**Genetic Variation, Breeding System Evolution, and Conservation of the Narrow Sand Dune Endemic Stellaria arenicola and the Widespread S. longipes (Caryophyllaceae)**

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# GENETIC VARIATION, BREEDING SYSTEM EVOLUTION, AND CONSERVATION OF THE NARROW SAND DUNE ENDEMIC *STELLARIA ARENICOLA* AND THE WIDESPREAD *S. LONGIPES* (CARYOPHYLLACEAE)[1]

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Genetic variation was examined by electrophoresis in 14 populations of *Stellaria arenicola,* an endemic of the Athabasca sand dunes in northern Saskatchewan, Canada, and seven populations of *S. longipes,* its progenitor. Three of the *S. longipes* populations were sympatric with the endemic. Populations of the endemic were found to have fewer alleles per polymorphic locus (2.21 vs. 2.37), fewer polymorphic loci (29.9 vs. 33.8), and lower genetic diversity (0.087 vs. 0.107) than populations of the progenitor. Genetic identities for all pairs of populations were high (0.932 to 1.000). The endemic had one novel allele and shared ten alleles with progenitor populations from the sand dunes that were not found in other populations of *S. longipes.* Populations of both species were found to partition most of their genetic variation within populations. An investigation of the multilocus outcrossing rates revealed that *S. arenicola* had higher rates of selfing and biparental inbreeding than *S. longipes.* This study suggests that partial genetic isolation through a shift in the breeding system, in addition to previously reported strong directional selection, has been important in the sympatric evolution of the endemic *S. arenicola.* The close genetic relationship between populations of *S. arenicola* and *S. longipes* found on the Athabasca sand dunes supports the suggestion that the endemic evolved while sympatric to the gene pool of the progenitor species that is found presently in the region.

Populations that are reproductively isolated may gradually exhibit genetic differentiation. For speciation to occur among sexual organisms, barriers to gene flow are generally required (Grant, 1981). Sympatric speciation represents a special case in the evolution of new species. There are few studies that have investigated the genetics or ecology of recently evolved sympatric species of plants. Shifts in breeding system accompanied by chromosomal changes (Gottlieb, 1973, 1974; Gottlieb and Pilz, 1976) and strong natural selection (Macdonald et al., 1987) were responsible for the evolution of some sympatric species. Evidence from population genetic studies generally supports the prediction that derivative species will have lower levels of genetic diversity than the progenitor (Gottlieb, 1973, 1974; Crawford and Smith, 1982b; Crawford, Ornduff, and Vasey, 1985; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989). If recently evolved sympatric species are still capable of limited gene flow with the progenitor, however, then they have the opportunity to acquire genetic variation from the larger gene pool after speciation has occurred.

Recently evolved species can often be classified as narrow endemics owing to their restricted geographic ranges. Knowledge of the ecology and genetics of narrow endemics is still limited (Karron, 1987; Pleasants and Wendel, 1989), but could provide relevant information on the fate of rare and endangered species. Plant species with limited ranges generally exhibit lower levels of genetic polymorphism (Karron, 1987; Hamrick and Godt, 1989). This reduced genetic variation has been attributed to strong directional selection, genetic drift, and/or the founder effect (Karron, 1987).

The boreal forest and arctic tundra have a variety of geological features that tend to be correlated with high rates of speciation (Kruckeberg, 1986), but these regions have very few endemic taxa (Kruckeberg and Rabinowitz, 1985). The Athabasca sand dunes in northern Saskatchewan, however, harbor one of the most important collections of rare plants in Canada, including ten endemic taxa (Raup and Argus, 1982). *Stellaria arenicola* Raup (Macdonald et al., 1987) and *Salix planifolia* ssp. *tyrrellii* (Raup) Argus (Argus and Steele, 1979) are the only endemics investigated to date with respect to habitat and morphological differentiation. Both of these endemics have evolved in sympatry with their progenitor taxon, and natural selection and partial genetic isolation have been implicated in their evolution.

The endemic plants of the Athabasca sand dunes provide an excellent opportunity to investigate the role of genetic isolation and natural selection as mechanisms responsible for speciation in sympatric species pairs. This study was conducted to test whether *Stellaria arenicola,* a recently evolved species and a narrow endemic, had lower levels of genetic variation than its widespread progenitor *S. longipes* Goldie. In order to measure the importance of isolating mechanisms in the evolution of the endemic, we evaluated the breeding system of the two species using progeny arrays to estimate the multilocus outcrossing rates. The relationship of *S. arenicola* to pop-

