



## Genetic and morphological divergence of *Euphorbia esula* and *E. maackii* in Korea (Euphorbiaceae)

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### 한국산 흰대극(*Euphorbia esula*)과 섬흰대극(*E. maackii*)의 유전적, 형태적 분화

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**ABSTRACT:** To understand morphological and genetic differentiation between *Euphorbia esula* and *E. maackii* we examined 12 morphological characters and 11 isozyme loci from 14 populations of two species. Species of *E. esula* complex ( $A = 1.63$ ,  $P = 44.83$ ,  $H_c = 0.198$ ) in Korea maintain nearly as high as the genetic diversity reported in East Asian *E. jolkinii* and *E. fauriei* while lower than those of *E. ebracteolata* and *E. pekinensis* in Korea. Although the ranges of most morphological character variation of the two species overlap, *E. esula* and *E. maackii* were well recognized by the combination of the morphological traits, and the result of UPGMA phenogram supports the two distinct species inhibited in Korea. However, isozyme data do not support the recognition of *E. esula* and *E. maackii*. The discordance between morphological and allozyme data should be explained by the recent divergence or gene flow via introgressive hybridization between two species.

**Keywords:** *Euphorbia esula*, *E. maackii*, morphology, genetic divergence

**적 요:** 흰대극과 섬흰대극의 형태적, 유전적 분화를 알아보기 위해 두 종의 14개 자연 집단으로부터 12개의 형태형질과 11개의 동위효소 유전자좌위를 조사하였다. 흰대극복합체의 유전적 다양성 측정치( $A=1.63$ ,  $P = 44.83$ ,  $H_c=0.198$ )는 기존의 동북아산 암대극과 두메대극의 보고와 유사하며, 한국산 붉은대극과 대극보다는 약간 낮은 수치를 보여주고 있다. 비록 대부분 두 종사이의 형태형질의 측정범위가 중복되나 흰대극과 섬흰대극은 형태형질의 조합에 의해 구별되며, 이를 기초로 한 전형질도는 한국에 두 종이 분포함을 지지해주고 있다. 하지만 동위효소 자료를 이용한 분석에서는 두 종이 구별되지 않았으며, 이와 같은 두 자료의 불일치는 두 종이 최근에 분화 하였거나 중간 형질이입에 의한 교잡에 의해 이와 같은 결과가 나온 것으로 추측된다.

**주요어:** 흰대극, 섬흰대극, 형태형질, 유전적 분화

The subgenus *Esula*, one of the largest subgenera in *Euphorbia*, is comprised of approximately 500 semi-succulent and herbaceous species distributed in the northern hemisphere

(Frajman and Schönswetter, 2011). Within the subgenus *E. esula* complex usually included several related species such as *E. esula* and *E. virgata* in Europe and United States while *E. octoradiata*, *E. nakaii*, *E. esula* and *E. lumulata* in Far East Asia. Because of worldwide distribution and intensive hybridization among these related species *E. esula* complex has been treated as a complicate taxonomic group in Europe

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and United States (Croizat, 1945). Recently, most of the related species have been treated as a single *E. esula* species by European taxonomists.

Within the subgenus about 10 perennial species including *E. esula* are distributed in South Korea (Park and Lee, 1988), and are abundant at the sandy sites along the coastal areas of Korea. Comparing other Euphorbias in Korea the *E. esula* and related species are characterized by the yellow and half-cycled bracts at the top of the main stems, and crescent-shaped glands (=nectaries) on the rim of the cyathium (Hurusawa, 1940; Croizat, 1945; Crompton et al., 1989; Webster, 1994). They also are reproduced by two different kinds of stems such as floristic shoots at spring season and sterile shoots at summer (Croizat, 1945).

Among the *E. esula* complex Nakai (1919) distinguished three taxa in Far East Asia: *E. lumulata* having the ear-shaped bract collected in Manchuria, *E. esula* having the round bract collected in Chemul-po and Soan island, and *E. esula* var. *latifolia* having the round bract and ovate leaves in Manchuria. Later, *E. lumulata* var. *obtusifolius* was reported by Hurusawa (1940) which had a smooth capsule collected at Pung-Do (Gyeonggi do). However, even in the recent flora of Korea *E. esula* species is accepted as an only species inhabiting in Korea. Ma and Wu (1992) treated *E. lumulata* as synonym of *E. esula* in China.

