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Genetic Diversity and Population Structure of *Liriope platyphylla* (Liliaceae) in Korea

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Genetic diversity and population structure of eleven *Liriope platyphylla* (Liliaceae) populations in Korea were determined using genetic variation at 20 allozyme loci. The percent of polymorphic loci within the enzymes was 55.9%. Genetic diversity at the species level and at the population level was high (*Hes* = 0.178; *Hep* = 0.168, respectively), whereas the extent of the population divergence was relatively low (G_{ST} = 0.064). F_{IS}, a measure of the deviation from random mating within the 11 populations, was 0.311. Total genetic diversity values (H_T) varied between 0.0 and 0.535, giving an average over all polymorphic loci of 0.323. The interlocus variation in within population genetic diversity (H_S) was high (0.305). An indirect estimate of the number of migrants per generation (*Nm* = 3.66) indicates that gene flow is high among Korean populations of the species. In addition, analysis of fixation indices revealed a substantial heterozygosity deficiency in some populations and at some loci. Mean genetic identity between populations was 0.988. It is highly probable that directional toward genetic uniformity in a relatively the homogenous habitat is thought to be operated among Korean populations of *L. platyphylla*.

Key words – Genetic diversity, population structure, *Liriope platyphylla*

Introduction

Most plants, especially for rhizomatous and stoloniferous species, have physical connections among ramets although its level of persistency is highly variable among species and habitats [23]. Studies of the genetic structure of apomictic plant populations have received revitalized interest in the past decade as a result of electrophoretic techniques, which allow us to better assess the genotypic composition of populations. A well-established general belief has been that asexually reproducing species lack genetic diversity and can be considered as evolutionary "dead-ends". Various studies have shown that asexually reproducing plants can be much more genetically diverse than originally thought [6]. Clearly, descriptive genetic work on both sexual and asexual plant populations is needed as well. Despite the importance of knowledge concerning genetic variation for providing information for conservation purpose and population genetic structure, detailed studies of the levels and distribution of genetic variation are not available for most species in Korea, particularly both sexual reproduction and asexually reproductive plants.

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Liriope platyphylla (Liliaceae) Wang et Tang is a widespread perennial herb occurring throughout boreal and temperate zones. *L. platyphylla* reproduces extensively by vegetative rhizomes and potentially by sexually produced seed. The species in Korea is endemic to several low mountains where it is found to elevations of 500 m below sea level. Leaves of this species are evergreen, alternate, linear with stipules lacking. Flowers are regular, perfect and hypogynous. *L. platyphylla* has been used in medicine and making tea in China and Korea. Recently, the species is important economically as garden ornamentals because the species has shown a strong resistance to environmental pollution. The purpose of this study was: 1) to estimate how much total genetic diversity is maintained in the species; 2) to describe how genetic variation is distributed within and among populations; and 3) to assess genetic structure of *L. platyphylla*. In addition, the basic question: Has the domestication process eroded the levels of genetic variation of the cultivated populations as has been shown in most cultivated species [5].

Materials and Methods

Sampling procedure

Liriope platyphylla was collected from six natural populations and five cultivated populations in Korea (Table 1).

Table 1. Population designation and collection localities of *Liriope platyphylla*

Code	Collection locality	Type
JEJ	Jeju Islands, Saekipo pref., Jeju-do	C
ANK	Ankang-meon, Pohang pref., Gyeongsangbuk-do	C
YOH	Yohang-meon, Haman pref., Gyeongsangnam-do	C
YOU	Youngam-meon, Youngam pref., Cheonlanam-do	C
DUC	Duckgu-meon. Uljin pref., Gyeongsnagbuk-do	C
BUS	Busan pref., Mt. Kyucheng, Gyeongsangbuk-do	W
YOD	Youngdong pref., Mt. Hackwha, Chungcheongbuk-do	W
SAN	Sancheong pref., Mt. Giri, Gyeongsangnam-do	W
CHO	Chengyang pref., Mt. Chilkap, Chungcheongbuk-do	W
KAP	Kapeng pref., Mt. Chiak, Gangwon-do	W
YAN	Yangyang pref., Mt. Solak, Gangwon-do	W

W: wild or natural population, C: cultivated population.

One leaf per plant was sampled during 2002 to 2005. More than 30 plants were collected from each population. Leaves gathered from all populations were stored in plastic bags for several days in a refrigerator until electrophoresis was carried out.