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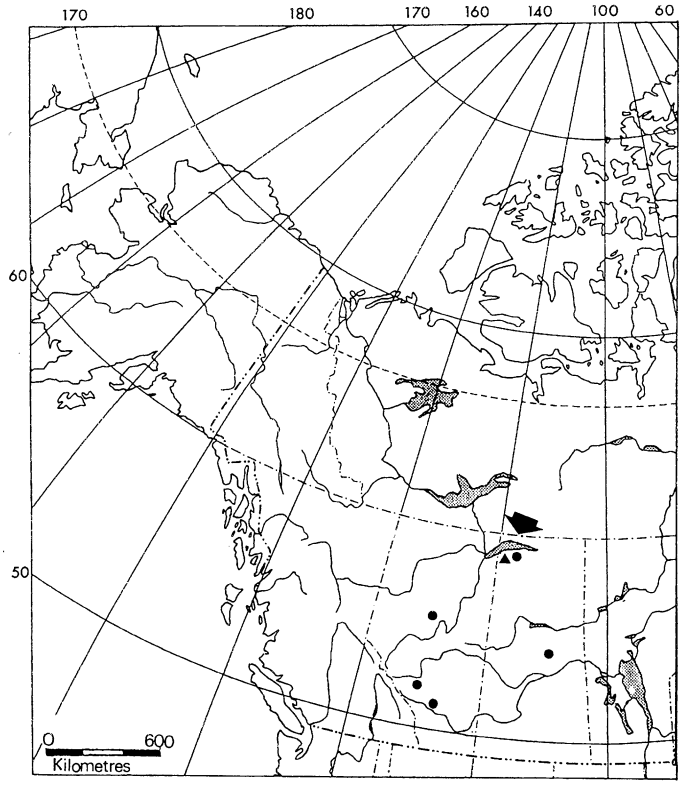


Fig. 1. Location of populations of the widespread *Stellaria longipes* (circles) and the endemic *S. arenicola* (triangle) from western Canada used in this study. The arrow points to the sand dunes on the south shore of Lake Athabasca.

ulations of *S. longipes* was of interest to test whether evidence suggested the endemic evolved from sympatric populations on the sand dunes or from populations presently found away from the sand dunes. Finally, we wanted to contribute to the growing body of knowledge concerning genetic diversity in rare species.

## MATERIALS AND METHODS

***Population sampling***—The locations of the populations that were sampled for this study can be found in Figs. 1 and 2. The numbers of populations and individuals, respectively, examined for each species were: *Stellaria arenicola* (14, 302), *S. longipes*—dunes (3, 58), and *S. longipes*—other (4, 83). Populations of the endemic *S. arenicola* were sampled throughout the range of the species. Populations of the related progenitor *S. longipes* were collected from the borders of the dune fields (Fig. 2) and in other habitats in Alberta and Saskatchewan (Fig. 1). Voucher specimens were deposited in the herbarium at the University of Alberta (ALTA). Seeds were collected from up to 50 individuals in each population. In addition, we collected progeny arrays that consisted of at least 30 seeds from each of 24 hermaphroditic individuals in two populations of each species. The collections were transported to the phytotron at the University of Alberta where the seeds were germinated and seedlings grown in soil. For the population collections, one progeny per parent was used in the electrophoretic analysis. For the progeny arrays, up to 24 progeny per mother plant were used.

***Electrophoresis***—Standard methods for starch gel electrophoresis were employed in this study (Soltis et al., 1983). Fresh pieces of actively growing leaf tissue were ground in cold Tris-HCl extraction buffer: 0.1 M Tris-HCl, pH 7.5, 4.0 mM 2-mercaptoethanol, 1.0 mM EDTA (disodium salt), 0.2 M sucrose, 0.6% polyvinyl-poly-pyrrolidone (5:1 ratio of 40 K:360 K m.w.), 2% PEG (8 K m.w.), 0.1% BSA, and 2.0 mM ascorbic acid. The supernatant was absorbed onto filter paper wicks, frozen at −20 C overnight, and electrophoresed the following morning. The filter paper wicks were loaded onto 12% starch gels.

Three systems were used to resolve the isozymes in this study. System I: gel buffer of one part 0.038 M LiOH·$H_2O$-0.188 M boric acid (pH 8.3), and nine parts 0.045 M Tris-7.0 mM citric acid (pH 8.4) (Soltis et al., 1983); electrode buffer containing only the lithium-borate constituent. System II: electrode buffer of 0.4 M citric acid·$H_2O$ (trisodium salt), 1.0 M HCl to pH 7.0; gel buffer of 0.02 M L-histidine·HCl monohydrate, 1.0 M NaOH to pH 7.0 (Soltis et al., 1983). System III: electrode buffer of 0.065 M L-histidine (free base)-0.065 M citric acid·$H_2O$ (pH 6.5); gel buffer containing electrode buffer and distilled water in a 1:3 ratio, respectively (Cardy, Stuber, and Goodman, 1983). System I was run at 50 mA for 30 min, then at 60 mA for 4–5 hr. System II was run at 100 mA for 30 min, then at 110 mA for 4–5 hr. System III was run at 30 mA for 4–5 hr. The electrophoresis was performed at 4 C.

