

## Genetic Diversity and Population Structure of *Pyrola fauriana* (Pyrolaceae) in Korea

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Received October 4, 2005 / Accepted November 29, 2005

Starch gel electrophoresis was used to estimate genetic diversity and population structure of *Pyrola fauriana* H. Andr. in Korea. The percentage of polymorphic loci within enzymes was 57.1%. The values of genetic diversity at the species level and at the population were higher than average values for herbaceous with similar life history traits ( $H_{es} = 0.149$ ;  $H_{ep} = 0.134$ , respectively), whereas the extent of the population divergence was relatively low ( $G_{ST} = 0.082$ ).  $F_{IS}$ , a measure of the deviation from random mating within the 12 populations, was 0.298. An indirect estimate of the number of migrants per generation ( $Nm = 2.81$ ) indicates that gene flow is moderate among Korean populations of the species. Analysis of fixation indices revealed a substantial heterozygosity deficiency in some populations and at some loci. This indicates that some populations sampled may have been substructured largely due to rhizomatous spread and decrease of population sizes.

**Key words** – Genetic diversity, population structure, *Pyrola fauriana*

Unlike most animals, plants cannot move to more favorable patches. Therefore, plants exhibit extensive plasticity in response to various environmental conditions. More precisely, natural selection promotes traits that increase the passage of genes to the next generation. This is, it promotes successful reproduction. Of course, survival is a prerequisite to production, but reproductive success can be enhanced by traits not associated with long survival times. For example, annual flowering plants are diverse and abundant, even though individuals do not live as long as perennial plants. Their survivorship are different, but they both have successful reproductive strategies. Many perennial plants multiply by both sexual and asexual reproduction. Numerous plant species can produce offspring that are genetically identical to each other and to the maternal plant[6]. This broad-sense asexual reproduction may be accomplished by vegetative spread or production of sexual propagules. 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[22].

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 [5,6,22]. 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 reproducing plants.

The family *Pyrolaceae* consists of 4 genera and 30-45 species distributed in cooler more temperate regions of the Northern Hemisphere. The genus *Pyrola* is most abundant in the boreal and Arctic areas[26]. Although Korean populations of *Pyrola fauriana* H. Andr. (*Pyrolaceae*) are rare and scattered, some local populations are frequently large.

Leaves of this species are evergreen, alternate, simple with stipules lacking. The stamens are 5. The pistil is composed of 5 united carpels with 5 locules and a superior ovary. Flowers are regular, perfect and hypogynous. *P. fauriana* is a profusely flowering spring perennial, with pinkish white flowers that are visited by a number of insect species. In this species, I have compiled and quantitatively analyzed what is known of the genetic structure of

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populations to examine whether any trends occur both within and among populations.

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; 3) to assess genetic structure of *P. fauriana* and 4) to characterize the population genetic structure to determine whether patches of the species as comprised of a single clone or a mixture of genets.

## Materials and Methods

### Sampling procedure

*P. fauriana* was collected from twelve natural populations in Korea (Fig. 1). One leaf per plant was sampled during 2002 to 2004. More than 28 plants were collected from each population. Leaves gathered from natural populations were stored in a refrigerator until electrophoresis was carried out.

### Enzyme electrophoresis

Leaves were homogenized by mechanical grinding to re-

lease enzymes from cell and organellar membranes with Tris-HCl grinding buffer-PVP solution described in Soltis et al.[23]. Electrophoresis was performed using 12.0% starch gel. Buffer systems and enzyme staining procedures from Soltis et al.[23] were used to assay twelve enzyme systems; peroxidase (PER), isocitrate dehydrogenase (IDH), glutamate oxaloacetate transaminase (GOT), fluorescent esterase (FE), 6-phosphogluconate dehydrogenase (PGD), alcohol dehydrogenase (ADH), octanol dehydrogenase (ODH), phosphoglucomutase (PGM), malic enzyme (ME), malate dehydrogenase (MDH), acid phosphatase (ACP), and shikimate dehydrogenase (SKD).

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. Although the genetic bases of the loci were not documented by controlled crosses, the isozymes expressed phenotypes that were consistent in subunit structure and genetic interpretation with most isozyme studies in plants, as documented by Weeden and Wendel[24].