As a part of monographic study of Far East Asian Euphorbiaceae, Hurusawa (1940) reported a new species *E. nakaii* from Jeju Island which has a oval bract and rough capsule, and considered it as a different species to *E. esula* in Europe. Also, he divided it into two intraspecific taxa, *E. nakaii* f. *littoralis* and *E. nakaii* f. *caespitosa*. He also treated *E. octoradiata* which was described as a new species at 1908 by Leveille and Vaniot as a synonym of *E. nakaii* form. *caespitosa*. However, Croizat (1941) considered both *E. nakaii* and *E. octoradiata* as a same species with *E. maackii* Meinsh. distributed in northern Manchuria and Siberian regions based on their holotypes. Thus, from the Croizat's point of view *E. esula* and *E. maackii* should be recognized in South Korea.

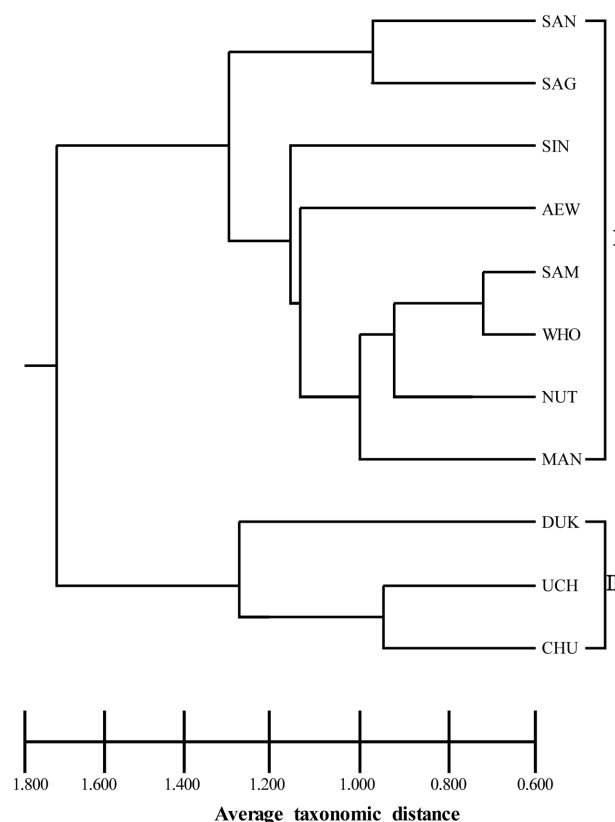
We examined Korean *E. esula* and *E. maackii* using morphological and genetic data to know the amount of genetic and morphological divergence among populations, and to propose a rigorous hypothesis whether the two species are a single species or an aggregate of several taxa.

## Materials and Methods

To understand morphological and genetic variation of Korean *E. esula* complex, we collected putative nine populations of *E.*

**Table 1.** Collection data for 14 populations representing Korean *E. esula* and *E. maackii* for electrophoretic and morphological divergence (Abbreviation for populations are given in parentheses).

Scientific name	Locality	Individual Numbers
<i>E. maackii</i>	Aewol (AEW; A)	Isl. Jeju 24
<i>E. maackii</i>	Shinchang-ri (SIN; B)	Isl. Jeju 28
<i>E. maackii</i>	Yongsu-ri (YON; C)	Isl. Jeju 24
<i>E. maackii</i>	Sagae-ri (SAG; D)	Isl. Jeju 21
<i>E. maackii</i>	Mt. Sanbang (SAN; E)	Isl. Jeju 27
<i>E. maackii</i>	Samchuk beach (SAM; F)	East Pop. 32
<i>E. maackii</i>	Nutjae beach (NUT; G)	East Pop. 39
<i>E. maackii</i>	Maengbang beach (MAN; H)	East Pop. 27
<i>E. maackii</i>	Whojong beach (WHO; I)	East Pop. 35
<i>E. esula</i>	Yong-ji Bong (YOG; J)	East Pop. 28
<i>E. esula</i>	Duckjuck Do (DUK; K)	West Pop. 31
<i>E. esula</i>	Pung Do (PUN; L)	West Pop. 24
<i>E. esula</i>	Chung-Podae beach (CHU; M)	West Pop. 29
<i>E. esula</i>	Uchung Do (UCH; N)	West Pop. 31



**Fig. 1.** UPGMA phenogram based on the average taxonomic distance of 12 morphological characters among 11 populations of Korean *E. esula* and *E. maackii*. I. *E. maackii*; II. *E. esula*.

**Table 2.** Morphological characters of 11 populations of Korean *E. esula* complex for clustering analysis. Numbers represent mean values (Unit = mm). (Abbreviation for populations are given in Table 1).

