analyzed. The outcrossing *P. lanceolata* had the highest level of electrophoretic variability and the lowest population differentiation. The inbreeding *P. major* showed the opposite: a low level of electrophoretic variability and a high population differentiation. *P. coronopus,* with an intermediate breeding system, had an intermediate level of variability and differentiation. In comparing the species, it appeared that *P. coronopus* and *P. major* showed good concordance in the distribution of both kinds of variability, each having only a slightly higher morphological than electrophoretic differentiation between populations. *P. lanceolata* showed a higher morphological than electrophoretic differentiation between populations. A comparison of populations, within species, revealed good concordance of electrophoretic and morphological variability only within *P. coronopus,* while some populations of the other two species had relatively lower morphological variability compared with electrophoretic variability.

Key words: Electrophoresis – Morphological variability – *Plantago* – Mating system

Introduction

Plants are ideal organisms for studying the role of the mating system in evolution, since there is a broad spectrum of mating systems among closely related species. The mating system can influence the genetic structure of populations to a great extent. Genetic structure has been studied experimentally, using electrophoretic data, and also from a theoretical point of view. It is usually the case that outbreeding species generally have high variability within populations and low heterogeneity among populations, whereas inbreeding species mostly possess low genetic variability within populations and significant population differentiation (e.g., Solbrig 1972; Brown 1979; Schoen 1982; Layton and Ganders 1984; Van Dijk et al. 1988). Hamrick et al. (1979) and Loveless and Hamrick (1984) analyzed the correlations of life-history characteristics and ecological factors with electrophoretic variability and genetic structure. Many factors were found to be significantly correlated with genetic variability, presumably through influences on gene flow and effective population size (N_e). A short generation length, animal pollination, low fecundity, limited seed dispersal, and seed dormancy, for example, tend to restrict gene flow, appear to lower N_e, and allow an increased loss of variability and a higher differentiation between (sub)populations (Levin and Kerster 1971). The breeding system, however, is recognized as having the strongest correlation with specific genetic structures, as outlined above (Hamrick 1982; Loveless and Hamrick 1984). Since other life-history characteristics and ecological factors can also be of significant importance, one should be cautious in relating the genetic structure or levels of variability to the breeding systems of the species compared; care should be taken to use closely related species with comparable life-history characteristics and ecological demands (Layton and Ganders 1984).

Electrophoretic variants can be considered in general as neutral markers, upon which the effects of limited gene flow and effective population size can be studied. Differences in morphological and life-history characteristics

* Grassland Species Research Group Publication No. 182

are more directly related to the environment as they are often under selection. Consequently, not only does the mating system affect morphological variability, diversifying selection may also have a profound effect on it. This may lead to increased differentiation between (sub)-populations. If, however, a species copes with environmental variability by means of phenotypic plasticity, selection for plasticity could even result in a lowered phenotypic differentiation compared to electrophoretic differentiation (Marshall and Jain 1968; Wu and Jain 1978; Carey 1983). Studies of the relation between electrophoretic and morphological variability showed different results. A positive correlation has been found in only a few studies. Bryant (1984) claimed that in these cases bottlenecks and/or inbreeding were often involved. Often no correlation was present and in many cases a higher morphological than electrophoretic differentiation was observed (e.g., Turner et al. 1979; Jain et al. 1980; Giles 1984; Ryman et al. 1984; Schwaegerle et al. 1986).

In the present study three *Plantago* species, *P. major, P. coronopus,* and *P. lanceolata,* are used to study electrophoretic variability and to evaluate the relationship between electrophoretic and morphological differentiation. This was realized by measuring electrophoretic and morphological variability in several populations within each species. For all three species populations from contrasting habitats were used. The species and populations sampled are described by Wolff (1991). In this way comparisons could be made within species and among species. The *Plantago* species have a diversity of mating systems: *P. lanceolata* is self-incompatible (outcrossing rate $t=1.0$), *P. coronopus* and *P. major* are self-compatible. *P. major* appeared to be highly self-pollinating ($t=0.0-0.1$), whereas *P. coronopus* usually had intermediate outcrossing rates ($t=0.5-0.9$) (Van Dijk et al. 1988; Wolff et al. 1988). Van Dijk et al. (1988) described the genetic structure of the three species using electrophoresis: it appeared that *P. major* showed the highest population differentiation, *P. lanceolata* the lowest, whereas *P. coronopus* had an intermediate position, which is in accordance with the general findings for species with comparable mating systems (Brown 1979). The measurement and analysis of morphological variation was described in a preceding paper (Wolff 1991). In the present study I will try to answer the question of whether the effect of the mating system on morphological variability is as important as that on electrophoretic variability, or whether other components, such as selection or plasticity, are als significant.