Enzyme electrophoresis

Leaves were homogenized by mechanical grinding to release enzymes from cell and organellar membranes with Tris-HCl grinding buffer-PVP solution described in Soltis et al. [24]. Electrophoresis was performed using 10% starch gel. Buffer systems and enzyme staining procedures from Soltis et al. [24] were used to assay twelve enzyme systems; peroxidase (PER), isocitrate dehydrogenase (IDH), glutamate oxaloacetate transaminase (GOT), fluorescent esterase (FE), 6-phosphoglugonate dehydrogenase (PGD), phosphoglucomutase (PGM), malic enzyme (ME), malate dehydrogenase (MDH), acid phosphatase (ACP), shikimate dehydrogenase (SKD), octanol dehydrogenase (ODH), and alcohol dehydrogenase (ADH). The procedures for starch gel electrophoresis were as reported by Soltis et al. [24].

For enzymes which resolved more than one zone of activity, the most anodal isozyme is arbitrarily designated 1, with the others sequentially assigned higher numbers. Likewise, alleles were designated sequentially with the most anodally migrating allozyme designated 'a' and progressively slower forms 'b', 'c', and so on. All *L. platyphylla* isozymes expressed phenotypes that were consistent in subunit structure and genetic interpretation with most isozyme studies in plants, as documented by Weeden and Wendel [25].

Analysis of data

A locus was considered polymorphic if two or more alleles were detected, regardless of their frequencies. Four standard genetic parameters were estimated using a computer program developed by Loveless and Schnabel; percent polymorphic loci (*P*), mean number of alleles per locus (*A*), effective number of alleles per locus (*Ae*), and gene diversity (*He*) [12]. Subscripts refer to species (s) or population (p) level parameters. Observed heterozygosity (*Hop*) was compared with Hardy-Weinberg expected value using Wright's fixation index (*F*) or inbreeding coefficients [26]. These indices were tested for deviation from zero by χ^2-statistics following Li and Horvitz [16]. Nei's gene diversity formulae (H_T, H_S, D_{ST}, and G_{ST}) were used to evaluate the distribution of genetic diversity within and among populations [20,21]. The G_{ST} coefficient estimates relative population differentiation. Nei's genetic identity (*I*) was calculated for each pairwise combination of populations [19]. The PC-MEGA3 program was used to conduct a cluster analysis on genetic distances via the unweighted pairwise groups method arithmetic average (UPGMA) [15]. The genetic structure within and among populations was also evaluated using Wright's [26] *F*-statistics: F_{IT}, F_{IS}, and F_{ST}. The F_{IT} and F_{IS} coefficients measure excesses of homozygotes or heterozygotes relative to the panmictic expectations within the entire samples and within populations, respectively. Two indirect estimates of gene flow were calculated. One estimate of *Nm* (the number of migrants per generation) was based on G_{ST} [26] and the other estimate was based on the average frequency of "rare" alleles found in only one population [1,22].

Results

Genetic diversity

Eleven of the 20 loci (55.0%) showed detectable polymorphism in at least two populations (Table 2). The remaining nine loci (*Per-2, Per-3, Pgd-2, Idh-1, Mdh-1, Got-1, Pmg-2, Odh,* and *Adh*) were monomorphic in all populations. There are significant differences in allelic frequencies in the two loci (*Skd* and *Me*) between wild and cultivated populations. An average of 44.1% of the loci was polymorphic within populations, with individual population values ranging from 40.0% to 50.0%. The majority of the polymorphic loci (*Per-1, Skd, Acp, Pgd-1, Idh-2, Mdh-2, Got-2,* and *Fe-2*) expressed three alleles, while the

Table 2. Percentage of polymorphic loci (*P*), mean number of alleles per polymorphic population (*Ap*), mean number of alleles per locus (*A*), effective number of alleles per locus (*Ae*), observed heterozygosity (*Hop*), Hardy-Weinberg expected heterozygosity or genetic diversity (*Hep*) for eleven populations of *L. platyphylla*

Pop[a].	*P*	*Ap*	*A*	*Ae*	*Hop* (SD)	*Hep* (SD)
JEJ	40.0	2.50	1.60	1.29	0.108 (0.012)	0.150 (0.048)
ANK	45.0	2.56	1.70	1.29	0.113 (0.013)	0.156 (0.047)
YOH	45.0	2.78	1.80	1.27	0.104 (0.013)	0.154 (0.046)
YOU	45.0	2.67	1.75	1.33	0.118 (0.013)	0.169 (0.049)
DUC	45.0	2.78	1.80	1.30	0.115 (0.013)	0.155 (0.050)
BUS	50.0	2.70	1.85	1.33	0.123 (0.014)	0.184 (0.047)
YOD	45.0	2.78	1.80	1.34	0.115 (0.013)	0.176 (0.050)
SAN	50.0	2.60	1.80	1.41	0.131 (0.013)	0.200 (0.054)
CHO	40.0	2.63	1.65	1.28	0.098 (0.012)	0.146 (0.049)
KAP	40.0	2.88	1.75	1.34	0.113 (0.013)	0.170 (0.053)
YAN	40.0	2.75	1.70	1.39	0.121 (0.013)	0.183 (0.056)
Mean	44.1	2.69	1.75	1.32	0.114 (0.004)	0.168 (0.056)

