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Genetic Diversity in Korean Populations of *Glycine soja* (Fabaceae)

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Glycine soja **Sieb. et Zucc., a predominantly selfing annual, has been served as a reservoir of germplasm for soybean, *G. max* (L.) Merr., cultivar improvement. This study describes the levels and distribution of genetic variation within and among 22 Korean populations of *G. soja* using starch gel electrophoresis. The species maintains very similar levels of genetic variability within populations observed in most other annuals. At the population level, the mean percent of polymorphic loci (P) was 32.6%, mean number of allele per locus (A) was 1.32, and mean expected heterozygosity (H_e) was 0.112. In addition, total genetic diversity (H_T) calculated only for polymorphic loci was 0.347. However, significant differences in allele frequencies among populations were found for all loci ($P<0.001$ in each case) and, on average, about 70% of the total variation in the species is common to all populations. Indirects estimate of the number of migrants per generation ($Nm=0.58$, calculated from mean G_{ST}) indicates that gene flow is low among Korean populations of the species. In addition, analysis of fixation indices revealed a substantial heterozygote deficiency in most populations and at all loci. This indicates that most populations sampled may have been substructed largely due to inbreeding (predominantly selfing) and restricted gene flow, coupled with founder effect and genetic drift. Considering a high genetic divergence among populations, it is recommended that several Korean populations of the species should be preserved, especially such as populations in the eastern and southeastern Korean peninsula with high variation.**

Keywords : *Glycine soja*, breeding system, genetic diversity, gene flow, population genetic substructure, conservation

Since the genetic variation provides the potential for evolutionary change in natural populations of plant species, its measurement has been one of the important topics of population genetics to understand the evolutionary factors affecting genetic structure. Allozyme study has been routinely used to describe the levels and distribution of genetic variation and the population genetic structure of a variety of groups of plants, because it provides the most abundant sources of data (Hamrick and Godt, 1989). More recently, Hamrick *et al.* (1991) suggested that allozyme diversity of a plant species can be used as a "yardstick" to measure the effectiveness of its *in situ* and *ex situ* conservation programs. Although the knowledge concerning genetic variation has been known to be one of important factors for providing information for conservation purposes, only few detailed studies on allozyme variation and population genetic structure are available for native plants in Korea (Chung, 1994a, b, c, d; Chung and Chung, 1994; Chung and Kang, 1994; Kim and Chung, 1995).

G. soja Sieb. et Zucc., a wild soybean, grows widely in China, a belt of Siberia adjacent northern China, Korea, Japan, and Taiwan (Kiang *et al.*, 1992). In Korea, the species grows naturally in riverbanks, roadsides, and waste places with patchy distribution. In addition, it commonly grows adjacent to cultivated soybean fields. The species is predominantly a

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selfer (Kiang *et al.*, 1992; S. Chung and M. Chung, pers. obs.) and it is diploid ($2n=40$: Hymowitz, 1970). The flower of *G. soja* has a purple corolla and seeds are 2-4 in each pod.

The natural populations of the species has served as a reservoir of germplasm for soybean cultivar improvement (Singh and Hymowitz, 1988). For this and other reasons, Chiang and his associates (Chiang, 1985; Kiang, 1987; Kiang and Chiang, 1991; Kiang *et al.*, 1992) studied on allozyme variation within several populations of the species in the East Asian countries. However, these works did not include studies on the population genetic structure and gene flow in the species. In addition, detailed studies on the levels of genetic diversity and genetic structure of Korean populations have not been carried out previously. In this study, we investigated allozyme variation and genetic structure in Korean populations of *G. soja* using starch gel electrophoresis.

MATERIALS AND METHODS

From 1991 to 1993 seeds were collected from 22 natural populations of *G. soja* in Korea (Fig. 1). 20 to 40 fruits (legumes) were collected from each population and one seed per each fruit was used in this study (Table 1). Since the plants in the field were often entangled, fruits were collected from individual plants separated at least by more than 2 m.

Horizontal starch gel electrophoresis was conducted to estimate allozyme variation maintained in the species. Seeds were moistened with 10 mL distilled water in petri dishes (10 cm in diameter) and incubated at 20℃ for 48 h for germination. Germinating seeds were collected in two days and homogenized with a multi-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 3 MM 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 the seven enzyme systems: alcohol dehydrogenese (ADH), fluorescent esterase (FE), malate dehydrogenase (MDH), and lactate dehydrogenase (LDH) were resolved on buffer system 2; isocitrate dehydrogenase (IDH), 6-phosphogluconate dehydrogenase (PGD), and aconitase (ACO) on buffer system 9. Electrophoretic phenotypes were interpreted on the basis of models for the soybean examined by Gorman and Kiang (1978). For enzymes with more than one locus, isozymes were sequentially numbered from the most anodal. Likewise, alleles were designated sequentially with the most anodally migrating alleles as a. *Fe-2* was being expressed, but it was not scored because of poor activity and/or resolution.