Fifteen enzyme systems were resolved in this study. Leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), glutamate oxalate-transferase (GOT), aldolase (ALDO), aconitase (ACO), alcohol dehydrogenase (ADH), and glutamate dehydrogenase (GDH) were resolved on system I. Malate dehydrogenase ([NAD]MDH), 6-phosphogluconate (PGD), phosphoglucose mutase (PGM), and malate dehydrogenase ((NADP)ME) were resolved on system II. Menadione reductase (MNR), isocitrate dehydrogenase (IDH), shikimic acid dehydrogenase (SKD), and glyceraldehyde-3-phosphate dehydrogenase (G3PDH) were resolved on system III. 6PGD, G3PDH, MDH, MNR, and PGM were used to assess outcrossing rates in the progeny array analysis.

Enzymatic assays followed Soltis et al. (1983), except for MNR and ADH (Wendel and Weeden, 1989). The locus specifying the most anodally migrating isozyme was designated as 1, the next 2, and so on. Similarly, the most anodal allozyme of a gene was labeled A, etc. Isozymes and allozymes were inferred by observing segregation of bands among individuals in the populations sampled, from segregation patterns in the open-pollinated progeny arrays, and from previous studies on the species (Cai and Chinnappa, 1989a, b; Cai, Macdonald, and Chinnappa, 1990). All populations were determined to be tetraploid ($2n = 52$) using the fuelgen staining method (Bayer, 1992) on root tips. The isozyme banding patterns conformed to those expected for tetrasomic inheritance. Homozygotes were scored as having four copies of the allele, balanced heterozygotes as having two copies of each allele, and unbalanced heterozygotes as having one and three copies of the respective alleles. Banding intensity was used to identify unbalanced heterozygotes. Allozyme frequencies at each locus were determined for each population; ge-

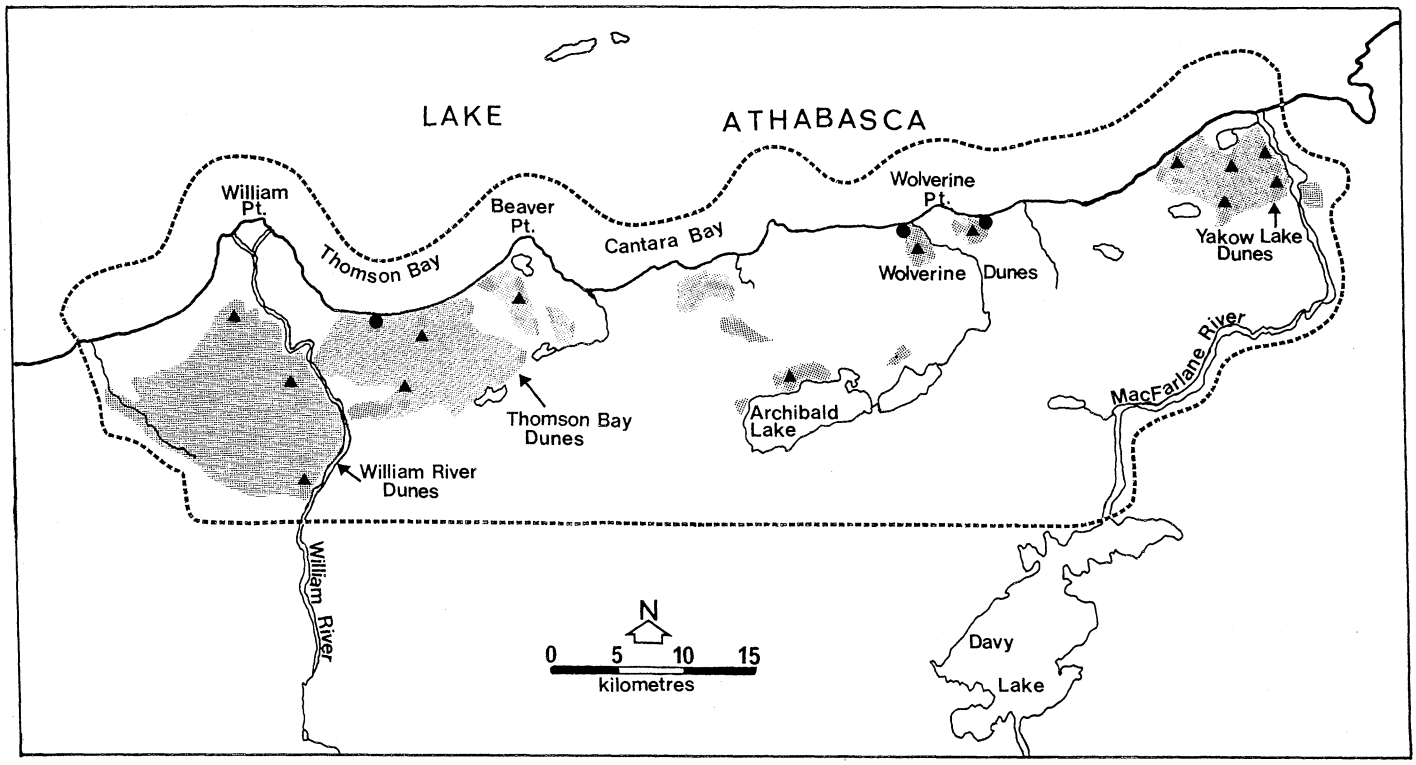


Fig. 2. Location of populations of the endemic *Stellaria arenicola* (triangles) and the widespread *S. longipes* (circles) used in this study from the Athabasca sand dunes. Active sand dunes are shaded on the map. The dotted line indicates the boundaries of the Athabasca Sand Dunes Wilderness Provincial Park.

notype frequencies were determined at each locus for the progeny arrays.

