Genetic Variation in Korean Populations of Wild Radish, *Raphanus sativus* var. *hortensis* f. *raphanistroides* (Brassicaceae)

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Raphanus sativus L. var. *hortensis* f. *raphanistroides* (wild radish: Brassicaceae), a herbaceous perennial, occurs only on beaches in East Asia. Genetic diversity and population structure of seven Korean populations were investigated using starch gel electrophoresis. Although the Korean populations are small, isolated with patchy distribution, the populations maintain a moderate level of genetic diversity; the mean percentage of polymorphic loci was 51.4%, mean number of alleles per locus was 1.84, and mean expected heterozygosity was 0.116. A combination of animal-outcrossing breeding system, wide geographical distribution, restricted ecological distribution, and a propensity for high fecundity may in part be explanatory factors contributing the moderate level of genetic diversity within populations. An overall excess of homozygotes relative to Hardy-Weinberg expectations (mean $F_{IS} = 0.116$) indicates that consanguineous mating occur within wild radish populations, leading to a family structure within a circumscribed area. Although populations of wild radish experience a limited gene flow, only 5% of the total genetic variation found in Korean wild radish populations examined is due to differences among populations (mean $G_{ST} = 0.052$). This value is considerably lower than the mean values of species with similar life history and ecological characteristics. However, significant differences were found in allele frequencies between populations for all polymorphic loci ($P<0.01$). It is supposed that directional selection toward genetic uniformity (similar gene frequencies) in a relatively homogenous habitat is thought to be operated among Korean wild radish populations.

Keywords : Breeding system, gene flow, genetic diversity, genetic substructure, *Raphanus sativus* var. *hortensis* f. *raphanistroides*, selection

Plant species adapted to a narrow set of environmental conditions should be less variable genetically than more ubiquitous species (Stebbins, 1942). In addition, species that occur as small isolated patches scattered over large geographic ranges are expected to experience significant genetic drift and high levels of population differentiation (Holinger and Gottlieb, 1991). However, knowledge of the population genetics of habitat specialists occurring in disjunct populations is still limited (Godt and Hamrick, 1993). With this in mind, we have studied on the allozyme

variation and genetic structure in populations of beaches and sand dune plants such as *Salsola komarovi* Iljin (Kim and Chung, 1995a) and *Calystegia soldanella* (L.) Roem. et Schutt. (Kim and Chung, 1995 b). In this study, we investigate levels and distribution of genetic variation of Korean populations in *Raphanus sativus* L. var. *hortensis* Backer f. *raphanistroides* Makino (wild radish: Brassicaceae), a herbaceous perennial, using starch gel electrophoresis.

Wild radish occurs only in sand dunes or sandy cliffs near sea sides in East Asia. It has been considered to be a naturalized taxon escaped from cultivated *R. sativus* L. (Kitamura ad Murata, 1987). The height of individuals of wild radish usually is 30-60

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cm. The flowers are purplish white and visited by *Apies* spp. and Bumbus spp. (M. Hur and M. Chung, pers obs.). Each fruit (5-8 cm long) contains 25 seeds, and the fruits do not open. The chromosome number is 2n=18 (Kitamura and Murata, 1987). These ecological and life history traits of wild radish allow us to predict low or moderate diversity within populations but high genetic differentiation between populations.

The purposes of this study were: 1) to estimate how much total genetic diversity is maintained in Korean populations of wild radish, 2) to describe how genetic variation is distributed within and among populations, and 3) to compare the levels of genetic diversity in Korean populations of wild radish with species having similar life history and ecological traits.

