American Journal of Botany 82(1): 121–130. 1995.

GENETIC DIVERSITY IN THE TETRAPLOID SAND DUNE ENDEMIC *DESCHAMPSIA MACKENZIEANA* AND ITS WIDESPREAD DIPLOID PROGENITOR *D. CESPITOSA* (POACEAE)[1]

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Electrophoretic variation was examined in 14 populations of tetraploid *Deschampsia mackenzieana,* an endemic of the Athabasca sand dunes in northern Saskatchewan, Canada, and 20 populations of its geographically widespread diploid progenitor, *D. cespitosa.* Three of the *D. cespitosa* populations were sympatric with the endemic on the Athabasca sand dunes. Populations of the endemic were found to have fewer alleles per locus (1.22 vs. 1.52), fewer alleles per polymorphic locus (2.17 vs. 2.70), lower percent polymorphic loci (18.9 vs. 30.5), and lower heterozygosity (0.062 vs. 0.119) than progenitor populations. Species level genetic diversity parameters also indicated that *D. mackenzieana* was genetically depauperate relative to its progenitor *D. cespitosa. Deschampsia mackenzieana* had no novel alleles but did share one allele with sympatric progenitor populations that did not occur in populations of *D. cespitosa* from other habitats. Although both species were found to partition most of their genetic diversity within populations, *D. mackenzieana* did have more of its limited genetic diversity partitioned among populations than *D. cespitosa.* The close genetic relationship between *D. mackenzieana* and sympatric populations of *D. cespitosa* may suggest the endemic tetraploid evolved from the sympatric diploid gene pool in the Athabasca sand dune region. The low levels of genetic diversity in *D. mackenzieana* suggest a restricted origin with limited gene flow from the progenitor since speciation.

There is considerable variation in the amount and pattern of allozyme diversity in species of plants, much of it correlated with different life history strategies or breeding systems (Hamrick and Godt, 1989). Genetic diversity is an important aspect of a species' evolutionary potential (Holsinger and Gottlieb, 1991; Ellstrand and Elam, 1993), yet some studies have been unable to demonstrate a relationship between genetic diversity and the ecological breadth of a species (Babbel and Selander, 1974; Mashburn, Sharitz, and Smith, 1978; Levin, Ritter, and Ellstrand, 1979; Huenneke, 1991).

Polyploidy has the potential to increase the genetic variability, evolutionary potential, and perhaps the ecological amplitude of a species (Hunziker and Schaal, 1983). Despite the exploitation of polyploidy in agronomic species (improved yield, hybridization, etc.), there is still little understanding of its adaptive value in populations of wild species (Rothera and Davy, 1986). Polyploidy is prevalent in higher plants (Grant, 1981), but polyploid evolution has been rigorously investigated in relatively few instances (Stebbins, 1985; Bayer, 1987; Bayer, Purdy, and Lebedyk, 1991; Novak, Soltis, and Soltis, 1991; Thompson and Lumaret, 1992).

[1] Manuscript received 22 March 1994; revision accepted 12 July 1994.

The authors thank Vernon L. Harms for information on the cytology of species from the Athabasca sand dunes; Shawn Francis, Ellen Macdonald, and Dallas Newby for assistance in the field; and Ellen Macdonald and two anonymous reviewers for comments on earlier versions of this manuscript. This research was supported by the Endangered Species Recovery Fund (World Wildlife Fund Canada), the Department of Indian and Northern Development (Northern Scientific Training Program), and the Canadian Circumpolar Institute (University of Alberta) to RJB and BGP, the Natural Sciences and Engineering Research Council (Canada) to RJB, and a Queen Elizabeth Doctoral Fellowship in Environmental Studies to BGP.

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Many isozyme studies of polyploid taxa have focused on determining the parentage of polyploids (Roose and Gottlieb, 1976; Bryan and Soltis, 1987; Rieseberg and Warner, 1987; Ashton and Abbott, 1992; Gastony, 1990) rather than the amount and pattern of genetic variation among closely related diploid and polyploid taxa (Soltis and Soltis, 1989). However, results from electrophoretic studies on *Tolmiea menziesii* (Soltis and Rieseberg, 1986; Soltis and Soltis, 1989), *Antennaria* species (Bayer, 1989), *Dactylis glomerata* (Lumaret and Barrientos, 1990), *Stellaria longipes* (Cai, Macdonald, and Chinnappa, 1990), and *Marshallia mohrii* (Watson, Elisens, and Estes, 1991) reveal that tetraploid taxa generally have higher numbers of alleles, polymorphic loci, and levels of heterozygosity than related diploid progenitor species.

Deschampsia mackenzieana Raup is an endemic grass of the Athabasca sand dunes in northwestern Saskatchewan, Canada (Raup, 1936; Raup and Argus, 1982). *Deschampsia mackenzieana* is related to the *D. cespitosa* (L.) P. Beauv. complex (Raup, 1936; Kawano, 1963). *Deschampsia cespitosa* is a geographically widespread species that is edaphically and morphologically variable (Kawano, 1963; Rothera and Davy, 1986). Tetraploid cytotypes of *D. cespitosa* have been recorded from Alaska (Kawano, 1963; Johnson and Packer, 1968) and Quebec (Hedberg, 1967) in North America as well as in Europe (Rothera and Davy, 1986). All other chromosome counts of *D. cespitosa* to the south and north of the Athabasca sand dunes have been diploid (Rothera and Davy, 1986). There are no previous reports on the cytology of *D. mackenzieana.*

This investigation was initiated to determine the amount and pattern of genetic variation in the sand dune endemic, *Deschampsia mackenzieana,* and its closely related, geographically widespread progenitor, *D. cespitosa.* We were interested in whether speciation affected the level of genetic diversity in the endemic *D. mackenzieana.* How-