Characters	<i>E. maackii</i>					
	AEW	SIN	SAG	SAN	SAM	NUT
1. Gland length	1.93	1.42	1.40	1.52	1.85	1.89
2. Gland width	0.98	0.79	0.67	0.75	1.03	1.00
3. Gland width/length	0.51	0.55	0.48	0.49	0.56	0.53
4. Capsule height/width	0.91	0.88	0.86	0.83	0.87	0.91
5. Anther height	0.69	0.71	0.72	0.71	0.85	0.86
6. Anther height/width	1.11	1.47	1.46	1.28	1.43	1.53
7. Seed height/width	1.72	1.50	1.58	1.74	1.68	1.70
8. Pedicel length	3.62	3.57	4.22	4.76	3.45	3.31
9. Filament length	1.97	1.98	2.21	2.05	2.31	2.12
10. The largest leaf width	11.1	13.3	15.7	15.5	14.2	12.9
11. Terminal stem leaf length/width	3.38	3.13	2.68	3.78	4.15	2.89

**Table 2.** Continued.

Characters	<i>E. maackii</i>			<i>E. esula</i>		
	MAN	WHO	DUK	CHU	UCH	
1. Gland length	2.34	1.76	1.69	1.02	1.40	
2. Gland width	1.14	0.91	1.14	0.67	0.85	
3. Gland width/length	0.49	0.52	0.67	0.66	0.60	
4. Capsule height/width	0.83	0.89	0.90	0.97	0.92	
5. Anther height	0.87	0.74	0.60	0.44	0.58	
6. Anther height/width	1.27	1.27	1.34	1.18	1.38	
7. Seed height/width	1.60	1.62	1.65	1.52	1.55	
8. Pedicel length	3.82	3.26	3.55	3.25	3.60	
9. Filament length	2.06	2.35	1.90	1.70	1.88	
10. The largest leaf width	11.3	10.8	2.30	5.04	4.31	
11. Terminal stem leaf length/width	3.40	3.31	5.79	5.67	5.34	
12. Terminal bract length/width	1.52	1.48	1.38	1.58	1.61	

*maackii* from Jeju island and east coast, and five populations of *E. esula* from west coast of Korean peninsula. Samples more than 10 individuals per population were stored in 70% alcohol to analyze morphological characters, and field collected young leaves from more than 20 individuals per population were used as enzyme source to analyze genetic variation. Collection localities of 14 populations showed on Table 1 and Fig. 5.

For clustering analysis using morphological characters, 12 quantitative characters from 10 individuals per population were measured (Table 2). The means of each measurement was used for data analysis. For clustering analysis using NTSYS Program (Rohlf, 1992), data were standardized by means of STD method, and the average taxonomic distance among populations was calculated. The UPGMA phenogram was

generated by taxonomic distance (Fig. 1).

For isozyme studies, a total of 361 individuals from 14 populations for *E. esula* and *E. maackii* were used for starch electrophoretic analysis. The extracting buffer is 0.1 M tris-HCL (pH 7.5) used 1 mM EDTA, 10 mM MgCl<sub>2</sub>, 10 mM KCl, 14 mM 2-mercaptoethanol, and 5–10 mg/mL solid polyvinylpyrrolidone (Gottlieb, 1981). The ground leaf materials using extracting buffer were put in 1.5 mL tubes, and stored at –70°C for electrophoresis. For running the gels, the extracts were centrifuged for 1 minute at 6000 rpm, and the supernatant was absorbed on the Whatman paper (#3) wicks. Nine enzymes were resolved on 11% starch gels with 4 buffer systems modified by Soltis et al. (1983).

System I has an electrode buffer of 0.065M L-histidine

titrated to pH 6.5 with 0.007M Citric acid monohydrate and a gel buffer of a 3:1 aqueous dilution of the electrode buffer. System II has an electrode buffer of N-(3-quinopropyl)-morpholine titrated to pH 6.1 with 0.04M Citric acid anhydrous and a gel buffer of a 20:1 aqueous dilution of the electrode buffer. System III has an electrode buffer of 0.18 M tris and 0.004 M EDTA titrated to pH 8.6 with 0.10 M Boric acid and a gel buffer of a 3:1 aqueous dilution of the electrode buffer. System IV has an electrode buffer (part A) of Lithium hydroxide titrated to pH 8.3 with 0.192 M Boric acid and part B of 0.052 M Tris titrated to pH 8.3 with citric acid anhydrous and a gel buffer is 1:9 of Part A : Part B. System I was used to resolve malic dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (6-PGD), and system II was used to resolve isocitrate dehydrogenase (IDH), phosphoglucosemutase (PGM), and system III was used to resolve malic enzyme (ME), phosphoglucoseisomerase (PGI), and system IV was used to resolve aspartate aminotransferase (AAT), alcoholdehydrogenase (ADH), triosephosphate isomerase (TPI).