Materials and methods

Populations sampled

Adult *P. major* plants were sampled from five populations, and *P. coronopus* and *P. lanceolata* plants from four populations. Two of the *P. major* populations belonged to the subspecies *major,* whereas the other three populations belonged to subspecies *pleiosperma.* Details on species and population characteristics are given in Wolff (1991).

Electrophoresis

Electrophoresis was carried out on horizontal polyacrylamide and starch gels as described by Van Dijk and Van Delden (1981), Wolff (1987) and Hofman (1988). The inheritance of the polymorphic enzyme variants used in the analysis was described by Van Dijk and Van Delden (1981), Van Dijk (1985), and Van Dijk et al. (1988).

Calculation of electrophoretic variability and outcrossing rates

To determine electrophoretic variability, 11 variable loci were used for *P. lanceolata,* 8 loci were used for *P. coronopus,* and 7 for *P. major.* The total number of loci was 36 in *P. major* and *P. coronopus* and 39 in *P. lanceolata* (Van Dijk et al. 1988). Allozyme variability in the populations was expressed as H_e, the mean expected heterozygosity over all loci (Nei 1975). The variance of H_e is the variance over loci according to Layton and Ganders (1984). Differences between populations in H_e were tested using the T-method of multiple comparisons among means (Sokal and Rohlf 1981). H_s in the mean H_e over populations of a species. Total variability of a species was expressed as H_T, the total expected heterozygosity in a species. The relation of variability within and between populations is given by $H_T = H_s + D_{ST}$, in which D_{ST} is the differentiation among populations (Nei 1973). The relative contribution of among- and within-population components to the total variability are expressed by H_s/H_T and D_{ST}/H_T (Loveless and Hamrick 1984; Layton and Ganders 1984).

Outcrossing rates in *P. major* and *P. coronopus* were calculated both from the fixation index and from a progeny analysis. The progeny analysis was performed with a multilocus estimation method (Shaw et al. 1981) and with a χ^2 iteration method, and was analogous to the method used in an earlier paper for *P. coronopus* (Wolff et al. 1988). The adult plant allele frequencies were used as pollen-pool allele frequency estimates. In each population, natural progenies from four to seven adult plants were analyzed, for a total per population of 153-579 descendants. Few mothers were used because of low frequencies of rare alleles; in such a case, it is more efficient to analyze progenies of only those mothers that have the rare genotype, presuming no allozyme-genotype specific outcrossing rates. One to four allozyme loci were used, depending on the variability available and the genotypes of the adult plants. The low number of loci used caused no problems, as *P. major* has low outcrossing rates (Shaw and Brown 1982). In populations Om (*major*) and Ud (*coronopus*), electrophoretic variability was too low to estimate outcrossing rates. The significance of the differences between outcrossing rates was tested using the T-method of multiple comparisons among means (Sokal and Rohlf 1981).

Results and discussion

From each population, as many adult plants as possible were analyzed for the polymorphic enzyme loci. For some populations, results from Van Dijk et al. (1988) were taken. Genotype and allele frequencies are not presented here, but are available on request. The electrophoretic variability and outcrossing rates in the populations are shown in Table 1. Further details on *P.*

Table 1. Levels of allozyme variability in populations of three *Plantago* species. P is the percentage of polymorphic loci, $\overline{H_e}$ is the mean gene diversity per locus, F is the fixation index and t_F and t_m are outcrossing rates, calculated from the fixation index or from a multilocus estimation method, respectively