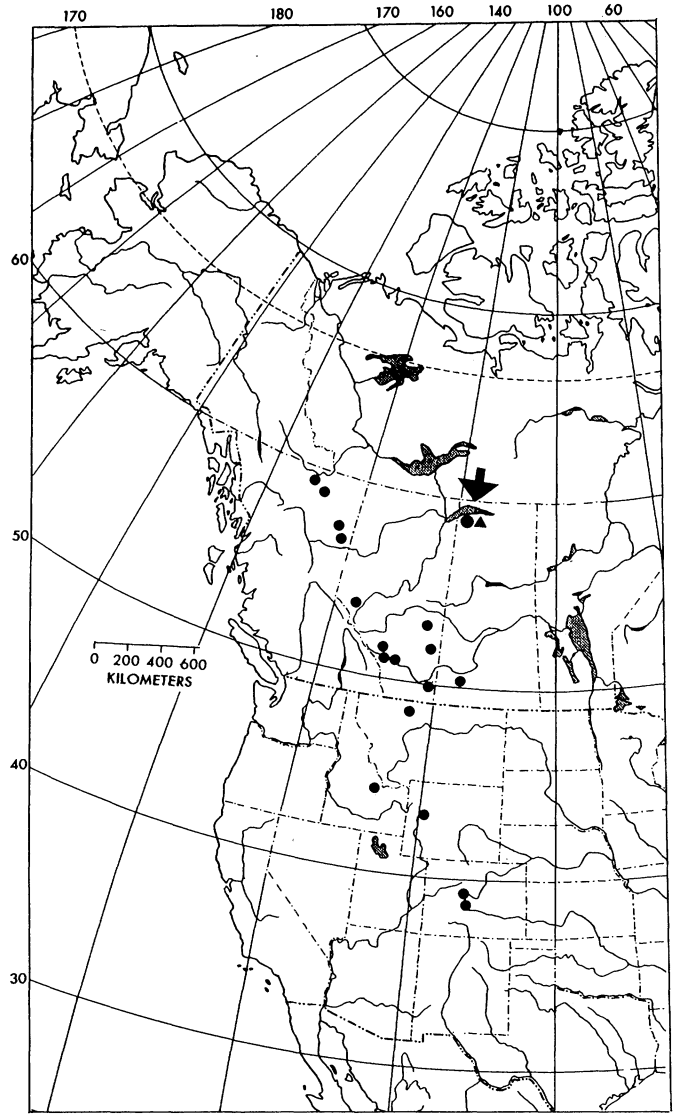

Fig. 1. Locations of populations of the widespread *Deschampsia cespitosa* (circles) and the endemic *D. mackenzieana* (triangles) from western North America used in this study. The arrow points to the sand dunes that occur on the south shore of Lake Athabasca.

ever, after determining the cytology of individuals of *D. mackenzieana* and *D. cespitosa,* the study became an investigation comparing populations of a diploid progenitor and tetraploid derivative species as well.

MATERIALS AND METHODS

Population sampling—The locations of the populations that were sampled for this study are found in Figs. 1 and 2, and Table 1. Populations of *Deschampsia mackenzieana* were sampled throughout the range of the species (Fig. 2), while populations of *D. cespitosa* were collected from the borders of the dune fields (Fig. 2) and from other habitats in western Canada and the United States (Fig. 1). The number of populations and individuals, respectively, examined for each species were: *D. mackenzieana* (14, 416) and *D. cespitosa* (20, 617). The number of populations and individuals collected for *D. cespitosa* from different regions were: Athabasca sand dunes (3, 100), northern Rocky Mountains (4, 120), central Rocky Mountains and plains (9, 271), and southern Rockies (4, 126).

Live plants were collected from up to 50 individuals in each population. Seeds representing open-pollinated progeny arrays were collected from sand dune populations of *Deschampsia mackenzieana* and *D. cespitosa.* The collections were transported to the phytotron at the University of Alberta where the live plants and germinated seeds were grown in soil. Mitotic chromosome counts were made from squashed actively growing root tips using the Feulgen staining technique (Purdy, Bayer, and Macdonald, in press). All populations of *D. mackenzieana* were found to be tetraploid ($2n = 52$), whereas all populations of *D. cespitosa* were found to be diploid ($2n = 26$).

Electrophoresis—Standard methods for starch gel electrophoresis were employed in this study (Soltis et al., 1983; Purdy, Bayer, and Macdonald, 1994). Fresh pieces of actively growing leaf tissue were ground in cold extraction buffer. 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 buffer systems were used to resolve the isozymes in this study. Thirteen enzyme systems were resolved. Leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), and glutamate oxalate-transferase (GOT) were resolved on system I (Purdy, Bayer, and Macdonald, in press). Malate dehydrogenase ([NAD]MDH), menadione reductase (MNR), glyceraldehyde-3-phosphate dehydrogenase (G3PDH), glucose-6-phosphate dehydrogenase (G6PDH), and acid phosphatase (ACP) were resolved on system II. 6-phosphogluconate (6-PGD), isocitrate dehydrogenase (IDH), malate dehydrogenase ([NADP]ME), phosphoglucose mutase (PGM), and shikimic acid dehydrogenase (SKD) were resolved on system III.

Enzymatic assays followed those outlined in Purdy, Bayer, and Macdonald (In press). 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, and from segregation patterns in open-pollinated progeny arrays. For tetraploid individuals, homozygotes were scored as having four copies of the allele, balanced heterozygotes as having two copies of each allele, 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.

