

Comparisons of allozyme variation of narrow endemic and widespread species of Far East *Euphorbia* (Euphorbiaceae)

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Abstract. Genetic variation from 19 populations representing four species of *Euphorbia* was compared using isozyme markers. *Euphorbia fauriei* and *E. garanbiensis* are rare endemic species in Korea and Taiwan, respectively while *E. pekinensis* and *E. jolkinii* are widespread in Korea and Taiwan. A low level of genetic variation and high genetic differentiation among populations was found in *E. garanbiensis*, which has a restricted distribution, small population sizes, gravity-dispersed seeds, and is possibly a self-pollinator. Alternatively, *E. garanbiensis* may have recently evolved from a continental progenitor or may be a relictual lineage from the continental flora. The high genetic diversity found in *E. fauriei* is unusual and may be explained by its recent origin from a widespread continental progenitor, *E. pekinensis*. An alternative explanation is that *E. fauriei* survived in refugia during the last glaciation in the Korean peninsula. The idea of progenitor-derivative species pairs between *E. pekinensis* and *E. fauriei* is supported by the high genetic identity values between the two species and the putative derivative *E. fauriei* having no unique allele and lacking some rare alleles present in the putative progenitor *E. pekinensis*.

Keywords: Allozyme variation; *Euphorbia fauriei*; *Euphorbia garanbiensis*; *Euphorbia jolkinii*; *Euphorbia pekinensis*.

Introduction

Most rare and endemic plant species have low levels of genetic variability due to the effects of small population sizes (Hamrick and Godt, 1989; Ellstrand and Elam, 1993; Gitzendanner and Soltis, 2000; Smith and Pham, 1996; Sherman-Broyles et al., 1992). When compared with wide-ranging taxa, rare species are heavily impacted by genetic drift, the founder effect, and directional selection with high levels of inbreeding decreasing genetic diversity by eliminating polymorphic loci and reducing alleles per polymorphic locus (Karron, 1987; Barrett and Kohn, 1991; Sherman-Broyles et al., 1992; Dodd and Helenurm, 2002; Gitzendanner and Soltis, 2000). However, recent comparative studies of genetic variation between rare and widespread species have demonstrated that several rare species were as polymorphic as their widespread congeners (Dodd and Helenurm, 2002; Gitzendanner and Soltis, 2000). Thus, it is difficult to state that species with small populations and limited geographic range always have low genetic diversity. A common approach to determining the cause of differences in genetic variation between rare and widespread species has been to compare phylogenetically related species pairs (Edwards and Wyatt, 1994; Dodd and Helenurm, 2002; Gitzendanner and Soltis, 2000).

Euphorbia jolkinii, *E. pekinensis*, and *E. fauriei* are herbaceous perennial species of Far Eastern *Euphorbia* subg. *Esula*. Phylogenetic studies of these species using morphological and chemical data found them to be closely related and to form a distinct clade (Park et al., 1999a). The

Korean endemic *E. fauriei* is a rare plant with a narrow distribution on Mt. Halla of Jeju Island and seemingly restricted to the open, rocky areas of the mountaintop (ca. 1,500 m). This species is diploid ($2n = 28$), insect pollinated, and perennial, growing to 10-20 cm in height. *Euphorbia pekinensis* is morphologically most similar to *E. fauriei*. It is a more widespread and morphologically variable species in Korea, Japan, and northeast China. Despite a high degree of morphological and cytological similarity between the two species, *E. fauriei* is well distinguished from *E. pekinensis* by several quantitative characters (Park et al., 2002). Recent cladistic analyses of morphological data indicate that these two species form a sister-group relationship (Park et al., 1999a). *Euphorbia jolkinii*, a sister group of *E. pekinensis* + *E. fauriei*, is a salt-tolerant species inhabiting rocky areas along the seacoasts of Korea, Japan, and Taiwan (Lin and Hsieh, 1991).

Euphorbia garanbiensis, a member of *Euphorbia* subg. *Chamaesyce*, is a rare endemic species of the Oluanpi Peninsula, the southernmost tip of Taiwan (Lin et al., 1991). It inhabits sandy areas and sea-cliffs along the coast with known populations restricted to a few localities in Pingtung County Taiwan (Lin et al., 1991). This species is a perennial, distinguished from the other three species by its prostrate habit and bearing conspicuous appendages on the rim of the cyathium. There have been few studies of the reproductive biology in *Euphorbia*, although self-pollination has been reported in several weedy species of the subg. *Chamaesyce* (Krombein, 1961; Ehrenfeld, 1976).