***Genetic analysis***—To estimate the extent of genetic variation within populations, the following statistics were computed: $A$, the mean number of alleles per locus; $A_P$, the mean number of alleles per polymorphic loci; $P$, the proportion of polymorphic loci when the most common allele has a frequency less than 0.95; and $H_E$, the expected panmictic heterozygosity. $T$-tests were used to test for significant differences among these population parameters. The partitioning of genetic diversity within and among populations was analyzed using measures proposed by Nei (1973). Genetic identities (Nei, 1972) were calculated as well. Population variation statistics ($A$, $A_P$, $P$, $H_E$) and standard genetic identities were calculated using the BIOSYS program (Swofford and Selander, 1981). Genetic diversity statistics were calculated using the GENESTAT-PC program (Whitkus, 1988). Principal components analysis (PCA) using the NT-SYS-pc program (Rohlf, 1987) helped evaluate the phenetic interpopulational relationships based on allele frequency distributions, with only polymorphic loci included in the analysis.

Outcrossing rates were determined using the multilocus outcrossing estimation program for tetraploids, TETRAT (Ritland, 1990). The single and multilocus outcrossing rates represent the proportion of progeny that are the result of outcrossing, 1.00 being the maximum value. TETRAT incorporates tetrasomic inheritance and can estimate four-gene fixation indices (Ritland, 1990). It determines the statistical variance of estimates by the bootstrap method. We performed 99 bootstraps per population.

## RESULTS

The 15 enzyme systems assayed in this study are coded by 27 putative loci. Some isozymes were excluded from our analysis because they were poorly resolved on our systems or have complex banding patterns (GOT-2, PGI-2, PGI-3, PGM-3). Eleven of the loci were monomorphic in all populations: *Aco-1, Aldo-1, Aldo-2, Got-1, Idh-2, Lap-1, Lap-2, Me-1, Pgi-1, Pgm-1,* and *Skd-2.* Sixteen loci, *Pgd-1, Pgd-2, Aco-2, Adh-1, G3pdh-1, Gdh-1, Got-2, Idh-1, Mdh-1, Mdh-2, Mdh-3, Mnr-2, Mnr-3, Pgm-1, Pgm-2,* and *Skd-1,* were polymorphic in at least some populations. A table of allele frequencies is available from the authors upon request.

Fifty-two alleles were detected at the 16 polymorphic loci. Thirty-one of these alleles were found in populations of the endemic species, and populations of the progenitor species located both on the Athabasca sand dunes and away from the sand dunes. Ten alleles were restricted to sand dune populations of both the endemic and progenitor species (*Pgm-1b, Pgm-2a, Adh-1a, Skd-1a, Pgd-1a, Mdh-1a, Mdh-2d, Mdh-3a, G3pdh-1a,* and *Gdh-1b*). One allele was unique to the endemic species (*Pgd-1d*) and one allele was unique to dune populations of the progenitor (*Mdh-2a*). Seven alleles were restricted to populations of the progenitor species located away from the sand dunes (*Pgd-2a, Pgd-2e, Got-2a, Mdh-1d, Mdh-3b, Aco-2a* and *Aco-*

TABLE 1. Summary of allozyme variation for 27 loci within 14 populations of the endemic *Stellaria arenicola* and seven populations of the widespread *S. longipes*. A locus was considered polymorphic if the most common allele frequency was less than 0.95.[a]