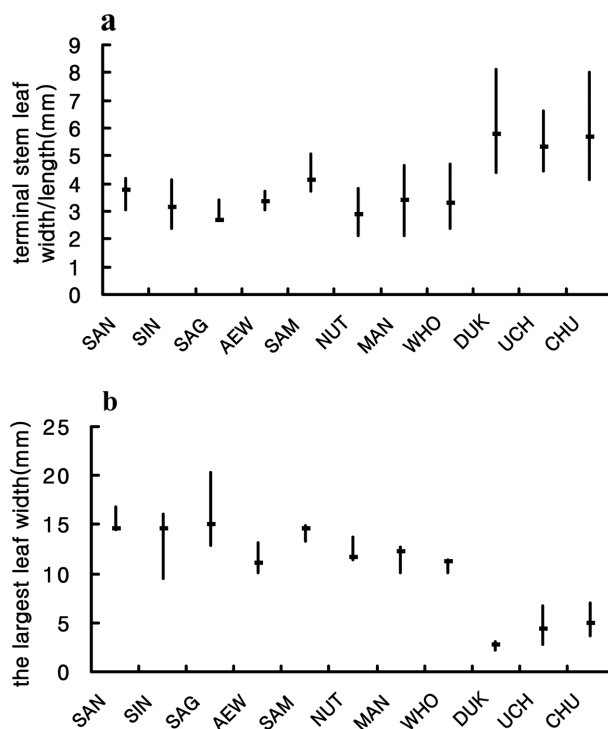
The BIOSYS-1 program (Swofford and Selander, 1981) was used to calculate allele frequency, and mean number of alleles per locus (A), percentage of polymorphic loci (P), mean expected heterozygosity ( $H_e$ ), Nei's (1972) genetic identity and distance. UPGMA phenogram was generated from Nei's genetic identity and Dice coefficients using presence-absence of allelic data.

## Results

**1. Morphological data analysis:** For UPGMA analysis and comparing morphological character difference, mean values of 12 quantitative characters of 11 populations of *E. esula* and *E. maackii* were presented on Table 2, and the UPGMA phenogram (Fig. 1) was generated by average taxonomic distance.

On the base of UPGMA tree the populations of *E. maackii* and *E. esula* were divided precisely as two clusters. The four *E. maackii* populations from east coast were clustered together, while those from Jeju Island were not grouping together (Fig. 1).

Except for the character 10 (largest leaf width) most morphological characters showed continuous variation (Table 2; Fig. 2). In order to know the significance of morphological characters distinguishing two species, T-test was done for 12 morphological characters. The length and width of gland, ratio of width to length of gland showed continuous variation, but *E. maackii* was longer than *E. esula* in the width of gland. But *E. esula* was greater than *E. maackii* in ratio of gland width to length ( $P < 0.001$ ), and *E. esula* was shorter than *E. maackii* in the height of anther, but *E. esula* was similar to *E. maackii*



**Fig. 2.** Ranges (lines) of the variation and mean values (dots) for (a) terminal stem leaf width/length (mm), (b) the largest leaf width (mm) in 11 populations of *E. maackii* (SAN-WHO) and *E. esula* (DUK-CHU).

in ratio of anther width to height ( $P > 0.05$ ). *E. maackii* was longer than *E. esula* in pedicel length and filament length ( $P < 0.001$ ). Two species were similar in ratio of terminal bract width to length ( $P > 0.05$ ), but *E. maackii* was greater than *E. esula* in the largest leaf width, and *E. esula* was significantly differ from *E. maackii* in ratio of terminal stem leaf width to length ( $P < 0.0001$ ) (Fig. 2).

**2. Isozyme data analysis:** Eleven loci, coding for seven enzymes, were scored from 14 populations of *E. esula* and *E. maackii*: one for *Me*, *Pgm*, *Tpi*, *Adh* and *Idh*; two for *6Pgd*, *Mdh* and *Pgi*. Allele frequencies for 11 polymorphic loci are summarized in Table 3. All loci showed more than two alleles. In *Pgm-2*, *Tpi-1*, *6Pgd-2*, *Mdh-1* and *Mdh-2*, all populations shared the same high-frequency alleles, and all populations of Jeju island had common alleles of high frequency in all loci except *Adh-2* (Table 3). Particularly, in locus *Me*, all populations of *E. maackii* except WHO had a fixed allele a/d, while all populations of *E. esula* had a unique b allele in *Me* locus. Unusually low frequency of b allele of *Me* locus was present in WHO population of *E. maackii*, and UCH population of *E. esula* had a *Me*<sup>d</sup> of high frequency which showed in only *E. maackii* (Table 3; Fig. 5).