Genetic analysis—To provide a measure of the level 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 locus; P, the proportion of polymorphic loci when the most common allele has a frequency less than or equal to 0.95; and H_E, the expected panmictic heterozygosity. Values for A, A_P, P, and H_E were calculated at the species

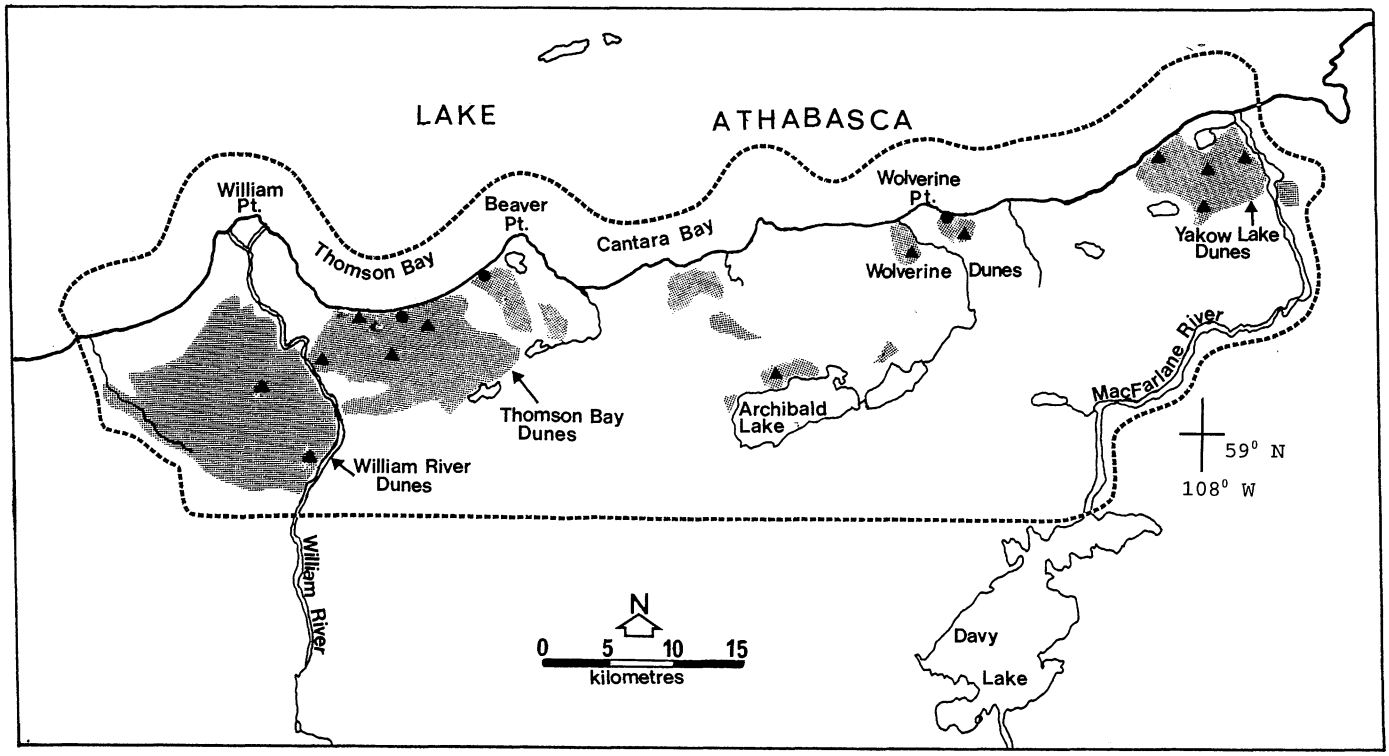

Fig. 2. Location of populations of the endemic *Deschampsia mackenzieana* (triangles) and the widespread *D. cespitosa* (circles) used in this study from the Athabasca sand dunes, Saskatchewan, Canada. Active sand dunes are shaded on the map. The dotted line indicates the boundaries of the Athabasca Sand Dunes Wilderness Provincial Park.

level, and for each population, which were then averaged for each species or geographic region. *T*-tests were used to test for significant differences among these population parameters when only two comparisons could be made, whereas ANOVA followed by Student-Newman-Keuls multiple range tests was employed when more than one comparison was to be made for a given population parameter.

The partitioning of genetic diversity within and among populations was analyzed using measures proposed by Nei (1973). We also calculated Wright's gene flow estimate (Nm_W, where $Nm_W = [1 - G_{ST}]/4G_{ST}$); and Slatkin's gene flow estimate (Nm_S, where $\log_{10}\bar{p}[1] = a\log_{10}[Nm_S] + b$; a and b depend on the number of individuals sampled in each subpopulation, and $\bar{p}[1]$ is the mean frequency of alleles unique to a single population) (Barton and Slatkin, 1986). The absolute population differentiation (D_M) was calculated using the formula: $D_M = sD_{ST}/(s - 1)$ where s is the number of subpopulations in the analysis and D_{ST} is the among population genetic diversity (Nei, 1973).

Genetic identities (Nei, 1972) were calculated as well. Population variation statistics 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 SYSTAT program (Wilkinson, 1990) helped evaluate the phenetic interpopulational relationships based on allele frequency distributions from polymorphic loci only. The PCA is presented with OTUs (populations) plotted onto the derived variables (principal axes) and alleles plotted at the end of vectors of the individual alleles relative to the PCA axes (Fig. 3).

RESULTS

The 13 enzyme systems assayed in this study are coded by 20 putative loci. Some isozymes were excluded from our analysis because they had complex banding patterns or overlapped with other loci (PGI, MDH, SKD). Eight of the loci were monomorphic in all populations: *6Pgd-1, Acp-1, Acp-4, G3pdh-2, Got-2, Lap-1, Me-1, Pgi-1.* Twelve loci—*6Pgd-2, Acp-2, Acp-3, G3pdh-1, Got-1, Idh-1, Idh-2, Lap-2, Me-2, Mnr-1, Pgm-1,* and *Pgm-2*—were polymorphic in at least some populations. A table of allele frequencies is available from the authors upon request.

