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High levels of genetic variation in Korean populations of *Sasamorpha borealis* (Poaceae)

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Abstract. Genetic and genotypic diversity of Korean populations in *Sasamorpha borealis* (Hack.) Nakai were investigated using allozymes as genetic markers. In Korea, *S. borealis* usually grows on hillsides under pine-oak understory. Many species of bamboos have the intermast period of "mast seeding." After spreading by extensive rhizomes for a specific period, nearly all adults in one area produce wind-pollinated flowers, set large quantities of seeds, and die. This study was undertaken to infer relationships between levels of genetic diversity and the reproductive biology of the species. Populations of *S. borealis* maintain high levels of genetic diversity: 51% of the loci examined were polymorphic and of mean genetic diversity (H_{eP} = 0.219). The mean number of multilocus genotypes per population was 18.4, and the mean genotypic diversity index (D_G) was 0.720. However, 31% of the total genetic variation was found among populations (G_{ST} = 0.310). Allele frequencies for all loci examined differed significantly among populations ($p < 0.001$). Average genetic identity for all pairs of populations was 0.833 (SD = 0.046). Indirect estimates of the number of migrants per generation (*Nm*) were 0.56 (calculated from G_{ST}) and 0.20 (calculated from the mean frequency of ten private alleles). Several biological and ecological traits found in *S. borealis* (widespread geographical distribution, long-lived habit, clonal reproduction with relatively high genotypic diversity, wind-pollinated breeding system, death of adults bearing large quantities of seeds, probable low gene flow among populations, selection for heterozyous genotypes in some of the sampled populations, the patterns of recolonization, effects of genetic drift, and local selective forces) may have played roles in shaping the population genetic structure of the species.

Keywords: Allozymes; Clonal diversity; Genetic diversity; Mast seeding; *Sasamorpha borealis*; Selection.

Introduction

Electrophoretic techniques for the study of clonal plants provide powerful genetic markers for recognizing individual plant genotypes (Berg and Hamrick, 1997). This approach has made it possible to better understand the spatial distributions of clones and the genotype diversity maintained within populations. According to a thorough review of studies of clonal plants (Ellstrand and Roose, 1987), species with predominantly vegetative reproduction generally have lower levels of genetic diversity than species that successfully produce progeny solely by sexual reproduction. Previous studies have revealed that vegetative reproduction and spread have a marked effect on the genetic structure of populations. As Eriksson (1993) pointed out, however, mechanisms for the maintenance of genetic variation in clonal plants are still controversial. For example, several results indicate that clonal reproduction could retard the loss of genetic diversity within populations because species with independent ramets could reduce the possibility of genet death (e.g., Parker and Hamrick, 1992; Berg and Hamrick, 1994; Lokker et al., 1994; Kim and Chung, 1995a,b; Mayers et al., 1998; Chung and Chung, 1999; Chung and Epperson, 1999). Others showed that clonal reproduction may act as an enhancer of genetic drift by reducing the effective size of local populations (e.g., Pleasants and Wendel, 1989; Bayer, 1990; Murawski and Hamrick, 1990; Aspinwall and Christian, 1992; Chung, 1994; Chung and Kang, 1996; Yeeh et al., 1996). Since the relationship between genetic diversity and mode of reproduction remains unclear, further study of clonal plants is called for.

According to a previous review of bamboo biology (Janzen, 1976), many of the more common Asian species spread by rhizomes for a species-specific period (e.g., *Sasa tessellata* has an intermast period of > 115 years). After reaching a specific period, most Asian bamboos produce wind-pollinated flowers, synchronously set large quantities of seed ("mast seeding"), and die (Janzen, 1976). The biology of bamboos may be of interest to plant population biologists. Here we report levels and partitioning of allozyme diversity within and among populations and the extent of clonal reproduction within populations of *Sasamorpha borealis* (Hack.) Nakai (Poaceae), a small bamboo. *Sasamorpha borealis* is widely distributed in the Korean peninsula and Japanese archipelago. In Korea, populations of *S. borealis* are large and commonly found on hillsides under pine-oak understory. Unfortunately, information on reproductive biology of the study species (e.g., the exact period of masting and the range of synchronization of the masting period in Korea) is not available.

