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Genetic Structure in Korean Populations of *Hosta capitata* (Liliaceae)

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I investigated levels of genetic diversity, population genetic structure, and gene flow in *Hosta capitata*, a herbaceous perennial native to South Korea and southwestern Japan. Starch gel electrophoresis was conducted on leaves collected from 310 plants in 19 Korean populations. Twenty-two of 25 putative loci examined were polymorphic in at least one population and the mean number of alleles per locus was 1.65. In addition, mean expected heterozygosity within populations (Hep=0.153) was higher than average values for species with similar life history traits. Significant differences in allele frequency were detected between populations at all loci ($P<0.01$), and slightly over 30% of the genetic variation was found among populations (G_{ST}= 0.308). Indirect estimates of the number of migrants per generation (*Nm*) (0.506, calculated from G_{ST}; 0.852, calculated from the mean frequency of ten private alleles) indicate that gene flow is restricted among the isolated Korean populations of *H. capitata*. Factors contributing to the high levels of genetic differentiation among populations of *H. capitata* include small and discrete populations, human disturbance, and low frequencies of pollinator foraging behavior.

Keywords : *Hosta capitata*, starch gel electrophoresis, genetic diversity, population genetic structure, gene flow

Studies of genetic variation within and among populations have provided information about evolutionary processes of plant species. The evolutionary change in natural populations is dependent on the existence of genetic variation and its distribution among populations. For this reason, the measurement of genetic variation of plant species has become one of major research areas in population genetics (Hamrick *et al.*, 1991).

Electrophoresis has provided the most abundant source of data for describing the levels and distribution of genetic variation and the population genetic structure of a variety of groups of plants. The accumulation of this information has provided insights into the relationships between allozyme diversity and life history traits (Brown, 1979; Gottlieb, 1981; Loveless and Hamrick, 1984; Hamrick and Godt, 1989; Hamrick *et al.*, 1991; Hamrick *et al.*, 1992). In addition, allozyme diversity can be used as a yardstick to measure the effectiveness of *in situ* and *ex situ* conservation programs (Hamrick *et al.*, 1991).

Hosta capitata (Koidz.) Nakai (Liliaceae), a herbaceous rhizomatous perennial, is an horticulturally important species with other hostas because of purple-colored, showy, and bell-shaped flowers and leaf texture. The species is native to South Korea (mainly in the southwestern Korean Peninsula) and southwestern Japan (Chung and Kim, 1991; Fujita, 1976). In Korea, most populations of the species are relatively small and isolated as compared to other Korean hostas (Chung *et al.*, 1991a), and few pollinators (*e.g.*, bees) were observed. Based on a recent review (Hamrick and Godt, 1989), the ecological and life history traits of *H. capitata* such as small and isolated populations, low fecundity, and insect pollination (Chung *et al.*, 1991a; Chung and Kim, 1991) allow me to predict high genetic differentiation between populations in this species. Here I report levels and partitioning of allozyme diversity within and among populations of *H. capitata* for the conservation purposes. The purpose of this study was: 1) to estimate how

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Table 1. Population code, locations (elevation) of 19 populations examined by electrophoretic analyses

Code	Locality (elevation, m)	N[a]	Collection number
1	Pooun-gun, Prov. Ch'ungch'ongbuk-do (ca. 600)	17	525
2	Sokrisan N.P., Prov. Ch'ungch'ongbuk-do (950)	11	526
3	Sokrisan N.P., Prov. Ch'ungch'ongbuk-do (ca. 990)	11	527
4	Chuwangsan N.P., Prov. Kyeongsangbuk-do (620)	21	528
5	Chirisan N.P., Nogodan, Prov. Chollanam-do (ca. 1300)	15	543
6	Chirisan N.P., Daejiryong, Prov. Chollanam-do (ca. 1400)	14	556
7	Daedunsan P.P., Wanju-gun, Prov. Chollabuk-do (ca. 520)	19	587
8	Tokyusan N.P., Prov. Chollabuk-do (ca. 680)	13	617
9	Gayasan N.P., Prov. Gyeongsangnam-do (ca. 650)	7	648
10	Moarksan P.P., Prov. Chollabuk-do (ca. 510)	22	713
11	Puan-gun, Prov. Chollabuk-do (ca. 700)	23	743
12	Sonunsan P.P., Prov. Chollabuk-do (ca. 520)	16	788
13	Naejangsan N.P., Prov. Chollabuk-do (ca. 600)	17	800
14	Kycryoungsan N.P., Prov. Ch'ungch'ongnam-do (ca. 570)	15	840
15	Jogaesan P.P., Prov. Chollanam-do (ca. 420)	19	936
16	Jukyang-meon, Hadong-gun, Prov. Gyeongsangnam-do (ca. 300)	20	1140
17	Mt. Jagol, Prov. Gyeongsangnam-do (ca. 500)	16	1160
18	Yonwhasan P.P., Prov. Gyeongsangnam-do (ca. 350)	17	1180
19	T'aeback city, Prov. Kangwon-do (ca. 900)	17	1456

