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Genetic Studies of *Oenothera odorata* Populations in Korea Based on Isozyme Analysis

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The genetic variation in Korean evening primrose (*Oenothera odorata* L.) populations was examined to estimate the level of allozyme variation within populations using starch gel electrophoresis. 7 of 13 loci (*Adh, Est-1, Est-2, Mdh-2, Pgd-2, Pgm-1*, and *Idh*) revealed (Ps=43. 2%) were polymorphic. The mean number of alleles per locus (A) and polymorphic locus (Ap) for populations were 1.64 and 2.46, respectively. The effective number of alleles (Aep) within populations relatively was low ranging from 1.08 to 1.22 with a mean of 1.14. Within populations, the mean number of allele per polymorphic loci (Ap) was 2.46, the mean number of alleles per locus (A) was 1.64, and the mean genetic diversity was 0.093. About 2.7% of the total allozyme diversity resided among populations (Mean G_{ST}=0.0274). F_{IS}, a measure of the deviation from random mating within 13 populations, was relative low (mean F_{IS}=-0.03636). The indirect estimate of gene flow, based on the mean G_{ST}, was high (Nm=8.88). Estimates of gene flow were consistent with low levels of genetic differentiation among populations.

Keywords: Korean evening primrose, allozyme variation, gene flow

Electrophoretic analysis is a valuable tool to measure the amount of genetic variability and the degree of genetic differentiation between populations. The relatively large number of enzymes for which isozymes or allozymes have been identified, as well as the codomiance of allele expression and the relative ease of electrophoretic separation have justified this recent trend. During the past 20 years, enzyme electrophoresis has been used to describe the population genetic structure of over 700 plant taxa (Hamrick and Godt, 1989; Chung, 1994, Chung and Kang, 1995). This information has contributed greatly to an understanding of the evolutionary history of individual species and related group of species (Crawford, 1983, 1989; Haufler, 1987), and has provided insights into the relationships between allozyme diversity and life history and ecological traits (Brown *et al.*, 1978; Loveless and Hamrick, 1984).

Plants may arrive in a new range though either accidental or deliberate introduction. Although the accidental entry of alien plants is almost undoubtedly more frequent, plants that are deliberately introduced gain benefits not available to accidental immigrants. There benefits may enhance the opportunity for naturalization.

Oenothera odorata is herbaceous and biannual. Leaves are alternate. Flower is regular, perfect, epigynous with a prominent colored by panthium, nectary glands inside toward the base; inflorescence of solitary flowers in axiles of leaves or in panicles; pollinated by insects other than bats, beetles, or wind, commonly self-pollinated. Sepals are 4, distinct. Petals are 4. Stamens are 8, filaments distinct, attached inside the hypanthium pistil compound of 4 united carpels. Loculés have same number as carpels. Fruits have loculicidal capsule. Transplantations of the evening primrose (*Oenothera odorata* L.) have been usually carried out from the south to north area in Korea.

In this research, we asked a series of questions concerning the genetic consequences of introduction, spread, and naturalization of this evening primrose. 1) What is the level of electrophoretically detectable genetic variation in these populations? 2) How does this level of variation compare among populations from different regions? 3) How is genetic variation within and between populations and regions partitioned? 4) What role does mating system play in

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flouncing the genetic structure of *Oenothera odorata* in introduced range?

MATERIALS AND METHODS

Enzyme extraction and electrophoresis

The seed crop from thirteen populations in Korea was randomly sampled for use in the electrophoretic studies. Table 1 lists the thirteen populations, their numeric codes, population size used in this study.

Horizontal starch gel electrophoresis was used to estimate allozyme variation. Electrophoresis was performed on 12% starch gels. Electrophoretic procedures followed the methods described by Soltis *et al.* (1983) with some modifications. Alcohol dehydrogenase (ADH), esterase (EST), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), Octanol dehydrogenase (ODH), and 6-phosphogluconate dehydrogenase (PGD), and phosphoglucomutase (PGM) were examined. Except as noted, gel and electrode buffers and enzyme staining procedures from Soltis *et al.* (1983) were used to assay the enzyme systems. Genetic interpretation of electrophoretic phenotypes was based on several lines of evidence. First, a phenotype that consistently occurred by itself in a population was considered to represent homozygosity for the locus or loci of that enzyme system. Diads (suite of two phenotypes commonly occurring together) of phenotypes were considered to represent one phenotype that was homozygous at all of its isozyme loci and another phenotype that was heterozygous at one of the loci. Triads (suite of three phenotypes commonly occurring together) of phenotypes obtained from a population sample were interpreted as two homozygous phenotypes and one heterozygous phenotype (Walters, 1988). Isozyme bands were assigned numbers for each putative locus, with the fastest migrating band numbered 1 and the next numbered 2 and so on. Likewise, alleles were designated sequentially, with the most anodally migrating alleles designated *a* and the next as *b*. Genotypic data and allele frequencies obtained from this study were listed Table 2.