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Materials and Methods

Population Samples

A total of 446 leaf samples were collected from ten populations of *S. borealis* in Korea (Figure 1). Population samples of 18 to 73 were employed. Population codes and sample sizes are given in Table 1. Because the species exhibits extensive clonal growth, samples were collected randomly at intervals of > 5m within patch or population to avoid biasing 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.

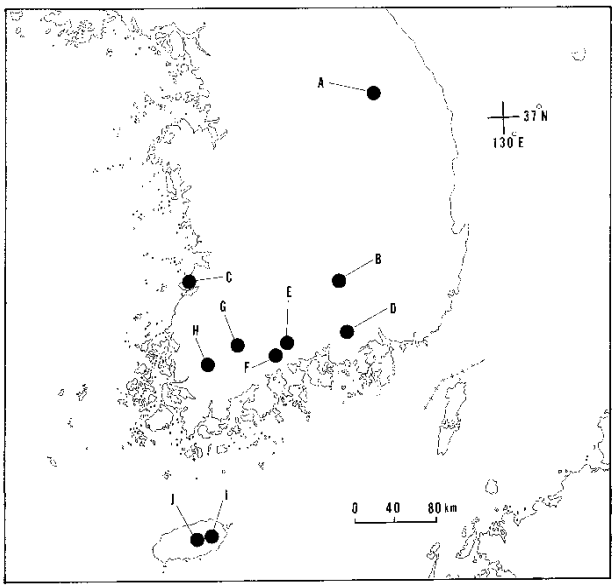

Figure 1. The location of the ten populations in Korea examined in this study (alphabetic codes as in Table 1).

Enzyme Extraction and Electrophoresis

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 and were stored at -70°C until needed for analysis. Electrophoresis was performed using 10.5% starch gels. Fourteen putative loci for *S. borealis* from nine enzyme systems were resolved using a Poulik buffer system, a modification (Haufler, 1985) of Soltis et al. (1983) system 6. The nine enzyme systems were acid phosphatase (ACPH), diaphorase (DIA), fluorescent esterase (FE), glutamate dehydrogenase (GDH), leucine aminopeptidase (LAP), peroxidase (PER), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), and triosephosphate isomerase (TPI). Enzyme staining followed protocols of Cheliak and Pitel (1984) for DIA and Soltis et al. (1983) for all others. Putative loci were designated sequentially, with the most anodally migrating isozyme designated 1, the next 2, etc. Likewise, alleles were designated sequentially with the most anodally migrating alleles designated a. 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 other isozyme studies in plants, as documented by Weeden and Wendel (1989).

Data Analyses

A locus was considered polymorphic if two or more alleles were detected, regardless of their frequencies. Five standard 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 polymorphic locus (AP), mean number of alleles per locus (A), effective number of alleles per locus (A_e),

Table 1. Summary of allozyme variation and clonal diversity for 14 loci within ten populations of *Sasamorpha borealis*[a].

Pop[b]	AL[c]	N[d]	P	AP	A	A_e	H_o (SD)	H_e (SD)	G	G/N	D_G	PG
A	950	27	42.86	2.00	1.43	1.39	0.378 (0.025)	0.200 (0.065)	4	0.148	0.556	0.593
B	480	57	64.29	2.56	2.00	1.39	0.262 (0.016)	0.227 (0.056)	38	0.667	0.978	0.123
C	20	44	35.71	2.00	1.36	1.24	0.227 (0.017)	0.125 (0.056)	3	0.068	0.342	0.795
D	350	73	57.14	2.00	1.57	1.55	0.500 (0.016)	0.281 (0.068)	2	0.027	0.106	0.862
E	450	32	50.00	2.29	1.64	1.42	0.362 (0.023)	0.222 (0.064)	15	0.469	0.938	0.156
F	430	65	57.14	2.50	1.86	1.35	0.237 (0.014)	0.209 (0.055)	32	0.492	0.514	0.185
G	320	57	64.29	2.33	1.86	1.49	0.251 (0.015)	0.270 (0.058)	42	0.737	0.983	0.105
H	300	32	57.14	2.13	1.64	1.47	0.333 (0.022)	0.245 (0.065)	24	0.750	0.976	0.125
I	750	18	35.71	2.40	1.50	1.38	0.294 (0.029)	0.183 (0.068)	8	0.444	0.883	0.222
J	1000	41	50.00	2.14	1.57	1.44	0.331 (0.020)	0.231 (0.066)	16	0.390	0.920	0.220
Mean		44.6	51.43	2.23	1.64	1.41	0.317 (0.006)	0.219 (0.020)	18.4	0.419	0.720	0.339