[a]: Abbreviation codes as in Table 1.

Table 3. Total genetic diversity (H_T), genetic diversity within population (H_S), deviations of genotype frequencies from Hardy-Weinberg expectations over all populations (F_{IT}) and within individual population (F_{IS}), and proportion of total genetic diversity partitioned among populations (G_{ST})

Locus	H_T	H_S	D_{ST}	F_{IS}	F_{IT}	G_{ST}
Per-1	0.535	0.524	0.011	0.247	0.263	0.021
Acp	0.510	0.450	0.010	0.249	0.264	0.020
Skd	0.372	0.290	0.081	0.536	0.637	0.219
Pgd-1	0.386	0.367	0.019	0.297	0.332	0.050
Idh-2	0.482	0.456	0.026	0.307	0.345	0.055
Mdh-2	0.079	0.075	0.004	0.220	0.255	0.046
Got-2	0.282	0.271	0.011	0.256	0.285	0.038
Fe-1	0.518	0.510	0.007	0.384	0.393	0.014
Fe-2	0.163	0.149	0.013	0.334	0.389	0.082
Pgm-1	0.144	0.131	0.013	0.297	0.358	0.087
Me	0.081	0.075	0.006	0.291	0.343	0.072
Mean	0.323	0.305	0.018	0.311	0.351	0.064

remaining ones expressed two (*Mdh-2*, *Pgm-1*, and *Me*) and four (*Fe-1*). The average number of alleles per locus (A) was 1.75 across populations, varying from 1.60 for the population with the lowest number of alleles and 1.85 for the population with the highest number of alleles. The effective number of alleles per locus (*Ae*) was similar at the species and the population level (*Aes* = 1.32; *Aep* = 1.32). The mean genetic diversity within populations was 0.168. Population SAN had the highest expected diversity (0.200), while Population CHO had the lowest (0.146). Genetic diversity (mean *Hep* = 0.177) at the wild populations was high, whereas the value at the cultivated populations (mean *Hep* = 0.157) was low. The *P*, *Ap*, and *A* are not significant differences among wild and cultivated populations, whereas, *Ae* and *Hep* were higher than those of cultivated populations.

Genetic structure

F_{IS}, a measure of the deviation from random mating within the 11 populations, was 0.374, and ranged from 0.000 (monomorphic locus) to 0.536 for *Skd* (Table 3). The observed high, significant, and positive F_{IS} value (0.311) indicates that there was a significantly in deficit of heterozygotes in the populations. Analysis of fixation indices, calculated for all polymorphic loci in each population, showed a substantial deficiency of heterozygotes relative to Hardy-Weinberg expectations (Table 4). For example, 88.4%

Table 4. Wright's fixation indices for eleven populations of *L. platyphylla*

Pop.	*Per-1*	*Acp*	*Skd*	*Pgd-1*	*Idh-2*	*Mdh-2*	*Got-2*	*Fe-1*	*Fe-2*	*Pgm-1*	*Me*
JEJ	0.131	0.044	-	-0.024	0.285	-	-	0.408**	0.385*	0.311	0.292
ANK	0.162	0.102	-	0.344	0.284	-	0.355	0.365*	0.322	0.385	0.272
YOH	0.372*	0.312	-	0.337	0.303	-	0.266	0.426**	-0.038	0.353	0.473*
YOU	0.296	0.274	-	0.344	0.320	-	0.234	0.403**	0.264	-0.39	0.356
DUC	0.280	0.221	-	0.279	0.278	-0.018	0.175	0.378*	0.372*	-	-0.016
BUS	0.303	0.338	0.596**	0.361	0.417*	-0.052	0.186	0.367*	-0.044	0.517	-
YOD	0.253	0.283	0.510**	0.349	0.328	0.356*	0.329	0.424**	-	0.267	-
SAN	0.255	0.361	0.497***	0.267	0.352*	0.281	0.246	0.393*	0.720	-0.038	-
CHO	0.232	0.299	0.683**	0.270	-0.020	-0.017	0.338*	0.382*	-	-	-
KAP	0.229	0.281	0.498**	0.388*	0.370*	-	0.314*	0.353	-	-	-
YAN	0.238	0.206	0.534***	0.263	0.338	0.435*	0.279	0.401*	-	-	-

Chi-square tests were used to determine if fixation indices were from an expected value (* = P < 0.05; ** = P < 0.01; *** = P < 0.001).