| Population | $N$ | $A$ | $A_P$ | $P$ | $H_E$ |
|---|---|---|---|---|---|
| *S. arenicola* | | | | | |
| N William Dune | 32 | 1.37 | 2.00 | 25.9 | 0.062 |
| C William Dune | 18 | 1.44 | 2.20 | 37.0 | 0.113 |
| S William Dune | 20 | 1.25 | 2.00 | 25.9 | 0.051 |
| C Thomson Dune | 20 | 1.37 | 2.25 | 29.6 | 0.088 |
| S Thomson Dune | 18 | 1.37 | 2.22 | 25.9 | 0.089 |
| Cantara Lake Dune | 32 | 1.33 | 2.12 | 29.6 | 0.086 |
| W Wolverine Dune | 20 | 1.44 | 2.50 | 29.6 | 0.086 |
| E Wolverine Dune | 24 | 1.48 | 2.62 | 25.9 | 0.094 |
| N McFarlane River | 24 | 1.55 | 2.15 | 33.3 | 0.091 |
| S McFarlane River | 18 | 1.37 | 2.25 | 29.6 | 0.089 |
| S Yakow Lake | 18 | 1.37 | 2.25 | 25.9 | 0.076 |
| SW Yakow Lake | 18 | 1.48 | 2.18 | 37.0 | 0.102 |
| NW Yakow Lake | 20 | 1.55 | 2.25 | 33.3 | 0.103 |
| Archibald Lake | 20 | 1.41 | 2.22 | 29.6 | 0.086 |
| *S. longipes* | | | | | |
| W Wolverine Point | 20 | 1.44 | 2.20 | 33.3 | 0.093 |
| E Wolverine Point | 18 | 1.63 | 2.55 | 40.7 | 0.116 |
| Thomson Bay | 20 | 1.56 | 2.36 | 40.7 | 0.127 |
| Ram Mountain, Alta. | 18 | 1.48 | 2.44 | 29.6 | 0.109 |
| Slave Lake, Alta. | 26 | 1.44 | 2.20 | 37.0 | 0.121 |
| Gem Lake, Sask. | 18 | 1.37 | 2.22 | 33.3 | 0.081 |
| Nose Hill, Alta. | 21 | 1.41 | 2.57 | 22.2 | 0.099 |
| Mean of *S. arenicola* | 21.6 | 1.41 | 2.23* | 29.9* | 0.087* |
| (SE) | 1.3 | 0.02 | 0.04 | 1.1 | 0.004 |
| Mean of *S. longipes* | 20.1 | 1.48 | 2.36* | 33.8* | 0.107* |
| (SE) | 1.1 | 0.03 | 0.06 | 2.5 | 0.006 |

[a] Sample size ($N$), mean number of alleles per locus ($A$), mean number of alleles per polymorphic locus ($A_P$), percent polymorphic loci ($P$), mean expected heterozygosity ($H_E$).
* $P < 0.05$.

*2c*). In addition, two alleles were found in populations of the endemic species and in the progenitor species located away from the sand dunes, but were not found in populations of the progenitor on the Athabasca sand dunes (*Mnr-2e* and *Skd-1c*). Most of the alleles having a restricted distribution occur in low frequency or in few populations. Only two loci (*Got-2* and *Pgd-2*) differed among groups for the most common allele.

The mean number of alleles per locus ($A$) ranged from 1.25 to 1.63 with a mean of 1.41 for the endemic populations and 1.48 for the progenitor populations (Table 1). The mean number of alleles per polymorphic locus ($A_P$) ranged from 2.00 to 2.62. The endemic populations had a mean $A_P$ of 2.23, and the progenitor populations had a mean $A_P$ of 2.36. Values of $P$, the percent polymorphic loci, ranged from 22.2 to 40.7 with a mean of 29.9 in the endemic and 33.8 in the progenitor populations. The expected panmictic heterozygosity ($H_E$) ranged from 0.051 to 0.127 with a mean of 0.087 in the endemic and 0.107 in the progenitor populations. $A_P$, $P$, and $H_E$ were significantly less ($P < 0.05$) in the endemic populations than populations of the progenitor taxon.

Gene diversity statistics were calculated and then averaged over all polymorphic loci (Table 2). The progenitor populations away from the sand dunes had the highest total genetic diversity, $H_T$ (0.212), the progenitor populations from the dunes had somewhat lower levels of genetic diversity (0.197), and the endemic populations had the lowest mean values of $H_T$ (0.163). The progenitor populations located away from the sand dunes had the highest level of population differentiation, $G_{ST}$ (0.183), while the progenitor populations from the sand dunes had the lowest level of population differentiation (0.041). The endemic populations had a mean $G_{ST}$ value of 0.102, intermediate to that of the other groups.

TABLE 2. Nei's (1973) statistics of genetic diversity for *Stellaria arenicola* and two groups of *S. longipes*. Values presented are means over all polymorphic loci.[a]

| Taxa | $H_T$ | $H_S$ | $G_{ST}$ |
|---|---|---|---|
| *S. arenicola* | 0.163 | 0.147 | 0.102 |
| *S. longipes*—dunes | 0.197 | 0.189 | 0.041 |
| *S. longipes*—other | 0.212 | 0.173 | 0.183 |

[a] $H_T$ = total gene diversity; $H_S$ = gene diversity within populations; and $G_{ST}$ = the proportion of total gene diversity found among populations.

Intraspecific and interspecific genetic identities averaged for the three groups are presented in Table 3. The populations were all closely related with the range of identities from 0.932 to 1.000. The endemic populations were more closely related to the progenitor populations from the sand dunes than those away from the sand dunes. Likewise, *S. longipes* populations from the sand dunes were more closely related to the sympatric *S. arenicola* populations than the allopatric populations of *S. longipes*. Populations of the progenitor located away from the sand dunes had the same mean identity with both progenitor and endemic populations from the sand dunes. Based on a PCA of allele frequency data, all sand dune populations were closely related regardless of the taxon, while the progenitor populations from non-sand dune habitats are grouped away from the sand dune populations (Fig. 3).

