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Spatial genetic structure among Korean populations of *Hosta minor* and *H. capitata* (Liliaceae)

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Abstract. I investigated the spatial distribution of genotypes among eight populations of *Hosta minor* and 19 populations of *H. capitata* from Korea using spatial autocorrelation analysis of enzyme polymorphisms. Both species are insect-pollinated, herbaceous perennials. Among 162 cases calculated for six distance classes among populations of both species, Moran's *I* was significant for 20 (12%) cases in *H. minor* and for 35 (21.6%) in *H. capitata*, respectively. In addition, the number of significant overall correlograms was different from each species (33.3%, 9/27 in *H. minor* vs. 11.1%, 3/27 in *H. capitata*). Eleven of 16 significant negative autocorrelations were observed for *H. capitata* in the longer distance classes (ca. 111–235 km boundary). On the other hand, no distinct trend with respect to distance was detected among populations of *H. minor*. The results of the study indicate that the level of gene flow among abundant, contiguous local populations of *H. minor* via winged seeds is higher than that of *H. capitata*, partly resulting from different distribution patterns and natural habitats of both species.

Keywords: Allozyme; Gene flow; *Hosta capitata*; *H. minor*; Moran's *I*; Spatial autocorrelation.

Introduction

Recent reviews of the plant allozyme literature have shown casual relationships between several life history and ecological traits of plants and the amount and patterns of genetic variation (e.g., Hamrick and Godt, 1989; Hamrick et al., 1992). For instance, species with narrow or endemic distributions maintain lower levels of genetic diversity than species with widespread distributions. Knowledge of geographic range, however, may not always be predictive of levels of genetic variation (Chung and Chung, 1994; Soltis and Soltis, 1991). This may be explained by the fact that species, even congeners, often differ in many other aspects of their biology. In their review of the plant allozyme literature, Hamrick and Godt (1989) included 653 taxa and classified each species for eight traits to find correlations between the traits and levels and distribution of genetic variation. Unfortunately, less than 50% of the variation among species was explained by their models, which is due to differences in the specific ecological, evolutionary history and other unknown factors among species (Hamrick et al., 1991). Spatial genetic patterns within and among populations affect the evolutionary dynamics of plant populations and species (Sokal and Oden, 1978b). An understanding of the pattern could give us a more explicit understanding of the evolutionary and ecological processes in plant species and thus has been of continued interest to evolutionary and conservation biologists (Heywood, 1991; Xie and Knowles, 1991). Spatial structure may be analyzed using spatial autocorrelation analysis (Sokal and Oden, 1978a). The analysis has only recently been applied to large scale structure on a number of animal species (e.g., Sokal and Oden, 1978a,b; Sokal, 1988) and plant species (e.g., Jensen, 1986; Sokal et al., 1986) and to fine scale genetic structure within populations (e.g., Dewey and Heywood, 1988; Epperson and Clegg, 1988; Knowles et al., 1992). These studies have revealed several advantages of spatial autocorrelation analysis because the analysis includes all pair comparisons in samples and it makes no assumptions about the spatial scale of the structure within a population (Epperson, 1989; Heywood, 1991).

Population differentiation among plant populations is significantly associated with breeding systems (Hamrick and Godt, 1989). In other words, gene flow via pollen in plant species is one of the primary factors shaping genetic structure among populations. *Hosta minor* (Baker) Nakai and *H. capitata* (Koidz.) Nakai, are insect-pollinated, herbaceous perennials. Populations of *H. minor*, a Korean endemic species, are large and abundant on hillsides and grasslands in the middle eastern and southern Korean Peninsula (Chung and Kim, 1991). Flowers are visited by bees (*Apis mellifera* L. and *A. cerana* F.; Chung pers. obs.). On the other hand, *H. capitata* 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 compared with other Korean hostas (Chung et al., 1991), and few pollinators (e.g., bees) were observed. Populations of *H. capitata* usually are found in pine-oak understories. The fruit of both species is a cylindrical capsule, with 10–30 small (3.0–5.5 mm) seeds in each capsule. Each seed is winged and dispersed by wind (Chung and Kim, 1991). Although both species are

diploids (2*n*=60), they are considered to be of ancient polyploid origin because of gene duplication on several enzyme systems such as phosphoglucomutase, phosphoglucoisomerase, 6-phosphogluconate dehydrogenase, and triosephosphate isomerase (Chung, 1990; Chung et al., 1991). Both species are similar in their seed dispersal mechanism and breeding system. As population differentiation is most affected by several ecological traits, we might expect that *H. minor* and *H. capitata* would exhibit similar patterns of spatial genetic structure among populations. The purpose of this study is to compare spatial genetic structure among populations of *H. minor* and *H. capitata*.