[a]Abbreviations: P, percentage of polymorphic loci; AP, mean number of alleles per polymorphic locus; A, mean number of alleles per locus; A_e, effective number of alleles per locus; H_o, observed heterozygosity; H_e, Hardy-Weinberg expected heterozygosity or genetic diversity; G, number of multilocus genotypes; D_G, multilocus genotypic diversity indices; G/N, number of genotypes per population samples ("proportion of distinguishable genotypes" per population); PG, probability of the most common multilocus genotype.
[b]Alphabetic codes as in Figure 1.
[c]Altitude (m).
[d]Sample size.

and gene diversity (H_e) (Berg and Hamrick, 1997). Subscripts refer to species (s) or population (p) level parameters.

Because *S. borealis* reproduces vegetatively, we assessed the amount of clonal diversity within and among populations. The first measure of clonal diversity we used was the "proportion of distinguishable genotypes" (Ellstrand and Roose, 1987). This is simply G/N, where G is the number of distinct genotypes in a population and N is the number of individuals sampled. The second measure was the probability of getting the most common genotype by chance in each population (PG). The third measure of multilocus genotype diversity (D_G) was calculated as a modification (Pielou, 1969) of the Simpson index: $D_G = 1 - \Sigma \{[n_i(n_i-1)]/[N(N-1)]\}$, where n_i is the number of individuals of genotype i and N is the total number of individuals in the population. Finally, for comparisons of genotype diversity among populations, numbers of "widespread genotypes" (genotype occurring in more than 75% of the populations) and "local genotypes" (genotypes occurring in only one population) were counted (Ellstrand and Roose, 1987).

Nei's (1973, 1977) 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. In addition, a chi-square statistic was used to detect significant differences in allele frequencies among populations for each locus (Workman and Niswander, 1970). Nei's (1972) genetic identity (I) was calculated for each pairwise combination of populations. We used NTSYS (Rohlf, 1988) to conduct a cluster analysis on genetic identities via the unweighted pairwise groups method using arithmetic average (UPGMA).

Two indirect estimates of gene flow were calculated. One estimate of *Nm* (the number of migrants per generation) was calculated based on F_{ST}, (equivalent to G_{ST}) as calculated in the study (Wright, 1951). The second estimate was based on the average frequency of private alleles (Slatkin, 1985; Barton and Slatkin, 1986).

Results

For *Sasamorpha borealis*, ten of the 14 scoreable loci were polymorphic in at least one population. *Gdh*, *Per-2*, *Pgi-1*, and *Tpi-1* were monomorphic in all ten populations. High levels of genetic variation within populations (Table 1) and the sample as a whole were observed: P_P and P_S of 51.4% and 71%, AP_P and AP_S of 1.64 and 3.60, and A_{eP} and A_{eS} of 1.41 and 1.74, and H_{eP} and H_{eS} of 0.219 and 0.332.

The number of multilocus genotypes in populations ranged from four to 42 (mean = 18.4), indicating that all populations were comprised of multiple genotypes. The proportion of resolved "distinguishable genotypes" (G/N) ranged from 0.027 to 0.750 with a mean of 0.419. The probability of getting the most common genotype by chance (PG) in each population ranged from 0.105 to 0.862 with a mean of 0.339. Genotype diversity indices (D_G) ranged from 0.106 to 0.983 with a mean of 0.720 (Table 1). Level of genotype diversity among populations was high. One hundred eight-four multilocus genotypes were found among the 446 samples from the ten populations. All multilocus genotypes were "local genotypes".