In the genus *Euphorbia*, the structure of the cyathium consists of four or five nectar-producing glands that have been considered an adaptation to insect pollination (Cronquist, 1968). A diverse array of insects, such as ants,

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bees, beetles and flies, were observed on the cyathium of *E. pekinensis* and *E. jolkinii* (Personal observation). Seeds of the three species are ovate, carunculate, and dispersed explosively.

This study investigates and compares the amount and distribution of genetic diversity in two island endemic *Euphorbia* species with two widespread relatives to evaluate the association between genetic diversity and geographic range.

Material and Methods

About 25 individuals per population from 19 populations representing four *Euphorbia* species were examined for isozyme variation (Table 1; Figure 1). Voucher specimens were deposited at the Herbarium of Kyung-Nam University (KNUH). Soluble enzymes were isolated from the fresh leaf tissue of field-collected plants and ground in an extracting buffer containing 0.1 M tris-HCl, pH 7.5, 1 mM EDTA (tetrasodium salt), 10 mM MgCl₂, 10 mM KCl, 14 mM 2-mercaptoethanol, and 5-10 mg/ml solid polyvinylpyrrolidone (Gottlieb, 1981). Leaf extracts were centrifuged in 1.5 ml tubes, and the supernatant absorbed onto wicks of Whatman 17 MM chromatography paper.

Eight enzymes were resolved on 12.5% starch gels utilizing two buffer systems. System I had an electrode buffer of 0.065 M L-histidine and 0.007 M citric acid, adjusted to pH 6.5 with NaOH. This gel buffer was a 1:3 dilution of the electrode buffer. System II consisted of an electrode buffer with 0.18 M tris, 0.1 M boric acid, and 0.004 M EDTA, pH 8.6. System I was used to resolve aldolase (ALD), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (6PGD), malic enzyme (ME) and phosphoglucomutase (PGM). System II was used to resolve the enzyme systems alcohol dehydrogenase (ADH), phosphoglucose isomerase (PGI), and triosephosphate isomerase (TPI). Enzyme-activity staining and agarose overlays generally followed the protocols of Soltis et al. (1983). Loci and alleles were numbered sequentially and lettered alphabetically, beginning with the most anodal form. The BIOSYS-1 program (Swofford and Selander, 1981) was used to calculate the mean number of alleles per locus (A), percentage of polymorphic loci (P), mean observed heterozygosity (H_o), and mean expected

heterozygosity (H_e) within the populations studied. For the analysis of population differentiation, Wright's (1965) F statistics were calculated. The F statistics include F_{IS} , an index of inbreeding, F_{IT} , the overall inbreeding coefficient, and F_{ST} , a measure of the genetic differentiation among subpopulations (Wright, 1965). Gene flow was estimated using Wright's (1951) formula $Nm = (1 - F_{ST}) / 4F_{ST}$. A UPGMA phenogram was produced by input of Nei's (1972) genetic identity values into the BIOSYS-1 program.

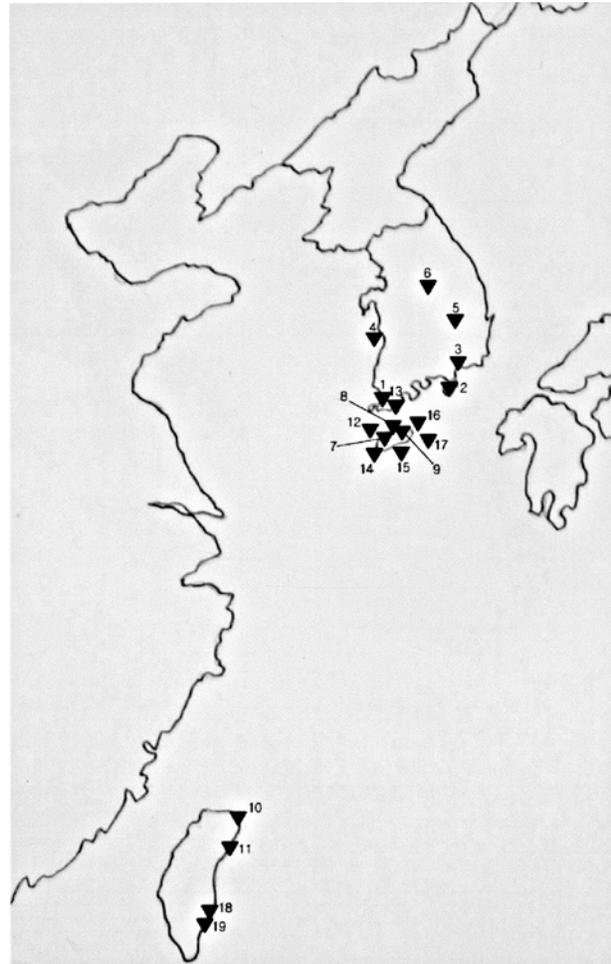


Figure 1. Collection localities for 19 numbered populations (Table 1) representing four species of *Euphorbia* from Taiwan and Korea.