Species	Population	P	$\overline{H_e}$	F	t_F	t_m
P. major	An ($n=48$)	14	0.052	0.889	0.059	0.013
	Kh ($n=42$)	14	0.039	0.948	0.027	0
	Om ($n=75$)	8	0.010	–	–	–
	Wd ($n=37$)	17	0.028	0.747	0.145	0.076
	Wv ($n=42$)	14	0.023	0.750	0.143	0.016
P. coronopus	Ud ($n=70$)[a]	0	0	–	–	–
	Wd ($n=135$)[a]	31	0.093	0.055	0.896	0.985[b]
	Sd ($n=20$)	8	0.024	−0.184	1	0.345
	Kw ($n=149$)[a]	31	0.088	0.149	0.741	0.932
P. lanceolata	Ud ($n=97$)[a]	28	0.104	0.118		
	Wd ($n=93$)[a]	36	0.124	0.084		
	Sp ($n=45$)	23	0.082	0.102		
	He ($n=90$)[a]	31	0.131	−0.011		

[a] Data from Van Dijk et al. (1988)
[b] Data from Van Dijk et al. (1988), as calculated from a gene flow model

Table 2. Distribution of allozyme variability in three *Plantago* species: within population (H_S) and between populations (D_{ST}) are both expressed as a percentage (given in brackets) of total variability (H_T) (data from Van Dijk et al. 1988)

Species	H_S	D_{ST}	H_T
P. lanceolata	0.127 (96)	0.006 (4)	0.133
P. coronopus	0.088 (89)	0.012 (11)	0.100
P. major (total)	0.047 (72)	0.018 (28)	0.065
P. major major	0.040 (90)	0.004 (10)	0.044
P. major pleiosperma	0.050 (93)	0.004 (7)	0.054

coronopus are presented in Wolff et al. (1988). Differences between populations in outcrossing rates were present both in *P. major* and in *P. coronopus* while this difference was larger in *P. coronopus*.

The expected mean heterozygosity ($\overline{H_e}$) was taken as a measure of variability, being a good estimator of allozyme variability (Nei 1975; Van Dijk 1985). The distribution of the allozyme variability in the three species was calculated from Van Dijk et al. (1988) (Table 2). *P. lanceolata* had the highest total and within-population variability. *P. major* had the highest contribution of the between-population component when both subspecies were involved. When the two subspecies of *P. major* were considered separately, *P. coronopus* showed the highest population differentiation.

Electrophoretic variability and outcrossing rates

The electrophoretic variability and its partitioning in the three *Plantago* species studied meets the expectations

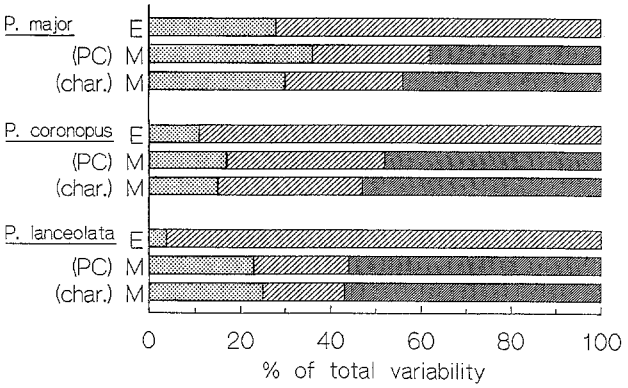

Fig. 1. Partitioning into a between-population and a within-population component of variability for electrophoretic (E) and morphological (M) variability expressed in percentages of total variability. Morphological variability is presented both as mean variability over a character set common to all three species and over PC for the same character set. For morphological variability, the within-family component is also indicated between populations; within populations; within families

derived from the breeding systems (e.g., Levin 1978; Brown 1979). The outcrossing species (*P. lanceolata*) has the highest total variability, the highest within-population variability, and the lowest between-population variability. The selfing species *P. major*, on the other hand, has the lowest within-population variability and the highest between-population differentiation.

It was striking that in *P. major* all outcrossing rates calculated from the fixation index were higher than outcrossing rates calculated from a progeny analysis, possibly indicating higher survival of the more heterozygous (outcrossed) individuals, although other explanations are also possible (see Wolff and Haeck 1990). Local differentiation for instance may give an underestimate of t, both in the fixation index method and in the multilocus progeny analysis method. Further, gametic disequilibrium, as probably present in most *P. major* populations, gives a small underestimation of t using a multilocus estimation procedure (Shaw et al. 1981).