There were 50 alleles at the 12 polymorphic loci. No alleles were restricted to the endemic taxon but *Idh-1c* was restricted to the sand dune populations of both species, occurring in at least some populations of *Deschampsia mackenzieana* and *D. cespitosa* with a frequency greater than 0.05. Three alleles not found in the endemic species—*6Pgd-2a, Acp-2e,* and *Lap-2d*—were found in *D. cespitosa* populations from both sand dune and nonsand dune habitats. Eighteen other alleles were found only in *D. cespitosa* populations in nonsand dune habitats. At ten polymorphic loci the endemic species shared the same most common allele with populations of the progenitor species. *Lap-2f* was the most common allele in *D. mackenzieana* and *D. cespitosa* populations from the sand dunes, while *Lap-2e* was the most common allele in the progenitor populations from nonsand dune habitats. Mean allele

TABLE 1. Population designation, collection location, habitat, and sample size for 14 populations of *Deschampsia mackenzieana* and 20 populations of *D. cespitosa* used in this study. Vouchers are at ALTA.

Population no.	Population location and habitat	Sample size
	D. mackenzieana—western dune fields	
wrd1	Central William River dune field. Lat. 59°03′N, Long. 109°20′W, elev. 244 m. Active sand dunes	32
wrd2	Southern William River dune field. Lat. 58°55′N, Long. 109°12′W, elev. 275 m. Active sand dunes	30
tbd1	Western Thomson Bay dune field. Lat. 59°05′N, Long. 109°11′W, elev. 244 m. Active sand dunes	30
tbd2	Eastern Thomson Bay dune field. Lat. 59°06′N, Long. 108°59′W, elev. 270 m. Active rolling dunes	17
tbd3	Central Thomson Bay dune field. Lat. 59°03′N, Long. 109°05′W, elev. 270 m. Active rolling dunes	32
tbd4	Thomson Bay shoreline. Lat. 59°05′N, Long. 109°10′W, elev. 215 m. Disturbed beach ridges	30
	D. mackenzieana—central dune fields	
cad1	East Wolverine dune field. Lat. 59°07′N, Long. 108°20′W, elev. 245 m. Active sand dunes	32
cad2	West Wolverine dune field. Lat. 59°08′N, Long. 108°25′W, elev. 245 m. Active sand dunes	30
cad3	Archibald Lake dune field. Lat. 59°02′N, Long. 108°35′W, elev. 305 m. Active sand dunes	29
	D. mackenzieana—eastern dune fields	
yld1	Northwestern Yakow Lake dune field. Lat. 59°11′N, Long. 108°10′W, elev. 220 m. Active sand dunes	30
yld2	Northern Yakow Lake dune field. Lat. 59°13′N, Long. 107°59′W, elev. 220 m. Active sand dunes	32
yld3	Eastern Yakow Lake dune field. Lat. 59°12′N, Long. 107°55′W, elev. 245 m. Active sand dunes	30
yld4	Southern Yakow Lake dune field. Lat. 59°09′N, Long. 108°05′W, elev. 250 m. Active sand dunes	30
yld5	Central Yakow Lake dune field. Lat. 59°10′N, Long. 108°00′W, elev. 240 m. Active sand dunes	32
	D. cespitosa—dunes	
asd1	Thomson Bay shoreline. Lat. 59°05′N, Long. 109°10′W, elev. 215 m. Moist beach habitat	36
asd2	Beaver Point shoreline. Lat. 59°08′N, Long. 108°50′W, elev. 215 m. Moist beach habitat	32
asd3	Wolverine Point shoreline. Lat. 59°07′N, Long. 108°20′W, elev. 215 m. Moist beach habitat	32
	D. cespitosa—north	
nor1	Buckinghorse River, B.C. Lat. 57°25′N, Long. 122°50′W, elev, 1,010 m. Gravel and silt floodplain	30
nor2	Liard River, B.C. Lat. 59°25′N, Long. 126°00′W, elev. 520 m. Sandy floodplain	30
nor3	Toad River, B.C. Lat. 59°10′N, Long. 125°50′W, elev. 855 m. Gravel floodplain	30
nor4	South Kihanni Chief River, B.C. Lat.. 57°15′N, Long. 122°40′W, elev. 795 m. Gravel floodplain	30
	D. cespitosa—central	
cen1	Cypress Hills, Alberta. Lat. 49°32′N, Long. 110°21′W, elev. 1,175 m. Moist prairie	30
cen2	Gold Butte, Montana, Lat. 48°45′N, Long. 111°35′W, elev, 1,375 m. Moist prairie	30
cen3	Wainright, Alberta. Lat. 52°45′N, Long. 110°50′W, elev. 645 m. Wet parkland meadow	27
cen4	Gooseberry Lake, Alberta. Lat. 52°06′N, Long. 110°45′ W, elev. 703 m. Sandy beach habitat	30
cen5	Webb, Saskatchewan. Lat. 50°18′N, Long. 108°13′W, elev. 735 m. Moist prairie	31
cen6	Nose Hill, Alberta. Lat. 51°08′N, Long. 114°10′W, elev. 1,285 m. Moist prairie	32
cen7	Waiperous Creek, Alberta. Lat. 51°25′N, Long. 115°05′W, elev. 1,500 m. Gravel floodplain	30
cen8	Ghost River, Alberta. Lat. 51°12′N, Long. 114°40′W, elev. 1,160 m. Gravel floodplain	30
cen9	Kinky Lake, Alberta. Lat. 53°17′N, Long. 117°45′W, elev. 1,130 m. Gravel beach habitat	31
	D. cespitosa—south	
sou1	Leadore, Idaho. Lat. 44°41′N, Long. 113°23′W, elev. 1,810 m. Moist prairie	31
sou2	Green River, Wyoming. Lat. 43°17′N, Long. 109°53′W, elev. 2,435 m. Wet subalpine meadow	33
sou3	Buffalo Springs, Colorado. Lat. 39°02′N, Long. 106°00′ W, elev. 2,885 m. Wet subalpine meadow	31
sou4	Hoosier Pass, Colorado. Lat. 39°21′N, Long. 106°02′W, elev. 3,600 m. Moist alpine meadow	31

frequencies indicated populations of *D. mackenzieana* and *D. cespitosa* differed for the most common allele at only one locus (*Mnr-1f* vs. *Mnr-1c*).