Table 1. Collection data for 19 populations representing four species of *Euphorbia* from Taiwan and Korea examined for electrophoretic studies. The number of individuals examined is in parentheses.

- Euphorbia pekinensis* (PEK). PEK 01 = Mokpo, Korea (26); PEK 02 = Isl. Koje, Korea (18); PEK 03 = Mt. Moohak, Korea (24); PEK 04 = Isl. Daechung, Korea (3); PEK 05 = Yongjibong, Daegu, Korea (15); PEK 06 = Dodamsambong, Korea (15).
- E. fauriei* (FAU). FAU 07 = Mt. Halla, Cheju-do, Korea (9); FAU 08 = Mt. Halla, 1,600 m, Cheju-do, Korea (23); FAU 09 = Mt. Halla, 1,500 m, Cheju-do, Korea (24).
- E. jolkinii* (JOL). JOL 10 = Wan-li, Taipei Co., Taiwan (27); JOL 11 = Homei, Taipei Co., Taiwan (28); JOL 12 = Isl. Beian, Cheju-do, Korea (35); JOL 13 = Isl. Bogil, Korea (10); JOL 14 = Suwul-bong, Cheju-do, Korea (35); JOL 15 = Jungmoon, Cheju-do, Korea (13); JOL 16 = Seiwha, Cheju-do, Korea (18); JOL 17 = Supgikogi, Cheju-do, Korea (35).
- E. garanbiensis* (GAR). GAR 18 = Oluanpi, Pingtung Co., Taiwan (26); GAR 19 = Northern coast of the Oluanpi, Pingtung Co., Taiwan (18).

Results

Eleven loci coding for eight enzymes were scored from 19 populations of four *Euphorbia* species. Two isozyme loci each of MDH, 6PGD and TPI could be scored. Only one isozyme locus of the remaining enzymes could be scored. Allele frequencies of 11 polymorphic loci are summarized in Table 2. Nine of 11 loci were polymorphic in *E. pekinensis*, *E. fauriei* and *E. jolkinii*, while eight loci (ADH-1, ALD-1, MDH-1, ME-1, 6-PGD-1, 6-PGD-2, TPI-1 and TPI-2) were monomorphic in Taiwan endemic *E. garanbiensis* (Table 2). *Euphorbia pekinensis* and *E. fauriei* consistently shared the highest-frequency alleles while *E. jolkinii* and these two species did not share the same high frequency allele in PGI-2 and PGM-1. *Euphorbia garanbiensis* (subg. *Chamesyce*), the most remotely related species among the four *Euphorbia*, only shared high-frequency alleles with the above three species of subg. *Esula* for ALD-1, 6-PGD-1 and PGM-1.

The mean number of alleles per locus in a population (A) ranged from 1.1 (GAR19) to 2.3 (JOL12); the proportion of polymorphic loci in a population (P) ranged from 81.8 (PEK01) to 9.1 (GAR19) (Table 3). The mean observed proportion of heterozygous loci in a population (H_o) ranged from 0.502 (JOL11) to 0.013 (GAR19) while the mean expected proportion of heterozygous loci (H_e) ranged from 0.315 (JOL11) to 0.012 (GAR19). The populations of *Euphorbia pekinensis* showed the highest mean values of A (1.8) and P (68.2) among species, in contrast to *E. garanbiensis*, which had the lowest mean values of A (1.2) and P (13.7) among species (Table 3). *Euphorbia jolkinii* had the highest mean values of H_o (0.368) and H_e (0.239), and *E. garanbiensis* the lowest mean values of H_o (0.019) and H_e (0.026).

Mean values of Nei's (1972) identity ranged within species from 0.832 for *E. pekinensis* to 0.921 for *E. fauriei* (Table 4). The pair-wise genetic identity values ranged between species from 0.264 to 0.881. Genetic identities ranged between species within subg. *Esula* from 0.881 to 0.664 while those of species pairs ranged between subg. *Esula* and subg. *Chamesyce* from 0.387 to 0.264. A UPGMA phenogram based on genetic identity values was constructed to examine the genetic relationship among populations of four *Euphorbia* species (Figure 2). Conspecific populations clustered together, with the exception of *E. fauriei* populations, which were nested in the *E. pekinensis* populations.