N.P.=National Park; P.P.=Provincial Park; [a]Sample sizes.

much total genetic diversity is maintained in the species, 2) to describe how genetic variation is distributed within and among populations, and 3) to compare my estimates with those for species having similar life history traits.

MATERIALS AND METHODS

Population samples

In 1987 and 1988, 310 samples of *Hosta capitata* rootstocks were collected from 19 localities in South Korea. Table 1 lists the 19 populations, their numeric codes, sample sizes, and vouchers used in this study. Collections of rootstocks from each site were made at least 2 m apart to reduce the likelihood of collecting clones. The rootstocks were transported to the Botany Plant Growth Facility at the University of Georgia where plants were grown under uniform conditions. Voucher specimens of all collections were deposited at GA, GNUC, KYO, MO, SNU, and US.

Isozyme extraction and electrophoresis

Crude leaf tissue extracts for horizontal starch gel electrophoresis were prepared using liquid nitrogen. The extraction buffer was that of Mitton *et al.* (1979). Wicks were stored at −60℃ until needed for analysis. Electrophoresis was performed using 11% starch gels. Except as noted, gel and electrode buffers and enzyme staining procedures from Soltis *et al.* (1983) were used to assay ten enzyme systems: phosphoglucomutase (PGM) was resolved on system 6; diaphorase (DIA) and glutamate oxaloacetate transaminase (GOT) on system 7; isocitrate dehydrogenase (IDH) on system 2; 6-phosphogluconate dehydrogenase (6-PGD) and malate dehydrogenase (MDH) on system 11; leucine aminopeptidase (LAP), triosphosphate isomerase (TPI), β-galactosidase (β-GAL), and fluorescent esterase (FE) on a modification (Haufler, 1985) of system 8. The staining procedures for diaphorase followed the method described by Cheliak and Pitel (1984). Putative loci were designated sequentially, with the most anodally migrating isozyme designated 1, the next 2, and so on. Likewise, alleles were designated sequentially with the most anodally migrating alleles designated a. All *H. capitata* isozymes expressed phenotypes that were consistent in subunit structures and genetic interpretation with most isozyme studies in plants as documented by Weeden and Wendel (1989).

Data analyses

A locus was considered polymorphic if two or more alleles were observed regardless of their frequencies. Four 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). Subscripts refer to species (s) or population (p) level parameters. The statistics for estimating these parameters is described 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). These indices were used to test significant deviations from an expected value ($F=0$) using the χ^2-statistic following Li and Horvitz (1953): $\chi^2=F^2N(a-1)$, df$=a(a-1)/2$, where N is the total sample size and a is the number of alleles at the locus.

Genetic variation among populations was examined in three ways. First, total genetic diversity (H_T), genetic diversity within populations (H_S), genetic diversity among populations (D_{ST}), and the proportion of genetic diversity found among populations (G_{ST}) were calculated following Nei's (1973, 1977) genetic diversity formula. Second, a χ^2-statistic was used to detect significant differences in allele frequencies among populations for each locus: $\chi^2=2NG_{ST}(a-1)$, df$=(a-1)(n-1)$, where n is the number of populations (Workman and Niswander, 1970). Third, Nei's (1972) genetic identity (I) was calculated for each pairwise combination of populations.