Data analysis

Percent polymorphic loci (P_P) was calculated by dividing the number of loci polymorphic in at least one population by the total number of loci analyzed. Mean number of alleles per locus (A_P) was determined by summing all alleles observed and dividing by the total number of loci. The effective number of alleles per locus (A_{EP}) was calculated for each locus by $1/\Sigma pi^2$, where p_i is the mean frequency of an allele. These values were then averaged across loci to obtain AEP. Heterozygosity at a locus is defined as $H_{EXP}=1-\Sigma p_i^2$, where p_i is the mean frequency of an allele (Nei, 1973). For each polymorphic locus, total gene diversity (H_T) was partitioned into diversity within populations (H_S) and diversity among populations (D_{ST}) as follows: $D_{ST}=H_S-H_T$. A measure of differentiation among populations, relative to total diversity, was calculated at each locus as $G_{ST}=D_{ST}/H_T$. G_{ST} values were averaged over all loci to obtain a species value for population divergence.

Population divergence was also examined by calculating Nei's genetic distance and identity parameters for all pairs of populations. In order to make clear the interrelationship among the 13 populations, genetic identity and genetic distance were calculated

Table 1. Collection localities for populations of *Oenothera odorata* as source for isozymes

Population	Pop. code	Pop. size	Altitude(m)	Collection area
Pusan	1	5×10^4	180	Kumjeong-gu, Pusan
Chinhae	2	10^4	100	Chinhae-si, Gyungsang nam-do
Yangsan	3	2×10^4	310	Yangsan-gun, Gyungsang nam-do
Uinyang	4	5×10^5	186	Uinyang-gun, Gyungsang nam-do
Naejangsan	5	5×10^3	540	Suchang-gun, Chollabuk-do
Kyongju	6	10^4	80	Kyongju-si, Gyungsang buk-do
Pohang	7	6×10^6	70	Pohang-si, Gyungsang buk-do
Gasan	8	10^4	200	Milyang-si, Gyungsang nam-do
Chupungyong	9	8×10^7	250	Youngdong-gun, Ch'ungch'ongbuk-do
Chengju	10	5×10^5	120	Chengju-si, Ch'ungch'ongbuk-do
Suwon	11	4×10^3	220	Sumon-si, Gyungki-do
Paeckdamsa	12	10^5	1500	Kangwon-do
Kangnung	13	2×10^3	60	Kangnung-si Gangwon-do

Table 2. Allozyme frequencies for nine polymorphic loci estimated in eight populations of *Oenothera odorata* L. from Korea. Abbreviations for populations and enzyme loci are given in Table 1