The positive values of F_{IS} and F_{IT} in *E. fauriei* and *E. garanbiensis* indicate a deficiency of heterozygotes while the significant negative values of them in *E. jolkinii* indicate an excess of heterozygotes when compared to the Hardy-Weinberg expectation (Table 5). Values of F_{ST} ranged from 0.237 in *E. fauriei* to 0.652 in *E. garanbiensis*. Mean F_{ST} was substantially higher for *E. garanbiensis* populations, indicating a large differentiation among populations. Gene flow among populations of each species using Wright's (1951) method ranged from $Nm = 0.133$ in *E. garanbiensis*, 0.463 in *E. pekinensis*, and 0.770 in *E. jolkinii* to 0.804 in *E. fauriei*.

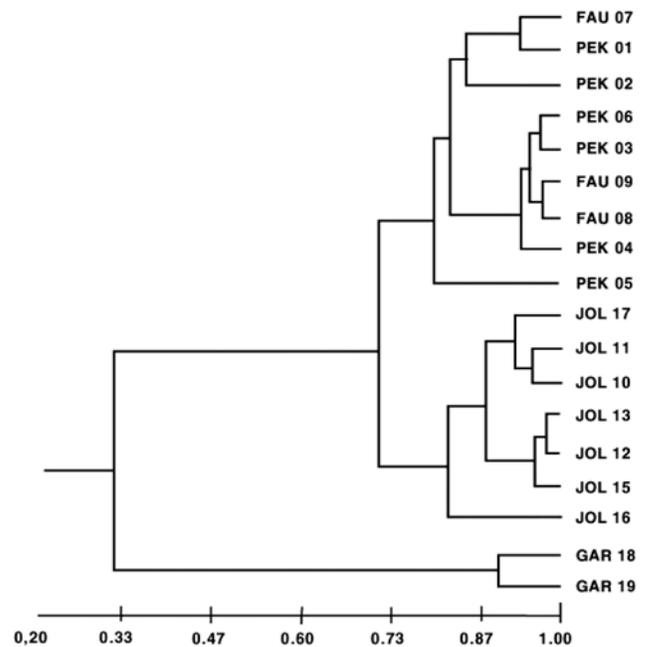


Figure 2. UPGMA phenogram derived from Nei's (1978) genetic identity among 19 populations of four *Euphorbia* species. The cophenetic correlation is 0.943. Species and population abbreviations refer to Table 1.

Discussion

Low Levels of Genetic Variation in Taiwan Endemic Euphorbia garanbiensis

In general, rare species exhibit significantly lower levels of genetic variation than their widespread congeners (Hamrick and Godt, 1989; Ellstrand and Elam, 1993; Gitzendanner and Soltis, 2000; Sherman-Broyles et al., 1992). This reduced amount of genetic variation in rare species may be due to chance events such as genetic drift and founder effects, strong directional selection, and high levels of inbreeding in small populations (Karron, 1991). *Euphorbia garanbiensis*, a rare endemic species in Taiwan, exhibits less genetic variation and higher levels of genetic differentiation among populations than *E. pekinensis*, *E. fauriei* or *E. jolkinii*. This agrees with previous studies of many rare species of flowering plants (Hamrick and Godt, 1989; Karron, 1991). The extremely low levels of genetic diversity shown in the *E. garanbiensis* populations are comparable to those reported for North American endemic *Euphorbia* species, *E. curtisii*, and *E. gracilior* (Park and Elisens, 1997). Some of the attributes of *E. garanbiensis*—such as restricted distribution, small population sizes, and gravity-dispersed seeds—may be responsible for the low levels of genetic diversity within, and high levels of differentiation among, populations. *Euphorbia garanbiensis* has much lower values of genetic variation in comparison to other species with similar life history characters, such as herbaceous perennials ($P = 28$; $A = 1.4$; $H_e = 0.1$), dicots ($P = 31.2$; $A = 1.46$; $H_e = 0.113$), endemic species ($H_e =$

Table 2. Summary allele-frequency data for 11 polymorphic loci among 19 populations of four species in *Euphorbia* from Taiwan and Korea.