**Table 3.** Allele frequencies of 11 polymorphic loci of 14 populations of Korean *E. esula* and *E. maackii*. (Abbreviation for populations are given in Table 1).

Locus	<i>E. maackii</i>						
	AEW	SIN	YON	SAG	SAN	SAM	NUT
<i>Me</i>							
a	0.500	0.500	0.500	0.500	0.500	0.500	0.500
b	-	-	-	-	-	-	-
c	-	-	-	-	-	-	-
d	0.500	0.500	0.500	0.500	0.500	0.500	0.500
<i>Pgm-2</i>							
a	-	0.056	0.111	-	-	0.121	0.041
b	0.500	0.481	0.444	0.500	0.500	0.431	0.486
c	0.500	0.481	0.444	0.500	0.500	0.379	0.486
d	-	-	-	-	-	0.086	-
<i>Tpi-1</i>							
a	1.000	1.000	1.000	1.000	1.000	0.984	0.814
b	-	-	-	-	-	0.016	0.186
<i>Adh-2</i>							
a	-	-	-	-	-	-	0.571
b	0.650	0.750	0.146	0.227	0.500	0.368	0.429
c	0.350	0.250	0.854	0.773	0.500	0.632	-
<i>6pgd-1</i>							
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000
b	-	-	-	-	-	-	-
<i>6pgd-2</i>							
a	-	-	-	-	-	-	-
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000
c	-	-	-	-	-	-	-
<i>Mdh-1</i>							
a	-	-	0.083	-	-	-	-
b	1.000	1.000	0.917	1.000	1.000	1.000	0.679
c	-	-	-	-	-	-	0.321
<i>Mdh-2</i>							
a	0.250	-	-	-	-	-	-
b	0.750	1.000	1.000	1.000	1.000	1.000	1.000
<i>Pgi-1</i>							
a	-	-	-	-	-	0.167	0.013
b	1.000	1.000	1.000	1.000	1.000	0.117	0.821
c	-	-	-	-	-	0.733	0.167
<i>Pgi-2</i>							
a	-	-	-	-	-	0.031	0.051
b	1.000	1.000	1.000	1.000	1.000	0.234	0.859
c	-	-	-	-	-	-	-
d	-	-	-	-	-	0.719	0.090
e	-	-	-	-	-	0.016	-
<i>Idh-2</i>							
a	-	-	-	-	-	-	-
b	0.600	0.827	0.979	0.417	0.500	1.000	1.000
c	0.400	0.173	0.021	0.583	0.500	-	-

**Table 3.** Continued.

Locus	<i>E. maackii</i>			<i>E. esula</i>			
	MAN	WHO	YOG	DUK	PUN	CHU	UCH
<i>Me</i>							
a	0.500	0.500	0.500	0.468	0.587	-	0.500
b	-	0.109	0.500	0.532	0.413	1.000	0.017
c	-	-	-	-	-	-	-
d	0.500	0.391	-	-	-	-	0.483
<i>Pgm-2</i>							
a	-	-	0.089	0.048	0.143	-	0.097
b	0.500	0.406	0.464	0.371	0.381	0.500	0.452
c	0.500	0.406	0.464	0.371	0.381	0.500	0.452
d	-	0.203	-	0.210	0.095	-	-
<i>Tpi-1</i>							
a	0.920	1.000	1.000	1.000	1.000	1.000	1.000
b	0.080	-	-	-	-	-	-
<i>Adh-2</i>							
a	-	-	-	-	-	-	-
b	0.694	0.717	0.115	0.232	0.152	1.000	0.233
c	0.306	0.283	0.885	0.768	0.848	-	0.767
<i>6pgd-1</i>							
a	1.000	1.000	1.000	0.806	1.000	-	1.000
b	-	-	-	0.194	-	1.000	-
<i>6pgd-2</i>							
a	-	0.100	-	-	-	-	-
b	1.000	0.900	1.000	1.000	0.521	0.500	1.000
c	-	-	-	-	0.479	0.500	-
<i>Mdh-1</i>							
a	-	-	-	0.097	-	-	-
b	1.000	1.000	1.000	0.903	1.000	1.000	1.000
c	-	-	-	-	-	-	-
<i>Mdh-2</i>							
a	-	-	-	0.032	-	-	-
b	1.000	1.000	1.000	0.968	1.000	1.000	1.000
<i>Pgi-1</i>							
a	-	-	-	-	-	-	-
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000
c	-	-	-	-	-	-	-
<i>Pgi-2</i>							
a	0.241	0.515	0.018	-	0.125	-	-
b	0.759	0.471	0.982	0.823	0.625	-	0.581
c	-	-	-	0.177	0.250	1.000	0.419
d	-	0.015	-	-	-	-	-
e	-	-	-	-	-	-	-
<i>Idh-2</i>							
a	-	-	-	0.333	-	1.000	-
b	0.933	0.926	0.778	0.667	1.000	-	0.404
c	0.067	0.074	0.222	-	-	-	0.596