Between-species comparison

For the level and partitioning of morphological variability in the three *Plantago* species, the same trend is partly found as that for electrophoretic variability (Wolff 1991). A summary of the results is given in Fig. 1, where variability is presented as a percentage of total variability and in Table 3, where several measures of variability are given. The coefficients of variability of characters (CV), the standard deviations of individual component scores on the principal component axes (PC), heritability estimates of characters (h^2), and estimations of the additive component of variability of PC (V_A/V_P PC) were calculated and used in the analysis as an average or as an average ranking (R) over characters. Differences in mat-

Table 3. Summary of electrophoretic (E) and morphological (M) variability found in the three species, expressed as total variability, between-population variability, and a mean within-population variability. Morphological variability is calculated as a mean or mean rank over the common subset of characters or as a mean of PC of the common character set. Species are ranked in decreasing order

Total variability	E (H_T)	lanc (0.133)	cor (0.100)	maj (0.065)
	M ($\bar{R}$ CV_S)	lanc (2.64)	cor (1.82)	maj (1.55)
Between populations	E (D_{ST})	maj (0.018)	cor (0.012)	lanc (0.006)
	M (mean%)	maj (30)	lanc (25)	cor (15)
	M (% PC)	maj (36)	lanc (23)	cor (17)
Within populations	E (H_S)	lanc (0.127)	cor (0.088)	maj (0.047)
	M ($\bar{R}$ CV_P)	lanc (2.64)	cor (2.00)	maj (1.36)
	M ($\bar{R}$ h^2)	lanc (2.40)	cor (1.80)	maj (1.80)
	M ($\overline{V_A/V_P}$ PC)	lanc (0.51)	cor (0.46)	maj (0.38)

ing systems seem to be associated with the level and the partitioning of variability, both electrophoretic and morphological, at the species level. However, a closer examination of Fig. 1 shows that for *P. major* and *P. coronopus,* levels of interpopulational variability are only slightly higher for morphological characters than for electrophoretic variation (30–36% versus 28% and 15–17% versus 11%, respectively). For *P. lanceolata,* however, there is a much higher degree of differentiation between populations at the morphological level than at the electrophoretic level (23–25% versus 4%). In this species it is probable that the populations are locally adapted, causing pronounced differentiation in morphological characters. *P. major* populations were only slightly more differentiated than *P. lanceolata* populations.

The agreement between electrophoretic and morphological differentiation and the absence of ecotypic differentiation in *P. coronopus* could be caused by plasticity for morphological characters. Such adaptive plasticity was hypothesized for *P. coronopus* by Schat et al. (1984) and Wolff (1991).

Within-species comparison

The measures for electrophoretic and morphological variability and the outcrossing rates (t_m) in the different populations within each species are summarized in Table 4. Only for *P. coronopus* is there concordance for the levels of electrophoretic and morphological variability, represented by $\overline{H_e}$, and rank of heritabilities, respectively: the correlation coefficient is 0.86 ($P=0.057$) and the nonparametric correlation is 1.00 ($P=0$). This suggests that in this species both kinds of variability may be influenced by the same forces in approximately the same way. The extremely low variability and the different morphology of the inland population (Ud) could be caused by an extremely small number of founders. Another, less likely, explanation is that in Ud selection favours both morphological and physiological extremity, whereas in the other populations, intermediate optima or fluctuating optima exist. This population is fully isolated from other (coastal) populations. The differences detected between the populations are, in most cases, caused by the deviating characteristics of the Ud population, e.g., an invariable and high degree of toothing. As this characteristic does not seem to have much ecological relevance, it may well be the result of the founder event. In *P. coronopus* a positive relation is found between outcrossing rates and variability. Although the number of populations is too small to draw firm conclusions, this again suggests that higher levels of inbreeding are associated with lower variability.