Locus	<i>E. pekinensis</i>						<i>E. fauriei</i>						<i>E. jolkini</i>						<i>E. garambiensis</i>	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
ADH-1	0.167	0.909	---	---	---	---	---	---	0.048	---	0.029	---	---	0.014	---	---	---	---	---	
a	0.833	0.091	1.000	0.667	---	1.000	1.000	0.917	0.952	0.704	0.735	1.000	0.986	---	0.500	1.000	---	---	---	
b	---	---	---	0.333	1.000	---	---	---	---	0.296	0.235	---	---	---	0.500	---	---	1.000	---	
c	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
d	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1.000	
ALD-1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	0.048	0.048	0.060	0.333	0.088	0.250	0.500	---	0.045	---	0.103	---	---	---	---	---	---	---	---	
b	1.000	0.881	0.900	0.667	0.853	0.750	0.500	0.904	0.955	1.000	0.897	1.000	0.972	0.955	1.000	1.000	1.000	1.000	1.000	
c	---	0.071	0.040	---	0.059	---	---	0.096	---	---	---	---	0.028	---	---	---	---	---	---	
MDH-1	0.054	---	0.117	0.333	---	0.111	---	0.056	---	---	---	---	---	---	---	---	---	---	---	
a	0.946	1.000	0.883	0.667	0.500	0.889	1.000	0.944	1.000	0.963	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
b	---	---	---	---	0.500	---	---	---	---	0.037	---	---	---	---	---	---	---	---	---	
c	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
MDH-2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	---	---	---	---	0.467	0.111	---	0.171	---	---	---	---	---	---	---	---	---	---	---	
b	---	0.100	0.625	1.000	0.533	0.611	---	0.629	0.690	---	---	---	---	---	---	---	---	---	---	
c	0.875	0.900	0.375	---	---	0.278	1.000	0.200	0.069	0.645	0.685	0.950	1.000	0.973	0.900	0.675	0.667	---	---	
d	---	---	---	---	---	---	---	---	---	---	0.013	---	0.027	0.100	0.125	0.208	0.948	1.000	---	
e	0.125	---	---	---	---	---	---	---	0.355	0.315	0.038	---	---	---	0.200	0.125	---	---	---	
f	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.052	---	---	
ME-1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	---	---	---	---	0.067	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
b	0.800	1.000	0.950	1.000	0.867	1.000	0.857	0.981	0.967	0.881	0.500	0.553	0.500	0.500	0.667	0.500	0.762	---	1.000	
c	0.200	---	0.050	---	0.067	---	0.143	0.019	0.033	0.119	0.500	0.447	0.500	0.500	0.333	0.500	0.237	---	---	
6PGD-1	0.636	0.050	---	---	---	0.056	0.300	---	---	0.711	0.500	0.934	1.000	0.203	1.000	---	---	---	1.000	
a	0.364	0.956	1.000	1.000	1.000	0.944	0.700	1.000	1.000	0.289	0.500	0.066	---	0.797	---	1.000	---	---	---	
b	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
c	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
6PGD-2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	---	---	---	---	---	---	---	---	---	0.158	---	0.463	0.500	---	---	---	---	---	---	
b	0.473	0.525	0.448	---	0.500	0.389	0.300	0.038	0.024	0.132	0.500	---	---	---	---	---	---	---	---	
c	0.527	0.475	0.552	1.000	0.500	0.611	0.700	0.962	0.976	0.711	0.500	0.538	0.500	1.000	0.700	1.000	0.400	---	---	
PGI-2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	---	---	---	0.500	---	---	0.071	---	---	---	---	0.026	---	---	---	---	---	---	0.931	
b	1.000	0.200	0.019	---	0.438	0.083	0.500	0.080	0.074	0.881	0.500	0.487	0.500	0.500	0.333	0.500	0.500	0.069	---	
c	---	0.500	0.981	0.500	0.375	0.917	0.429	0.780	0.630	---	---	0.026	---	---	0.333	---	---	---	---	
d	---	0.300	---	---	0.188	---	---	0.140	0.296	0.119	0.500	0.461	0.500	0.500	0.333	0.500	0.500	---	---	
PGM-1	0.054	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	0.946	0.900	1.000	1.000	1.000	0.889	1.000	1.000	0.929	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
b	---	0.100	---	---	---	0.111	---	---	---	---	---	---	---	---	---	---	---	---	---	
c	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
TPI-1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	---	---	---	---	---	0.059	---	---	---	---	---	---	---	---	---	---	---	---	---	
b	0.688	0.725	0.963	0.833	0.853	0.912	0.958	1.000	0.967	0.500	0.630	0.500	0.500	0.500	0.500	0.500	0.500	1.000	---	
c	0.313	0.275	0.037	0.167	0.147	0.029	0.042	---	0.033	0.500	0.352	0.045	---	---	0.500	0.500	0.500	---	---	
d	---	---	---	---	---	---	---	---	---	---	---	0.455	0.500	0.500	0.500	---	---	---	---	
TPI-2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
a	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
b	0.906	0.906	0.750	1.000	1.000	0.900	1.000	1.000	1.000	1.000	0.926	1.000	1.000	1.000	1.000	0.500	0.917	---	1.000	
c	0.094	0.094	0.250	---	---	0.100	---	---	---	---	0.074	---	---	---	---	0.500	0.083	---	---	