The distribution of genetic diversity within and among populations was evaluated using Wright's (1965) F-statistics: F_{IT}, F_{IS}, and F_{ST}. These measures represent relative excess of homozygotes or heterozygotes compared with panmictic expectations relative to all populations (F_{IT}), within populations (F_{IS}), and among populations (F_{ST}). F_{IT} was calculated using the direct method: $F_{IT}=1-$Ho/He, where Ho is the observed number of heterozygotes in the whole population and He is the expected number, based on mean allele frequencies. The relationships between these measures are: $(1-F_{IT})=(1-F_{IS})(1-F_{ST})$, which assumes random population differentiation. Deviations of F_{IT} and F_{IS} from zero were also tested using the χ^2-statistic (Li and Horvitz, 1953). Gene flow among populations was estimated indirectly from the allozyme data by two methods. The first estimate of the number of migrants per generation (Nm) was obtained based on Wright's (1931) formula as modified by Crow and Aoki (1984): $Nm=(1-F_{ST})/4F_{ST}\alpha$, ($F_{ST}=G_{ST}$), where $\alpha=[n/(n-1)]^2$. The second estimate was based on the average frequency of private alleles (Slatkin, 1985; Barton and Slatkin, 1986): $\log_{10}[P(1)]=a\log_{10}Nm+b$, where a and b are variables related to population size and P (1) is the mean frequency of private alleles.

RESULTS

Genetic diversity

Twenty-two of the 25 loci resolved ($P_S=88\%$) were polymorphic in at least one of the 19 populations. The mean percent of polymorphic loci within populations (P_P) was 43.8%, ranging from 24% in population 9 to 72% in population 16 (Table 2). Seventy-eight alleles were scored across all loci, indicating that, on average, more than three alleles were found at each locus ($A_S=3.12$). Mean number of alleles

Table 2. Estimates of genetic diversity for 19 *Hosta capitata* populations based on 25 allozyme loci[a]

POP[b]	Ho_P (SD)	He_P (SD)	P_P	Ae_P	A_P
1	0.115 (0.057)	0.134 (0.042)	40.000	1.260	1.480
2	0.120 (0.056)	0.096 (0.035)	32.000	1.170	1.360
3	0.131 (0.061)	0.100 (0.035)	28.000	1.170	1.320
4	0.126 (0.042)	0.155 (0.046)	36.000	1.300	1.400
5	0.101 (0.055)	0.102 (0.037)	32.000	1.190	1.400
6	0.140 (0.066)	0.195 (0.042)	52.000	1.340	1.640
7	0.091 (0.047)	0.123 (0.036)	44.000	1.210	1.560
8	0.142 (0.062)	0.151 (0.040)	48.000	1.260	1.520
9	0.116 (0.057)	0.088 (0.035)	24.000	1.160	1.280
10	0.127 (0.041)	1.126 (0.040)	32.000	1.230	1.360
11	0.126 (0.042)	0.133 (0.036)	52.000	1.220	1.600
12	0.165 (0.056)	0.151 (0.046)	36.000	1.300	1.480
13	0.200 (0.050)	0.180 (0.044)	52.000	1.340	1.600
14	0.184 (0.067)	0.164 (0.041)	44.000	1.290	1.560
15	0.234 (0.057)	0.183 (0.045)	48.000	1.340	1.720
16	0.262 (0.065)	0.265 (0.041)	72.000	1.470	2.040
17	0.255 (0.064)	0.202 (0.048)	56.000	1.410	1.840
18	0.191 (0.064)	0.217 (0.045)	60.000	1.410	1.920
19	0.134 (0.051)	0.146 (0.040)	44.000	1.260	1.520
Mean	0.156 (0.013)	0.153 (0.009)	43.790	1.280	1.650

[a]Abbreviations (subscript p refers to population level parameter): 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. [b]Numerical codes as in Table 1.

per locus within populations (A_P) was 1.65. The highest number of alleles detected per locus was 5 for 6-PGD1. The average number of alleles per polymorphic locus was 3.40. The effective number of alleles per locus at the species level (Ae_S) and at the population level (Ae_P) were 1.45 and 1.28, respectively, indicating that many of the alleles were present at very low frequencies. Genetic diversity at the species level (He_S) and at the population level (He_P) were 0.294 and 0.153, respectively. Population 16 had the highest expected diversity (0.265), while 2, 3, 5 and 9 had the lowest (0.088-0.102).