MATERIALS AND METHODS

From 1993 to 1994 seeds were collected from seven populations of wild radish in Korea (Fig. 1). Twenty to 123 fruits were collected from each population and one seed per fruit was used in this study. Seeds were moistened with 10 mL distilled water in petri dishes (10 cm in diameter), and incubated at 20°C for 48 h for germination. Germinating seeds were collected in two days, and homogenized with a mu-
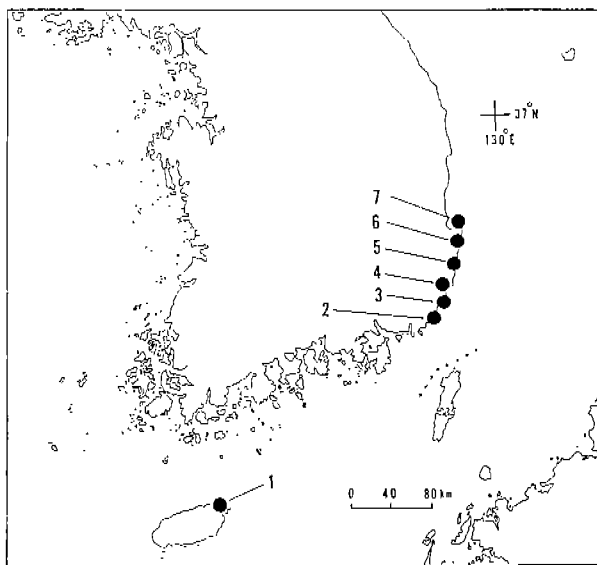

Fig. 1. The location of seven sampled populations of *R. sativus* var. *hortensis* f. *raphanistroides* in Korea.

lti-pod plate and glass rod with phosphate buffer described in Huh (1984). The crushed extract was absorbed onto 5×8 mm wicks cut from Whatman 3MM chromatography paper. Electrophoresis was performed using 12% starch gels. Gel and electrode buffer systems and enzyme staining procedures from Soltis *et al.* (1983) were used to assay six enzyme systems: glucose-6-phosphate isomerase (GPI) and 6-phosphogluconate dehydrogenase (PGD) were resolved on system 2; isocitrate dehydrogenase (IDH) and phosphoglucomutase (PGM) on system 6; alcohol dehydrogenase (ADH) and malate dehydrogenase (MDH) on system 11. All stain recipes were identical to those described by Soltis *et al.* (1983). Electrophoretic phenotypes were read in the conventional manner with those loci migrating farthest from the origin being designated as 1, the next farthest 2, etc. Within a locus the fastest allele was named a, the next b, etc. Because no controlled crosses were made to analyze segreation of the isozyme banding patterns, all alleles and loci designations are "putatively" decided based on subunit structure and genetic interpretation with most isozyme studies in plants as documented by Weeden and Wendel (1989).

A locus was considered polymorphic if two or more alleles were detected, regardless of their frequencies. Four standard genetic parameters were estimated using a computer program developed by M. D. Loveless and A. Schnabel; percent polymorphic loci (P), mean number of alleles per locus (A), effective number of alleles per locus (Ae), and gene diversity (He) (Hamrick *et al.*, 1992).

Observed heterozygosity was compared to Hardy-Weinberg (H-W) expected value using Wright (1922) fixation index or inbreeding coefficients (*F*). These indices were tested for deviation from zero by x^2-statistics following Li and Horvitz (1953).

Nei's (1973, 1977) gene diversity formulae (H_T, H_S, D_{ST}, and G_{ST}) were used to evaluate the distribution of genetic diversity within and among populations. In addition, an x^2-statistic was used to detect significant differences in allele frequency among populations for each locus (Workman and Niswander, 1970). Nei's (1972) genetic identity (I) was calculated for each pairwise combination of populations. The genetic structure within and among population was also evaluated using Wright's (1965) *F*-statistics: F_{IT},

Table 1. Allele frequencies for nine polymorphic loci estimated in seven Korean populations of *R. sativus* var. *hortensis* f. *raphanistroides*. Abbreviations for populations and enzyme loci are given in Fig. 1 and text, respectively