Table 3. Average values for mean sample size per locus (N), mean number of alleles per locus (A), proportion of polymorphic loci (P), mean observed proportion of heterozygous loci (H_o), and mean expected proportion of heterozygous loci (H_e) in 19 populations of four *Euphorbia* species from Taiwan and Korea.

Species/population	N	A	P	H_o	H_e
<i>E. pekinensis</i>					
PEK01	25.4	1.8	81.8	0.225	0.240
PEK02	18.0	2.0	81.8	0.255	0.236
PEK03	23.9	1.8	54.5	0.168	0.179
PEK04	3.0	1.5	45.5	0.303	0.230
PEK05	14.5	1.9	63.6	0.167	0.271
PEK06	14.7	2.0	81.8	0.267	0.233
Mean	16.6	1.8	68.2	0.231	0.232
<i>E. fauriei</i>					
FAU07	8.7	1.6	45.5	0.215	0.217
FAU08	23.0	1.8	45.5	0.093	0.134
FAU09	23.5	1.9	36.4	0.107	0.136
Mean	18.4	1.8	42.5	0.138	0.162
<i>E. jolkinii</i>					
JOL10	26.9	1.8	54.5	0.312	0.224
JOL11	27.4	1.8	63.6	0.502	0.315
JOL12	34.5	2.3	81.8	0.437	0.279
JOL13	9.5	1.4	36.4	0.364	0.192
JOL14	34.6	1.6	36.4	0.297	0.181
JOL15	12.9	1.6	45.5	0.239	0.217
JOL16	17.5	1.6	54.5	0.423	0.279
JOL17	35.5	1.6	54.5	0.373	0.229
Mean	24.9	1.7	53.4	0.368	0.239
<i>E. garanbiensis</i>					
GAR18	25.7	1.2	18.2	0.025	0.040
GAR19	17.4	1.1	9.1	0.013	0.012
Mean	21.5	1.2	13.7	0.019	0.026

0.063), early successional species ($H_e = 0.14$), and out-crossed species ($P = 36$; $A = 1.5$; $H_e = 0.12$) (Hamrick and Godt, 1989; Hamrick et al., 1991). Besides, *E. garanbiensis* has also lower mean values for all measures of genetic variation when compared to other *Euphorbia* species (Table 6).

One alternative hypothesis for the low genetic diversity found in Taiwan endemic *E. garanbiensis* is that it may have recently evolved from a continental progenitor, or, alternatively, it may be a relictual lineage from the continental flora. Genetic drift and bottleneck after colonization events may have reduced the genetic variation of the species (Sherman-Broyles et al., 1992; Ayres and Ryan, 1999). Comparisons of insular endemic and mainland plant species show that most of the insular endemic species are less

variable than their continental congeners (Dejode and Wendel, 1992; Frankham, 1997).

The heterozygote deficiencies in populations of *E. garanbiensis* may be explained by the somewhat inefficient sexual reproduction and seed dispersal mechanism of this species (Pleasants and Wendel, 1989). Although most of the *Euphorbia* species are insect pollinated, a few cases of self-pollination have been reported in *Euphorbia* subg. *Chamaesyce* as a result of their mostly small, prostrate habits and their inconspicuous inflorescences (Ehrenfeld, 1976). Inefficient seed dispersal mechanisms along with the isolation of populations in *E. garanbiensis* would prevent efficient gene flow between populations and, therefore, promote genetic differentiation among populations. Comparison of isozyme variation among *Euphorbia* species

Table 4. Mean values for Nei's (1978) unbiased genetic identity coefficient for pair-wise comparisons of populations among four species in *Euphorbia* from Taiwan and Korea.

Species	PEK	FAU	JOL	GAR
PEK	0.832			
FAU	0.881	0.921		
JOL	0.664	0.711	0.894	
GAR	0.308	0.264	0.387	0.902

Table 5. Summary of F -statistics for mean values of 11 loci from four species of *Euphorbia*.