Materials and Methods

A total of 443 leaf samples collected from eight populations (133 individuals) of *H. minor* and 19 populations (310 individuals) of *H. capitata* in Korea (Figure1) was used in the study. Isozyme extraction and electrophoresis, and interpretation of isozyme banding patterns (loci and alleles designation) have been described previously (Chung, 1990; Chung et al., 1991). Except as noted, gel and electrode buffers and enzyme staining procedures from Soltis et al. (1983) were used to assay four and six enzyme systems for *H. capitata* and *H. minor*, respectively: system 6 resolved phosphoglucomutase (PGM) for both species and phosphoglucoisomerase (PGI) for *H. minor*; diaphorase (DIA) on system 7; isocitrate dehydrogenase (IDH) on system 2; 6-phosphogluconate dehydrogenase (PGD) on system 11; for *H. minor*, triosephosphate isomerase (TPI) on a modification (Haufler, 1985) of system 8. The staining procedures for DIA followed the method described by Cheliak and Pitel (1984).

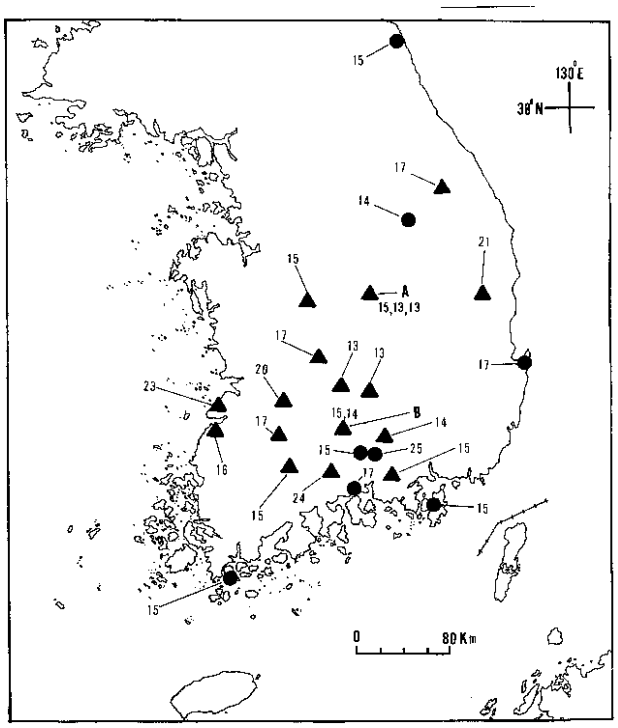

Figure 1. The location of 27 sampled populations in Korea. Closed circles indicate *Hosta minor* (eight populations) and closed triangles represent *H. capitata* (19 populations) respectively. A and B indicate three (ca. 5 km boundary) and two populations (ca. 10 km boundary), respectively, were collected. Sample size is indicated in each population.

A locus was considered polymorphic only if the most common allele occurred at a frequency of 0.95 or less in the population (a 95% criterion). For spatial autocorrelation analysis, the mean frequency values were assigned to each population for alleles at each locus. Every possible pair of populations was considered as a join and was assigned to one of six distance classes based on the geographic distance between them. These six distance classes were constructed by equalizing sample sizes among the classes. The distance classes for *H. minor* are 0<49, 49<119, 119<140, 140<175, 175<283, and 283<383 km. For *H. capitata*, they are 0<43, 43<70, 70<83, 83<110, 110<137, and 137<235 km. Moran's *I* values were calculated for interpopulational distance classes by

$$I = N \sum_i \sum_j (W_{ij} \Sigma_i \Sigma_j) \left(\sum_i \sum_j W_{ij} \Sigma Z_j^2 \right)^{-1}$$

(Sokal and Oden, 1978a). Here, N is the number of populations, W_{ij} is the join on weighting matrix, where W_{ij} is set as one if *i*th and *j*th population are in the distance class and zero otherwise, $Z_i = X_i - \bar{X}$, $Z_j = X_j - \bar{X}$, the variables X_i and X_j are the mean allele frequency scores for *i*th and *j*th population, respectively, and $\bar{X}$ is the mean score for all populations. The value of *I* ranges between +1 (complete positive autocorrelation, i.e., paired populations have identical values) and -1 (complete negative autocorrelation). Each *I* value was used to test significant deviations from the expected values, E(*I*)=-1/(*N*-1) (Cliff and Ord, 1981). A significant positive value of Moran's *I* indicates that the neighboring populations in the distance class considered tend to have different gene frequencies, whereas a significant negative value suggests that they tend to have different scores. Overall significance of individual correlograms was tested using Bonferroni's criteria (Sakai and Oden, 1983). All calculations and statistical analyses were performed using the SAAP program (ver. 4.3) written by D. Wartenberg.