Measurements of genetic variation within and among populations of two species are presented in table 4. The mean

**Table 4.** Level of genetic variation for 11 loci within 14 populations of Korean *E. esula* and *E. maackii*.

Populations	Sample size	<i>A</i>	<i>P</i>	<i>H<sub>e</sub></i>
<i>E. maackii</i> (Jeju island)				
AEW	22.4	1.5	45.5	0.216
SIN	27.5	1.5	36.4	0.157
YON	23.5	1.5	36.4	0.143
SAG	18.5	1.4	36.4	0.175
SAN	24.8	1.4	36.4	0.187
Means	23.4	1.5	38.2	0.176
<i>E. maackii</i> (East Pop.)				
SAM	30.1	2.0	45.5	0.231
NUT	35.5	1.9	63.6	0.258
MAN	24.7	1.5	54.5	0.192
WHO	32.4	1.8	54.5	0.226
Means	30.1	1.8	54.5	0.227
<i>E. esula</i> (West Pop.)				
YOG	26.7	1.5	36.4	0.153
DUK	28.7	1.9	63.6	0.262
PUN	21.7	1.7	45.5	0.230
CHU	26.8	1.2	18.2	0.093
UCH	30.4	1.6	45.5	0.224
Means	26.8	1.6	41.8	0.192

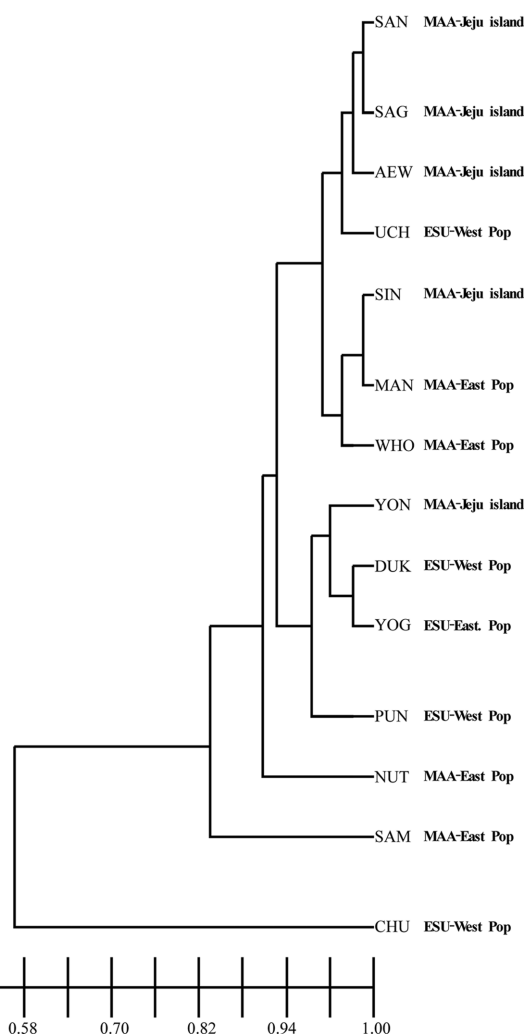
(*A* = mean number of alleles per locus; *P* = percentage of loci polymorphic; *H<sub>e</sub>* = expected heterozygosity).