### 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 (LYNSPROG) developed by Loveless and Schnabel; percent polymorphic loci ( $P_p$ ), mean number of alleles per locus ( $A$ ), effective number of alleles per locus ( $A_e$ ), and gene diversity ( $H_e$ )[11].  $A_e$  is calculated as the reciprocal of the sum of squares of allele frequencies. Subscripts refer to species (s) or population (p) level parameters. Observed heterozygosity ( $H_o$ ) was compared with Hardy-Weinberg expected value using Wright's fixation index ( $F$ ) or inbreeding coefficients[29]. These indices were tested for deviation from zero by  $\chi^2$ -statistics following Li and Horvitz[14].

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[16-18]. In addition,  $\chi^2$ -statistics were used to detect significant differences in allele frequencies among populations for each locus[27]. Nei's genetic identity ( $I$ ) was calculated for each pairwise combination of populations[16]. I used the PC-SAS program[20]

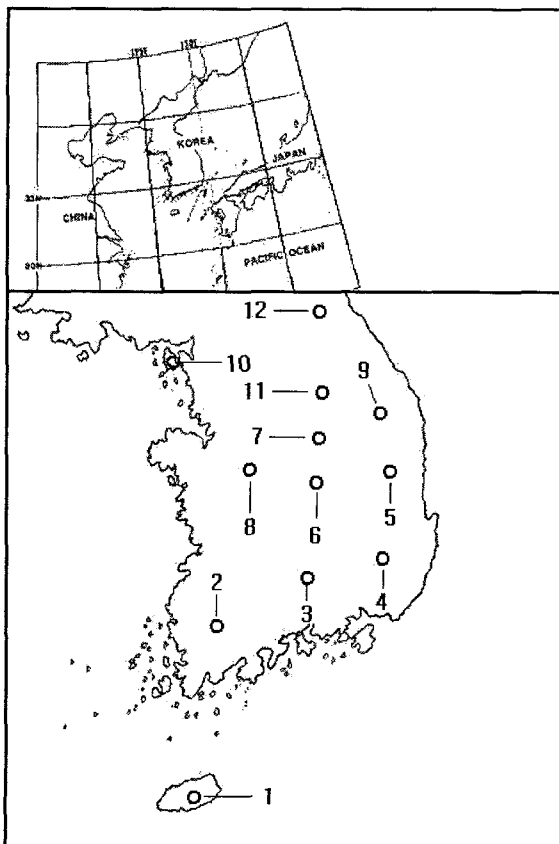


Fig. 1. Collection localities for populations of *P. fauriana* as sources for isozyme analysis.

to conduct a cluster analysis on genetic distances via the unweighted pairwise groups method arithmetic average (UPGMA).

The genetic structure within and among populations was also evaluated using Wright's *F*-statistics[28]:  $F_{IT}$ ,  $F_{IS}$ , 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. The  $F_{ST}$  coefficient estimates relative population differentiation. Deviation of  $F_{IT}$  and  $F_{IS}$  from zero were tested using  $\chi^2$ -statistics[14]. Two indirect estimates of gene flow were calculated. One estimate of  $Nm$  (the number of migrants per generation) was based on  $F_{ST}$ [28] and the other estimate was based on the average frequency of "rare" alleles found in only one population [1.21].

## Results

### Genetic diversity

Twelve of the 21 loci studied (57.1%) showed detectable polymorphism in at least two populations. The remaining nine loci (*Per-2*, *Per-3*, *Idh-1*, *Mdh-2*, *Got-1*, *Fe-3*, *Fe-4*, *Pgd-1*, and *Adh*) were monomorphic in all populations. An average of 40.5% of the loci were polymorphic within populations, with individual population values ranging from 33.3% to 47.6%. The average number of alleles per locus (*A*) was 1.61 across populations, varying from 1.48 for the population with the lowest number of alleles and 1.71 for

the population with the highest number of alleles (Table 1). The effective number of alleles per locus was similar at the species and the population level ( $A_{es} = 1.24$ ;  $A_{ep} = 1.23$ ). The mean genetic diversity within populations was 0.134. Population 8 had the highest expected diversity (0.171), while population 1 had the lowest (0.106). Genetic diversity at the species level was high, whereas the value at the population level was somewhat lower ( $H_{es} = 0.149$ ;  $H_{ep} = 0.134$ ).