Results

A total of 27 alleles for both species were used for spatial autocorrelation analysis on the basis of a 95% criterion for considering a polymorphic locus. If two alleles were detected at each locus, only one allele was considered because either allele would provide the same information. The spatial autocorrelation coefficients, Moran's *I*, for both species are presented in Tables 1 and 2. For *H. minor*, Moran's *I* values in all eight populations were calculated for the 27 alleles surveyed. Moran's *I* was significant in 20 of 162 cases (12%). The overall correlogram for *Pgi-1*^{c}, *Tpi-3*^{a}, and *Tpi-3*^{c} was significant (Table 1). In the distance class 1 (0<49 Km), three positive and three

Table 1. Spatial autocorrelation coefficients (Moran's *I*) of 27 alleles among populations of *Hosta minor* for six distance classes (1–6).

Allele	1	2	3	4	5	6	*P*[a]
Pgm-1	-0.89**	0.38	-0.21	0.09	-0.27	-0.01	0.054
Pgm-2	-0.03	-0.44	-0.73	0.21	0.21	-0.17	0.585
Pgm-3[a]	-0.57	-0.21	0.43	0.29	-0.68	-0.09	0.493
Pgm-3[b]	-0.50	-0.17	-0.13	-0.70	0.71*	-0.14	0.087
Pgm-3[c]	-0.83*	0.16	0.11	-0.40	0.19	-0.18	0.208
Pgi-1[a]	0.37	0.12	-0.75	-0.33	0.05	-0.33	0.516
Pgi-1[b]	0.76**	-0.87*	-0.24	-0.10	0.29	-0.37	0.054
Pgi-1[c]	0.63*	-0.98**	-0.11	0.02	0.20	-0.27	0.029
Pgi-2	-0.10	-0.15	0.33	-0.38	-0.47	0.02	0.668
Dia-1	-0.80*	-0.00	0.62*	-0.37	-0.10	-0.18	0.225
Dia-2[a]	-0.38	-0.15	0.15	-0.48*	0.18	-0.16	0.237
Dia-2[b]	0.00	0.00	-0.84*	0.16	-0.33	0.04	0.277
Dia-2[c]	0.30	0.18	-0.97*	-0.59	0.03	0.30	0.067
Dia-2[d]	-0.11	-0.04	-0.85*	-0.06	0.12	0.08	0.172
Dia-3[a]	0.11	0.15	-0.36	0.12	0.05	-0.91**	0.057
Dia-3[b]	-0.01	0.02	-0.84	0.11	-0.42	0.17	0.300
Dia-3[c]	-0.11	0.33	-0.01	-0.12	-0.67	-0.25	0.364
Pgd-1[a]	0.39	-0.34	-0.04	-0.63	0.02	-0.13	0.471
Pgd-1[b]	-0.22	-0.38	-0.00	0.08	-0.10	-0.22	1.000
Pgd-1[c]	-0.35	-0.31	-0.14	0.32	-0.37	-0.05	0.812
Idh-2[a]	-0.43	-0.31	0.14	-0.09	-0.09	-0.09	0.472
Idh-2[b]	0.62*	-0.62	-0.89*	-0.03	0.22	-0.15	0.118
Idh-2[c]	-0.04	-0.17	-0.91*	0.36	0.12	-0.20	0.125
Idh-2[d]	0.04	-0.68	-0.57	0.27	0.09	-0.05	0.506
Tpi-3[a]	0.17	0.28	-0.07	0.05	0.08	-0.89**	0.000
Tpi-3[b]	-0.23	-0.35	0.07	-0.40	0.21	-0.13	0.438
Tpi-3[c]	0.38	0.44*	-0.03	-0.18	0.12	-0.93**	0.000

[a]Overall correlogram significance (Bonferroni approximation).
* = P < 0.05; ** = P < 0.01.

Table 2. Spatial autocorrelation coefficients (Moran's *I*) of 27 alleles among populations of *Hosta capitata* for six distance classes (1–6).