**Table 5.** Mean values (ranges) for Nei's (1972) genetic identity coefficients between *E. maackii* and *E. esula*.

Species	<i>E. maackii</i>	<i>E. esula</i>
<i>E. maackii</i>	0.933 (0.825-0.999)	
<i>E. esula</i>	0.843 (0.476-0.987)	0.818 (0.578-0.984)

number of alleles per locus in a population (*A*) between two species was no difference, but that of Jeju island populations (*A* = 1.5) of *E. maackii* was a lower value than those of east populations (*A* = 1.8) of the same species. The proportion of polymorphic loci in a population (*P*) ranged from 18.2 to 63.6. *E. maackii* from east populations showed higher mean values of *P* than those of Jeju island populations of the same species (Table 4). The mean expected proportion of heterozygous loci (*H<sub>e</sub>*) ranged from 0.093 to 0.262, and those of Jeju island populations (*H<sub>e</sub>* = 0.176) of *E. maackii* was a lower value than those of east populations (*H<sub>e</sub>* = 0.227) of the same species.

Mean values of Nei's (1972) genetic identity ranged within species from 0.933 for *E. maackii* to 0.818 for *E. esula*. Mean genetic identity between two species was 0.843 and this was

**Fig. 3.** UPGMA phenogram using Nei's genetic identity among 14 populations of Korean *E. esula* and *E. maackii*.

higher than value among populations of *E. maackii* (Table 5).

The UPGMA phenogram based on Nei's Genetic Identity showed that conspecific populations did not cluster together, but Jeju island populations of *E. maackii* didn't generate one cluster (Fig. 3). The UPGMA phenogram using the Dice coefficient of genetic character (Fig. 4) generated a cluster of Jeju island populations of *E. maackii*.

## Discussion

**The validity of *Euphorbia maackii* and *E. esula*:** Because of worldwide distribution and intensive variability of vegetative characters in *E. esula* complex several species such as *E. nakaii*, *E. octoradiata*, *E. esula* and *E. lunulata* have been reported in Korea by several authors (Nakai, 1919; Hurusawa, 1940). After careful examination of type specimens Croizat

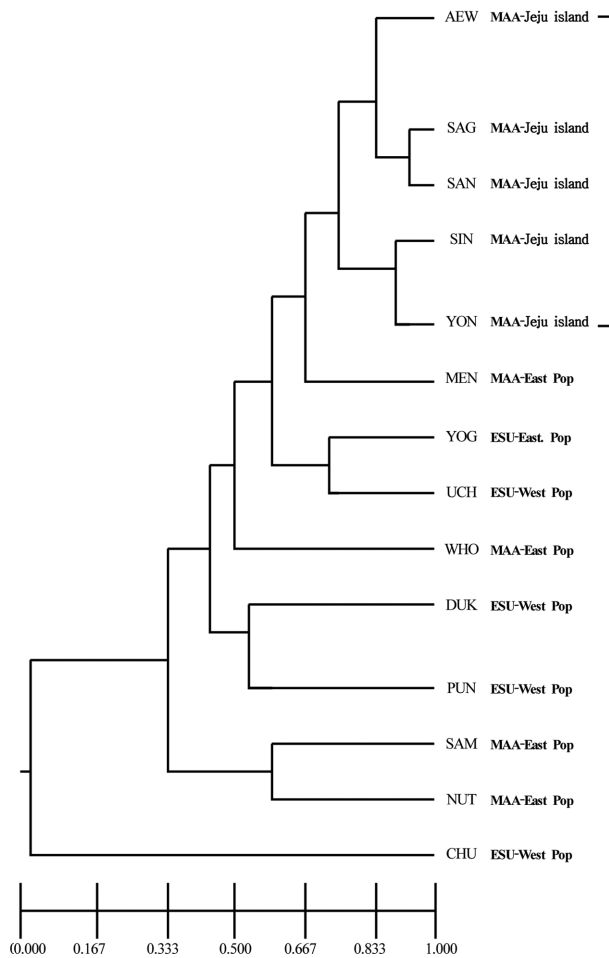


Fig. 4. UPGMA phenogram using Dice coefficients from isozyme phenotypes based on 14 populations of *E. esula* and *E. maackii*.

(1941) insisted *E. nakaii* and *E. octoradiata* as same species, and treated them as synonyms of *E. maackii*. According to the Croizat's treatment, only *E. esula* and *E. maackii* are distributed in Korea, and two species are partially distinguished from each other by the shape of leaves. Hurusawa (1940) recognized a new species *E. nakaii* which is now treated as *E. maackii* had ovate leaves contrary to having linear leaves of European *E. esula*. Although the ranges of most morphological characters of the two species overlap, *E. esula* and *E. maackii* were well recognized by the combination of the morphological traits, and the UPGMA phenogram supports the two distinct species inhibited in Korea.