Genetic structure

Analysis of fixation indices, calculated for all polymorphic loci in each population, showed an overall deficiency of heterozygotes relative to Hardy-Weinberg expectations. Although nearly 57% of fixation indices were negative (109/192), only 35 of those departed signigficently from zero ($P<0.05$). An excess of heterozygotes was found in all populations at the DIA3 locus. PGMI and GOT3 had excess heterozygotes over half of the populations. In contrast, 60 of 83 positive fixation indices were significently diffenrent from zero ($P<0.05$), indicating a deficiency of heterozygotes at those loci and in those populations, and half of those showed absence of heterozygotes ($F=1$): DIA2 (1 population); GOTI (12 populations); LAP3 (5 populations); MDH1 (5 populations); 6-PGD1 (4 populations); and PGM2 (3 populations).

Wright's F-coefficients showed that significant deficiencies of heterozygotes exist for 11 and 14 of the 22 polymorphic loci at the level of population and the sample as a whole, respectively (Table 3). In contrast, 8 and 4 loci at the population level and the sample as a whole showed signigicant excess of heterozygosity, and at the population level and at the sample as a whole. Three loci (DIA1, IDH1, and TPI2) and 4 loci (D1A1, TPI1, FE2, and FE3), however, did not deviate Hardy-Weinberg expectations

Table 3. Estimates of genetic diversity parameters for 22 polymorphic loci examined for 19 *Hosta capitata* populations

Locus	H_T	H_S	F_{IS}[b]	F_{IT}[b]	G_{ST}	χ^2(DF)
PGM1	0.491	0.419	−0.493***	−0.279***	0.147	239.642 (54)***
PGM2	0.320	0.155	0.293***	0.657***	0.514	841.434 (54)***
PGM3	0.447	0.340	0.373***	0.524***	0.240	308.927 (54)***
DIA1	0.010	0.009	−0.070^{NS}	−0.005^{NS}	0.061	37.617 (18)**
DIA2	0.050	0.039	0.666***	−0.743***	0.232	143.520 (18)***
DIA3	0.537	0.516	−0.797***	−0.724***	0.040	158.231 (54)***
GOT1	0.428	0.216	0.970***	0.985***	0.494	306.314 (18)***
GOT2	0.326	0.252	0.194***	0.376***	0.226	232.271 (36)***
GOT3	0.564	0.292	−0.138***	0.411***	0.483	476.179 (36)***
PGD1	0.260	0.080	0.639***	0.888***	0.691	544.351 (72)***
PGD2	0.621	0.412	0.232***	0.491***	0.337	425.936 (54)***
IDH1	0.078	0.068	0.006^{NS}	0.133*	0.127	134.602 (54)***
IDH2	0.468	0.320	0.215***	0.464***	0.317	250.999 (36)***
MDH1	0.105	0.081	1.000***	1.000***	0.233	225.822 (36)***
MDH2	0.078	0.064	−0.267***	0.411***	0.483	173.348 (36)***
LAP	0.050	0.038	0.661***	0.743***	0.242	150.219 (18)***
LAP	0.325	0.141	0.360***	0.722***	0.566	388.264 (36)***
TPI1	0.054	0.045	−0.221***	−0.021^{NS}	0.164	214.727 (36)***
TPI2	0.495	0.116	−0.029^{NS}	0.759***	0.766	773.041 (54)***
TPI3	0.261	0.177	−0.725***	−0.172***	0.321	270.978 (36)***
FE2	0.124	0.105	−0.141**	0.040^{NS}	0.158	128.904 (36)***
FE3	0.069	0.053	−0.331***	−0.320^{NS}	0.224	202.581 (36)***
Mean	0.280	0.179	0.109	0.349	0.308	

[a]Abbrevations: H_T, total genetic diversity; H_S, genetic diversity within populations, F_{IT} and F_{IS}, deviations of genotype frequencies from Hardy-Weinberg expectations over all populations and within individual populations, respectively; G_{ST} ($=F_{ST}$), proportion of total genetic diversity partitioned among populations. A χ^2 test for allele frequency heterogeneity between populations is also given. **, $P<0.01$; ***, $P<0.001$. [b]Asterisks indicate F-coefficients significantly different from zero (*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$).