Significant differences in allele frequencies among populations were found for all ten polymorphic loci ($p < 0.001$ in each case). The G_{ST} values ranged from 0.089 for *Pgi-3* to 0.597 for *Pgm-2* (Table 2), and on average, about 69% of the total variation in the species was common to all populations. In addition, ten private alleles were found in five populations: A (*Dia*^{e}, 0.500), B (*Acph*^{b}, 0,018; *Lap*^{a,e}, 0.035, 0.079; *Tpi-2*^{c}, 0.018), D (*Lap*^{b}, 0.500), E (*Fe*^{c}, 0.016), G (*Pgm-1*^{c}, 0.009), and I (*Acph*^{a}, 0.389; *Fe*^{a}, 0.083). The indirect estimate of gene flow based on the mean G_{ST} was low (*Nm* = 0.56) and similar to the estimate based on private alleles (*Nm* = 0.20). Average genetic identity for all pairs of populations was low (I = 0.834, SD = 0.046).

Genetic structure among populations was also evaluated by testing whether genetic relatedness of neighboring populations was greater than expected by chance.

Table 2. Nei's (1973,1977) statistics of genetic diversity for ten polymorphic loci in *Sasamorpha borealis*[a].

Locus	H_T	H_S	D_{ST}	G_{ST}
Acph	0.2304	0.1357	0.0947	0.4109***
Dia	0.4790	0.3812	0.0979	0.2043***
Fe	0.6245	0.4190	0.2055	0.3290***
Lap	0.5253	0.4209	0.1045	0.1988***
Per-1	0.3154	0.2108	0.1046	0.3315***
Pgi-2	0.5468	0.3385	0.2083	0.3809***
Pgi-3	0.4873	0.4441	0.0433	0.0888***
Pgm-1	0.2315	0.1538	0.0777	0.3355***
Pgm-2	0.7095	0.2859	0.4236	0.5971***
Tpi-2	0.4926	0.3806	0.1120	0.2274***
Average	0.4642	0.3171	0.1472	0.3104

[a]Abbreviations: H_T, total genetic diversity; H_S, genetic diversity within populations; D_{ST}, genetic diversity among populations; G_{ST}, proportion of the total genetic diversity partitioned among populations. A chi-square test for allele frequency heterogeneity between populations: *** = $p < 0.001$.

Three correlation matrices were constructed comparing each pair of populations; the physical distances between populations, pairwise values of Nei's genetic distance, and pairwise F_{ST} (= G_{ST}) values (Slatkin, 1993). The Mantel Z test (carried out using NTSYS) showed no correlation in either of the two pairs of matrices (physical distances vs. Nei's genetic distance, $r = 0.074$, $p >> 0.05$; physical distances vs. pairwise F_{ST} values, $r = 0.193$, $p >> 0.05$). Again, the UPGMA phenogram shows very weak correspondence between genetic and geographic distance (Figure 2).

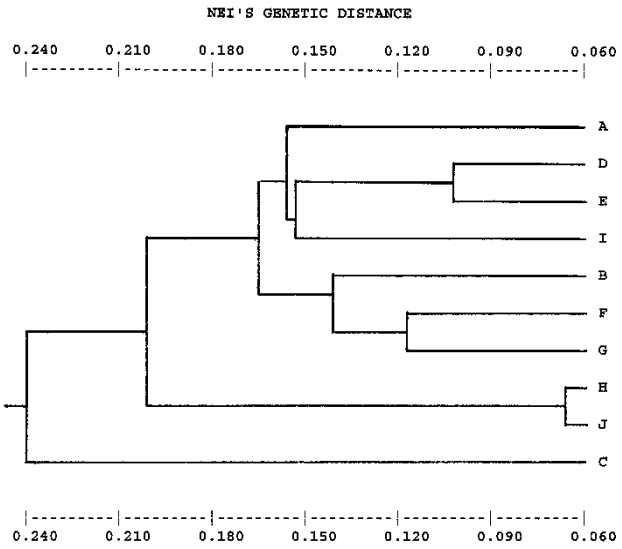

Figure 2. Phenogram from UPGMA cluster analysis based on Nei's (1972) genetic distance between the ten populations of *Sasamorpha borealis*.