Deschampsia mackenzieana had considerably less genetic variation than *D. cespitosa*. At the population level, the endemic species had lower average A (1.22 vs. 1.52), A_P (2.17 vs. 2.70), P (18.9 vs. 30.5), and H_E (0.062 vs. 0.119) than the widespread progenitor species (Table 2, $P < 0.01$). Values for A, A_P, and P were significantly less at the species level in *D. mackenzieana* than in *D. cespitosa* (Table 2). Subdividing the progenitor populations into geographic regions revealed similar amounts of genetic variation for populations in all four regions. In all comparisons, *D. mackenzieana* had less genetic diversity than *D. cespitosa* populations from any given geographic region (Table 2).

Total genetic diversity at polymorphic loci (H_T) for *Deschampsia mackenzieana* was 0.189, but the proportion of allozyme diversity among populations (G_{ST}) was 0.268, indicating that there was considerable genetic differentiation among populations (Table 3). *Deschampsia cespitosa* had a higher mean total genetic diversity (H_T = 0.249) than *D. mackenzieana,* but a lower amount of population differentiation (G_{ST} = 0.212), despite the much larger geographic collecting range. An analysis of the progenitor populations subdivided on the basis of geographic region indicates that *D. cespitosa* maintains higher total- and within-population genetic diversity than the endemic *D. mackenzieana.* Values for G_{ST} are lower for all geographic subdivisions of the progenitor when compared to the endemic taxon (Table 3).

Nm_W estimates were lower for *Deschampsia mackenzieana* than for *D. cespitosa* (Table 3), while Nm_S estimates were higher for the tetraploid endemic than the diploid progenitor. The absolute measure of genetic differentiation among populations (D_M) was similar between *D. mackenzieana* and *D. cespitosa* (Table 3).

Genetic identities among the *Deschampsia mackenzieana* populations ranged from 0.943 to 1.000 with a mean of 0.976 (Table 4). Genetic identities among the *D. cespitosa* populations ranged from 0.893 to 0.999 (Table 4). *Deschampsia mackenzieana* had highest genetic identities with the progenitor populations of *D. cespitosa* from the Athabasca sand dunes and lowest genetic identities with

TABLE 2. Summary of allozyme variation for 20 loci within 14 populations of the endemic *Deschampsia mackenzieana* and 20 populations of the widespread *D. cespitosa* from four geographic regions. A locus was considered polymorphic if the most common allele frequency was less than 0.95.[a,b]

Taxa and region	Population	A	A_P	P	H_E
D. mackenzieana	wrd1	1.25	2.25	20	0.047
	wrd2	1.20	2.00	20	0.072
	tbd1	1.20	2.00	20	0.062
	tbd2	1.20	2.00	20	0.074
	tbd3	1.15	2.00	10	0.051
	tbd4	1.15	2.00	15	0.054
	cad1	1.15	2.00	10	0.027
	cad2	1.35	2.17	30	0.104
	cad3	1.30	2.20	25	0.073
	yld1	1.15	2.50	10	0.026
	yld2	1.15	2.50	10	0.047
	yld3	1.30	2.50	30	0.083
	yld4	1.25	2.00	25	0.081
	yld5	1.25	2.25	20	0.070
	Mean	1.22a	2.17a	18.9a	0.062a
	(SE)	0.02	0.05	1.9	0.006
D. cespitosa—dunes	asd1	1.50	2.43	35	0.112
	asd2	1.50	2.43	35	0.104
	asd3	1.50	2.43	35	0.139
	Mean	1.50b	2.43ab	35.0b	0.118b
	(SE)	0.00	0.00	0.0	0.011
D. cespitosa—north	nor1	1.35	2.40	25	0.095
	nor2	1.55	2.37	40	0.189
	nor3	1.65	2.63	40	0.168
	nor4	1.60	2.71	35	0.122
	Mean	1.54b	2.53ab	35.0b	0.144b
	(SE)	0.07	0.08	3.5	0.021
D. cespitosa—central	cen1	1.30	2.50	20	0.062
	cen2	1.75	3.33	30	0.139
	cen3	1.50	2.80	25	0.084
	cen4	1.40	2.75	20	0.091
	cen5	1.40	2.33	30	0.095
	cen6	1.45	2.50	30	0.109
	cen7	1.70	3.00	35	0.124
	cen8	1.38	2.40	25	0.090
	cen9	1.65	3.17	30	0.143
	Mean	1.50b	2.75b	27.2b	0.104b
	(SE)	0.05	0.12	1.7	0.009
D. cespitosa—south	sou1	1.50	2.25	40	0.142
	sou2	1.65	2.85	35	0.138
	sou3	1.45	3.25	20	0.105
	sou4	1.70	3.40	25	0.121
	Mean	1.58b	2.94b	30.0b	0.127b
	(SE)	0.06	0.26	4.6	0.009
D. mackenzieana	population	**1.22	**2.17	**18.9	**0.062
	(SE)	0.02	0.05	1.9	0.006
	species	*1.55	**2.22	45	0.083
	(SE)	0.15	0.15	—	0.034
D. cespitosa—all	population	**1.52	**2.70	**30.5	**0.119
	(SE)	0.03	0.09	1.6	0.007
	species	*2.90	**4.17	60	0.148
	(SE)	0.46	0.49	—	0.049

[a] 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).