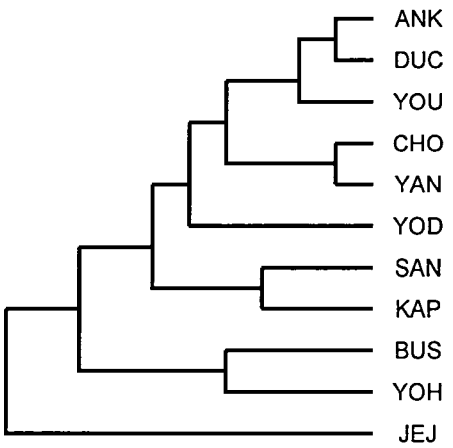

Fig. 1. A dendrogram for eleven *Liriope platyphylla* populations based on allozyme analysis. Abbreviations for codes are listed in Table 1.

of fixation indices were positive (76/86), and 31 of those departed significantly from zero ($p < 0.05$). Only ten of indices were negative, indicating an excess of heterozygotes at *Pgd-1* (population JEJ), *Idh-2* (population CHO), *Mdh-2* (Populations 4 and 8), and *Me* (population DUC). In all wild populations, genotypic frequencies at *Skd* locus does not conformed to Hardy-Weinberg expectations. Total genetic diversity values (H_T) varied between 0.0 and 0.535, giving an average over all polymorphic loci of 0.323. The interlocus variation in within population genetic diversity (H_S) was high (0.305). On a per locus basis, the proportion of total genetic variation due to differences among populations (G_{ST}) ranged from 0.014 for *Fe-1*to 0.219 for *Skd* with a mean of 0.064, indicating that about 6.4% of the total allozyme variation was among populations. The estimate of gene flow based on G_{ST} was slightly high among Korean populations of *L. platyphylla* (Nm = 3.66). Values of genetic distance (D) were below 0.030. Genetic identity values among pairs of populations range from 0.973 to 0.999. The similarity among *L. platyphylla* populations can be seen in the UPGMA dendrogram, where total populations cluster at a below genetic distance 0.788.

Discussion

Genetic diversity

L. platyphylla maintains more diversity in most populations than the average plant species. For example, its mean genetic diversity at 0.178 is slightly higher than that of temperate-zone species (0.146), species with a reproduction mode that is sexual and asexual (0.138), species with a long-lived perennial herbaceous (0.205), and that of widespread geographic ranges (0.202) [11]. The percent polymorphic loci at species level was 55.0%. The value is higher than species with a reproduction mode that is sexual and asexual (43.8%), long-lived perennial herbaceous (39.3%), and temperature-zone species (48.5%), but it is similar to species with widespread geographic ranges (58.9%) [11]. Its average number of alleles per locus was 2.82; this value is higher than that of species with a reproduction mode that is sexual and asexual (1.69) and long-lived perennial herbaceous (1.42), species with widespread geographic ranges (2.29), and temperate-zone species (1.91) [11]. These comparisons suggest that genetic diversity of *L. platyphylla* is higher than that of its associates, the temperate-zone species. Ellstrand and Roose [6], in a review of studies of population genetic structure of primarily obligate clonal plant species, concluded that clonal plant species tend to have intermediate levels of genetic diversity. The results of the present study are not consistent with the general conclusion of Ellstrand and Roose [6] about the levels of genetic diversity. The relatively high level of genetic variation found in *L. platyphylla* is consistent with several aspects of its biology. First, geographic range has been shown to be strongly associated with the level of variation maintained within populations and at the species level [12]. Widely distributed plant species tend to maintain more variation than more narrowly distributed species. Although *L. platyphylla* in Korea is distributed patchily, the species is wide geographic ranges of the Northern Hemisphere including East Asia. Second, the breeding system of a species is an important determinant of variability at both the species and population levels. *L. platyphylla* has a short style and tall stamens (almost pin type). Therefore, this species appears to be predominantly by insects. Predominantly outcrossing species maintain higher levels of intrapopulation genetic variation predominantly inbreeding species [3,9]. Third, long-lived perennial species, like *L. platyphylla*, generally maintains relatively higher levels of variation than annuals and short-lived perennials [17]. As populations of *L. platyphylla* are older, opportunities for the accumulation of mutations should be high. Fourth, the reproduction type of *L. platyphylla* is an important role of genetic variability. In addition, vegetative reproduction and spread can also affect the genetic structure of populations [18]. Cook [4] argued that clonal