Discussion

The species level parameters are more useful because population level values are influenced by both the level of variation in the species as a whole as well as how that variation is distributed among the populations (Berg and Hamrick, 1997). The levels of genetic variation found in *S. borealis* sampled were high in relation to the mean values of long-lived herbaceous perennials. According to a recent review of plant allozyme literature (Hamrick and Godt, 1989), long-lived herbaceous perennials ($N = 4$) have a mean percent polymorphic loci (P_S) of 39.6%, mean number of alleles per locus (A_S) of 1.42, mean effective number of alleles per locus (A_{eS}) of 1.28, and mean genetic diversity (H_{eS}) of 0.205. For *S. borealis* P_S is 71%, A_S is 2.86, A_{eS} is 1.74; and H_{eS} is 0.332. The H_T values (Table 2) for all the polymorphic loci are quite high indicating rather even allele frequencies from the pooled values. This is unusual since usually for most species there are at least a few loci with very common alleles (i.e., > 0.95).

Why was genetic diversity in populations of *S. borealis* so high? Usually, the combined traits of breeding system and geographical distribution are correlated significantly with levels of genetic diversity within populations (Hamrick and Godt, 1989). Populations of outcrossing, wind-pollinated species have considerably higher levels of genetic diversity than selfing species and animal-pollinated species with mixed mating systems (i.e., partially selfed, partially outcrossed) (Hamrick and Godt, 1989). Bamboos are apparently wind-pollinated since they have inflorescences like those of other grasses (Janzen, 1976). Plant species with geographically widespread distributions usually tend to maintain higher levels of allozyme diversity than plants with more restricted ranges (Karron et al., 1988). *Sasamorpha borealis* is widely distributed in Japan and Korea.

Clonal reproduction could also affect the levels of genetic diversity and population genetic structure of plant populations (Cook, 1983, 1985). The average genotypic diversity index for *S. borealis* is higher ($D_G = 0.72$) than the average (0.62) reported by Ellstrand and Roose (1987) in their review of genotypic diversity in clonal plants. The mean "proportion of distinguishable genotypes" per population for *S. borealis* is also higher (0.42 vs. 0.17). Population D had the highest value of H_e (0.281), but the lowest values of G (2), G/N (0.027), and D_G (0.106). This was caused by the abundance of two multilocus genotypes which are heterozygous at seven out of ten polymorphic loci. Population G had the highest G, G/N, and D_G (42, 0.737, and 0.983, respectively), but as expected, it also had the lowest PG (0.105).

In every population but population G the level of observed heterozygosity (H_o) was higher than the expected heterozygosity (H_e). In fact there is a trend in the data (Table 1): the more genotypes that are observed, the closer the H_o and H_e values become, i.e., those populations with few genotypes have a large excess of heterozygotes (Spearman rank correlation, $r_s = -0.903$, $p < 0.001$). This may indicate the existence of selection for heterozygous genotypes in these populations. The abundance of ramets with a high frequency of heterozygous genotypes at several loci in some of the sampled populations (e.g., populations A, C, D, and I) is responsible for the high levels of allozyme diversity in *S. borealis*.

Chung and Kang (1994) stressed the importance of high fecundities for maintaining high genetic diversity in plant populations. The adult mast-seeding bamboos usually die after bearing numerous seeds in a mast year to remove the intense shade that they often cast (Nicholson, 1922) or to decrease competition with large numbers of their own seedings (Janzen, 1976). As *S. borealis* has a relatively long, branched rhizome, independent ramets could reduce the probability of genet death. These factors may also be important for *S. borealis* maintaining high levels of allozyme variation.