Locus	Allele	Populations												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Adh	a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0134	0.0000	0.0100	0.0168
	b	1.0000	0.9959	0.9965	0.9933	1.0000	1.0000	0.9934	0.9853	1.0000	0.9866	1.0000	0.9733	0.9698
	c	0.0000	0.0041	0.0035	0.0067	0.0000	0.0000	0.0066	0.0147	0.0000	0.0000	0.0000	0.0167	0.0134
Mdh-3	a	0.1053	0.0923	0.0000	0.0000	0.9138	0.0000	0.0000	0.0652	0.0200	0.0373	0.0929	0.1000	0.0833
	b	0.8158	0.8692	1.0000	1.0000	0.0862	1.0000	0.9327	0.8913	0.9800	0.9104	0.8464	0.9000	0.9167
	c	0.0789	0.0385	0.0000	0.0000	0.0000	0.0000	0.0673	0.0435	0.0000	0.0522	0.0607	0.0000	0.0000
Pgd-2	a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0375	0.0581	0.0792	0.0375	0.0625
	b	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.9688	0.8469	0.8875	0.9070	0.8583	0.9625	0.9375
	c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0313	0.1531	0.0750	0.0349	0.0625	0.0000	0.0000
Pgm-1	a	0.0930	0.0676	0.0513	0.0294	0.0263	0.0455	0.0385	0.0532	0.0714	0.0814	0.0455	0.1087	0.1196
	b	0.9070	0.9324	0.9487	0.9706	0.9737	0.9545	0.9487	0.9255	0.8810	0.8837	0.9167	0.8587	0.8478
	c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0128	0.0213	0.0476	0.0349	0.0379	0.0326	0.0326
Est-1	a	0.0408	0.0222	0.0341	0.0116	0.0000	0.0303	0.0286	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	b	0.9592	0.9778	0.9659	0.9884	1.0000	0.9697	0.9714	1.0000	0.9500	0.9444	0.8864	1.0000	1.0000
	c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0500	0.0556	0.1136	0.0000	0.0000
Est-2	a	0.0761	0.1163	0.1667	0.1600	0.1471	0.1778	0.1630	0.1531	0.1635	0.1818	0.1887	0.1827	0.2100
	b	0.7283	0.7093	0.7000	0.6700	0.6765	0.7111	0.7283	0.6837	0.6635	0.6455	0.6509	0.6538	0.6300
	c	0.1957	0.1744	0.1333	0.1700	0.1765	0.1111	0.1087	0.1633	0.1731	0.1727	0.1604	0.1635	0.1600
Idh-2	a	0.0732	0.0750	0.0745	0.0455	0.0349	0.0625	0.0875	0.0833	0.1087	0.1100	0.0600	0.1125	0.1111
	b	0.9268	0.9250	0.9255	0.9545	0.9651	0.9375	0.9125	0.9167	0.8804	0.8700	0.9200	0.8280	0.8333
	c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0109	0.0200	0.0200	0.0625	0.0556

Table 3. Percentage of polymorphic loci (Pp), mean number of alleles per locus (A) and polymorphic loci (Ap), effective number of allelels per locus (Aep), observed heterozygosity (Hop), Hardy-Weinberg expected heterozygosity or genetic diversity (Hep) for eight populations of *Oenothera odorata* L.

Pop	Pp	Ap	A	Aep	Hop (SD)	Hep (SD)
1	38.46	2.40	1.54	1.14	0.107 (0.012)	0.098 (0.039)
2	46.15	2.33	1.62	1.11	0.085 (0.011)	0.078 (0.038)
3	38.46	2.20	1.46	1.09	0.065 (0.010)	0.057 (0.036)
4	38.46	2.20	1.46	1.10	0.059 (0.010)	0.055 (0.038)
5	30.77	2.25	1.38	1.10	0.062 (0.010)	0.062 (0.038)
6	30.77	2.25	1.38	1.08	0.054 (0.009)	0.050 (0.035)
7	53.85	2.29	1.69	1.10	0.076 (0.011)	0.070 (0.034)
8	46.15	2.50	1.69	1.15	0.103 (0.012)	0.099 (0.041)
9	46.15	2.67	1.77	1.14	0.091 (0.011)	0.092 (0.042)
10	53.85	2.71	1.92	1.18	0.119 (0.012)	0.119 (0.042)
11	46.15	2.83	1.85	1.22	0.160 (0.012)	0.148 (0.045)
12	46.15	2.67	1.77	1.17	0.109 (0.013)	0.108 (0.045)
13	46.15	2.67	1.77	1.18	0.117 (0.013)	0.113 (0.046)
MEAN:	43.20	2.46	1.64	1.14	0.093 (0.003)	0.088 (0.011)

(Nei, 1972). The distribution of genetic variation within and among the 13 populations of *Oenothera odorata* was analyzed using *F* statistics (Wright, 1965; Nei, 1977). As defined by Wright (1951), in a subdivided population F_{IT} and F_{IS} are the correlations among gametes within individuals relative to the total population and relative to the subpopulation, respectively. The fixations index $F_{IS}=1-H_O/H_S$ was calculated for each sample using unbiased estimates of H_O (observed heterozygosity of total population) and H_S (mean value of within-population heterozygosity) averaged over loci as described by Nei and Chesser (1983). The fixations index F_{IT} was calculated by $F_{IT}=1-H_O/H_T$. F_{ST} is the correlation of random gametes within subpopulations and can be interpreted as a measure of the amount of differentiation among populations. $F_{ST}=1-H_S/H_T$, where H_S is mean value of within-population heterozygosity and H_T is the expected heterozygosity of the total population. The F_{ST} values reported for each locus are weighted averages over alleles.