However, when the UPGMA tree using morphological data is compared to the trees of isozyme data there is little correspondence. Based on the UPGMA tree using allozyme data the populations of each species did not form the same cluster in morphological data. The discordance between morphological and allozyme data should be explained by the

recent divergence or gene flow between two species. Comparing genetic identity within populations of *E. esula* high genetic identity between two species also supports the recent divergence of two species. Similar patterns of recent origin and low level of genetic divergence between species were exemplified in species of *Euphorbia* section *Tithymalopsis* (Park and Elisens, 1997), *Allium* species (Smith and Pham, 1996), *Sullivantia* (Soltis, 1982) and *Coreopsis* (Cosner and Crawford, 1990). Even they are well differentiated morphologically, there may be little time to elapse genetically since divergence.

Gene flow via introgressive hybridization between *E. esula* and *E. maackii* may occur, and it should make two populations of two species mix at *Me* locus. For example, except for Whojoun population (Fig. 5, I = WHO) *E. maackii* was fixed by the allele *a/d* of *Me* locus. WHO population possessed *Me<sup>b</sup>* at low (0.109) frequency which is a unique and high frequency allele at the populations of *E. esula*. Besides, Uchung-do population (Fig. 5, N) of *E. esula* also possessed *Me<sup>d</sup>* (0.483) as high frequency allele which is a unique and fixed allele at the populations of *E. maackii*.

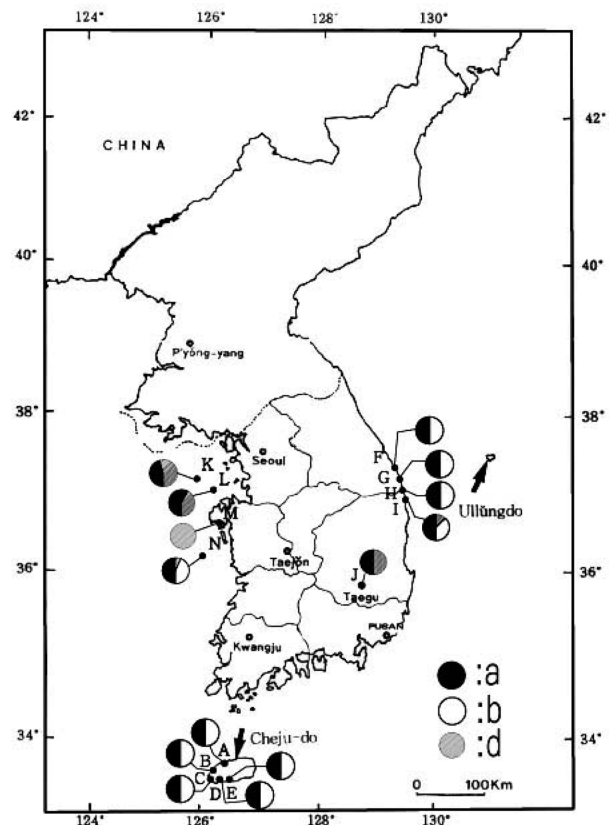


Fig. 5. Distribution of allelic frequencies of *Me* locus in 14 populations of Korean *E. esula* and *E. maackii* (A: AEW, B: SIN, C: YON, D: SAG, E: SAN, F: SAM, G: NUT, H: MAN, I: WHO, J: YOG, K: DUK, L: PUN, M: CHU, N: UCH).

**The genetic variation of *E. maackii* and *E. esula*:** Species of *E. esula* complex in Korea maintain nearly as high as the genetic diversity reported in East Asian *E. jolkini* ( $A = 1.7$ ,  $P = 53.4$  and  $H_e = 0.239$ ) and *E. fauriei* ( $A = 1.8$ ,  $P = 42.5$  and  $H_e = 0.162$ ) while lower than those of *E. ebracteolata* ( $A = 2.3$ ,  $P = 86.7$  and  $H_e = 0.358$ ) and *E. pekinensis* ( $A = 1.8$ ,  $P = 68.2$  and  $H_e = 0.232$ ) in Korea (Park, 2004). Comparing to the north American *Euphorbia* species *E. esula* complex maintained a relatively high level of genetic diversity (Park and Elisens, 1997). However, within the species *E. maackii* the populations from Jeju island maintain a low level of allozyme diversity relative to other continental populations of same species (Table 4). Besides, high genetic identities (0.95-0.99) reflected a single cluster of Jeju island populations from UPGMA phenogram using Dice coefficients (Fig. 5). These patterns of genetic divergence may reflect a recent a single introduction to Jeju island from continental progenitor populations.

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