For the other two species, *P. major* and *P. lanceolata,* there is no concordance between morphological and electrophoretic variability; neither parametric nor nonparametric correlations are significant ($P>0.30$). Random drift and founder events influence both kinds of variability; therefore, at least in part, different forces must act on morphological and electrophoretic variants. Alternatively, the relative importance of the forces varies due to the presumed overall neutrality of allozyme variants and selection for particular sets of morphological variants. Selection is strongly directional for particular morphological characters in some populations, leading to a loss of morphological variability (Wolff and Van Delden 1987; Wolff 1991). In *P. major* the population with the lowest $\overline{H_e}$ (Om) has a high total variability and an intermediate genetical, morphological variability. The population with the lowest t_m has a high variability; whithin this species there seems to be no relation between levels of outcrossing and variability. Selection is probably an important factor for morphological differentiation. In highly uniform sites only a limited number of genotypes will be left, whereas in sites in which the habitat is patchy, there is a possibility for microdifferentiation (Allard et al. 1968; Carey 1983): Especially in population Wv, occurring in a harsh and uniform habitat, strong unidirectional selection for an extreme trodding- and soil compaction-resistant ecotype is probably responsible for the loss of morphological variability. Differences between populations within one subspecies are often as large as between subspecies; see, e.g., the number of seeds per capsule. Therefore, each population can be seen as a specialized ecotype, allowing several subdivisions within the subspecies. Population Wd is a *P. major* ssp. *major* roadside type, whereas population Wv is a lawn type (Van Dijk 1984). In *P. major* ssp. *pleiosperma,* the population An comes from a riverside, characteristically with a higher number of seeds per capsule than the other two, more ruderal, *pleiosperma* populations. Because many ecotypes within a subspecies can be distinguished in *P.*

Table 4. Summary of electrophoretic (E), morphological (M) variability, and outcrossing rates (t_m) found in the populations of the three species. Rank orders for CV_P, standard deviation of PC, h^2 of characters and of PC are determined. In the right column populations are given in decreasing order: populations connected by a common line are not significantly different at the 5% level (Student-Newman-Keul's test). Populations for which it was not possible to obtain an estimate of the outcrossing rate are indicated by ‡

Plantago major	Variability					Rankorder				
Population	An	Kh	Wd	Wv	Om					
E $\overline{H_e}$	0.052	0.039	0.028	0.023	0.010	An	Kh	Wd	Wv	Om
M $\bar{R}$ CV_P	3.38	2.88	3.62	1.58	3.74	Om	Wd	An	Kh	Wv
$\overline{SD}$ PC	0.82	0.83	0.84	0.59	0.87	Om	Wd	Kh	An	Wv
M $\bar{R}$ h^2	3.14	3.69	3.00	1.88	3.29	Kh	Om	An	Wd	Wv
$\overline{V_A/V_P}$ PC	0.32	0.42	0.26	0.26	0.29	Kh	An	Om	Wd	Wv
t_m	0.013	0	0.076	0.016	‡	Wd	An	Wv	Kh	
Plantago coronopus										
Population	Wd	Kh	Sd	Ud						
E $\overline{H_e}$	0.093	0.088	0.024	0		Wd	Kh	Sd	Ud	
M $\bar{R}$ CV	2.68	2.96	3.36	1.00		Sd	Kh	Wd	Ud	
$\overline{SD}$ PC	0.94	0.87	1.24	0.57		Sd	Wd	Kh	Ud	
M $\bar{R}$ h^2	3.11	2.75	2.61	1.54		Wd	Kh	Sd	Ud	
$\overline{V_A/V_P}$ PC	0.66	0.48	0.50	0.31		Wd	Sd	Kh	Ud	
t_m	0.98	0.93	0.34	‡		Wd	Kh	Sd		
Plantago lanceolata										
Population	He	Wd	Ud	Sp						
E $\overline{H_e}$	0.131	0.124	0.104	0.102		He	Wd	Ud	Sp	
M $\bar{R}$ CV	2.98	2.33	1.90	2.79		He	Sp	Wd	Ud	
$\overline{SD}$ PC	0.94	0.92	0.84	0.80		He	Wd	Ud	Sp	
M $\bar{R}$ h^2	1.98	2.95	2.48	2.60		Wd	Sp	Ud	He	
$\overline{V_A/V_P}$ PC	0.46	0.63	0.48	0.51		Wd	Sp	Ud	He	

major subdivision different from the subspecies division seems relevant (see Van Dijk 1985).