Genetic divergence among populations was also estimated by calculating Nei's genetic identity and distance for all pairs of populations. A correlation between genetic distance and linear geographical distance was manually calculated. In addition, cluster analysis on genetic identities was conducted via the unweighted pairwise groups method using arithmetic average (UPGMA) using SAS (SAS, 1989). Finally, estimate of *Nm* (the number of migrants per generation) was obtained using Wright's (1951) equation as modified by Crow and Aoki (1984): $F_{ST}=1/$

Table 4. Wright's fixation indices for eight populations of *Oenothera odorata* L.

Locus	Populations												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Adh	0.000	0.000	0.000	-0.003	0.000	0.000	-0.003	-0.011	0.000	0.495	0.000	-0.017	-0.020
Mdh-2	-0.156	-0.107	0.000	0.000	-0.085	0.000	-0.062	-0.078	-0.010	-0.065	-0.128	-0.095	-0.076
Pgd-2	0.000	0.000	0.000	0.000	0.000	0.000	-0.022	-0.169	-0.082	-0.070	-0.115	-0.026	-0.053
Pgm-1	-0.090	-0.058	-0.041	0.008	-0.014	-0.036	-0.030	-0.052	-0.086	-0.088	-0.059	-0.119	-0.132
Est-1	-0.032	-0.011	-0.024	0.000	0.000	-0.016	-0.015	0.000	-0.040	-0.047	-0.123	0.000	0.000
Est-2	0.040	-0.066	-0.183	0.586	0.048	-0.074	-0.097	0.079	0.129	0.100	-0.093	0.145	0.109
Idh-2	-0.066	-0.068	-0.069	0.056	-0.024	-0.053	-0.082	-0.078	-0.111	-0.116	-0.059	-0.141	-0.136

Table 5. Total genetic diversity (H_T), genetic diversity within population (H_S), deviations of genotype frequencies from Hardy-Weinberg expectations over all populations (F_{IT}) and within individual populations (F_{IS}), and proportion of total genetic diversity partitioned among populations (G_{ST}) of *Oenothera odorata* L.

Locus	H_T	H_S	F_{IS}	F_{IT}	F_{ST}	G_{ST}[b]	χ^2(DF)[a]
Adh	0.0166	0.0165	0.0487	0.0585	0.0103	0.0103	
Mdh-2	0.1775	0.1709	-0.1192	-0.0777	0.0371	0.0371	0.9049(12)
Pgd-2	0.1106	0.1043	-0.1092	-0.0454	0.0576	0.0576	98.0505(24)
Pgm-1	0.1552	0.1526	-0.0925	-0.0740	0.0169	0.0169	147.1597(24)
Est-1	0.0761	0.0724	-0.0849	-0.0322	0.0486	0.0486	34.4482(24)
Est-2	0.4875	0.4849	0.0191	0.0242	0.0052	0.0052	111.5765(24)
Idh-2	0.1713	0.1686	-0.1069	-0.0893	0.0159	0.0159	14.4554(24)
							47.3808(24)
Mean	0.1707	0.1672	-0.0636	-0.0337	0.0274	0.0274	

[a] Chi-square for allele freq. heterogeneity (DF)

(αNm+1), where $\alpha=[n/(n-1)]^2$ and n is the number of populations.

RESULTS

For the Korean evening primrose, 7 of 13 loci (*Adh, Est-1, Est-2, Mdh-2, Pgd-2, Pgm-1*, and *Idh*) revealed (Ps=43.2%) were polymorphic in at least one population. *Idh-1, Est-3, Mdh-1, Mdh-3, Odh, Pgd-1* and *Pgm-2* were monomorphic in all thirteen populations (Table 2). Frequencies of the *a* allele at the *Adh* locus were somewhat lower in the southern populations (from Pop. 1 to Pop. 9). This was also the case for the *Pgm-1* locus (*c* allele) and *Idh-2* locus (*c* allele). The number of alleles detected per polymorphic locus was three. The percent of loci polymorphic per population (Pp) ranged from 30.77 to 53.85%, with a mean of 43.20% (Table 3). The mean number of alleles per locus (A) and polymorphic locus (Ap) for populations were 1.64 and 2.46, respectively. The effective number of alleles (Aep) within populations relatively was low ranging from 1.08 to 1.22 with a mean of 1.14. In addition, mean expected heterozygosity (Hep) for genetic diversity within populations was similar with that for the overall values for the sample as a whole (SD= 0.003). But the values of Hep in the northern populations (Pops. 10, 11, 12 and 13) were somewhat higher than those of Hep in the southern populations (Pops. 1~7). In addition, genetic diversity at the species level and at the population level was 0.092 and 0.008, respectively. Overall, mean observed heterozygosity at the population level similar to the expected value (Hop=0.093; Hep=0.088).