[b] Lowercase letters indicate values differ between groups for population genetic statistics ($P < 0.05$). * and ** indicate values differ between species at $P < 0.05$ and $P < 0.01$, respectively. Species level genetic diversity values were calculated by treating all populations within the species as one population.

progenitor populations from the northern and central geographic regions (Table 4). *Deschampsia cespitosa* populations from the sand dunes had higher interspecific genetic identities with the sympatric endemic taxon (0.962) than intraspecific identities with allopatric populations of *D. cespitosa* (0.935 to 0.949) (Table 4). The PCA of allele frequencies also indicated the close genetic relationship of the sympatric *D. mackenzieana* to *D. cespitosa* pop-

TABLE 3. Nei's (1973) statistics of genetic diversity and estimates of gene flow for *Deschampsia mackenzieana* and four groups of *D. cespitosa*. Values presented are means over all polymorphic loci within a species or geographic group.[a]

Species and region	Number of Pops.	Number of Loci	H_T	H_S	G_{ST}	Nm_W	Nm_S	D_M
D. mackenzieana	14	9	0.189	0.138	0.268	0.684	1.636	0.054
D. cespitosa	20	12	0.249	0.196	0.212	0.933	0.850	0.055
dunes	3	6	0.333	0.294	0.116	1.915	0.959	0.058
north	4	9	0.399	0.318	0.202	0.991	0.212	0.107
central	9	10	0.232	0.205	0.116	1.898	0.779	0.030
south	4	9	0.332	0.280	0.157	1.349	0.658	0.070

[a] H_T = total gene diversity; H_S = gene diversity within populations; G_{ST} = the proportion of total gene diversity found among populations; Nm_W = Wright's gene flow estimate; Nm_S = Slatkin's gene flow estimate; and D_M = absolute population differentiation.

ulations from the Athabasca sand dunes (Fig. 3). There was no strong association of *D. cespitosa* populations from the north, central, and south geographic regions with populations from their respective geographic region (Fig. 3). The PCA revealed that *Lap-2, Acp-2,* and *Acp-3* were the loci that differentiated the sand dune populations of both *D. mackenzieana* and *D. cespitosa* from other progenitor populations (Fig. 3).

DISCUSSION

Amount and pattern of genetic diversity—*Deschampsia mackenzieana* is both a recently evolved species and a narrow endemic. Evidence from population genetic studies suggests derivative species have lower amounts of genetic diversity than their progenitors (Gottlieb, 1973, 1974; Crawford and Smith, 1982a, b; Crawford, Ornduff, and Vasey, 1985; Pleasants and Wendel, 1989; Purdy, Bayer, and Macdonald, 1994). In addition, plant species with limited geographic ranges typically have lower levels of genetic polymorphism (Karron, 1987; Loveless and Hamrick, 1988; Hamrick and Godt, 1989; Pleasants and Wendel, 1989; Falk and Holsinger, 1991; Sherman-Broyles et al., 1992), although not always (Bayer and Crawford, 1986; Karron et al., 1988; Linhart and Premoli, 1993).

Deschampsia mackenzieana has considerably less genetic diversity at the species and population levels than the widespread progenitor *D. cespitosa,* which supports the trend seen in the majority of studies. Levels of genetic variation (*A, P,* H_E) in *D. cespitosa* were comparable to other species with similar life history characteristics: monocots, widespread geographic range, boreal-temperate distribution, wind-pollinated (Hamrick and Godt, 1989). Although *D. cespitosa* occurs over a wide range of habitats and geographic regions, genetic diversity was comparable among sand dune, northern, central, and southern regions for *A,* A_P, *P,* and H_E. *Deschampsia mackenzieana* had significantly lower levels of population and species level genetic diversity than its widespread progenitor, but comparable with the mean values for other endemic taxa (Hamrick and Godt, 1989).

The observed reduction in genetic polymorphism in the endemic taxon may be due to founder effect, genetic drift, strong directional selection, and/or a change in breeding system (Karron, 1987). *Deschampsia cespitosa* is known to be self-incompatible (Rothera and Davy, 1986; Bush and Barrett, 1993), and our attempts to produce offspring as a result of selfing in *D. mackenzieana* were unsuccessful. Consequently, *D. mackenzieana* and *D. cespitosa* probably have similar rates of outcrossing. Because the endemic taxon maintains large and extensively distributed populations within its restricted range (Raup and Argus, 1982), genetic drift is unlikely to account for the loss of genetic diversity observed. In light of these facts (Barrett and Kohn, 1991), a genetic bottleneck in the founding population of *D. mackenzieana* is the most likely explanation for the reduced levels of species and population level genetic variation. However, because of differences in habitats of the two species, strong directional selection cannot be ruled out as a factor resulting in the reduction of genetic diversity in *D. mackenzieana.*

Deschampsia cespitosa had considerably higher total- (H_T) and within-population (H_S) genetic diversity than the endemic *D. mackenzieana,* a trend seen in other studies (Hamrick and Godt, 1989). Interestingly, populations of *D. mackenzieana,* despite being collected over a very small geographic area, exhibited higher populational differentiation (G_{ST}) than any regional group of *D. cespitosa.*

TABLE 4. Matrix of gene identities (Nei, 1972) averaged over populations of *Deschampsia mackenzieana* and *D. cespitosa* from four geographic regions. Ranges are given in brackets.