The endemic, *S. arenicola*, had a lower outcrossing rate ($P < 0.05$) than *S. longipes* populations from the sand dunes (Table 4). Single locus outcrossing rates differed between the two taxa and from multilocus outcrossing rates within taxa (Table 4). When single locus estimates of outcrossing are lower than multilocus estimates, biparental inbreeding (outcrossing between relatives) may be occurring (Shaw, Kahler, and Allard, 1981). The two-, three-, and four-gene fixation indices were positive, indicating that the plants practice some selfing. The lower three- and four-gene fixation indices indicate that localized mating is causing some level of biparental inbreeding to occur in these populations.

## DISCUSSION

***Amount and pattern of genetic variation***—Although Stebbins (1942) suggested long ago that endemic taxa were genetically depauperate, it wasn't until techniques became available to reveal protein and DNA variation that this statement could be extensively tested. Information on the population biology and genetics of endemic, regional, and widespread species has increased in recent years. In a recent summary of allozyme variation in plant species, Hamrick and Godt (1989) found that the geographic range of a species accounted for the largest amount of genetic variation in population and species level statistics. Species

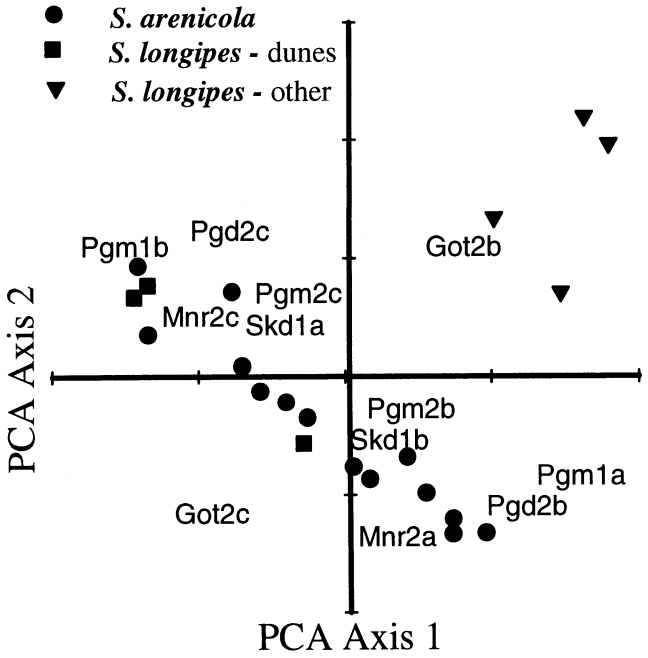


Fig. 3. Principal components analysis of allele frequencies from populations of the endemic *Stellaria arenicola* and the widespread *S. longipes*. The first two principal components explain 26% and 24% of the total variance, respectively. Positions for OTUs (populations) and variables (alleles) are presented.

with small ranges typically have less genetic variation than regional or widespread taxa (Gottlieb, 1973; Karron et al., 1988; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989; Bayer, 1992).

Our isozyme data indicated that *Stellaria arenicola* has lower genetic variation at the population level than *S. longipes*. This was demonstrated in the mean number of alleles per polymorphic locus, percent polymorphic loci, and panmictic heterozygosity. Other studies of recently evolved sympatric species have found the derivative to be depauperate in genetic variation (Gottlieb, 1973, 1974), although not always (Gottlieb and Pilz, 1976). Strong directional selection, or changes in allele frequencies due to chance (drift, founder effects), are factors thought responsible for the reduction in genetic variation in endemic species (Karron, 1987). Inbreeding and founder effects were responsible for the reduced genetic variation in *Stephanomeria malheurensis*, a recently evolved sympatric species endemic to one mountain in Oregon (Gottlieb, 1973). Macdonald et al. (1987) previously suggested that strong selection for sand dune-adapted traits was responsible for the evolution of the endemic *S. arenicola*.

TABLE 4. Estimates of outcrossing rates and gene fixation indices for *Stellaria arenicola* and *S. longipes* from the Athabasca sand dunes. Standard errors are enclosed in brackets.

| Parameter | Taxa[a] | |
|---|---|---|
| | *S. arenicola* | *S. longipes* |
| Outcrossing rate | | |
| Multilocus outcrossing rate | 0.667 (0.046)a | 0.802 (0.048)b |
| Single locus outcrossing rate | 0.523 (0.043)a | 0.714 (0.060)b |
| Difference | 0.145 (0.021)* | 0.088 (0.025) |
| Fixation indices | | |
| Two-gene fixation index | 0.201 (0.023) | 0.167 (0.017) |
| Variance of two-gene fixation index | 0.106 (0.012) | 0.077 (0.011) |
| Three-gene fixation index | 0.085 (0.016) | 0.072 (0.015) |
| Four-gene fixation index | 0.072 (0.015) | 0.059 (0.014) |
| No. of families | 40 | 34 |
| No. of progeny over all families | 791 | 635 |

[a] Lowercase letters indicate values differ between species ($P < 0.05$).
* Indicates single and multilocus outcrossing rates differ ($P < 0.05$).

