

Allozyme Diversity in Korean Populations of *Calystegia soldanella* and *C. japonica* (Convolvulaceae): Implications for Conservation

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We investigated levels and distribution of genetic variation in Korean populations of *Calystegia soldanella* and *C. japonica*, clonally reproducing herbaceous perennials. *Calystegia soldanella* is one of ecologically important beach plants growing only on sand and beach dunes in Europe, East Asia, the Pacific Islands, and the west coast of North America. In contrast, *C. japonica* usually grows on small mounds of paddy fields, roadsides, and waste places with patchy distribution. Starch gel electrophoresis was conducted on leaves collected from 13 populations of *C. soldanella* and eight populations of *C. japonica*. The levels of genetic variation of the two species are very comparable; means of expected heterozygosity (H_e) were 0.100 and 0.099 for *C. soldanella* and *C. japonica*, respectively. These values were also very similar to those for species with similar life-history and ecological traits. However, the proportion of total genetic diversity partitioned among populations (G_{ST}) of *C. soldanella* (0.146) was considerably lower than that of *C. japonica* (0.383). In addition, means of Nei's genetic identity (I) for *C. soldanella* and *C. japonica* were 0.985 and 0.900, respectively, which supports a restricted gene flow resulting from obligate clonal reproduction of *C. japonica*. Significant differences in allele frequency were detected among populations at eight and nine of nine polymorphic loci for *C. soldanella* and *C. japonica* ($P < 0.01$), respectively. Considering the ecological importance of *C. soldanella*, the isolated beach populations coupled with present destruction of natural habitats of the species may result in erosion of genetic diversity in the near future. In this respect, conservation efforts should be focused on those populations that currently maintain the most genetic diversity such as those populations in the eastern and southeastern Korean Peninsula and Hamduck Beach, Cheju Island.

Keywords: *Calystegia soldanella*, *C. japonica*, sand dune and beach plants, genetic diversity, clonal reproduction, conservation

Allozyme study has been routinely used to estimate genetic variation and to describe population genetic structure of over 700 plant taxa (Hamrick and Godt, 1989). However, relatively few allozyme studies of comparison between completely or obligately asexual species and its sexual congener are available in the plant allozyme literature (cf., Pleasants and Wendel, 1989). According to a recent review on

plant allozyme literature (Hamrick and Godt, 1989), isozyme data for sexual and asexual plants available until 1988 were only 54 taxa, which contrasts to 352 taxa with only a sexual mode of reproduction. As Hamrick and Godt (1989) pointed out, however, generalization concerning the relationships between genetic diversity and modes of reproduction can be made for plant species is still unclear, pending further studies on sexual and asexual plant species (Ellstrand and Roosc, 1987).

Allozyme diversity can be used as a yardstick to

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measure the effectiveness of *in situ* and *ex situ* conservation programs (Hamrick *et al.*, 1991). Recently, attention has focused on allozyme studies of the rare and endangered species or species under severe environmental and human stresses because sound management of these species requires an understanding of genetic structure of the species (Wyatt, 1992).

In this study, we investigated levels and distribution of genetic variation in the two clonally reproducing species, *Calystegia soldanella* (L.) Roem. et Schutt. and *C. japonica* Choisy, using allozyme markers. *Calystegia soldanella*, a herbaceous perennial vine growing on only beaches and sand dunes, is widely distributed in Europe, East Asia, the Pacific Islands, and the west coast of North America (Kitamura *et al.*, 1986). *Calystegia soldanella* is an ecologically important species because it enhances formation and/or stabilization of sand dunes and beaches (Mun, 1984). The species is clonally reproduced by underground rhizomes, and insect-pollinated. The species is diploid ($2n=22$; Kitamura *et al.*, 1986), and the stems are elongated and prostrate, which assists in the accumulation of more sand. Despite the ecological importance of this species, the natural habitats of *C. soldanella* in Korea have been severely destroyed (M. Chung, pers. obs.).