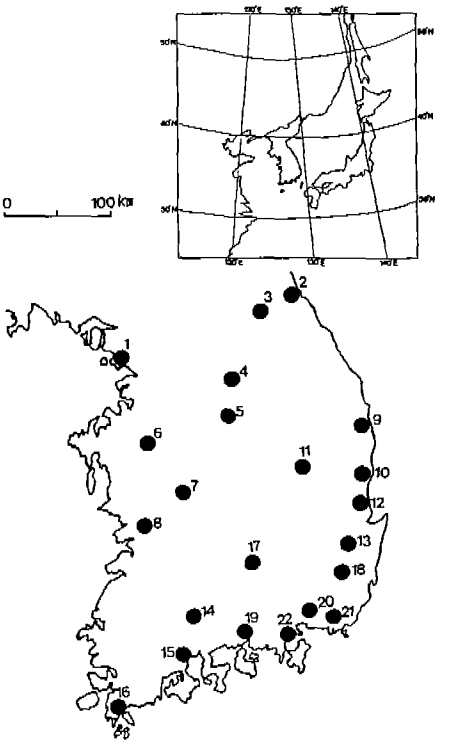

Fig. 1. The location of the 22 sampled populations of *G. soja* in Korea.

Loci with two or more alleles were considered polymorphic, 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 (A_e), and mean expected heterozygosity (H_e), assuming Hardy-Weinberg equilibrium. The statistics of these parameters were described in detail in Hamrick *et al.* (1992) and Chung and Chung (1994).

Observed heterozygosity was compared to Hardy-Weinberg expected values using Wright's (1922) fixation indices (F) of inbreeding coefficients. These indices were tested for deviations from zero by a χ^2-

Table 1. Estimates of genetic variation within 22 populations of *G. soja*. Abbreviations: N, number of seeds examined; P, percent polymorphic loci; A, mean number of alleles per locus; A_e, effective number of alleles per locus; H_o, observed heterozygosity; H_e, expected heterozygosity; SE, standard error

Pop. code	N	P	A	A_e	H_o (SE)	H_e (SE)
1	28	18.2	1.18	1.13	0.000 (0.000)	0.077 (0.011)
2	22	36.4	1.36	1.26	0.017 (0.005)	0.146 (0.014)
3	27	27.3	1.27	1.16	0.003 (0.002)	0.094 (0.011)
4	24	18.2	1.18	1.10	0.004 (0.003)	0.060 (0.010)
5	29	36.4	1.36	1.30	0.041 (0.007)	0.165 (0.014)
6	30	36.4	1.09	1.17	0.006 (0.003)	0.106 (0.013)
7	32	18.2	1.36	1.15	0.000 (0.000)	0.081 (0.012)
8	25	36.4	1.36	1.15	0.000 (0.000)	0.104 (0.010)
9	24	36.4	1.27	1.34	0.000 (0.000)	0.176 (0.016)
10	23	27.3	1.36	1.14	0.008 (0.004)	0.080 (0.012)
11	25	36.4	1.36	1.24	0.011 (0.005)	0.133 (0.013)
12	29	36.4	1.45	1.16	0.022 (0.006)	0.101 (0.010)
13	31	45.5	1.27	1.24	0.000 (0.000)	0.144 (0.013)
14	25	27.3	1.36	1.18	0.071 (0.000)	0.094 (0.014)
15	24	36.4	1.36	1.18	0.000 (0.000)	0.106 (0.012)
16	22	36.4	1.27	1.16	0.000 (0.000)	0.109 (0.010)
17	27	27.3	1.45	1.17	0.007 (0.003)	0.095 (0.012)
18	25	45.5	1.36	1.16	0.030 (0.007)	0.112 (0.009)
19	29	36.4	1.36	1.18	0.003 (0.002)	0.111 (0.012)
20	26	36.4	1.36	1.23	0.000 (0.000)	0.129 (0.014)
21	28	36.4	1.36	1.24	0.016 (0.005)	0.146 (0.013)
22	30	27.3	1.32	1.17	0.000 (0.000)	0.106 (0.012)
Mean	26.6	32.6	1.32	1.19	0.011	0.113
SE		0.63	0.01	0.01	0.001	0.002

statistics following Li and Horvitz (1953).