As expected from the chi-square tests, F_{IS}, a measure of the deviation from random mating within 13 populations, was relatively low (mean F_{IS}=-0.03636). In locuswide calculations, deficiency of heterozygosity was detected at the *Adh* and *Est-2* loci, whereas a slight excess of heterozygosity was observed at five loci (*Mdh-2, Pgd-2, Pgm-1, Est-1* and *Idh-2*). In addition, Wright's *F* coefficients showed that significant excesses of heterozygotes exit for each six of the thirteen polymorphic loci 169th at the level of population and the sample as a whole (Table 4). On a per locus basis, the G_{ST} values ranged from 0.0052 for *Est-2* to 0.0576 for *Pgd-2* with mean of 0.0274 and about 98% of the total variation

Table 6. Estimates of genetic identity (above diagonal) and distance (below diagonal) based upon the data from the polymorphic loci

Pop.	1	2	3	4	5	6	7	8	9	10	11	12	13
1	-	.9997	.9981	.9986	.9986	.9977	.9981	.9979	.9978	.9980	.9974	.9980	.9972
2	.0003	-	.9992	.9992	.9992	.9989	.9990	.9986	.9986	.9988	.9982	.9989	.9983
3	.0019	.0008	-	.9998	.9993	.9999	.9997	.9983	.9991	.9989	.9979	.9987	.9984
4	.0019	.0008	.0002	-	.9996	.9996	.9993	.9983	.9991	.9989	.9980	.9985	.9983
5	.0014	.0008	.0007	.0004	-	.9992	.9993	.9983	.9987	.9988	.9981	.9980	.9977
6	.0023	.0011	.0001	.0004	.0008	-	.9997	.9981	.9989	.9987	.9978	.9984	.9982
7	.0019	.0010	.0003	.0007	.0007	.0003	-	.9986	.9989	.9989	.9980	.9982	.9979
8	.0021	.0015	.0017	.0017	.0017	.0019	.0014	-	.9991	.9986	.9983	.9980	.9976
9	.0022	.0012	.0009	.0009	.0013	.0011	.0011	.0009	-	.9997	.9989	.9990	.9989
10	.0020	.0012	.0011	.0011	.0012	.0013	.0011	.0014	.0003	-	.9993	.9993	.9993
11	.0026	.0018	.0021	.0020	.0019	.0022	.0020	.0017	.0011	.0007	-	.9983	.9983
12	.0020	.0011	.0013	.0015	.0020	.0016	.0018	.0020	.0010	.0007	.0017	-	.9999
13	.0028	.0017	.0016	.0017	.0023	.0018	.0021	.0024	.0011	.0007	.0017	.0001	-

in the species was common to all populations (Table 5). However, significant differences in allele frequency among populations were not found for all thirteen loci (P>0.01). The indirect estimate of gene flow, based on the mean G_{ST}, was high (Nm=8.88). Estimates of gene flow were consistent with low levels of genetic differentiation among populations. Average genetic identity for all pairs of populations was 0.998 (Table 6). The UPGMA dendrogram provided a few insights into the genetic structuring of the thirteen populations (Fig. 1). The cluster analysis revealed few patterns of geographic relationships among populations. Populations 1 and 2, 9 and 10 had relatively high genetic similarities, although they share no geographic relationship. Population 8 (Gasan) was the most highly differentiated population by a substantial margin.