(Table 3). The values of F_{IS} (Table 3) varied from 1,000 to −0.796. This range of values of the inbreeding coefficient were substantially greater than those expected, suggesting that the unknown evolutionary forces acting differ in their impacts upon 22 loci. Similar trends were observed in *H. minor* (Chung, 1994) and in Korean populations of *Eurya japonica* (Theaceae) a dioecious, broad-leaved evergreen woody perennial (Chung and Kang,1994). The mean F_{IT} (0.349) was high, suggesting an overall deficiency of heterozygotes if the species is considered as a single panmictic unit.

The G_{ST} values ranged from 0.040 for D1A3 to 0.766 for TPI2 (Table 3), and overall, slightly less than 70% of the total variation in the species is common to all populations. Significant differences in allele frequencies were found among populations for all polymorphic loci ($P<0.01$). Ten private alleles were found in seven populations: 1 (PGM2^b), 9 (PGM1^a), 11 (D1A1^a), 16 (1DH1^a), 17 (6-PG1^d and TPI3^a), 18 (6-PGD1^e and TPI2^d) and 19 (PGM3^a and TPI^a). Average genetic identity for all pairs of populations was 0.876 (SD=0.034), within the range of values expected for conspecific populations (Crawford, 1989). Indirect estimate of the number of migrants per generation (Nm) were 0.506, and 0.852 calculated from G_{ST} and the mean frequency of 10 private alleles.

DISCUSSION

Genetic diversity

Hosta capitata maintains relatively high levels of allozyme variation compared to the average plant species. At the species level, mean percent polymorphic loci (P_S) for the average plant species is 50.5%, mean number of alleles (A_S) is 0.97, and mean genetic deversity (He_S) is 0.149 (Hamrick and Godt, 1989). In contrast, for *H. capitata*, P_S is 88%; A_S, 3.12; and He_S, 0.294. The same trend is observed at the population level. Mean percent polymorphic loci (P_P) for the average plant species is 34.2%, mean number of alleles per locus (A_P) is 1.53, and mean genetic diversity within populations (He_P) is 0.113 (Hamrick and Godt, 1989). Within *H. capitata* populations, P_P is 43.8%; A_P, 1.65; and He_P, 0.153. A comparison of genetic variation maintained within *H. capitata* and within plant species with similar life history traits (reviewed in Hamrick *et al.*, 1992) can also be made. Long lived herbaceous species with a predominantly animal-outcrossing mode of reproduction and wind-dispersed seeds, and regional geographic range have a mean percent polymorphic loci (P_S) of 50%, mean number of alleles per locus (A_S) of 1.93, and mean genetic diversity (He_S) of 0.144. At the population level, species with these traits have P_P of 36%, A_P of 1.55, and He_P of 0.115. The values for *H. capitata* (see above) are higher than the mean of the species as a whole with similar life history traits. At the population level, however, the estimates for *H. capitata* are very comparable to these for species with similar life history traits. Based on a recent review of the plant population genetics literature (Hamrick and Godt, 1989), features such as patterns of geographical distribution, breeding system, taxonomic status, life form, seed dispersal, and successional status influence levels and partitioning of genetic diversity. The relatively high levels of genetic variation observed in *H. capitata* comparable to several aspects of its biology. Geographic range has been shown to be strongly associated with the level of variation maintained within populations (Hamrick *et al.*, 1979). Widely distributed plant species tend to maintain more variation than more narrowly distributed species. Populations of *H. capitata* distributed in South Korea and southwestern Japan. Except *H. capitata*, and *H. clausa*, other 22 to 23 *Hosta* species are native to Korea, Japan and China (Chung *et al.*, 1991b; Fujita, 1976). Breeding system is also directly associated with variation within populations (Gottlieb, 1981). Predominantly outcrossing species tend to maintain more variation within their populations than species with higher proportions of self-pollination. *H. capitata* native to Korea appears to be predominantly outcrossing because most of the flowers have pronounced spatial separation (herkogamy) of mature anthers and stigmas impeding self-pollination. In addition, only a few individuals of the species set fruit in a screened green house (Chung *et al.*, 1991a), and artificially self-pollinated fruits bear only a few seeds (Chung, unpubl. data). *H. capitata*, a perennial that sprouts from a rhizome, may be rather long-lived. Long-lived species tend to maintain higher levels of genetic variation within their populations (Hamrick *et al.*, 1979), presumably because of the large number of generations present in any given population (Levin, 1977). Combinations of these fac-