### Genetic structure

Chi-square tests indicated significant deviations from Hardy-Weinberg expectation. As expected from the chi-square tests,  $F_{IS}$ , a measure of the deviation from random mating within the 12 populations, was 0.298, and ranged from 0.188 for *Odht* to 0.425 for *Skd* (Table 2). The positive  $F_{IS}$  value (0.298) indicates that there was a significant 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. For example, 86.2% of fixation indices were positive (81/94), and 54 of those departed significantly from zero ( $p < 0.05$ ). Thirteen of these indices were negative, indicating an excess of heterozygotes at those loci and in these populations. On a per locus basis, the proportion of total genetic variation due to differences among populations ( $G_{ST}$ ) ranged from 0.030 for *Fe-1* to 0.179 for *Me* with a mean of 0.082, indicating that about 8% of the total

Table 1. Percentage of polymorphic loci (*Pp*), 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 twelve populations of *P. fauriana*.

Pop <sup>a</sup> .	N <sup>b</sup>	<i>Pp</i>	<i>Ap</i>	<i>A</i>	<i>Ae</i>	<i>Hop</i> (SD)	<i>Hep</i> (SD)
1	37	38.1	2.25	1.48	1.17	0.079 (0.011)	0.106 (0.035)
2	38	38.1	2.50	1.57	1.23	0.098 (0.011)	0.132 (0.043)
3	32	38.1	2.63	1.62	1.18	0.078 (0.011)	0.117 (0.037)
4	32	38.1	2.50	1.57	1.24	0.093 (0.012)	0.136 (0.043)
5	35	38.1	2.63	1.62	1.24	0.089 (0.012)	0.125 (0.046)
6	33	47.6	2.50	1.71	1.29	0.109 (0.013)	0.165 (0.044)
7	33	42.9	2.56	1.67	1.25	0.098 (0.012)	0.147 (0.042)
8	34	47.6	2.50	1.71	1.32	0.112 (0.012)	0.171 (0.048)
9	36	33.3	2.71	1.57	1.20	0.076 (0.011)	0.116 (0.042)
10	28	38.1	2.50	1.57	1.22	0.090 (0.012)	0.125 (0.043)
11	31	42.9	2.56	1.67	1.31	0.116 (0.013)	0.164 (0.049)
12	29	42.9	2.22	1.52	1.15	0.093 (0.012)	0.104 (0.034)
Mean	33.2	40.5	2.50	1.61	1.23	0.094 (0.003)	0.134 (0.012)

a : Numerical codes as in Fig. 1.

b : Number of individuals in the sample.

Table 2. 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 populations ( $F_{IS}$ ), and proportion of total genetic diversity partitioned among populations ( $G_{ST}$ ) of *P. fauriana*.

Locus	$H_T$	$H_S$	$F_{IT}$	$F_{IS}$	$G_{ST}$
<i>Per-1</i>	0.454	0.431	0.298	0.259	0.052
<i>Acp</i>	0.492	0.474	0.265	0.237	0.037
<i>Skd-1</i>	0.225	0.190	0.515	0.425	0.156*
<i>Pgd-1</i>	0.388	0.365	0.376	0.338	0.058
<i>ldh-2</i>	0.419	0.384	0.405	0.355	0.077
<i>Mdh-1</i>	0.104	0.098	0.263	0.218	0.058
<i>Got-2</i>	0.264	0.254	0.236	0.205	0.039
<i>Fe-1</i>	0.458	0.444	0.384	0.365	0.030
<i>Fe-2</i>	0.114	0.104	0.317	0.250	0.090*
<i>Pgm-1</i>	0.163	0.147	0.413	0.353	0.094*
<i>Me</i>	0.035	0.029	0.491	0.380	0.177*
<i>Odh</i>	0.021	0.018	0.278	0.188	0.111*
Mean	0.261	0.245	0.353	0.298	0.082*

\* $p < 0.05$ .

allozyme variation was among populations (Table 2). Values of genetic distance (D) were below 0.02 except in pairs involving populations 11 and 2. The estimates of gene flow based on  $G_{ST}$  was moderate among Korean populations of *P. fauriana* ( $Nm = 2.81$ ). The estimate of inter-population gene flow using only one rare allele frequency was 0.41. Genetic identity values among pairs of populations range from 0.978 to 0.997. The similarity among *P. fauriana* populations can be seen in the UPGMA dendrogram, where total populations cluster at a below genetic distance 0.826 (Fig. 2). The UPGMA and correlation

analysis show very weak correspondence between genetic distance and geographical distance. Only two most isolated populations (1 and 10) give any hint of a relationship between geographic and genetic distance. Data on allele frequencies and fixation indices are too lengthy to include here, but these data are available upon request from authors.