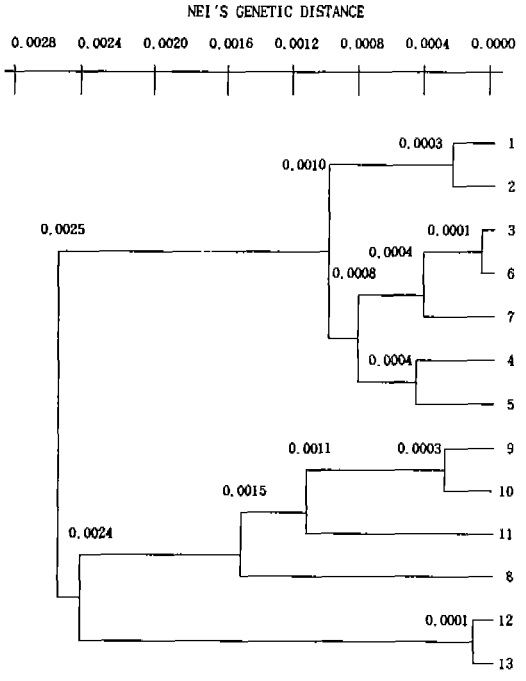

Fig. 1. Phenogram from UPGMA cluster analysis based on Nei's (1972) genetic distance between the thirteen populations of *Oenothera odorata* in Korea.

DISCUSSION

Based on recent reviews of the plant allozymes diversity literature (Hamrick and Godt, 1989), feature, such as breeding system, patterns of geographical distribution, taxonomic status, life form, seed dispersal, and successional status influences amount and distribution of genetic diversity within and among populations. At the population level, *Oenothera odorata*, with 43.20% of the loci polymorphic, is less variable than many plants with like characteristics. For example, the average proportion of polymorphic loci for short-lived herbaceous annuals 51.0% (Hamrick and Godt, 1989). Other measures of genetic variation, such as effective number of alleles (A_E) and genetic diversity (He) are similar to the means reported for annual herbaceous (Hamrick and Godt, 1989).

The genotypic diversity within populations of *Oenothera odorata* is also consistent with values reported for other clone-forming species (Ellstrand and Roose, 1987).

A substantial heterozygeneity in allele frequencies among *Oenothera odorata* populations in Korea is

suggested by a *G*st value of 0.0274. This value is low compared to species that share the same suite of traits: dicots, temperate plants, annual herbaceous, plants with sexual reproduction, and outcrossing plants with seed dispersed by insects (Hamrick and Godt, 1989).

Although not the primary thrust of this investigation, there were significant heterogygotes deficiencies with local *Oenothera odorata* populations. Because Mendelian inheritance of isozyme phenotype has been previously demonstrated at most of the loci we examined, the phenomenon is likely evidence of nonrandom mating (Chung *et al.*, 1995; Huh *et al.*, 1995). In all 13 populations, the observed heterozygosity exceeded the expected heterozygosity by 5.5-14.8% (Table 3). While the bulk of our data supports the conclusion that little population substructuring or differentiation has occurred, the consistent though nonsignificant deficiency of heterozygotes may be due to one or more of several factors. Brown (1979) has reviewed this so-called heterozygosity paradox wherein outbreeders show a deficit of heterozygotes while inbreeders show a surplus of heterozygotes, relative to expectations. Although we cannot exclude such possible explanations as dominant alleles at modifier loci, and negative heterosis, it seems more likely that the pooling of individuals from several breeding groups (Wahlund effect) is responsible. In some cases, the study mountains and hills were fairly large and heterogeneous, and hence heterozygote deficiencies may be attributable to uninternal lumping across spatial subdivisions (Wahlund effect). Low levels of genetic (electrophoretic) variation have been of thirteen reported within populations of introduced plant species (Barett and Richardson, 1986, Gray, 1986, Barett and Husband, 1990, Novak *et al.*, 1995). Allozyme variability in *Oenothera odorata* is different to compare with the results for other species because most of these species are polyploid and apomicts. Most of the variation among seed sources was due to differentiation of sources located on the perimeter of the natural range. Seed sources were not particularly distinct.

When all sources were considered, no differences between the eastern and eastern regions of the range were detected. In addition, neither genetic identity nor expected heterozygosity was correlated with elevation, latitude, or longitude.

Although a correlation between geographic distance and isozyme divergence was also detectable among 13 populations of the *Oenothera odorata*, we found no significant correlation between divergence and environmental difference measured directly from fatic acid and biotic variables and thus attributed the divergence-distance correlation to variance in interpopulation gene flow alone, independent of effects from natural selection (Huh *et al.*, unpublished).

There is obviously considerable variation in *Nm* among population (Table 4). However, many of the values of *Nm* are approximately 2 or smaller, which gives considerable scope for genetic divergence resulting from random genetic drift (Slakin, 1987; Chung and Chung, 1994).

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