Calystegia japonica is also a herbaceous perennial vine and is widely distributed in China, Korea, and Japan (Kitamura *et al.*, 1986). In Korea, the species grows usually on small mounds of paddy fields, along roadsides, rarely colonizing sites or waste places which have been recently disturbed. Populations of *C. japonica* are typically small and distributed in patches. Usually the ovary of *C. japonica* does not mature fully (Kitamura *et al.*, 1986) and mature capsules also have not been encountered during field trips by the authors, indicating that the species is a nearly obligate clonal plants propagating predominantly by rhizomes. The species is also diploid ($2n=22$) (M. Chung, unpubl. data).

The purposes of the study were: 1) to estimate how much genetic diversity is maintained in the two species; 2) to describe how genetic variation is distributed within and among populations of the species; 3) to compare the levels and distribution of genetic diversity of the species with those having similar life-history traits; and 4) to make a conclusion about which Korean populations of *C. soldanella* in Korea

should be protected.

MATERIALS AND METHODS

A total of 750 leaf tissues was collected from 13 populations (425 individuals) of *C. soldanella* and eight populations (325 individuals) of *C. japonica* in Korea (Fig. 1). Population code and sample size were given in Table 1. Because the species exhibit clonal growth, samples were collected randomly at intervals of more than 2 m within each populations or patches to avoid repeated sampling of the same genet and biased samples toward certain clones. Leaf samples were placed in plastic bags wrapped with a wet paper towel and stored on ice and transported to the laboratory. Samples were then stored at 4°C until protein extraction.

Leaf samples were cut finely, and crushed with a mortar and pestle. A phosphate-polyvinylpyrrolidone extraction buffer (Mitton *et al.*, 1979) was added to the leaf samples to facilitate crushing and to aid enzyme stabilization. The crushed extract was absorbed onto 4×6-mm wicks cut from Whatman 3 MM chromatography paper, then stored at -70°C until needed for analysis. Electrophoresis was performed using 10.5% starch gel. Fifteen putative loci for *C. soldanella* and *C. japonica* from seven enzyme sys-

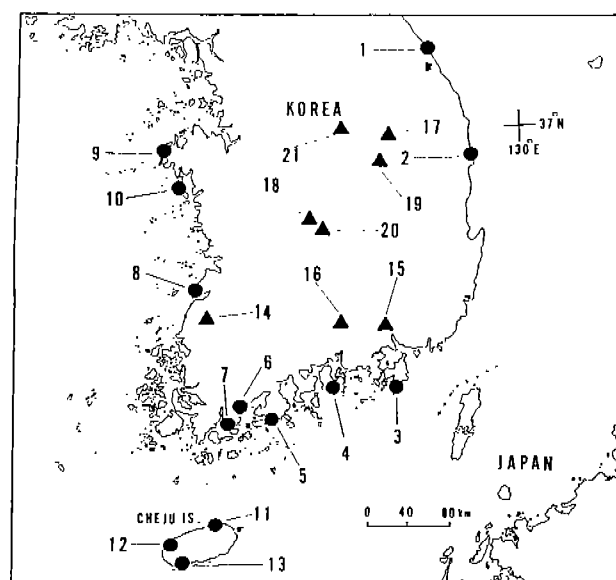


Fig. 1. Locations of the 21 sampled populations in Korea. Closed circle (1-13) indicate *Calystegia soldanella* and closed triangles (14-21) represent *C. japonica*, respectively.

Table 1. Summary of allozyme variation for 15 loci within 13 populations of *Calystegia soldanella* and eight populations of *C. japonica*. Abbreviations: N, sample size; P, percentage of polymorphic loci; A, mean number of alleles per locus; Ae, mean effective number of alleles per locus; He, expected heterozygosity; SE, standard error