Populations of *Stellaria longipes* were found to have higher total genetic diversity, and higher within-population genetic diversity than the endemic *S. arenicola* (Table 2), similar to the pattern found in other studies (Hamrick and Godt, 1989). Population differentiation is most affected by the breeding system of the organism under study (Hamrick and Godt, 1989) and not by the geographic range of the species. The higher population differentiation of the progenitor *S. longipes* is likely due to the more extensive geographic distribution of the populations collected for this study and the greater interpopulational distances characteristic of the progenitor. The three *S. longipes* populations from the sand dunes show very low population differentiation compared to the endemic *S. arenicola*, although both were collected over a similar range. Higher population differentiation in the endemic would be expected if populations were isolated and small; however, the endemic is quite abundant within its limited range. Other factors that might reduce gene flow among populations of the endemic, such as a shift in breeding system, could account for the higher population differentiation observed.

***Breeding systems***—Previous studies suggested a shift to inbreeding, from primarily outcrossing, contributed to the evolution of the endemic *Stellaria arenicola* (Chinnappa and Morton, 1984). Macdonald et al. (1987) found reduced protandry in populations of the endemic and pro-

TABLE 3. Matrix of gene identities (Nei, 1972) averaged over populations of *Stellaria arenicola* and *S. longipes* from the sand dunes and from other habitats. Ranges are given in parentheses.

| Species | *N* | *S. arenicola* | *S. longipes*—dunes | *S. longipes*—other |
|---|---|---|---|---|
| *S. arenicola* | 14 | 0.989 (0.977–0.999) | | |
| *S. longipes*—dunes | 3 | 0.990 (0.980–1.000) | 0.995 (0.992–0.997) | |
| *S. longipes*—other | 4 | 0.959 (0.932–0.982) | 0.959 (0.947–0.980) | 0.983 (0.976–0.991) |

genitor *Stellaria* species on the sand dunes as well as a slight shift to earlier flowering in the endemic. A major shift in breeding system to selfing from obligately outcrossing was responsible for the evolution of at least one other sympatric species pair (Gottlieb, 1973). Variation among individuals in the proportions of offspring produced by selfing, or outcrossing, has been studied in relatively few instances (Brown, Burdon, and Jarosz, 1989). Although it has been suggested that geographically restricted taxa exhibit greater self-compatibility and higher levels of inbreeding than closely related widespread congeners, the evidence accumulated to date is inconclusive (Karron, 1987, 1989).

Our electrophoretic analysis of progeny arrays revealed a significantly higher rate of selfing in *Stellaria arenicola* populations relative to *S. longipes* populations on the Athabasca sand dunes. In addition, evidence provided by comparisons of the single and multilocus outcrossing rates and the relationships of the two-, three-, and four-gene fixation indices suggests that some of the selfing is due to biparental inbreeding, or outcrossing with relatives (Shaw, Kahler, and Allard, 1981; Bayer, Ritland, and Purdy, 1990). Although we found a significant difference in outcrossing rate between *S. arenicola* and *S. longipes,* breeding systems of the two species could still be considered to be relatively similar. Other studies have found even higher variation in outcrossing rates among populations of single species (Glover and Barrett, 1986; Holtsford and Ellstrand, 1989).

Morphological aspects and demography of the endemic on the sand dunes might be partly responsible for the lower outcrossing rates. *S. arenicola* was found to have more flowers on individual ramets and to have significantly more of its ramets in reproductive mode than individuals of *S. longipes* (Macdonald et al., 1987). This might significantly affect pollinator foraging, resulting in higher geitonogamous pollination (crossing between flowers from the same genetic individual). In addition, established individuals of the endemic tend to stabilize the sand around them, providing a good habitat for seed germination and seedling establishment (B. Purdy, personal observation). This results in large clumps of *S. arenicola* that appear as genets but are in fact a conglomeration of isozymically closely related individuals (B. Purdy, unpublished data). A patchy distribution of clumps of *S. arenicola* results in pollinators foraging among many flowers within clumps before moving off to new patches. This would result in significant within-family outcrossing, responsible for the observed functional inbreeding. Higher inbreeding may have been instrumental in the rapid evolution of the endemic *S. arenicola* by allowing fixation of adaptive gene complexes and by reducing gene flow with sympatric populations of the progenitor *S. longipes.*

***Origin of Stellaria arenicola***—It has been predicted that recently derived species exhibit: 1) high genetic similarity with the progenitor taxon; 2) less genetic variation than the progenitor; 3) a subset of the allelic diversity found in the progenitor; and 4) few, if any, unique alleles, due to inadequate time for new mutations to accumulate (Gottlieb, 1973). Predictions concerning the allelic relationships of recently derived species with their progenitor species have been supported by a number of studies (Gottlieb, 1973, 1974; Crawford and Smith, 1982a, b; Crawford, Ornduff, and Vasey, 1985; Gottlieb, Warwick, and Ford, 1985; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989). All of these predictions are supported by the present study.