The *P. lanceolata* populations are more homogeneous with respect to the levels of electrophoretic variability than the inbreeding species *P. major*. However, discrepancies between the level of electrophoretic and morphological variability are also present here. He, the population with high electrophoretic variability, has the lowest $\overline{h^2}$ of the four populations. Strong directional selection in a homogeneous habitat may be responsible for the low morphological variability here, too. This finding is in accordance with results from Wolff and Van Delden (1987), who concluded that directional selection and favorable genetic correlations caused the reduction of additive-genetic morphological variability in this population. The completely isolated *P. coronopus* population from Ud has an extremely low variability, and this holds partly true also for the Ud population of *P. lanceolata*. Both species have probably experienced comparable historical events: a small founder population and isolation from other populations. These effects most likely reduced genetic variability to a larger extent in the self-compatible species *P. coronopus* than in the self-incompatible *P. lanceolata*.

Concluding remarks

The three *Plantago* species used in this study are closely related. Since the different species have been, as much as possible, collected from the same sites, relevant comparisons can be made. The species do not have identical life-history characteristics or ecological demands. *P. coronopus* often behaves as an annual or biennial, *P. lanceolata* is a perennial species, while *P. major* can have varying generation lengths from annual (e.g., the riverside ecotype of the ssp. *pleiosperma*) to perennial. Hamrick et al. (1979) found that species with shorter generation lengths often possessed less electrophoretic variability. The level of electrophoretic variation in *P. coronopus* is considerable and is not diminished by the effect of a short life cycle. The shorter lifetime cannot, therefore, be the cause of the lack of morphological differentiation due to low genetic variability.

How the different levels of outbreeding evolve remains an open question. The consequences of outcrossing and of self-pollination have been discussed by several authors, e.g., Jain (1976) and Schemske (1983). For *P. lanceolata,* the short-term and the long-term advantages of outcrossing seem to be valid, namely, the maintenance of variability and the avoidance of deleterious effects of homozygosity (Van Damme 1983), respectively. For *P. major,* short-term adaptation to specific local stress conditions seems advantageous, while in many populations variability is probably maintained by the patchy pattern of selection. *P. coronopus* has an intermediate position. Local morphological adaptation is apparently not profitable or not possible for this species as no population differentiation occurs (Waite and Hutchings 1982; Wolff 1991). To favor complete outcrossing a strong advantage by heterosis is necessary (Schemske 1983). From results of a garden experiment in which progeny obtained from selfing was compared to outcrossed progeny, this advantage seems not to be present to such an extent (K. Wolff, unpublished results). The intermediate position of *P. coronopus* between obligate selfing and obligate outcrossing allows an increased probability of fertilization in low density populations, while as much of the benefit of heterotic effects as is possible is obtained by outcrossing.

The evolutionary fate of highly inbreeding species such as *P. major* has been debated extensively by many authors (e.g., Stebbins 1957; Allard et al. 1968; Jain 1976). They concluded that inbreeding has rarely, if ever, allowed new lines of adaptations and may be seen as an evolutionary dead end. This may be true on a large evolutionary scale for strict selfers, but does not hold true when populations on a small time scale are considered. Most predominantly selfing species have variable outcrossing rates. An outburst of outcrossing, even a rare one, may be sufficient to maintain variability and a potency for (micro)evolution (Adams and Allard 1982). Mean gene diversity in selfers may not be so different from diversity in outcrossers; when genotype diversity over all loci is considered, however, often only a few genotypes appear to be present in a particular population of the selfing species (Layton and Ganders 1984; Golenberg and Nevo 1987; this study, results not shown). Multilocus associations of allozyme loci seem to be more general in selfers than in outcrossers (Brown 1979). It is logical to assume that multilocus associations for morphological characters are also present in selfers but not in outcrossers, as was shown to be the case in studies by Van Dijk (1984) and Wolff (1987). These associations make differentiation between populations in selfers more probable. One can think of populations of a selfing species as being composed of many rather inbred lines with a low within-family component of variability. The number of different inbred lines in a population depends on population size, habitat diversity, and the modes and severity of selection (Allard et al. 1968; Layton and Ganders 1984). The relatively high genetic variability of morphological characters implies much potential for future evolution in selfers (Abbott 1986). However, one should be cautious: significant heritabilities found in the greenhouse may be hidden by environmental causes in the field, and unfavorable genetic correlations may prevent further evolution (Mitchell-Olds and Rutledge 1986).