Species	F_{IS}	F_{IT}	F_{ST}
<i>E. pekinensis</i>	-0.057	0.314	0.351
<i>E. fauriei</i>	0.109	0.320	0.237
<i>E. jolkinii</i>	-0.575	-0.189	0.245
<i>E. garanbiensis</i>	0.267	0.745	0.652

Table 6. Comparison of Genetic diversity data for rare and widespread *Euphorbia* species of this study (indicated in bold) and compiled from the literature.

Species	Distribution	A	P	H_e	F_{ST}/G_{ST}	Reference
<i>E. corollata</i>	Widespread	1.5	36.9	0.147	0.307	Park & Elisens, 1997
<i>E. pubentissima</i>	Widespread	1.5	33.3	0.144	0.399	Park & Elisens, 1997
<i>E. curtisii</i>	Rare	1.2	15.0	0.070	0.332	Park & Elisens, 1997
<i>E. discoidalis</i>	Rare	1.6	35.4	0.145	0.425	Park & Elisens, 1997
<i>E. gracilior</i>	Rare	1.2	14.6	0.052	0.601	Park & Elisens, 1997
<i>E. mercurialina</i>	Rare	1.3	27.1	0.117	0.160	Park & Elisens, 1997
<i>E. polyphylla</i>	Rare	1.5	33.4	0.138	0.538	Park & Elisens, 1997
<i>E. strictior</i>	Rare	1.2	19.5	0.098	0.337	Park & Elisens, 1997
<i>E. wrightii</i>	Widespread	1.2	10.4	0.043	0.785	Park & Elisens, 1997
<i>E. ebracteolata</i>	Widespread	2.3	86.7	0.358	0.163	Park et al., 1999
<i>E. octoradiata</i>	Widespread	1.8	54.5	0.227		Jung, 2000
<i>E. esula</i>	Widespread	1.6	41.8	0.192		Jung, 2000
<i>E. pekinensis</i>	Widespread	1.8	68.2	0.232	0.351	
<i>E. fauriei</i>	Rare	1.8	42.5	0.162	0.237	
<i>E. jolkinii</i>	Widespread	1.7	53.4	0.239	0.245	
<i>E. garanbiensis</i>	Rare	1.2	13.7	0.026	0.652	

(Table 6) clearly demonstrates that high levels of genetic differentiation is a general pattern within the genus. Although outcrossing is predominant within the genus, high genetic differentiation values may be related to the typical seed-dispersal mechanism (eg. gravity-dispersed, ant-dispersed) for *Euphorbia* species.

High Genetic Variation in Korean Endemic *Euphorbia fauriei*

The results of this analysis indicate that genetic variation of the Korean endemic species, *E. fauriei*, is nearly as high as the genetic variability in previously reported widespread *Euphorbia* species such as *E. corollata* and *E. pubentissima* in North America, and *E. octoradiata* and *E. esula* in Far East Asia (Table 6). Although the genetic variation of *E. fauriei* is less variable than that of the widespread *E. pekinensis*, the values greatly exceed those of the Taiwan endemic, *E. garanbiensis*, and previously reported insular endemic species (DeJoode and Wendel, 1992). Although, theoretically, restricted species maintain less genetic diversity than more widespread species (Hamrick and Godt, 1989), some rare species maintain levels of diversity equal to or exceeding that of widespread congeners (Gitzendanner and Soltis, 2000). Thus, geographic distribution is not always a good indicator of the genetic diversity of the species (Lewis and Crawford, 1995; Gitzendanner and Soltis, 2000). High genetic diversity in rare species is usually associated with the unique history of the species such as its recent origin from a widespread ancestor, multiple origin, hybridization, refugia origin, and ecological traits such as the ability to survive in diverse habitats (Smith and Pham, 1996; Godt and Hamrick, 1998; Gitzendanner and Soltis, 2000).

The relatively high genetic diversity and high intraspecific values of genetic identity found in the island endemic *E. fauriei* suggests that it may have recently originated from a widespread continental progenitor, *E. pekinensis*.