Locus	Allele	Populations						
		1	2	3	4	5	6	7
Got-1	a	0.757	0.850	0.900	0.917	0.917	0.967	0.923
	b	0.243	0.150	0.100	0.083	0.083	0.033	0.067
	N	37	30	30	30	30	30	30
Adh	a	0.000	0.020	0.017	0.042	0.006	0.000	0.000
	b	1.000	0.980	0.983	0.916	0.994	1.000	1.000
	c	0.000	0.000	0.000	0.042	0.000	0.000	0.000
	N	70	50	60	60	87	60	72
Gpi-2	a	1.000	1.000	1.000	1.000	1.000	0.813	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.187	0.000
	N	90	35	35	30	30	30	40
Idh-2	a	0.098	0.300	0.060	0.042	0.136	0.159	0.165
	b	0.874	0.700	0.890	0.917	0.864	0.826	0.810
	c	0.028	0.000	0.040	0.042	0.000	0.015	0.025
	N	123	50	50	60	70	69	79
Mdh-1	a	0.017	0.041	0.038	0.079	0.125	0.125	0.128
	b	0.983	0.905	0.962	0.921	0.875	0.875	0.863
	c	0.000	0.054	0.000	0.000	0.000	0.000	0.009
	N	60	37	60	66	76	80	51
Pgd-1	a	0.080	0.229	0.038	0.035	0.023	0.066	0.026
	b	0.920	0.771	0.937	0.960	0.954	0.901	0.949
	c	0.000	0.000	0.025	0.005	0.023	0.033	0.025
	N	50	35	40	100	44	30	39
Pgd-2	a	0.000	0.043	0.000	0.014	0.050	0.000	0.040
	b	0.995	0.799	0.936	0.946	0.800	0.975	0.940
	c	0.005	0.158	0.064	0.040	0.150	0.025	0.020
	N	95	57	62	74	20	20	50
Pgm-2	a	0.163	0.077	0.073	0.044	0.058	0.076	0.100
	b	0.800	0.854	0.866	0.776	0.859	0.864	0.831
	c	0.037	0.069	0.061	0.210	0.093	0.000	0.069
	N	120	65	41	57	86	59	65
Pgm-3	a	0.000	0.000	0.000	0.000	0.125	0.000	0.000
	b	0.931	0.962	0.952	0.904	0.779	0.963	0.930
	c	0.069	0.038	0.048	0.096	0.096	0.037	0.070
	N	102	52	42	47	52	54	50

N, sample size.

F_{IS} and F_{ST}. The F_{IT} and F_{IS} coefficients measure excesses of homozygotes or heterozygotes relative to the panmictic expectations within the entire samples and within populations, respectively. The F_{ST} coefficient estimates relative population differentiation. Deviation of F_{IT} and F_{IS} from zero was tested using x^2-statistics (Li and Horvitz, 1953).

RESULTS

For *Raphanus sativus* var. *hortensis* f. *raphanistroides*, nine of 15 loci (60%) were revealed polymorphic in

at least one population. *Got-2, Gpi-1, Idh-1, Mdh-2, Mdh-3,* and *Pgm-1* were monomorphic in all seven populations. Allele frequencies for nine polymorphic loci estimated in seven Korean populations were presented in Table 1. The mean number of alleles per locus was 2.07, and the effective number of alleles was 1.74. At the population level, relatively low mean estimates of genetic variation observed; P of 51.4%, A of 1.84, and Ae of 1.16 (Table 2). In addition, mean expected heterozygosity or genetic diversity within populations (0.116) was similar with that for the overall values for the sample as a whole

Table 2. Estimates of genetic diversity within seven populations of *R. sativus* var. *hortensis* f. *raphanistroides*. Abbreviations: P, percentage of polymorphic loci; A, mean number of alleles per locus; Ae, effective number of alleles per locus; Ho, observed heterozygosity; He, Hardy-Weinberg expected heterozygosity or genetic diversity; SD, standard deviation. Population numbers correspond to those in Fig. 1

Population	Ho (SD)	He (SD)	P	Ae	A
1	0.087 (0.028)	0.108 (0.034)	46.67	1.15	1.60
2	0.095 (0.041)	0.151 (0.042)	53.33	1.22	1.74
3	0.070 (0.037)	0.083 (0.022)	53.33	1.10	1.73
4	0.085 (0.035)	0.106 (0.029)	53.33	1.14	1.87
5	0.101 (0.039)	0.127 (0.035)	53.33	1.17	1.80
6	0.116 (0.042)	0.121 (0.031)	53.33	1.16	1.73
7	0.096 (0.037)	0.116 (0.031)	46.67	1.16	1.80
Mean	0.093 (0.014)	0.116 (0.012)	51.43	1.16	1.84

(0.119).