The levels of electrophoretic and morphological differentiation as found between populations within species may partly be influenced by statistical methods and the morphological characters used. The fact that no discrepancy between the two types of variation is found in one of the species (*P. coronopus*) but is present in the other two species, however, makes explanations other than the techniques used more probable. Morphological variability more than likely evolves by a selective mode, while electrophoretic variability is thought to be mostly neutral (Turner et al. 1979). In some selfing species, adaptive plasticity can be seen to be a result of selection, namely, as a solution for coping with environmental heterogeneity, e.g., in *Bromus mollis* (Wu and Jain 1978) and in *Avena barbata* (Marshall and Jain 1968). *P. coronopus,* a self-compatible species with relatively high outcrossing rates, copes with environmental differences by adaptive plasticity (for a definition, see Wu and Jain 1978). Van Dijk (1985) states that *P. lanceolata* is plastic (a generalist), compared to the specialist *P. major.* However, our study reveals genetic differentiation in *P. lanceolata,* whereas for *P. coronopus* adaptive plasticity is plausible. Although caution should be exercised when comparing electrophoretic and morphological variability, since the relationships between genes and morphology are unknown (Lewontin 1984), between-species comparisons seem to be fruitful. The mating system has a strong influence on the genetic structure of populations and species, as seen from the electrophoretic data. Morphological

variability and its distribution is influenced by the mating system, but is also dependent on the extent to which a species shows adaptation through genetic differentiation or through plasticity.

Acknowledgements. I wish to thank W. Van Delden and S. Tonsor for their helpful suggestions and comments on this paper. These investigations were supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by The Netherlands Organization for the Advancement of Pure Research (ZWO).

References

Abbott RJ (1986) Life-history variation associated with the polymorphism for capitulum type and the outcrossing rate in *Senecio vulgaris* L. Heredity 56:381–391

Adams WT, Allard RW (1982) Mating system variation in *Festuca microstachys*. Evolution 36:591–595

Allard W, Jain S, Workman JL (1968). The genetics of inbreeding populations. Adv Genet 14:55–131

Brown AHD (1979) Enzyme polymorphism in plant populations. Theor Popul Biol 15:1–42

Bryant EH (1984) A comparison of electrophoretic and morphometric variability in the face fly, *Musca autumnalis*. Evolution 38:455–458

Carey K (1983) Breeding system, genetic variability, and response to selection in *Plectritis* (Valerianaceae). Evolution 37:947–956

Giles BE (1984) A comparison between quantitative and biochemical variation in the wild barley *Hordeum murinum*. Evolution 38:34–41

Golenberg EM, Nevo E (1987) Multilocus differentiation and population structure in a selfer, wild emmer wheat, *Triticum dicoccoides*. Heredity 58:451–456

Hamrick JL (1982) Plant population genetics and evolution. Am J Bot 69:1685–1693

Hamrick JL, Linhart YB, Mitton JB (1979) Relationship between life-history characteristics and electrophoretically detectable genetic variation in plants. Annu Rev Ecol Syst 10:173–200

Hofman A (1988) Starch gel electrophoresis: a tool for studying the phylogenetic systematics and population genetics of mosses. In: Glime JM (ed) Methods in bryology. Proc Bryol Methods Workshop, Mainz, Hattori Botanical Laboratory, Nichinan, Japan, pp 353–358

Jain SK (1976) The evolution of inbreeding in plants. Annu Rev Ecol Syst 7:469–495

Jain SK, Wu L, Vaidya KR (1980) Levels of morphological and allozyme variation in Indian amaranths: a striking contrast. J Hered 71:283–285

Layton CR, Ganders FR (1984) The genetic consequences of contrasting breeding systems in *Plectritis* (Valerianaceae). Evolution 38:1308–1325

Levin DA (1978) Genetic variation in annual *Phlox:* self-compatible versus self-incompatible species. Evolution 32:245–263

Levin DA, Kerster HW (1971) Neighborhood structure in plants under diverse reproductive methods. Am Nat 105:345–354

Lewontin RC (1984) Detecting population differences in quantitative characters as opposed to gene frequencies. Am Nat 123:115–124

Loveless MD, Hamrick JL (1984) Ecological determinants of genetic structure in plant populations. Annu Rev Ecol Syst 15:65–95