## Discussion

A moderate amount of genetic diversity exists at the

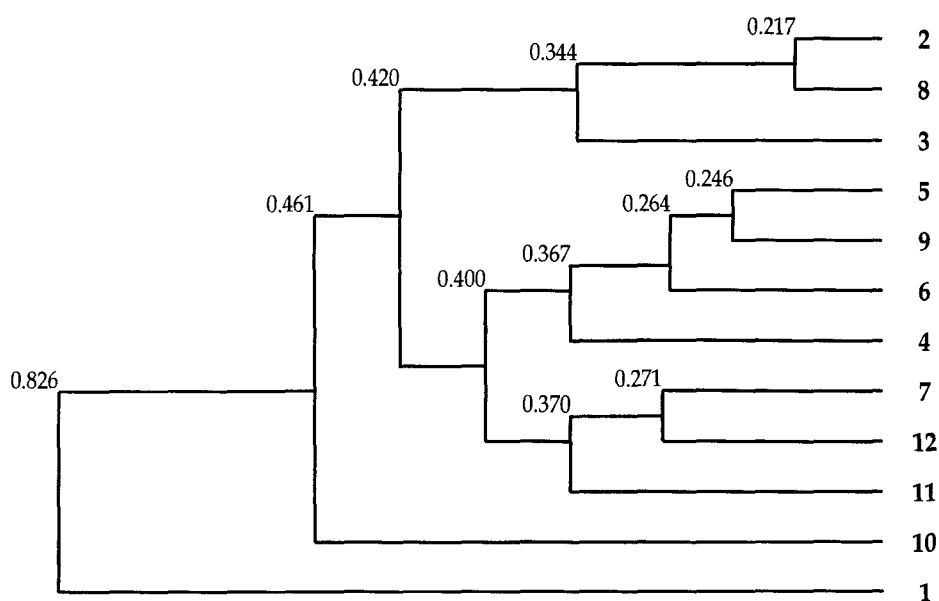


Fig. 2. A dendrogram showing the phylogenetic relationships among the twelve populations of *P. fauriana* based on data of genetic distance obtained by starch gel electrophoresis. Numbers of populations are given in Fig. 1.

species level for *P. fauriana*. For example, its genetic diversity at 0.149 is slightly higher than species with a reproduction mode that is sexual and asexual (0.138), species with a short-lived perennial herbaceous (0.116), but it is similar to species with temperature-zone species (0.146), and it is lower than that of widespread geographic ranges (0.202)[10]. The percent polymorphic loci in the studied sample was 40.5%, which is lower than temperature-zone species (48.5%), and species with widespread geographic ranges (58.9%), but it is similar to species with a reproduction mode that is sexual and asexual (43.8%)[10]. Its average number of alleles per locus was 2.14; this value is lower than that of species with widespread geographic ranges (2.29), but it is higher than those of species with a reproduction mode that is sexual and asexual (1.69) and short-lived perennial herbaceous (1.70)[10]. These comparisons suggest that genetic diversity levels of *P. fauriana* are as high as its associates, the temperature-zone species. It is most interesting to note its levels of genetic diversity are comparable to other species with the same reproductive mode (both sexual and asexual). Ellstrand and Roose[5], 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[5] about the levels of genetic diversity. Although *P. fauriana* is similar to that of woody species, its genetic diversity is much higher than that of herbaceous.

The relatively high level of genetic variation found in *P. fauriana* 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[9,10]. Widely distributed plant species tend to maintain more variation than more narrowly distributed species. Although *P. fauriana* in Korea is distributed patchily, the species is wide geographic ranges of the Northern Hemisphere including East Asia. Actually, Asian regions such as China, Korea, Japan, and Siberian are well known for various other species. Second, the breeding systems of a species is an important determinant of variability at both the species and population levels. *P. monor* has a tall style and 5 short stamens. The length of style is about twice of that of stamen. *P. fauriana* is predominantly an outcrossing, insect-pollinated species. This combination is well-known to be associated with high