Allele	1	2	3	4	5	6	*P*[a]
Pgm-1[a]	-0.06	-0.12	-0.10	-0.09	0.02	0.02	0.906
Pgm-1[b]	0.05	-0.17	-0.10	-0.18	0.01	0.06	1.000
Pgm-1[c]	0.07	-0.33*	-0.19	0.06	0.05	0.02	0.159
Pgm-1[d]	0.04	-0.50**	0.04	0.21*	-0.02	-0.07	0.004
Pgm-2[a]	-0.01	-0.01	-0.08	0.01	-0.19*	-0.06	0.270
Pgm-2[b]	-0.02	-0.12	0.06*	-0.13	-0.13	-0.02	0.105
Pgm-2[c]	-0.29	0.10	-0.20	0.33**	-0.22	-0.09	0.042
Pgm-2[d]	-0.33*	0.12	-0.25	0.27*	-0.13	-0.03	0.080
Pgm-3[a]	0.00	0.05	-0.05	-0.06	0.03	-0.31*	0.084
Pgm-3[b]	0.05	-0.03	0.00	-0.01	0.07	-0.41**	0.028
Pgm-3[c]	0.07	-0.07	-0.03	-0.04	0.07	-0.32*	0.165
Dia-1	-0.02	-0.01	-0.10	-0.09	-0.10	-0.02	1.000
Dia-2	-0.05	-0.09	-0.02	-0.05	0.06	-0.16	0.398
Dia-3[a]	-0.05	-0.05	0.12*	-0.18	-0.13	-0.03	0.175
Dia-3[b]	0.28*	0.15	0.17	-0.18	-0.47**	-0.27	0.021
Dia-3[c]	0.34**	0.31**	-0.12	-0.32	-0.48**	-0.08	0.020
Dia-3[d]	0.12	-0.13	0.15*	-0.05	-0.26*	-0.14	0.250
Pgd-1	-0.13	-0.28	-0.13	0.28*	0.06	-0.14	0.079
Pgd-2[a]	0.46**	0.13	0.09	-0.52**	-0.10	-0.37*	0.005
Pgd-2[b]	0.11	-0.03	0.24*	-0.14	0.04	-0.53**	0.001
Pgd-2[c]	0.24*	0.22*	-0.15	-0.38*	-0.18	-0.09	0.145
Idh-1[a]	-0.06	-0.09	-0.02	-0.05	0.06	-0.16	0.398
Idh-1[b]	0.41**	-0.08	-0.17	-0.22	0.04	-0.30*	0.000
Idh-1[c]	0.54**	-0.08	-0.23	-0.27	0.02	-0.31*	0.000
Idh-2[a]	-0.18	0.22*	-0.05	-0.17	0.02	-0.18	0.087
Idh-2[b]	0.02	0.21*	-0.05	-0.28	-0.25	0.01	0.239
Idh-2[c]	0.01	0.20*	-0.05	-0.28	-0.25	0.01	0.281

[a]Overall correlogram significance (Bonferroni approximation).
* = P < 0.05; ** = P < 0.01.

negative *I* values were significantly different from the expected value (E[*I*])=-0.143 (Table 1). Beyond the distance class, 11 negative and three positive cases were significantly different from the expected value, indicating that populations are somewhat genetically heterogeneous beyond the distance class 1. For *H. capitata*, Moran's *I* was significant in 35 of 162 (21.6%) cases, and 19 of 35 values were positive (Table 2). The 19 positive values were only observed from distance classes 1 (0<43 km) to 4 (83<110 km), indicating overall genetic similarity within the distance classes. On the other hand, 11 negative values in the distance classes 5 (110<137 km) and 6 (137<235 km) were significantly different from the expected value E[*I*]=-0.056 (Table 2). The overall correlogram for *Pgm-1*[d], *Pgm-2*[c], *Pgm-3*[b], *Dia-3*[b], *Dia-3*[c], *Pgd-2*[a], *Pgd-2*[b], *Idh-1*[b], and *Idh-1*[c] were significant (Table 2).