Population code	N	P	A	Ae	He (SE)
<i>C. soldanella</i>					
1	50	33.3	1.80	1.27	0.130 (0.014)
2	50	40.0	1.47	1.24	0.128 (0.014)
3	50	33.3	1.52	1.32	0.148 (0.016)
4	25	33.3	1.47	1.32	0.153 (0.016)
5	25	33.3	1.67	1.31	0.146 (0.016)
6	25	33.3	1.47	1.20	0.098 (0.013)
7	25	33.3	1.47	1.16	0.090 (0.011)
8	22	20.0	1.33	1.12	0.075 (0.010)
9	28	20.0	1.33	1.12	0.068 (0.010)
10	40	26.7	1.40	1.19	0.096 (0.013)
11	35	40.0	1.53	1.20	0.111 (0.013)
12	25	13.3	1.13	1.09	0.048 (0.008)
13	25	6.7	1.13	1.09	0.012 (0.003)
<i>C. japonica</i>					
14	25	26.7	1.33	1.16	0.089 (0.017)
15	50	40.0	1.47	1.28	0.158 (0.019)
16	50	33.3	1.33	1.15	0.085 (0.016)
17	50	40.0	1.47	1.24	0.122 (0.019)
18	50	26.7	1.33	1.15	0.078 (0.016)
19	50	20.0	1.27	1.17	0.079 (0.018)
20	25	26.7	1.27	1.15	0.081 (0.016)
21	25	40.0	1.40	1.14	0.097 (0.013)
Mean of <i>C. soldanella</i>					
	32.7	28.2	1.44	1.19	0.100 (0.004)
Mean of <i>C. japonica</i>					
	40.6	31.7	1.36	1.18	0.099 (0.006)

terms were resolved using two gel/electrode buffer systems. A Poulick buffer system (Haufler, 1985), a modification of Soltis *et al.* (1983) system 8, resolved phosphoglucosmutase (PGM), leucine aminopeptidase (LAP), triosephosphate isomerase (TPI), and phosphoglucosomerase (PGI). A morpholine citrate buffer system (Chung and Kang, 1994), a modification of Clayton and Tretiak (1972), was used to resolve 6-phosphoglucosnate dehydrogenase (PGD), peroxidase (PER), and isocitrate dehydrogenase (IDH). All stain recipes were identical to those described by Soltis *et al.* (1983). Although the genetic bases of the loci were not documented by controlled crosses, all calystegia isozymes expressed phenotypes that were consistent in subunit structure and genetic interpretation with most isozyme studies in plants

as documented by Weeden and Wendel (1989). 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. *Lap-2* was being expressed, but it was not scored because of poor activity and/or resolution.

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 or expected heterozygosity (He) assuming Hardy-Weinberg law (Hamrick *et al.*, 1992). Subscripts refer to species (S) or population (P) level parameter. *T*-tests were used to test for significant differences among these population parameters.

The partitioning of genetic diversity within and among populations at each polymorphic locus was estimated using Nei's gene diversity formulae (Nei, 1973, 1977) and averaged to provide a single estimate for each species. G_{ST} values were tested for significance by a χ^2 -statistic proposed by Workman and Niswander (1970). Nei's genetic identities and distances (Nei, 1972) were calculated for each pairwise combination of populations and species. Nei's genetic distance were also used to evaluate the divergence time between *C. soldanella* and *C. japonica*. Assuming mutations are neutral and mutation rate is roughly 10^{-7} per year for electrophoretically detectable proteins, a crude estimate of divergence time could be obtained: $t = 5 \times 10^6 D$ (Nei, 1987), where *D* is genetic distance.

RESULTS

Calystegia soldanella and *C. japonica* maintain a very similar level of genetic variation. Nine of the 15 loci resolved ($P_s = 60\%$) were polymorphic in at least one population for *C. soldanella* and *C. japonica*. *Lap-1*, *Tpi-1*, and *Idh-3* were monomorphic in all 13 populations of *C. soldanella*, whereas *Tpi-2*, *Idh-1*, and *Idh-3* were monomorphic in all eight populations of *C. japonica*. *Pgi-1*, *Pgd-2*, and *Idh-2* were monomorphic for both species. Two or more alleles were observed for 15 loci of *C. soldanella* and *C. ja-*

ponica, with the total average numbers of alleles for the species (A_s) being 2.33 and 2.13, respectively. The average effective number of alleles was 2.01 for *C. soldanella* and 1.82 for *C. japonica*. Overall genetic diversity (H_e), however, was lower in *C. soldanella* than *C. japonica* (0.136 vs. 0.178).