The degree of population differentiation observed in *S. borealis* was higher than those of plants with similar life history characteristics (reviewed in Hamrick and Godt, 1989). Long-lived herbaceous perennials ($N = 2$, $G_{ST} = 0.213$), species with widespread geographic range ($N = 87$, $G_{ST} = 0.213$), and those with sexual and asexual mode of reproduction ($N = 54$, $G_{ST} = 0.213$) have lower mean G_{ST} values than *S. borealis* ($G_{ST} = 0.310$). This is supported

by low mean genetic identities for each pairwise combination of populations (mean I = 0.834). In addition, significant differences were found in allele frequencies among populations for all nine polymorphic loci ($p < 0.001$). Genotypic diversity among populations was large. No "widespread genotypes" were observed. In addition, all multilocus genotypes were "local genotypes." These data suggest that the present populations might have been founded from sexually produced seed rather than by asexual fragmentation and dispersal of preexisting clones. The high G_{ST} value suggests that gene flow among populations is low. Indirect estimates of the number of migrants per generation (*Nm*) were 0.56, calculated from G_{ST}, and 0.20, calculated from the mean frequency of ten private alleles.

Other explanations for the high G_{ST} value, however, could be suggested. It is probable that populations become established and reestablished by an infrequent reproductive event. Most or all of the adult plants flower and then die to be replaced by seedlings. If the population is reestablished from only a few seedlings, the resulting adult population will consist of only a few reproductive adults and experience a genetic bottleneck. Such a bottleneck could also develop if several seedlings become established but only a few genets survive. Thus, it may be the pattern of recolonization rather than gene flow that has produced the large population structure observed. In addition, the relatively high G_{ST} value observed may have resulted in part from the fact that some of the sampled populations have very few genetically distinct individuals. Thus, regardless of the sample size these low number of genets could cause elevated G_{ST} values. The mean G_{ST} value (0.209) based on six populations (populations B, E, F, G, and J) with higher numbers of multilocus genotypes (>15) was lower than that for all populations (0.310).

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韓國 *Sasamorpha borealis* (Poaceae) 族群的高度遺傳變異

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利用異源酵素 (allozyme) 作爲遺傳標誌來研究探討韓國 *Sasamorpha borealis* (Hack.) 族群之遺傳及基因型歧異性 (genotypic diversity)，在韓國 *S. borealis* 通常生長於山腹位於松樹一橡樹下層。很多種竹子都有產生種子的時期，當經過廣泛的地下莖生長散佈一段時期後，同一區域內幾乎所有的成株都會產生風授粉過的花，並結大量的種子，然後死亡。本研究主要探討種的遺傳歧異性與生殖生物學間的關係。*S. borealis* 族群維持相當高的遺傳歧異性：約 51% 檢試的基因座是多型性的且其平均遺傳歧異性爲 Hep = 0.219，每一族群之多基因座基因型的平均數目爲 18.4，平均基因型歧異性指數 (D_G) 爲 0.720 。然而族群間 (G_{ST} = 0.310) 約有 31% 的遺傳變異，不同族群間 (P<0.001) 所有檢試的基因座其對偶基因頻率有極顯著的差異，其所有比對後的平均遺傳同一性 (average genetic identity) 約爲 0.833 (SD = 0.046)，間接估算每代間移動者的數目約爲 0.56（從 G_{ST} 上計算）及 0.20（從每十個對偶基因的平均頻率上計算）。*S. borealis* 之幾個生物學及生態學上的性狀（廣泛的地質上分佈、長期存留的棲息地、具高度基因型歧異性的營養系繁殖、風授粉的育種系統、成株死亡時產生大量的種子、可能的低的族群間遺傳流動 (genetic flow)、某些取樣族群中異源基因型的篩選、再移殖的型式、遺傳漂變 (genetic drift) 的效應、及局部的篩選力量）或許對於種之族群遺傳結構之形成扮演重要角色。

關鍵詞：異源酵素；營養系歧異性；遺傳歧異性；果實內結成種子；*Sasamorpha borealis*；篩選。