Discussion

The results of this study indicate that the pattern of genetic distribution in *H. minor* is different from that of *H. capitata*. For example, 11 of 16 significant negative autocorrelations were observed for *H. capitata* in the longer distance classes (ca. 111–235 km boundary), and this implies that genetically more different populations are spaced farther apart. In addition, all 19 significant positive autocorrelation coefficients in distance classes 1 to 4 (ca. 0–110 km boundary) were detected among populations of *H. capitata*. Although three significant negative values were observed in the longest distance class, no distinct trend was observed among populations of *H. minor*. Among 162 cases calculated for all distance classes among populations of *H. minor* and *H. capitata*, Moran's *I* was significant for 20 (12%) cases in *H. minor* and for 35 (21.6%) in *H. capitata*, respectively. In addition, a higher number of significant overall correlograms was observed in *H. capitata* (9 vs. 3). Considering the similarity of the breeding systems (predominantly outcrossing because of herkogamy) and seed dispersal mechanisms (via wind) between the two species, the observed spatial pattern of genetic structure between them is somewhat surprising. The higher percentage of significant Moran's *I* values in *H. capitata* over *H. minor* indicates that the amount of gene flow among populations of *H. minor* is greater than that of *H. capitata*. Based on 22 polymorphic allozyme loci, Chung (1994a) reported that the partitioning of genetic variation among populations (Nei's [1973, 1977] G_{ST}) among the 19 Korean *H. capitata* populations (G_{ST}= 0.308) was considerably higher than those of mean values for similar life history traits. The high mean G_{ST} value observed in *H. capitata* is also indicative of a low level of gene flow. An indirect estimate of the number of migrants per generation (*Nm*) based on the mean G_{ST} was low (0.56). On the other hand, about 16% was due to differences among populations of the total variation found in *H. minor* on the basis of 19 polymorphic allozyme loci (G_{ST}=0.158; Chung, 1994b). In addition, indirect gene flow estimate of *Nm* (1.33) based on the G_{ST} was moderate, but this level was considerably higher than that for *H. capitata*. For neutral genes, below *Nm*=1 genetic drift is the predominant factor affecting population structure, whereas above *Nm*=4 gene flow replaces drift (J. Hamrick of University of Georgia, pers. comm.). Thus, it appears that both genetic drift and gene flow may play roles in shaping the genetic structure in the Korean populations of *H. minor*. Species with more continuously distributed populations should experience more gene flow than species with discrete, isolated populations and therefore have relatively lower variation among populations (e.g., Gibson and Hamrick, 1991; Chung and Kang, 1994). Most Korean populations of *H. capitata* surveyed are small, isolated, and grow on dense pine-oak understory in hillsides and mountains (alt. ca. 500–1,400 m); whereas most populations of *H. minor* are large and abundant (several thousand individuals per local population), and contiguously distributed on hillsides along coastal areas (alt. ca. less than 100 m), over the eastern and southern Korean Peninsula (Chung, pers. obs.). The present distribution patterns of *H. minor* and *H. capitata* in Korea can be explained by the Pleistocene paleoclimatic history of the Korean Peninsula. It is supposed that, since the Ice Age (the glacial "Würm"), the glacial remnants of *H. capitata* have retreated exclusively to calcarious mountainous regions (the southwestern Korean Peninsula) (Fujita, 1976), resulting in a relatively small effective population size. On the other hand, the remnant of *H. minor* has adapted to the warm coastal hillsides in the southern and southeastern Korean Peninsula. Gene flow via pollen between scattered or isolated populations of *H. capitata* seems improbable given the apparent lack of specialized pollinators (Chung, pers. obs.). In addition, as *H. capitata* usually grows in pine-oak understory, foraging behavior by flower visitors or pollinators would be limited (Chung, pers, obs.), and winged seeds would be dispersed in a relatively short distance. On the other hand, considering the distribution pattern and natural habitats of *H. minor*, it is highly probable that gene flow would be moderate among contiguously distributed local populations via winged seeds (Chung, 1994b). These differences may in part contribute to the observed spatial genetic structure among populations found in the two species.

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韓國 *Hosta minor* 和 *H. capitata* (Liliaceae)族群之空間遺傳結構

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本文分析多型性酵素之空間自相關性，以探討韓國 8 個 *Hosta minor* 和 19 個 *H. capitata* 族群其基因型之空間分布。此二品種均為蟲媒花，多年生草本。計算六個間距區內族群 162 個案例，其中 *H. minor* 有 20 個（約 12%），*H. capitata* 有 35 個案例（約 21.6%）有顯著之 Moran's *I* 值。此外，此二品種具顯著總相關之數目也不同（在 27 個案例中，*H. minor* 有 9 個案例，約佔 33.3% ，而 *H. capitata* 有 3 個案例，約佔 11.1%)。在 16 個有顯著負自相關之案例，有 11 個是位於較遠間距區（111-235 公里範圍）之 *H. capitata* 族群。然而在 *H. minor* 族群未見有這種跟距離有關的趨勢。結果顯示經由翅果散布之 *H. minor* 族群其基因流轉高於 *H. capitata* ，部份肇因於兩者之分布型式及自然生長環境不同。

關鍵詞：同功酵素；基因流轉； *Hosta minor* ； *H. capitata* ； Moran's *I* ；空間自相關。