Analysis of fixation indices, calculated for all polymorphic in each population of Korean wild radish, showed an overall excess of homozygotes relative to H-W expectations, 47% of fixation indices were positive (24/51), and 16 of those departed significantly from zero ($P<0.05$). However, all 27 negative fixation indices were not significantly different from zero (Table 3). In addition, Wright's F-coefficients showed that significant excesses of homozygotes exist for each six of the nine polymorphic loci at the level of population and the sample as a whole (Table 4). The value of F_{IS} varied from -0.231 to 0.332, with a mean of 0.116 (Table 4). This range

Table 4. Total genetic diversity (H_T), genetic diversity within populations (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 *R. sativus* var. *hortensis* f. *raphanistroides*

Locus	H_T	H_S	$F_{IS}{}^{a}$	$F_{IT}{}^{a}$	$G_{ST}{}^{b}$
Got-1	0.200	0.191	0.205***	0.241***	0.045**
Adh	0.032	0.031	-0.049^{ns}	-0.013^{ns}	0.035***
Gpi-2	0.040	0.033	-0.231**	-0.021^{ns}	0.171***
Idh-2	0.266	0.257	0.255***	0.279***	0.032***
Mdh-1	0.147	0.143	-0.106*	-0.080^{ns}	0.024***
Pgd-1	0.141	0.134	0.230***	0.266***	0.048***
Pgd-2	0.137	0.129	0.117*	0.169***	0.059***
Pgm-2	0.302	0.296	0.294***	0.307***	0.019***
Pgm-3	0.152	0.146	0.332***	0.356***	0.036***
Mean	0.157	0.151	0.116	0.224	0.052

[a] Asterisks indicate F-coefficients significantly different from zero (ns not significant; *$P<0.05$; **$P<0.01$; ***$P<$ 0.001). [b] Asterisks indicate significant allele frequency heterogeneity among populations based on a x^2 test (*$P<0.05$; **$P<0.01$; ***$P<0.001$).

of values of inbreeding coefficients was greater than expected, suggesting that the unknown evolutionary forces have varied impact upon nine loci.

The G_{ST} values ranged from 0.019 for *Pgm-2* to 0.171 for *Gpi-2* (Table 4), and on average, about 95% of the total variation in the species is common to all populations (mean $G_{ST}=0.052$). However, significant differences in allele frequency among populations were found for all nine loci ($P<0.01$). Average genetic identity for all pairs of populations was 0.995.

Table 3. Wright's fixation indices (F) for seven populations of *R. sativus* var. *hortensis* f. *raphanistroides*. Chi-square tests were used to determine if fixation indices were different from an excepted value ($F=0$). Population that were monomorphic for a particular locus are indicated with a dash. Population numbers correspond to those in Fig. 1

Locus	Population						
	1	2	3	4	5	6	7
Got-1	0.421*	0.357^{ns}	-0.093^{ns}	-0.073^{ns}	0.356^{ns}	-0.017^{ns}	-0.054^{ns}
Adh		-0.010^{ns}	-0.009^{ns}	-0.058^{ns}	$-$	$-$	$-$
Gpi-2	$-$	$-$	$-$	$-$	$-$	-0.212^{ns}	$-$
Idh-2	0.104^{ns}	0.529***	0.357**	-0.058^{ns}	0.214^{ns}	0.310**	0.284**
Mdh-1	-0.009^{ns}	-0.062^{ns}	-0.063^{ns}	-0.032^{ns}	-0.079^{ns}	-0.136^{ns}	-0.136^{ns}
Pgd-1	0.462***	0.681***	-0.037^{ns}	-0.032^{ns}	-0.024^{ns}	-0.067^{ns}	-0.027^{ns}
Pgd-2	$-$	0.224^{ns}	0.470***	-0.039^{ns}	-0.164^{ns}	$-$	-0.039^{ns}
Pgm-2	0.015^{ns}	0.472***	0.301^{ns}	0.607***	0.222*	0.172^{ns}	0.276*
Pgm-3	0.237**	-0.030^{ns}	-0.038^{ns}	0.392**	0.535***	-0.029^{ns}	0.544***

ns not significant; *$P<0.05$; **$P<0.01$; ***$P<0.001$.