Species	1	2	3	4	5
D. mackenzieana	0.976 (0.943–1.000)				
D. cespitosa—dunes	0.962 (0.926–0.993)	0.983 (0.972–0.996)			
D. cespitosa—north	0.912 (0.878–0.943)	0.935 (0.905–0.954)	0.958 (0.940–0.994)		
D. cespitosa—central	0.915 (0.878–0.943)	0.935 (0.893–0.962)	0.966 (0.932–0.995)	0.985 (0.969–0.999)	
D. cespitosa—south	0.929 (0.903–0.955)	0.949 (0.921–0.966)	0.966 (0.936–0.988)	0.975 (0.955–0.994)	0.973 (0.962–0.990)

The three populations of the progenitor taxon collected from the sand dunes over a distribution similar to the endemic had very low levels of population differentiation. This result differs from that seen in most studies where endemic taxa generally partition their genetic diversity in the same pattern as related widespread taxa (Hamrick and Godt, 1989). Values of G_{ST} are relative and depend on the amount of genetic diversity present (Nei, 1973). The absolute measure of population differentiation (D_M) revealed that differences between populations of *Deschampsia mackenzieana* are of the same magnitude as differences between populations of the genetically diverse *D. cespitosa.*

Estimates of gene flow among populations of *Deschampsia mackenzieana* differ significantly depending on the method used to calculate the parameter. Wright's estimate of gene flow (Nm_W), which is derived from the value of G_{ST}, is lower for the endemic than any group of *D. cespitosa.* In contrast, Slatkin's estimate of gene flow (Nm_S), based on the number of private alleles in populations, suggests higher gene flow for *D. mackenzieana* than any group of *D. cespitosa.* This suggests the private alleles that occur in the endemic have very low frequencies, and that most of the differentiation seen in *D. mackenzieana* is attributed to frequency differences of alleles that are found in more than one population.

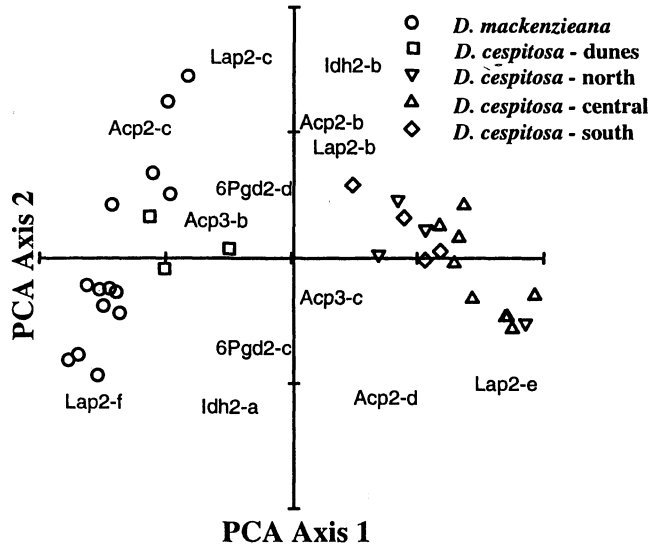

Fig. 3. Principal components analysis of allele frequencies from populations of the endemic *Deschampsia mackenzieana* and the widespread *D. cespitosa.* The first two principal components explain 60.8% and 9.6% of the variance, respectively. Positions for OTUs (populations) and variables (alleles) are presented.

Origin of Deschampsia mackenzieana—There are a number of predictions that have been made regarding the relationship between progenitor and derivative taxa (Gottlieb, 1973; Pleasants and Wendel, 1989), all of them met in this study. First, the intraspecific identities among populations of *Deschampsia mackenzieana* were similar to the interspecific identities with populations of *D. cespitosa* from the sand dunes. Second, the sand dune populations of *D. cespitosa* had higher identities with the endemic taxon than with other populations of the same species. Third, there was less genetic variation in the derivative taxon than that found in the progenitor. Fourth, the allelic diversity in *D. mackenzieana* is a subset of the gene pool of *D. cespitosa,* and there are no alleles unique to the derivative species, likely due to inadequate time for mutations to accumulate.

The data suggest that *Deschampsia mackenzieana* may be derived from the gene pool of sympatric *D. cespitosa* populations that occurred on the Athabasca sand dunes during speciation and that *D. mackenzieana* is a recently derived species (Crawford, 1983). *Deschampsia mackenzieana* probably functions as a distinct species with its own gene pool due to the reproductive barrier resulting from different ploidy levels. Morphological and cytological hybrids have not been found on the sand dunes despite the co-occurrence of *D. cespitosa* and *D. mackenzieana* in a number of locations (B. Purdy, personal observation).

Effects of polyploidy—Two chromosomal races ($2n$ = 26, 52) of *Deschampsia cespitosa* have been reported from Britain (Rothera and Davy, 1986). Cytological evidence (Rothera and Davy, 1986) and isozyme data (Bush and Barrett, 1993) suggest that the diploid cytotypes ($2n$ = 26) are, in fact, ancient tetraploids. Reports on the inheritance of isozymes in *D. cespitosa* have differed (Gehring and Linhart, 1992; Bush and Barrett, 1993). Colorado populations of *D. cespitosa* were found to have a disomic pattern of inheritance at all isozyme loci investigated (Gehring and Linhart, 1992). Ontario populations of *D. cespitosa* had this pattern of inheritance at some loci, while other loci revealed complex banding patterns indicating gene duplication, with isozymes of 6PGD, PGI, MDH, and DIA appearing to be duplicated (Bush and Barrett, 1993).

In our study, PGI and MDH produced complex banding patterns and appeared to be duplicated based on the occurrence of interlocus heteromeric molecules. These isozymes were excluded from further genetic analysis. However, in the western North American populations of *Deschampsia cespitosa* used in our study, 6PGD did not appear to be duplicated. Segregation patterns of open pollinated progeny arrays revealed a disomic pattern of inheritance of isozymes in the diploid *D. cespitosa,* similar to that reported by Gehring and Linhart (1992), and a tetrasomic pattern of inheritance in the tetraploid *D. mackenzieana.*

Polyploidy is now regarded to be an integral component of the ecological and evolutionary dynamics of plant populations and species (Thompson and Lumaret, 1992). Central questions regarding polyploidy include the processes responsible for the origin of polyploids, ecological conditions favoring the establishment and coexistence of different cytotypes, and colonization patterns of newly formed polyploids.