Marshall DR, Jain SK (1968) Phenotypic plasticity of *Avena fatua* and *A. barbata*. Am Nat 102:457–467

Mitchell-Olds T, Rutledge JJ (1986) Quantitative genetics in natural plant populations: A review of the theory. Am Nat 127:379–402

Nei M (1973) Analysis of gene diversity in subdivided populations. Proc Natl Acad Sci USA 70:3321–3323

Nei M (1975) Molecular population genetics and evolution. North-Holland, Amsterdam

Ryman N, Lagercrantz U, Andersson L, Chakraborty R, Rosenberg R (1984) Lack of correspondence between genetic and morphologic variability patterns in Atlantic herring (*Clupea harengus*). Heredity 53:687–704

Schat H, Bos AH, Scholten M (1984) The mineral nutrition of some therophytes from oligotrophic slack soils. Acta Oecologia/Oecol Plant 5 No. 2:119–131

Schemske DW (1983) Breeding system and habitat effects on fitness components in three neotropical *Costus* (Zingiberaceae). Evolution 37:523–539

Schoen DJ (1982) Genetic variation and the breeding system of *Gilia achilleifolia*. Evolution 36:361–370

Schwaegerle KH, Garbutt K, Bazzaz FA (1986). Differentiation among nine population of *Phlox*. I. Electrophoretic and quantitative variation. Evolution 40:506–517

Shaw DV, Brown AHD (1982) Optimum number of marker loci for estimating outcrossing in plant populations. Theor Appl Genet 61:321–325

Shaw DV, Kahler AL, Allard RW (1981) A multilocus estimator of mating system parameters in plant populations. Proc Natl Acad Sci USA 78:1298–1302

Sokal RR, Rohlf FJ (1981) Biometry, W. H. Freeman, San Francisco

Solbrig OT (1972) Breeding system and genetic variation in *Leavenworthia*. Evolution 26:155–160

Stebbins GL (1957) Self-fertilization and population variability in the higher plants. Am Nat 91:337–354

Turner JRG, Johnson MS, Eanes WF (1979) Contrasted modes of evolution in the same genome: allozymes and adaptive change in *Heliconius*. Proc Natl Acad Sci 76:1924–1928

Van Damme JMM (1983) Gynodioecy in *Plantago lanceolata* L. II. In heritance of three male sterility types. Heredity 50:253–273

Van Dijk H (1984) Genetic variability in *Plantago* species in relation to their ecology. 2. Quantitative characters and allozyme loci in *P. major*. Theor Appl Genet 68:43–52

Van Dijk H (1985) Genetic variability in *Plantago* species in relation to their ecology. PhD thesis, University of Groningen, The Netherlands

Van Dijk H, Van Delden W (1981) Genetic variability in *Plantago* species in relation to their ecology. 1. Genetic analysis of the allozyme variation in *Plantago major* subspecies. Theor Appl Genet 60:285–290

Van Dijk H, Wolff K, De Vries A (1988) Genetic variability in *Plantago* species in relation to their ecology. 3. Structure of populations of *P. major, P. lanceolata,* and *P. coronopus*. Theor Appl Genet 75:518–528

Waite S, Hutchings MJ (1982) Plastic energy allocation patterns in *Plantago coronopus*. Oikos 38:333–342

Wolff K (1987) Genetic analysis of ecological relevant morphological variability in *Plantago lanceolata* L. 2. Localization of quantitative trait loci. Theor Appl Genet 73:903–914

Wolff K (1991) Genetic analysis of morphological variability in three *Plantago* species with different mating systems. Theor Appl Genet 81:111–118

Wolff K, Haeck J (1990) Genetic analysis of ecological relevant morphological variability in *Plantago lanceolata* L. VI. Relation between allozyme heterozygosity and some fitness components. J Evol Biol 3:243–255

Wolff K, Van Delden W (1987) Genetic analysis of ecological relevant morphological variability in *Plantago lanceolata* L. I. Population characteristics. Heredity 58:183–192

Wolff K, Friso B, Van Damme JMM (1988) Outcrossing rates and male sterility in natural populations of *Plantago coronopus*. Theor Appl Genet 76:190–196

Wu KK, Jain SK (1978) Genetic and plastic response in geographic differentiation of *Bromus rubens* populations. Can J Bot 56:873–879