levels of allozyme variation[2,7,8]. In addition, vegetative reproduction and spread can also affect the genetic structure of populations[15]. Cook[3] 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. Furthermore, *P. fauriana* in Korea could be characterized as weedy. 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[5]. 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[12] have also argued that physiological independence among ramets may maintain genetic diversity by buffering clones against localized, patch specific selection forces. Third, short-lived perennial species, like *P. fauriana*, generally maintains relatively higher levels of variation than annuals. The observation of *P. fauriana* examined revealed that the plants with old rhizomes possible had been harvested for domestic medicine for at least several hundred years. As populations of *P. fauriana* are older, opportunities for the accumulation of mutations should be high [13]. Fourth, the reproduction type of *P. fauriana* is an important role of genetic variability. Sexual reproduction could act to enhance the genetic variation and asexual reproduction could maintain the enhanced genetic variation. *P. fauriana* commonly reproduces by sexually produced seeds. But, *P. fauriana* usually propagates by asexually produced rhizomes when several strong environmental disadvantages influenced on the habitats of this species. Stigma of *P. fauriana* is exsected. It has been suggested that exsected anthers are disadvantaged by heavy rainfall whereby pollen may be lost before it can be collected by a pollinator[25]. Of course, exsected stigma may be more difficulty to receive pollen from short stamens. Since large flowers are presumable more costly to make and the benefit of wider flowers must saturate at very high pollinator visiting rates, the optimal corolla width is expected to be flower where pollinators are more abundant[25]. Unfortunately, the flower width of *P. fauriana* is small and the color of flower is pinkish white. Therefore flowers of this species fewer visitors.

Nei *et al.*[18] have shown that the reduction in average heterozygosity per locus depends not only on the size of

the population bottleneck, but also on the subsequent rate of population growth. If population growth is reduced, reduction in average heterozygosity is large, even given a small number of founder. Some population sizes in Korea have a tendency to decrease gradually because of several artificial factors such as using of medicine, construction of Buddhist temples, and burial grounds. It is a tradition in Korea for Buddhist temples and tombs to be constructed in the forest. Regardless of growth rate, however, populations undergoing bottlenecks tend to lose low frequency alleles, reducing polymorphism and the number of alleles per polymorphic locus [8].

Considering the factors mentioned above (small population sizes and the species' low frequency), our indirect estimate of gene flow  $Nm$  (2.81) is moderate.  $Nm$  values greater than 1 are considered high enough to counteract the effects of genetic drift or major factor in *P. fauriana* populations. Although  $Nm$  estimates, which are derived from  $G_{ST}$ , can be affected by other factors (e.g. selection, drift, and mutation), the gene flow estimate is probably caused by seed dispersal via wind. In Korea, *P. fauriana* inhabits understory *Pinus*-, *Larix*-dominated forest. This might be attributable to their growth strategies such as winter-seed dispersal and vegetative reproduction. It is difficult to pollinate by insect in dense forest. But, in late fall and early winter, numerous light seeds of *P. fauriana* are spread over a deciduous forest by wind.

In addition, significant differences were found in allele frequencies between populations for all fourteen polymorphic loci. Mean genetic identity between populations ( $I = 0.990$ ) was somewhat above the mean identity ( $I = 0.945$ ) reported by Gottlieb [8] for 22 species and Crawford ( $I = 0.946$ ) reported for 32 species [4]. It is unclear how the populations are genetically homogeneous. It is highly probable that directional toward genetic uniformity in a relatively homogeneous habitats (i.e. mountain habitats and shaded ground) is thought to be operated among Korean populations of *P. fauriana*.

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**초록 : 한국내 주걱노루발의 유전적 다양성과 집단구조**

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한국내 주걱노루발의 유전적 다양성과 집단구조를 평가하기 위해 전분 젤 전기영동을 사용하였다. 효소내 다형현상을 나타내는 대립유전자좌위는 57.1%였다. 종 수준(*Hes* = 0.149)과 집단 수준(*Hep* = 0.134)에서 유전적 다양도는 유사한 생활사를 가진 초본류의 평균값에 비해 높았다. 반면에 집단간 분화정도는 비교적 낮았다 (*G<sub>ST</sub>* = 0.082). 열 두 집단내 임의교배에서 편차는 0.298이었다. 간접적으로 평가한 세대당 이주하는 개체수(*N<sub>m</sub>* = 2.81)는 이 종의 한국 집단내 보통 수준을 유지하고 있었다. 고정지수 분석 결과 많은 집단과 대립유전자좌위에서 이형접합체의 결핍이 있었다. 이는 주걱노루발에서 가근의 번식능력과 한국내 조사된 주걱노루발 집단의 크기 감소에 기인한다.