The mean genetic identity between pairs of *S. arenicola* populations was the same as that between populations of the endemic and sand dune populations of *S. longipes.* In fact, genetic identities indicated that populations of *S. longipes* from the sand dunes were more similar to populations of the endemic species than they were to *S. longipes* populations located away from the sand dunes.

As predicted, the endemic *Stellaria arenicola* contained less genetic variation than *S. longipes.* The level of genetic variation in species of recent origin is a function of the genetic variation in the ancestral populations and the variation represented in the founding individuals. At all polymorphic loci except *Got-2* and *6Pgd-2,* the endemic and progenitor populations shared the same most common allele. The data on patterns of allelic diversity and on genetic identity among populations strongly suggests the endemic *S. arenicola* is derived from the sympatric gene pool of the progenitor *S. longipes* that occurs presently on the Athabasca sand dunes. Further, the high identities suggest a recent origin for the endemic, and/or continued gene flow among derivative-progenitor populations, and is similar to other recent progenitor-derivative pairs where morphological divergence has occurred despite a lack of divergence at isozyme loci (Gottlieb, 1981; Crawford, 1983; Gottlieb, Warwick, and Ford, 1985; Loveless and Hamrick, 1988).

The sympatric evolution of the endemic *S. arenicola* has probably resulted in higher population genetic variation than would occur had the sand dune endemic evolved allopatrically because gene flow can still occur between the two species as they are reproductively compatible (Chinnappa and Morton, 1984) and co-occur in a number of areas on the sand dunes (Macdonald et al., 1987).

The flora of the Athabasca sand dunes represents one of the world's few boreal groups of endemic plants (Raup and Argus, 1982), a region known for its paucity of endemic species (Kruckeberg and Rabinowitz, 1985). Rapid speciation has occurred in other sand dune systems since the Pleistocene (Bowers, 1984; Pavlick, 1989). High rates of endemism in dune systems have been attributed to adaptation of plants to moving sand and barriers to dispersal and establishment (Bowers, 1984). The endemic taxa found on the Athabasca sand dunes occur both allopatric and sympatric to their progenitor species (Argus and Steele, 1979; Raup and Argus, 1982), and all but one have traits that could be considered adaptive for survival in a shifting sand dune environment. All of the endemic species are considered to have evolved after the sand dunes were formed at the end of the Pleistocene, 8,000 years ago (Raup and Argus, 1982).

***Conservation***—This study focused on the population genetic aspects of the sand dune endemic *Stellaria arenicola,* a species derived from the widespread *S. longipes.* Comparisons of the amount and pattern of genetic variation in this recently derived species with its progenitor were similar to other studies of similar species pairs and agreed with theoretical expectations. Despite the strong

selection pressures on the sand dunes (Argus and Steele, 1979; Macdonald et al., 1987) and the inbreeding that is occurring in the endemic populations, *S. arenicola* still maintains relatively high genetic variation at the population level relative to populations of the widespread *S. longipes* from which it has evolved, and shows only moderate population differentiation.

One focus of a larger study was to investigate the population distribution and population genetics of the sand dune endemics to develop management plans for the vegetation of the Athabasca sand dunes, and because the endemic plants are candidates for the endangered species list in Canada. All populations of *S. arenicola* occur on isolated northern dune habitats not accessible by roads, and are protected by ecological reserve or wilderness provincial park status. The main threat to the populations of the endemic *S. arenicola* seen presently would be if gene flow with the progenitor were to increase to a level obscuring the morphological distinction of the endemic populations. Previous studies have shown, however, that strong selection pressure is keeping the progenitor genotypes from establishing on the harsher moving sand dune environment (Macdonald et al., 1987). Because there is little differentiation among populations of *S. arenicola* at isozyme loci, most of the gene pool for this restricted species can presently be captured in a few large populations. The largest populations also occur on the largest dune fields where the other sand dune endemics are most common. These are the areas where population monitoring should be focused in the future.

We are presently investigating the amount and pattern of genetic variation in other sand dune endemics to compare with the results found in this study. *Deschampsia mackenzieana* Raup is an endemic grass found only on the Athabasca sand dunes that has evolved sympatrically with its widespread progenitor species *D. cespitosa* (L.) P. Beauv. *Salix silicicola* Raup and *Armeria maritima* ssp. *interior* (Raup) Pors. are two endemic taxa that are allopatric with progenitor populations of *Salix alaxensis* (Anderss.) Cov. and *Armeria maritima* ssp. *labradorica* (Wallr.) Hult., known to occur in more northerly locations. It will be of interest to observe the effect of sympatric and allopatric progenitor populations on the amounts and patterns of genetic variation found in the endemic plants from the Athabasca sand dunes.

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