DISCUSSION

The levels of genetic variation found within Korean wild radish populations were similar to the mean values of short-lived herbaceous perennial. According to a recent review of plant allozyme literature (Hamrick and Godt, 1989), short-lived herbaceous plants at the population (N=159) level maintain a mean polymorphic loci of 28.0%, mean number of alleles per locus of 1.40, mean effective number of alleles per locus of 1.12, and mean genetic diversity of 0.096. For the Korean populations of wild radish, these estimates are 51.4%, 1.18, 1.16, and 0.116, respectively. These levels of genetic variation of wild radish could be explained by several biological aspects of the plant. Breeding system is strongly associated with levels of genetic variation within populations (Gottlieb, 1981). Populations of selfing species and animal-pollinated species with mixed mating systems (i.e., partially selfed, partially outcrossed) have considerably lower levels of genetic diversity than that of outcrossing, wind-pollinated species (Hamrick and Godt, 1989). Wild radish has been known to exhibit gametophytic-sporaphytic self-incompatibility (Lewis et al., 1988). In addition, dehiscent anthers are physically separated from the receptive stigma (herkogamy), indicating animal-outcrossing breeding system.

In general, species or taxa with widespread geographic distribution maintain a higher level of genetic diversity than those with narrow or endemic distributions (Karron et al., 1988). In addition, species with discrete populations in patchy distribution have relatively low levels of variation within populations than those with more continuously distributed populations (Chung, 1994; Chung and Kang, 1996a; Kim and Chung, 1995c). Although wild radish has wide geographic range, it has restricted ecological distribution; it grows only on sand dunes and beaches or disturbed areas near sea in East Asia. Like wild radish, species with a relatively narrow niche and discrete, isolated populations ("habitat specialists"), in general, maintain less genetic variation within populations than species with continuous, abundant populations growing on broad-niched mainland habitats ("habitat generalists") (Nevo et al., 1984).

Usually, plant species with high fecundities main-

tain high genetic diversity within species (Chung and Kang, 1994; Chung and Kang, 1995). Wild radish has high flower production and relatively high seedmass compared to other rapidly cycling species, and individual plant produce hundreds of seeds in the field and greenhouse conditions (Mazer and Stick, 1991). It is highly probable that a combination of several factors such as animal-outcrossing breeding system, widespread geographical distribution, restricted ecological distribution and a propensity for high fecundity, may in part serve to maintain a moderate level of allozyme diversity found in Korean wild radish.

In general, many outcrossing species show heterozygotes that are lower than expected, despite theoretical predictions that heterozygosity should be favored in outcrossing plants (Brown, 1979). An overall deficiency of heterozygotes was observed in wild radish (Tables 3 and 4). Although wild radish is self-incompatible, the heterozygotes deficiencies in several populations and at several loci (Table 3) indicate that consanguineous mating might occur in populations of Korean wild radish. A previous study by Devlin and Ellstrand (1990) also indicated that pollen flow in wild radish was limited and the mating among neighboring plants occurred at a high frequency. In addition, seeds of wild radish disperse only short distance (Togunaka and Ohnishi, 1992). Randomness of the spatial distribution of genotypes at four isozyme loci of a natural population of Japanese wild radish was tested by spatial autocorrelation analysis (Togunaka and Ohnishi, 1992). The authors reported significant aggregation of an identical allele at two loci, indicating that a significant small scale genetic structure was present. Although genetically related individuals were aggregated in the short distance, samples were collected in this study from several patches per population. If these aggregates are small subpopulational patches or demes differing to some extent in allele frequencies, their pooling during electrophoretic study would result in a Wahlund effect (Wahlund, 1928). Factors such as mating among neighboring plants and genetic subdivision due to limited gene flow could lead to a family structure within a circumscribed area.