Allozyme variation at the population level was lower than at the species level (Table 1). For example, the percentage of polymorphic loci (P_p) was never higher than 41% in any population, with means of 28.2% for *C. soldanella* and 31.7% for *C. japonica*, respectively, which did not significantly differ between the species ($t=0.83$, $P>0.5$). Also, mean number of alleles per locus (A_p), mean effective number of alleles per locus (A_{ep}), and mean genetic diversity within populations did not differ between *C. soldanella* and *C. japonica*: 1.44 vs. 1.36, $t=1.18$, $P>0.1$; 1.19 vs. 1.18, $t=0.14$, $P>0.8$; 0.100 vs. 0.099, $t=0.10$, $P>0.9$, respectively.

Significant differences in allele frequencies among populations were found at eight and nine of nine polymorphic loci for *C. soldanella* and *C. japonica* ($P<0.01$), respectively (Table 2). Total genetic diversity at the polymorphic loci (H_T) for *C. japonica* was high (0.296), but the proportion of genetic diversity among populations (G_{ST}) was 0.383, indicating slightly less than 62% of the total variation is common to all eight populations. On the other hand, *C. soldanella* also had a high mean H_T (0.227), but the mean G_{ST} value was 0.146, lower than that of *C. japonica*. In addition, average genetic identity for all pairs of populations of *C. soldanella* ($I=0.958$, $SE=0.001$) was higher than for *C. japonica* ($I=0.900$, $SE=0.007$). Mean genetic identity between the species was 0.811. The crude estimate of divergence time, as derived from the mean interspecific genetic distance, was

1.056^b years.

DISCUSSION

Genetic diversity within and among populations

The levels of genetic variation found within Korean populations of *C. soldanella* is very comparable with those of *C. japonica*. Based on a recent review of plant allozyme literature (Hamrick and Godt, 1989), the mean estimates for each of the four parameters of genetic variation (P , A , A_e , and H_e) are also very comparable with those for the nearly 160 herbaceous species and 60 sexual-asexual plant species.

Recent reviews of plant allozyme literature (*e.g.*, Brown, 1979; Hamrick *et al.*, 1979; Gottlieb, 1981; Hamrick and Godt, 1989; Loveless and Hamrick, 1984; Hamrick *et al.*, 1992) have shown causal relationships between allozyme diversity and life-history and ecological traits. Therefore, the life-history and ecological characteristics of the two *Calystegia* species may give us some hints to explain moderate levels of allozyme variability maintained in the two species. For example, Hamrick and Godt (1989) has shown that levels of allozyme variation within populations is strongly correlated with geographic range. Usually, plant species with geographically widespread distributions tend to maintain higher level of allozyme diversity than those with more restricted ranges (Karron *et al.*, 1988). Although several exceptions have been noted (*e.g.*, Godt and Hamrick, 1993; Chung, 1994a) species with discrete populations with patchy distributions have relatively lower level of variation within populations than those with more continuously distributed populations (Chung and Kang, 1994). In addition, plant species with restricted ecological distribution would have less genetic variation than those growing on heterogeneous habitats ("niche-width hypothesis" by Van Valden [1965]) (*e.g.*, Wolff and Jefferies, 1987; Cole and Biesboer, 1992; Purdy *et al.*, 1994; Kim and Chung, 1995). Although *C. soldanella* is widely distributed in Europe, East Asia, the Pacific Islands, and the west coast of North America, it grows only on sand and beach dunes. Populations of *C. japonica* also have a wide geographic range in East Asia and usually are pat-

Table 2. Nei's (1973, 1977) statistics of genetic diversity for *Calystegia soldanella* and *C. japonica*. Values presented are means over all polymorphic loci. Abbreviations: H_T , total genetic diversity; H_s , genetic diversity within populations; and G_{ST} , proportion of total genetic diversity partitioned among populations