tors may contribute to the maintenance of relativily high levels of variation within *H. capitata*. It is of interest to compare the levels of genetic variation within *H. capitata* with those for *H. yingeri*, a Korean endemic, known from only in Taehuksan, Sohuksan, and Hong Islands. Although *H. yingeri* is a narrow endemic, it maintains higher level of genetic variation within species (P_S=64%; P_P=59%; A_S=2.32; A_P=1.92; He_S=0.313; and He_P=0.250: Chung and Chung, 1994) than more widely distributed its congener, *H. capitata*. Chung and Chung (1994) suggested that factor such as large effective population sizes, high fecundity, the persistence of multiple generations within populatons, predominantly outcrossing breeding system, seed disperal by wind in the open habitats and large size of pollinator visitation areas in the open coastal island habitats, or combinations of these factors may be explanatory factors contributing to the maintenance of the high levels of genetic variation found in *H. yingeri*. Although *H. capitata* occurs wider than *H. yingeri*, most populations are small and isolated, which seems to be one of the major factors contributing to lower level of genetic variation within the species than *H. yingeri*. From the results, it seems that geographic distribution is not a good predictor of levels of genetic diversity for *Hosta* species.

Genetic structure

The analysis of fixation indices showed a considerable amount of heterozygote deficiencies (mean F_{IS} =0.109). Although the species has winged seeds, the dispersal distance seems to be short under rich pine-oak forests, which may favor the establishment of clusters of related individuals. In addition, the pollinator visitation areas appears to be small (Chung, pers. obs.), indicating probable mating among relatives. Such structure could lead to biparental inbreeding, causing heterozygote deficiences. This patchy distribution of related individuals should generate a Wahlund effect resulting from the species fragmentation into discrete breeding units. Sampling has been done at several patches per population. It is highly probable that the combination of these factors may contribute to heterozygote deficiences within populations. The most significant deviation observed in *H. capitata* from plants with similar life istory characterisics, however, is the partitioning of genetic variation among populations. Species with regional geographic range (G_{ST}=0.216), outcrossing-animal breeding system (G_{ST}=0.197), seed dispersal by wind (G_{ST}=0.143), and long-lived herbaceous perennial (G_{ST}=0.213) have lower mean G_{ST} values than that of *H. capitata* (G_{ST}=0.308), which is supported by low mean genetic identities for each pairwise combination of populations (I= 0.876). Genetic differentiation among populations is principally a function of gene flow among populations *via* pollen and seeds dispersal (Loveless and Hamrick, 1984). The high mean G_{ST} value observed in *H. capitata* suggests that gene flow among populations is low. Indirect estimates of *Nm* based on G_{ST} values (0.506) and the private alleles (0.852), were lower than those obtained for other species with similar life history traits (Hamrick, 1987). For neutral genes, an *Nm* values of 1.0 is considered necessary to prevent divergence due to genetic drift (Wright, 1931). The levels of gene flow calculated here are of insufficient magnitude to counterbalance genetic drift. Thus, it appears that genetic drift may play one of roles in shaping the genetic structure of the populations. Most populations of *H. capitata* are discrete and isolated, which may in part account for the high levels of genetic differentiation among populations. Similar results were observed in *Pinus halepensis* Mill. This species, distributed in discrete populations around the Mediterranean Sea, has 30% of its variation among populations (Schiller *et al.*, 1986). Historically, populations of *H. capitata* have been disturbed by collecting leaves for vegetables in rural areas. Also, *H. capitata* usually grows in pines and oaks understory. It is highly probable that in the rich pines and oaks understory pollinator foraging behavior would be limitted (Chung pers. obs.), and winged seeds would be dispersed in a relatively short distance. These factors may result in higher levels of genetic differentiation among populations.