Although level of gene flow within and among populations of wild radish was restricted (Togunaka and Ohnishi, 1992), only 5% of the total genetic va-

riation found in Korean wild radish examined is due to differences among populations (mean $G_{ST}=0.052$). In addition, mean genetic identity between populations ($I=0.995$) was somewhat above the mean identity ($I=0.945$) reported by Gottlieb (1981) for 22 species. According to an allozyme literature reviewed by Hamrick and Godt (1989), short-lived herbaceous perennials, widespread species, species with animal-outcrossing breeding system, and species with gravity seed dispersal mechanism have mean G_{ST} values of 0.237, 0.210, 0.197, and 0.277, respectively. The degree of population differentiation observed in Korean wild radish was considerably low relative to those values. This is surprising and may not be expected from Korean populations of wild radish. It is unclear how allele frequencies among seven populations are relatively similar. It is supposed that similar selective forces on a very similar habitat of wild radish (i.e., dry and beach habitat) might have resulted in a considerable genetic uniformity in Korean wild radish. A few example of the similar results were available on allozyme literature. For example, *Impatiens hypophylla* Makino (Balsaminaceae), a herbaceous annual, is a rare endemic to a few locations of southwestern Japan and southeastern Korea. Although Korean populations of the species are small and isolated, and also the gene flow among discontinuous populations are limited, they differed little in gene frequencies among populations (mean $F_{SI}=0.059$: Chung and Kang, 1996b). Similar results were also observed in geographically isolated populations of *Maniola jurtina* (L.), a sedentary butterfly (mean $F_{ST}=0.015$: Goulson, 1993). Since this value of F_{ST} was close to those for known migrant Lepidopterian species and was far lower than those of known sedentary Lepidopterian species, Goulson concluded that similar selection at all sites examined maintained similar gene frequencies in isolated populations.

ACKNOWLEDGMENTS

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韓國産 갯무 自然集團의 遺傳的 多樣性

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적   요

갯무(십자화과)는 다년생 초본이며 동아시아 해변가에서 자생하고 있다. 한반도에 자생하는 7군데 집단을 대상으로 유전적 다양도 및 구조를 밝히기 위해 전분 전기영동을 사용했다. 비록 조사된 갯무집단은 작고 격리되어 있지만, 이들 집단들은 대부분 다년생 초본에서 보이는 수준을 유지하고 있음이 밝혀졌다. 예를 들면, 집단내 평균유전좌위의 다양성은 51.4%를 보였고 유전좌위당 대립인자의 수는 1.84였으며 집단내 평균 유전적 다양도는 0.116을 나타내었다. 이들 이유로는 곤충에 의한 타가수분, 넓은 지리적 분포, 한정된 생태적 분포, 다산성의 조합된 요소가 현재 집단내 유전적 다양도를 유지하는데 기여되고 있다고 볼 수 있다. 자가수정계수분석에 의하면 전반적으로 동형접합자들이 많이 존재하는 것으로 나타났다(평균 F_{IS}=0.116). 부분적인 근친교배 및 제한된 유전자들이 집단내에 하부구조를 형성했기 때문일 것이다. 이런 현상에도 불구하고 집단간의 분화도는 5% 밖에 되지 않았다. 이 값은 갯무와 생활사적 및 생태학적으로 유사한 식물과 비교해 볼 때 매우 낮게 나타났다. Nei의 집단간 유전적 동질성값도 높은 값인 0.995를 보였다. 이런 결과는 아마 갯무의 생육지가 환경이 비슷한 해안가에서 유사한 자연도태압이 한반도 갯무 집단에 영향을 주고 있다고 할 수 있다.

주요어 : 교배계, 유전자이동, 유전자다양성, 유전적 하부구조, 한반도, 자생 갯무집단, 자연도태

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