Nei's (1973, 1977) gene diversity formula (H_T, H_S, D_{ST}, and G_{ST}) were used to evaluate the distribution of genetic diversity within and among populations. A χ^2-statistics was used to detect significant differences in allele frequencies among populations for each locus and in each population (Workman and Niswander, 1970). Nei's (1972) genetic identity (I) was calculated for each pairwise combination of populations. A correlation between genetic identity and geographical distance was calculated using PC-SAS (SAS Institute, Inc., 1989). In addition, we used NT-SYS (Rohlf, 1988) to conduct a cluster analysis on genetic identities via the unweighted pairwise group methods using arithmetic average (UPGMA). Finally, an indirect estimate of gene flow (*Nm*, the number of migrants per genneration) was calculated based on Wright's (1951) formula.

RESULTS

Five of the 11 loci (45%) examined were polymorphic in at least one of the 22 populations. *Adh-1, Mdh-2, Fe-1, Pgd-1, Ldh*, and *Aco* were monomorphic in all 22 populations studied. The mean percent of polymorphic loci within populations (*P*) was 32.6 %, ranging from 18.2% (populations 1, 4, and 7) to 45.5% (populations 13 and 18) (Table 1). Mean number of allele per locus (A) within the species and populations were 1.45 and 1.32, respectively. At the species and the population levels, the mean effective numbers of alleles per locus (A_e) were 1.48 and 1.19, respectively. Mean genetic diversity (H_e) estimates at the species and the population levels were 0.158 and 0.112, respectively.

Analysis of fixation indices, calculated for all polymorphic loci in each population, showed a substantial deficiency of heterozygotes relative to Hardy-Weinberg expectations. For example, 95% of fixation indices were positive (75/79), and all of those departed significantly from zero ($P<0.05$). In contrast, of four negative fixation indices, only one was significantly different from zero ($P<0.05$) (Table 2).

Heterogeneity χ^2 tests indicated that significant differences in allele frequencies among populations were found for all polymorphic loci ($P<0.001$ in each case). On a locus basis, the proportion of total genetic variation due to differences among populations (G_{ST}) ranged from 0.152 for *Fe-3* to 0.535 for *Idh*, with a mean of 0.299 (Table 3). On average, about 70% of the total variation resided within populations, indicating that gene flow among populations was highly restricted. The number of migrants per generation ($Nm=0.58$) is concordant with the significant differentiation in allele frequencies among populations. Average genetic identity for all pairs of populations was 0.940 (standard error=0.003), well within the range of values expected for conspecific population (Crawford, 1989). The UPGMA dendrogram, however, gave few insights into the genetic structuring among the 22 populations (Fig. 2). In a good agreement with the UPGMA phenogram, no significant correlation between genetic distance and geographic distance was found ($r=0.161$, df=229, $P>0.05$) and indicated that only about 2% of the variation in genetic distance was due to geographic distance.

Table 2. Fixation indices (F) for five polymorphic loci in populations of *G. soja*. Chi-square tests were used to determine if fixation indices were differcnt from an expected values ($F=0$). Populations that were monomorphic for a particular locus are indicated with a dash

Locus	Population										
	1	2	3	4	5	6	7	8	9	10	11
Adh-2	–	0.48*	0.93***	0.89***	0.35^{ns}	0.83**	1.00***	–	1.00***	1.00***	0.70**
Idh	–	–	–	–	–	–	–	1.00***	–	–	1.00***
Mdh-1	1.00***	1.00***	–	–	0.75***	1.00***	–	1.00***	1.00***	–	–
Fe-3	–	1.00***	1.00****	–	1.00***	1.00***	–	1.00***	1.00***	−0.03^{ns}	1.00***
Pgd-2	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***

Table 2. (Continued)

Locus	Population										
	12	13	14	15	16	17	18	19	20	21	22
Adh-2	0.82***	1.00***	–	1.00***	1.00***	0.85***	0.69***	1.00***	1.00***	0.56**	1.00***
Idh	1.00***	1.00***	−0.95***	–	–	–	1.00***	1.00***	1.00***	1.00***	–
Mdh-1	−0.09***	1.00***	–	1.00***	1.00***	–	1.00***	0.79	–	1.00***	1.00***
Fe-3	–	1.00***	1.00****	1.00***	1.00***	1.00***	0.08^{ns}	–	1.00***	–	–
Pgd-2	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***	1.00***

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

Table 3. Genetic diversity statistics (Nei, 1973, 1977) for five polymorphic loci in *G. soja*