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LITERATURE CITED

Barton, N.H. and M. Slatkin. 1986. A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. *Heredity* **56**: 409-415.

Brown, A.D.H. 1979. Enzyme polymorphism in plant populations. *Theor. Pop. Biol.* **15**: 1-42.

Cheliak, W.M. and J.A. Pitel. 1984. Techniques for starch gel electrophoresis of enzyme from forest species. *Information Report PI-X-42*, Petawawa National Forestry Institute, Agriculture Canada, Canadian Forestry Service, Chalk River, Ontario, pp. 1-49.

Chung, M.G. 1994. Gentic variation and population structure in Korean endemic species: III. *Hosta minor* (Liliaceae). *J. Plant Res.* (in press).

Chung, M.G. and H.G. Chung. 1994. Allozyme diversity and population genetic structure in Korean Endemic species: II. *Hosta yingeri* (Liliaceae). *J. Plant Biol.* **37**: 141-149.

Chung, M.G., J.L. Hamrick, S.B. Jones and G.S. Derda. 1991a. Isozyme variation within and among populations of *Hosta* (Liliaceae) in Korea. *Syst. Bot.* **16**: 667-684.

Chung, M.G., S.B. Jones, J.L. Hamrick and H.G. Chung. 1991b. Morphometric and isozyme analysis of the genus *Hosta* (Liliaceae) in Korea. *Plant Species Biol.* **6**: 55-69.

Chung, M.G. and S.S. Kang. 1994. Genetic variation and population structure in Korean populations of *Eurya japonica* (Theaceae). *Am. J. Bot.* **81**: 1077-1082.

Chung, M.G. and J.W. Kim. 1991. The genus *Hosta Tratt.* (Liliaceae) in Korea. *Sida* **14**: 411-420.

Crawford, D.J. 1989. Enzyme electrophoresis and plant systematics. *In* Isozymes in Plant Biology, D.E. Soltis and P.S. Soltis (eds.). Dioscorides, Portland, pp. 146-164.

Crow, J.F. and K. Aoki. 1984. Group selection for a polygenic behavioral trait: Estimating the degree of population subdivision. *Proc. Natl. Acad. Sci. USA* **81**: 6073-6077.

Fujita, N. 1976. The genus *Hosta* (Liliaceae) in Japan. *Acta Phytotax. Geobot.* **27**: 66-96. (in Japanese)

Gottlieb, L.D. 1981. Electrophoretic evidence and plant populations. *Progr. Phytochem.* 7: 1-46.

Hamrick, J.L. 1987. Gene flow and distribution of genetic variation in plant populations. *In* Differentiation Patterns in Higher Plants. K. Urbanska (ed.). Academic Press, New York, pp. 53-67.

Hamrick, J.L. and M.J.W. Godt. 1989. Allozyme diversity in plant species. *In* Plant Population Genetics, Breeding and Genetic Resources. S.D.H. Brown, M.T. Clegg, A.L. Kahler and B.S. Weir (eds.). Sinauer, Sunderland, pp. 43-63.

Hamrick, J.L., M.J.W. Godt, D.A. Murawski and M.D. Loveless. 1991. Correlations between species traits and allozyme diversity: Implications for conservation biology. *In* Genetics and Conservation of Rare Plants. D. A. Falk and K.E. Holsinger (eds.). Oxford University Press, New York, pp. 75-86.

Hamrick, J.L., M.J.W. Godt and S.L. Sherman-Broyles. 1992. Factors influencing levels of genetic diversity in woody plant species. *New Forests* **6**: 95-124.