Species	No. of loci	H_T	H_s	G_{ST}	Significance
<i>C. soldanella</i>	9	0.227	0.177	0.146	8 loci $P<0.01$
<i>C. japonica</i>	9	0.296	0.168	0.383	9 loci $P<0.01$

chily distributed. It is probable that strongly directional natural selection toward genetic uniformity in homogeneous beach and sand dune environments and habitats might be operated on *C. soldanella*. In addition, vegetative reproduction and spread could have a marked effect on the genetic structure of plant populations (Murawski and Hamrick, 1990; Chung, 1994b). Clonal reproduction could lead to retard the loss of genetic diversity within populations, because species with independent ramets could reduce the probability of genet death (Cook, 1983). *Calystegia soldanella* reproduces asexually by underground rhizomes and sexually by seeds, whereas *C. japonica* propagates mainly by rhizomes. These and other unknown factors may account for the observed levels of genetic variation within populations of *C. soldanella* and *C. japonica* in Korea. Based on a recent review of the study of clonal plant species (Ellstrand and Roose, 1987), species with a predominantly vegetative reproduction and rarely through sexual reproduction generally maintain lower level of genetic diversity than those successfully produce progeny by sexual reproduction as a reproductive alternative to vegetative reproduction. However, the present data strongly suggest that this statement is not applicable to the two *Calystegia* species in Korea.

Although the levels of genetic variation of *C. soldanella* are very comparable with those of *C. japonica*, the G_{ST} value of *C. soldanella* (0.146) is considerably lower than that for *C. japonica* (0.383). The level of genetic divergence of *C. soldanella* is lower than mean values reported for species with similar life-history characteristics, whereas the mean G_{ST} value of *C. japonica* is higher than those reported for most species with similar life-history traits. For example, herbaceous perennials and plant species with widespread geographic range and sexual and asexual mode of reproduction have mean G_{ST} values of 0.223 ($N=121$), 0.210 ($N=87$), and 0.213 ($N=54$), respectively (Hamrick and Godt, 1989). It is interesting to note that population differentiation is most affected by the breeding system of the plant species and not by the geographic range of the species (Hamrick and Godt, 1989). For example, wind-pollinated, outcrossed species have a mean G_{ST} value (0.099, $N=134$) five times lower than the selfing ones (mean $G_{ST}=0.510$, $N=78$), whereas animal-pollinated ones have an intermediate mean G_{ST} value (0.207, $N=$

184). Although the breeding systems of the two species are unknown, it is probable that the species are predominantly outcrossing because of herkogamy. The possibility of geitonogamy, however, should not be ruled out because flowers are axillary from numerous axils of elongated and prostrate stems.

As Korean populations of *C. soldanella* are surrounded by hillsides, gene flow into adjacent areas or populations via pollen dispersal by insects is unlikely. In addition, no specialized primary seed dispersal mechanism is apparent in the species. When one considers these factors and relatively low level of genetic divergence among populations observed in the species (mean $I=0.985$), a secondary seed movement might have occurred among locations of the species. Seed dispersal by sea water might have occurred among populations located on the beach front at the high tide line (Devall and Thien, 1989).

Populations of *C. japonica* are discontinuous or isolated and have patchy distribution. This type of populations are expected to show increased levels of genetic differentiation as gene flow decreases (Loveless and Hamrick, 1984). In addition, no fruits has been observed in populations of *C. japonica* during field trips (M. Chung, pers. obs.). As expected, Korean populations of *C. japonica* have a high mean G_{ST} value, low mean genetic identity among populations ($I=0.900$), and significant differences in allele frequencies for all polymorphic loci ($P<0.001$).

The divergence time between *C. soldanella* and *C. japonica* is approximately one million years, as deduced from the average interspecific genetic distance. Mean genetic identity between species ($I=0.811$) was above the range of mean identity (0.65–0.70) reported by Gottlieb (1981) and Crawford (1983). However, the two species have adopted the different ecological strategies, as they have adapted to specific environments. As a consequence of such different ecological strategies adopted by each species, interspecific reproductive isolation would prevent any exchange of genes at the interspecific level. Individuals with apparent hybrid enzyme phenotype were not detected in this study.