Locus	No. of alleles	H_T	H_S	D_{ST}	G_{ST}[a]
Adh-2	2	0.4876	0.3701	0.1176	0.2411***
Idh	2	0.2000	0.0930	0.1071	0.5353***
Mdh-1	2	0.3130	0.1972	0.1158	0.3701***
Fe-3	2	0.2346	0.1990	0.0356	0.1517***
Pgd-2	2	0.5000	0.4029	0.0971	0.1941***
Mean	2	0.3470	0.2524	0.0946	0.2985

Abbreviations: H_T, total genetic diversity; H_S, genetic diversity within populations; D_{ST}, genetic diversity among populations; and G_{ST}, proportion of total genetic diversity partitioned among populations. [a]Asterisks indicate significant allele frequency heterogeneity among populations based on a χ^2 test (***P<0.001)

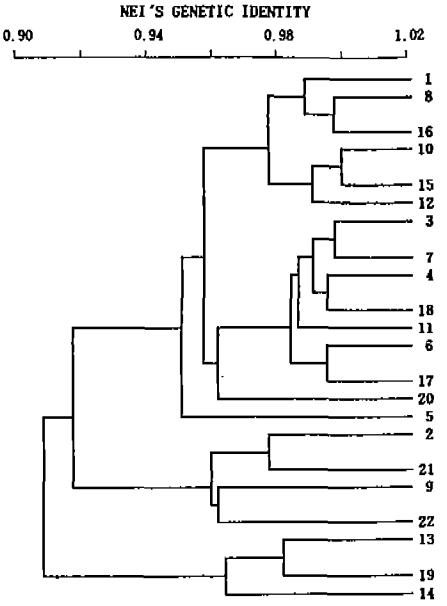

Fig. 2. Phenogram from UPGMA cluster analysis based on Nei's (1972) genetic identities between the 22 populations of *G. soja* in Korea.

DISCUSSION

Korean populations of *G. soja* maintain a comparable level of genetic variability observed in most annuals. For example, at the species and the population levels, mean percentage of polymorphic, mean number of alleles, mean effective number of alleles, and mean genetic diversity of 226 annuals reviewed by Hamrick *et al.* (1992) were 49.2 and 29.4%, 2.02 and 1.45, 1.22 and 1.14, and 0.154 and 0.101, respectively. Korean *G. soja* showed 45 and 32.6% of mean percentage of polymorphic loci, 1.45 and 1.32 of ave-

rage number of alleles per locus, 0.158 and 0.112 of mean effective number of alleles, and 0.148 and 0.19 of mean expected heterozygosity at the species and the population levels, respectively. As expected, levels of allozyme variation found in four Japanese populations of *G. soja* (Kiang *et al.*, 1992) also similar to those in this study. This moderate level of genetic variation of *G. soja* is easily explained with biological aspects of the species. Genetic variation within populations is significantly associated with breeding systems (Hamrick and Godt, 1989). Predominantly self-pollinating species tend to maintain less genetic variation within populations than those with higher proportions of outcrossing (Gottlieb, 1981) because of restricted gene flow via pollen and/or genetic drift. *G. soja* is a predominantly selfing annual (Kiang and Gorman, 1983), and its seeds are dispersed around the mother plants (S. Chung and M. Chung, pers. obs.). Although the species is predominantly self-pollinated, it is abundant and occurs widely in East Asia. In general, species with widespread distribution maintain higher level of genetic diversity than those with narrow or endemic distributions (Hamrick and Godt, 1989). In addition, it has been observed that each mature plant generates 50-100 fruits, indicating high reproductive capacity (S. Chung and M. Chung, pers. obs.). It is highly probable that widespread geographical distribution and a propensity for high fecundity may in part be factors that serve to maintain a moderate level of allozyme diversity found in *G. soja* in Korea.

A substantial heterozygote deficiency in most populations and at all loci explicitly reflects a predominant selfing breeding system of *G. soja*. Considering the breeding system of the species, most populations (or locations) would consist of several discrete breeding units. In addition, sampling has been done at several patches per population, which could generate a Wahlund effect (Hartl and Clark, 1989) contributing partly to heterozygote deficiencies observed in this study.