Hamrick, J.L., Y.B. Linhart and J.B. Mitton. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. *Annu. Rev. Ecol. Syst.* **10**: 173-200.

Haufler, C.H. 1985. Enzyme variability and modes of evolution in *Bommeria* (Pteridaceae). *Syst. Bot.* **10**: 92-104.

Levin, D.A. 1977. The organization of genetic variability in *Phlox drummondii*. *Evolution* **31**: 477-494.

Li, C.C. and D.G. Horvitz. 1953. Some methods of estimating the inbreeding coefficient. *Am. J. Human Genet.* **5**: 107-117.

Loveless, M.D. and J.L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. *Annu. Rev. Ecol. Syst.* **15**: 65-95.

Mitton, J.B., Y.B. Linhart, K.B. Sturgeon and J.L. Hamrick. 1979. Allozyme polymorphisms detected in mature needle tissue of ponderosa pine. *J. Heredity* **70**: 86-89.

Nei, M. 1972. Genetic distance between populations. *Am. Nat.* **106**: 283-292

Nei, M. 1973. Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci. USA* **70**: 3321-3323.

Nei, M. 1977. *F*-statistics and analysis of gene diversity in subdivided populations. *Annu. Human Genet.* **41**: 225-233.

Schiller, G., M.T. Conkle and C. Grumwald. 1986. Isozyme variation among native stands and populations of aleppo pine in Israel. *Israel J. Bot.* **35**: 161-174.

Slatkin, M. 1985. Rare alleles as indicators of gene flow. *Evolution.* **39**: 53-65.

Soltis, D.E., C.H. Haufler, D.C. Darrow and G.J. Gastony. 1983. Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules. *Am. Fern J.* **73**: 9-27.

Weeden, N.F. and J.F. Wendel. 1989. Genetics of plant isozymes. *In* Isozymes in Plant Biology. D.E. Soltis and P.S. Soltis (eds.). Dioscorides, Portland, pp. 46-72.

Workman, P.L. and J.D. Niswander. 1970. Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Papago. *Am. J. Human Genet.* **22**: 24-49.

Wright, S. 1922. Coefficients of inbreeding and relationship. *Am. Nat.* **56**: 330-338.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics* **16**: 97-159.

Wright, S. 1965. The interpretation of population structure by *F*-statistics with special regard to systems of mating. *Evolution* **19**: 395-420.

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韓國產 일월비비추 自然集團의 遺傳的 構造

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적 요

한국 및 일본 남서부에 자생하는 다년생 초본인 일월비비추를 대상으로 유전적 다양성, 집단유전적 구조 및 유전자 이동을 조사했다. 19군데의 자연집단에서 310개체를 대상으로 잎을 채취하여 전분전기영동법을 시행하였다. 조사된 25종류의 유전좌위 중 22종류는 적어도 한 집단 이상에서 다형성을 나타냈고 각 유전좌위 당 평균 대립인자의 수는 1.65였으며, 집단내에서 보이는 평균 유전적 다양도(He_P=0.153)는 일월비비추와 유사한 생활환적 특징을 가지는 식물들의 평균값보다 높았다. 조사된 모든 유전좌위에서 집단간에서 통계학적으로 중요하게 대립인자의 빈도차가 나타났으며(P<0.01), 전체 유전적 변이 중 집단간의 변이는 30%를 차지하게 되었다(G_{ST}=0.308). 세대 당 집단간 이동 개체의 수(Nm)의 측정은 간접적 방법으로 행해졌다. Nm은 G_{ST}에 의한 방법으로는 0.506이었으며 오직 한 집단에서만 나타난 1개의 대립인자에 의한 측정으로는 0.852였다. 이 값들은 한국산 일월비비추 집단간에 유전자 이동이 제한되고 있다는 것을 의미한다. 일월비비추에 보이는 높은 집단간의 분화도를 나타내는 데 기여한 요인들로서 집단들의 크기가 작고, 격리되어 있으며, 인간에 의한 간섭과 수분매개체의 활동이 낮다는 점 등을 들 수 있다.

주요어 : 일월비비추, 전분전기영동법, 유전적 다양도, 집단 유전적 구조, 유전자 이동

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