Implications for conservation

Although *C. soldanella* is one of ecologically important species which stabilize beach dunes, the natu-

ral habitats of the species in Korea have been severely destroyed because of recent increase in dune-bank construction and human disturbance in summer season (M. Chung, pers. obs.). Because this study was only conducted on the Korean populations, the present estimates of genetic variability may underestimate the true levels of genetic diversity of *C. soldanella* as a whole. However, as one of the objectives of this study was to provide information about the genetic resources of the species in Korea, here we suggest some proposal to maintain the Korean populations of the species. The species in Korea maintains a moderate level of genetic variability within populations compared with those with similar life-history and ecological traits. Also, relatively low but a significant level of interpopulational genetic divergence in *C. soldanella* exists. The isolated beach populations of *C. soldanella* in Korea coupled with present destruction of natural habitats by building beachbanks and human disturbance may result in erosion of genetic diversity in the near future. The proportion of among population component of the total genetic variation is of primary importance for the conservation of genetic diversity or the evolutionary potential of species (Hamrick and Godt, 1989). Considering the present data such as a relatively low mean G_{ST} value, at least a few populations should be preserved to conserve most genetic diversity found in Korean populations of *C. soldanella*, giving priority to populations with high variation such as populations 1 to 5 (the eastern and southeastern Korean Peninsula) and 11 (Hamduck Beach, Cheju Island). Populations of 1, 5, and 11 also harbor five private alleles. These six populations could be used as sources of genetic diversity for the restoration of genetically depauperate populations. However, very little was known about the biology of the species, including information on its mating systems, breeding structure, pollen and seed dispersal, and demography. Such information on *C. soldanella* should provide valuable information for developing its more adequate conservation strategy.

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韓國產 갯메꽃 및 메꽃 (메꽃科) 集團의 遺傳的 多樣性 保存에 대한 暗示

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적 요

한반도에 자생하는 갯메꽃 및 메꽃은 주로 영양적으로 번식하는 식물인데 이 두 종을 대상으로 집단내의 유전적 수준과 집단간의 유전적 분포를 조사했다. 갯메꽃은 생태적으로 중요한 사구 식물 중 하나이며 유럽, 동아시아, 태평양연안 및 구미대륙의 서해안의 사구 및 모래해안에만 자생한다. 반면에 메꽃은 밭 혹은 논 주위, 도로가, 혹은 버려진 땅 등에 주로 살며 동북아시아에 자생한다. 갯메꽃 13군데 집단 (425개체) 및 메꽃 8군데 집단 (325개체)를 대상으로 전분전기영동법이 행해졌다. Hardy-Weinberg 법칙에 준하여 계산된 이형접합자 기대치 (H_e)에 기준을 둘 때 이 두 종의 유전적 다양도는 거의 같았다. 즉, 갯메꽃은 0.100이었고 메꽃은 0.099를 나타내었다. 또한 이런 값은 이들 두 종과 생활사적 생태적 특질이 유사한 다른 종들의 평균치와 매우 유사하였다. 그러나, 집단간의 분화도 (G_{ST})는 갯메꽃 (0.146)이 메꽃 (0.383)보다 상당히 낮았으며 Nei의 종 내 집단간의 동질성 (I)도 갯메꽃 (0.985)이 메꽃 (0.900)보다 훨씬 높았다. 이는 주로 메꽃은 열매가 맺지않고 무성적으로 번식하는데 기인되는 집단간의 유전자 이동이 제한되고 있음을 암시하고 있다. 조사된 9군데 다형성 유전좌위 중 8군데 (갯메꽃) 및 9군데 (메꽃) 전부에서 집단간의 대립인자 빈도의 차이가 통계학적으로 유의성이 있는 것으로 나타났다 ($P < 0.01$). 갯메꽃의 생태적 중요성을 고려해 볼 때, 집단들은 격리되어 있고 현재 이 종의 생육지가 파괴되고 있어서 이 종이 지니는 유전적 다양도 (진화적 잠재력)는 앞으로 낮아질 수 있을 것이다. 만약 이것이 사실이라면, 현재 유전적 다양도가 가장 높은 집단들 (예를들면, 동해안, 동남해안 및 제주도 함덕 해수욕장)을 보존하는데 주력해야 될 것이다.

주요어: 갯메꽃, 메꽃, 사구 및 모래해안 자생식물, 유전적 다양성, 영양번식, 보존

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