Genetic differentiation among populations is principally a function of gene flow among populations via pollen and seeds dispersal (Loveless and Hamrick, 1984). Predominantly selfing species with discrete, isolated populations should experience a limited gene flow (Richards, 1986). Of the total variation observed in *G. soja*, about 30% is due to differences among populations (G_{ST}=0.299). This level of genetic divergence is higher than mean G_{ST} value of 584 plant species (0.228) reported by Hamrick *et al.* (1992). The high level of genetic divergence among Korean populations of *G. soja* suggests that gene flow is low. Indirect gene flow estimate of *Nm* (0.58) was low, reflecting a predominantly selfing breeding system and gravity seed dispersal mechanism exhibited by the species. For neutral gene, a *Nm* value of 1 is considered necessary to prevent divergence due to genetic drift (Wright, 1931). In other words, given limited gene flow, populations are expected to diverge genetically due to drift, the random loss of alleles due to small population size (genetic bottleneck) resulting from founder effect (Wright, 1931). Thus, the level of gene flow in Korean populations of *G. soja* is insufficient to counterbalance genetic drift. However, the level of genetic divergence observed in this study is slightly lower than mean value (G_{ST}=0.355) based on 226 annuals reviewed by Hamrick *et al.* (1992). It is supposed that infrequent secondary gene flow would be possible by the seed movement by soil brought from other places under road and riverbank construction in Korea (S. Chung and M. Chung, pers. obs.). It is of interest to note that the level of genetic differentiation found among four Japanese populations (G_{ST}=0.197: Kiang *et al.*, 1992) was considerably lower than that for Korean populations examined. This may be in part due to different sample sizes between the two studies. Twenty-two populations were sampled in this study (ca. 400 km range), but four Japanese populations were collected within 120 km distance along reverbanks. Kiang *et al.* (1992) suggested that gene flow via seeds from upstream to downstream populations growing along riverbanks in four Japanese populations be occurred. The seeds in intact pods and those caught in dry pod walls can float on water for over 24 h (Kiang *et al.*, 1992). These two factors may account for the lower level of genetic differentiation observed in four Japanese populations of the species.

The relatively small populations in patchy distribution that currently characterize the Korean populations of *G. soja* coupled with present destruction of natural habitats by riverbank and road construction may result in erosion of genetic diversity in a near future. Hamrick and Godt (1989) noted that the degree of genetic differentiation among plant po-

pulations is of primary importance for the conservation of genetic diversity and the evolutionary potential of the species under consideration. Based on the data available such as a considerably high G_{ST} value compared with a mean value of plant species, it is recommended that several populations of the species in Korea should be preserved, giving priority to populations primarily with high variation such as populations mostly in the eastern and southeastern Korean Peninsula (populations 2, 5, 9, 11, 13, 18, 20, and 21; Fig. 1). These populations could be used as sources of genetic diversity for the restoration of genetically depauperate populations in the future.

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韓國產 돌콩 自然集團의 遺傳的 多樣性

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적 요

자가수분이 주된 교배계인 돌콩은 1년생 초본이며 대두의 품종개량을 위한 생식질원으로 이용되어 오고 있다. 본 연구에서는 전분 전기영동법을 사용하여 획득한 한반도내 22군데 자연집단내 · 간에서의 유전적 변이의 수준과 분포를 기술하고 있다. 이 종이 지니는 집단내의 유전적 변이도는 대부분의 다른 일년생 초본에서 보이는 수준이었다. 예를 들면, 집단내 평균 유전좌위의 다형성(P)은 32.6%를 보였고 유전좌위당 대립인자의 수(A)는 1.32였으며 집단내 평균 유전적 다양도(H_e)는 0.112를 나타내었다. 또한 다형성 유전좌위만 고려한 전체 유전적 다양도는 0.347이었다. 그러나 조사된 모든 다형성 유전좌위에서 집단간의 대립인자의 빈도의 차이가 통계학적으로 유의성이 있는 것으로 나타났으며($P<0.001$) 평균적으로 이 종이 지니는 전체 유전적 다양도 중 약 70% 정도가 조사된 모든 집단에 공통으로 나타났다. 평균 G_{ST} 값으로부터 간접적으로 구한 세대당 집단간 이동개체수($N_m=0.58$)는 이 종의 한반도내 집단간의 유전자이동은 낮다는 것을 암시하고 있다. 자가수정계수분석에 의하면 이형접합자의 부족이 상당한 수준에서 보였다. 이 이유로는 자가수분이 주된 교배계이며, 제한된 유전자이동, 유전적 부동 및 창시자효과 때문이라고 해석된다. 집단간의 유전적 분기수준이 높은 점을 감안해 볼 때 유전적 변이가 높은 한반도의 동해안 및 남쪽지역의 집단들을 주로해서 몇 군데 집단들이 보존되어야 될 것이다.

주요어: 돌콩, 자가수분, 유전적 다양성, 유전자 이동, 집단하부구조, 보존

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