Cladistic analyses using morphological and chemical data proposed a sister-group relationship between the two species (Park et al., 1999a). Isozyme data suggest that genetic identity between *E. fauriei* and *E. pekinensis* ($I = 0.881$) is higher than within *E. pekinensis* ($I = 0.832$), supporting the recent origin of *E. fauriei*. One alternative explanation for the high genetic variation is occupation of refugia in the south coastal areas of the Korean peninsula during the last glaciations. Species that resided in refugia tended to maintain high levels of genetic diversity due to population stability during the glacial cycles (Qiu and Parks, 1994; Lewis and Crawford, 1995). Present populations of *E. fauriei* appear to be of multiple origin from widely distributed refugia during the last glaciations on the Korean peninsula. The importance of refugia in the southern part of the Korean peninsula has been proposed for such species as *Eurya japonica* (Chung and Kang, 1994), *Hemerocallis hakuunensis* (Kang and Chung, 1997), and *Euphorbia ebracteolata* (Park et al., 1999b).

Progenitor-Derivative Species Pairs between *Euphorbia pekinensis* and *E. fauriei*

Among the species pairs within the subgenus *Esula*, *E. pekinensis* and *E. fauriei* showed the highest identity values in comparison to those of any other pairs. Mean genetic identity values between *E. pekinensis* and *E. fauriei* ($I = 0.881$) were higher than those within *E. pekinensis* ($I = 0.832$), strongly supporting the sister-group relationship between *E. pekinensis* and *E. fauriei* proposed by a phylogenetic analysis using morphological and chemical data (Park et al., 1999a). The genetic variation pattern of the two species is very similar to those for progenitor-derivative species pairs (Gottlieb, 1973; Crawford and Smith, 1982). *Euphorbia pekinensis*, widespread in its distribution, exhibits more genetic variation than *E. fauriei*, which is restricted in its distribution. *Euphorbia fauriei* has no unique allele and lacks some rare alleles present in

E. pekinensis (Table 2), suggesting that the island endemic *E. fauriei* may be a derived species, probably from the widespread continental progenitor species, *E. pekinensis*.

Euphorbia jolkinii: a Disjunct Population System in Korea and Taiwan

The typical seed dispersal mechanism, by gravity or ant, for *Euphorbia* species probably contributes to low levels of gene flow among populations, resulting in high differentiation among populations (Table 6). Although the populations of *E. jolkinii* are separately distributed in Korea and Taiwan, *E. jolkinii* has lower values of F_{ST} relative to the other three *Euphorbia* species (Table 5). In addition to this, *Euphorbia jolkinii* has much lower values of F_{ST} in comparison to previously reported *Euphorbia* species (Table 6). Relative to the previous reports of *Euphorbia* species, the genetic differentiation among *E. jolkinii* populations was low and indicated little genetic divergence among populations. *Euphorbia jolkinii*, a salt-tolerant species, inhabits rocky areas along the seacoasts in Korea and Taiwan. Long distance seed dispersal in *E. jolkinii* along the sea current could result in increasing gene flow among populations. Even though few cases have been reported of plant species dispersing by water, *Asclepias perennis*, an inhabitant of floodplains, has significantly high Nm values and relatively low G_{ST} values (Edwards and Wyatt, 1994). Edwards and Wyatt (1994) suggested that the multidirectional dispersal along interconnected floodplains may be similar to wind dispersal, and therefore could increase gene flow.

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遠東大戟科植物窄小地區分佈及廣為分佈之物種間同功異構酶之比較

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採自大戟科四個物種共 19 個族群之基因變異經由若干異構酶標誌加以分析。*Euphorbia fauriei* 及 *E. garanbiensis* 分別為韓國及台灣之稀有在地種，而 *E. pekinensis* 及 *E. jolkinii* 則在韓國及台灣廣為分佈。*E. garanbiensis* 具有限地區分佈，族群小，藉重力傳播之種子，及可能為自花授粉諸特點；我們發現此物種具低階的遺傳變異但有高階的遺傳分化。或者，*E. garanbiensis* 最近剛從某一大陸祖先物種演化過來，或可能是古大陸物種之遺留後代。*E. fauriei* 之高遺傳變異乃不尋常且可解釋為它的最近源生自某一分佈廣闊之大陸種，*E. pekinensis*。另一交替的說法是：*E. fauriei* 乃上次冰河期在韓國半島避難物種之殘存後代。支持 *E. pekinensis* 及 *E. fauriei* 兩者間有祖先—後代關係的數據來自於：兩者間存在之高遺傳等同性，以及假想後代 *E. fauriei* 缺少獨特之等位基因，也缺少某些存在於假想祖先 *E. pekinensis* 之稀有等位基因。

關鍵詞： *Euphorbia fauriei* ; *Euphorbia garanbiensis* ; *Euphorbia jolkinii* ; *Euphorbia pekinensis* ; 異構酶之變異。