Electrophoretic investigations have focused on determining the parentage of polyploids, whether the polyploids were allotetraploids or autotetraploids in origin, and amounts of divergence among cytotypes or potential amounts of gene flow across cytotypes (Roose and Gottlieb, 1976; Bayer and Crawford, 1986; Bryan and Soltis, 1987; Rieseberg and Warner, 1987; Gastony, 1990; Ashton and Abbott, 1992). Polyploidy is a mechanism that allows plants to increase heterozygosity and hence, genetic

diversity. This is especially true in small populations where the effects of genetic drift could be compensated for by the added heterozygosity that both autopolyploids and allopolyploids possess. The majority of isozyme studies on diploid and polyploid derivatives have found polyploids to have higher heterozygosity, higher number of alleles per locus, and more polymorphic loci than their diploid progenitors (Soltis and Rieseberg, 1986; Bayer, 1989; Cai, Macdonald, and Chinnappa, 1990; Lumaret and Barrientos, 1990; Watson, Elisens, and Estes, 1991).

Deschampsia mackenzieana does not follow this trend and is genetically depauperate when compare to its diploid progenitor. Although formal genetic analysis of progeny from controlled crosses was not performed in this study, the following points suggest that *D. mackenzieana* is an autotetraploid. Fixed heterozygosity was not seen at any locus, the same number of loci were observed in the diploid and tetraploid cytotypes, and, in progeny arrays from naturally outcrossed mother plants, segregation of heterozygotes into balanced and unbalanced heterozygotes as well as homozygotes, i.e., tetrasomic inheritance, was observed. Although autotetraploids are thought to be less common than allotetraploids, they have been observed to maintain higher genetic diversity than their diploid progenitors (Soltis and Rieseberg, 1986; Lumaret and Barrientos, 1990).

Gene flow with diploid progenitor populations was probably important for the high levels of genetic diversity noted in the tetraploid *Dactylis glomerata* (Lumaret and Barrientos, 1990). A genetic bottleneck in the founding population of *Deschampsia mackenzieana,* coupled with minimal gene flow with the genetically diverse diploid cytotypes of *D. cespitosa,* might be responsible for the small gene pool observed in this sand dune endemic. In addition, the low levels of genetic diversity in *D. mackenzieana* may suggest a single polyploidization event leading to the species origin.

Niche differentiation is thought to be required for the coexistence of newly formed polyploids with their diploid progenitors (Thompson and Lumaret, 1992) and has been demonstrated in the *Antennaria rosea* complex (Bayer, Purdy, and Lebedyk, 1991), *Dactylis glomerata* (Lumaret et al., 1987), and *Deschampsia cespitosa* (Rothera and Davy, 1986). In each of these studies the tetraploid cytotypes were more common in disturbed habitats. In Britain, *D. cespitosa* diploid plants were more common in woodlands while tetraploid plants dominate in areas where disturbance has recently or historically occurred (Rothera and Davy, 1986). On the Athabasca sand dunes, the tetraploid *D. mackenzieana* clearly occupies the disturbed habitat of active sand dunes while the diploid *D. cespitosa* occurs primarily on stabilized moist sand habitats along the shores of lakes and rivers. Tetraploid *Dactylis glomerata* (Lumaret and Barrientos, 1990) flowered earlier than diploid cytotypes, an observation that is consistent with phenological observations made on populations of *Deschampsia mackenzieana* and *D. cespitosa* from the Athabasca sand dunes (B. Purdy, personal observation).

Unlike the studies on *Dactylis glomerata* in Spain (Lumaret and Barrientos, 1990) and *Deschampsia cespitosa* in Britain (Rothera and Davy, 1986), the diploid *D. cespitosa* and the tetraploid *D. mackenzieana* are morphologically distinct (Raup, 1936; Kawano, 1963). *Deschampsia mackenzieana* differs from *D. cespitosa* in having larger, only two-flowered spikelets, and in its spreading panicles (Raup, 1936). The endemic species also differs from *D. cespitosa* in having smooth lemmas with awns attached near the middle instead of scabrous lemmas with awns from near the base, and in having strongly involute leaves with short ligules instead of flat leaves with longer ligules (Raup, 1936). The morphological distinctness of *D. mackenzieana* is maintained when grown in the same habitat as *D. cespitosa* (B. Purdy, personal observation), despite the high amounts of phenotypic plasticity observed in the diploid *D. cespitosa* (Rothera and Davy, 1986). Yet the close genetic relationship between diploid populations of *D. cespitosa,* in particular those populations from the Athabasca sand dunes, and the tetraploid *D. mackenzieana,* suggests a close phylogenetic relationship.

Conclusions—*Stellaria arenicola* was previously the only Athabasca sand dune endemic that has been the subject of a population genetic investigation (Purdy, Bayer, and Macdonald, 1994). Although *S. arenicola* was found to have less genetic diversity than its closely related geographically widespread progenitor taxon, *S. longipes,* the sympatric progenitor populations were thought to play a role in providing genetic variation to the endemic populations. The genetic isolation experienced in *Deschampsia mackenzieana* due to its tetraploid cytology is likely responsible for the marked reduction in genetic diversity found within populations of the endemic species. *Deschampsia mackenzieana* is well adapted to the active sand dune habitat, and is one of the most important dune stabilizing species on the Athabasca sand dunes (Raup and Argus, 1982). However, as a result of speciation on the Athabasca sand dunes, *D. mackenzieana* may have a reduced ability for future evolution, unless opportunities arise for the immigration of new allelic diversity into future populations.

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