growth could act to retard the loss of genetic diversity within populations. If a small amount of gene flow and/or mutation add new clones to a population from time to time, clonal variation may be maintained. Thus, if clonalization occurs by multiple genotypes, the ephemeral nature of woody populations may preclude significant loss of genetic variation while those populations are extant [6].

Genetic structure

Species with independent ramets could spread the risk of mortality among ramets, thus reducing the probability of genet death and preserving genetic diversity. Hartnett and Bazzaz [13] have also argued that physiological independence among ramets may maintain genetic diversity by buffering clones against localized, patch specific selection forces. Sexual reproduction could act to enhance the genetic variation and asexual reproduction could maintain the enhanced genetic variation [2]. *L. platyphylla* commonly reproduces by sexually produced seeds. But, *L. platyphylla* usually propagates by asexually produced rhizomes when several strong environmental disadvantages influenced on the habitat of this species. The species has physical connections among ramets. There asexual reproduction assures the stabilization and persistence of a phenotype that is well adapted to be the immediate environment [14].

The high levels of genetic variation found in both the wild and cultivated populations for *L. platyphylla* consistent with the general pattern of erosion of genetic variation in cultivated plants [5,8]. But, the *P*, *A*p, and *H*op were not significantly different among wild and cultivated populations. The tiny differences of variation among wild and cultivated populations of *L. platyphylla* may also be due in part to high levels of gene flow (3.66) among populations and/or high effective population sizes, generated, at least in part, by the combination of following factors: first, gene flow is very probable, as the wild subpopulations usually grow close to each other, and cultivated populations also can grow near wild populations; second, individuals are perennial and can live for at least 5 years, thus increasing effective population sizes [7]; third, farmers can move the wild plants for the purpose of domestication.

The considerable amount of heterozygote deficiencies is notable (F_{IS} = 0.311). Although the species has many seeds, the dispersal distance seems to be short under rich pine (*Pinus densiflora* and *P. rigida*) forests, which may favor the establishment of clusters of related individuals. In addition, no specialized seed dispersal mechanisms were known in the species. *L. platyphylla*, cannot completely rule out the possibility mating among relatives via localized pollinator behavior rather than selfing could occur within populations. Such structure could lead to biparental inbreeding, causing heterozygote deficiencies. In addition, this patch distribution of related individuals should generate a Wahlund effect. Our sampling included individuals from several patches per population, resulting in an overall deficiency of heterozygotes. It is probably that the combination of these factors may contribute to high levels of heterozygote deficiencies within populations.

In addition, significant differences were found in allele frequencies between populations for all eleven polymorphic loci. Mean genetic identity between populations (I = 0.988) was somewhat above the mean identity (I = 0.945) reported by Gottlieb [10] for 22 species. It is unclear how the populations are genetically homogeneous. It is highly probable that directional toward genetic uniformity in a relatively the homogeneous habitat (i.e. low mountain habitats, shaded ground, and a little swampy land) is thought to be operated among Korean populations of *L. platyphylla*.

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한국내 분포하는 맥문동(*Liriope platyphylla*) 11집단에 대한 20 알로자임 대립유전자좌위에서 유전적 다양성과 집단구조를 조사하였다. 효소내 다형성을 나타내는 빈도는 55.9%였다. 종과 집단 수준에서 유전적 다양도는 각각 0.178, 0.168로 높았으며, 집단간 분화 정도는 낮았다(G_{ST} = 0.064). 전체 11 집단에서 임의교배에 의한 편차는 0.311이였다. 전체 유전적 다양성는 0~0.535였다. 유전적 다양도 중 집단내 변이는 높았다(H_S = 0.305). 세대간 이주하는 개체수는 약 3.66으로 이 종의 한국내 집단간 유전자 흐름이 높음을 시사한다. 또한 라이트의 고정지수 분석 결과 많은 대립유전자좌위와 집단에서 이형접합자의 결핍이 존재하고 있었다. 집단간 유전적 동질성은 0.988이였다. 이는 맥문동의 분포지가 한국내 유사한 환경에 놓여 있고 집단이 방향적 동질성을 가지고 있음을 시사한다.