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Genetic Variation and Population Structure of *Carex breviculmis* (Cyperaceae) in Korea

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We determined the genetic diversity and population structures of *Carex breviculmis* (Cyperaceae) populations in Korea, using genetic variations at 23 allozyme loci. *C. breviculmis* is a long-lived herbaceous species that is widely distributed in eastern Asia. A high level of genetic variation was found in 15 populations. Twelve enzymes revealed 23 loci, of which 11 were polymorphic (47.8%). Genetic diversity at the speciesand population levels were 0.174 and 0.146, respectively. Total genetic diversity (H_T = 0.363) and within-population genetic diversity (H_S = 0.346) were high, whereas the extent of the population divergence was relatively low (G_{ST} = 0.063). Deviation from random mating (F_{IS}) within the 15 populations was 0.206. An indirect estimate of the number of migrants per generation (Nm = 3.69) indicated that gene flow was extensive among Korean populations of this species. Analysis of fixation indices revealed a substantial heterozygote deficiency in some populations and at some loci. Genetic identity between populations was high, exceeding 0.956.

Keywords: *Carex breviculmis*, genetic diversity, population structure

The genus *Carex* is one of the largest (>2000 species) and most widespread of the flowering-plant genera. This group of perennials occurs throughout the world in moist habitats (Reznicek, 1990). Although cosmopolitan, most species are temperately distributed, with centers of diversity in North America and eastern Asia (Ball, 1990; Reznicek, 1990; Naczi, 1992; Starr et al., 1999). *Carex breviculmis* R. Brown is a long-lived herb found mainly in the deciduous and coniferous forests of Korea, China, and Japan. It can reproduce either clonally or sexually via monoecious flowers. Rhizomes generally are horizontal, with shallow elongations or prostrate stem-rooting at the nodes. Plants are covered with scale-like modified leaves, and are upturned at their apices. Buds in the axils of the scales may grow into aboveground stems.

Stems of *C. breviculmis* are used to produce mats, straw ropes, and materials for mud brick. In addition, the fibrous root systems form extensive networks in the soil, which makes this species an economically important tool for preventing soil erosion. This particular property is exploited during the development of effective watersheds, stabilizing the soil along fragile field embankments, deforested areas, and in places prone to mud slides.

Despite its global distribution and ecological importance, detailed studies of genetic variation are not available for most *Carex* species in eastern Asia (Starr et al., 1999). These include approximately 348 species in Korea and Japan. However, genetic diversity has been studied in northern rhizomatous *Carex* species (McClintock and Waterway, 1993; Vellend and Waterway, 1999). The objectives of our study were to estimate how much allozyme diversity is maintained in the species, and to describe how genetic variation is distributed within and among populations. In addition, we compared the genetic diversity and population structure of *C. breviculmis* with plant species having similar life-history characteristics.

MATERIALS AND METHODS

Sampling Procedure and Enzyme Electrophoresis

C. breviculmis was collected from 15 populations in Korea, from 1997 to 1999. More than 50 plants (one

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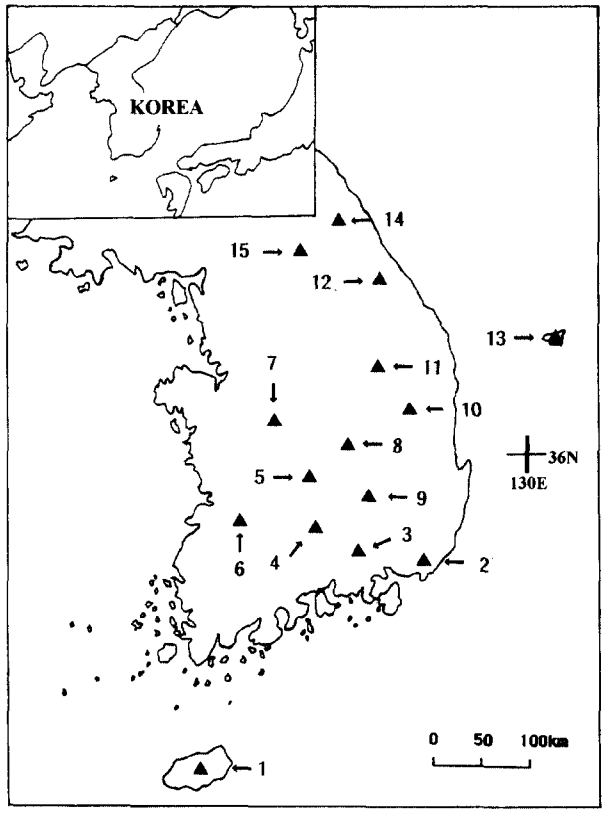

Figure 1. Collection sites for populations of *C. breviculmis* for isozyme analysis. **1**, Mt. Hanla, Cheju Island; **2**, Changjen-dong, Kymjeung-gu, Pusan-ci; **3**, Chisu-myen, Chinju-ci, Gyeongsangnam-do; **4**, Yongjeung-myen, Kure-gun, Chonllanam-do; **5**, Mt. Naechang, Cheungup-ci; Chonllabuk-do; **6**, Kaenae-myen, Changsu-gun, Chonllabuk-do; **7**, Mt. Muju, Muju-gun, Chonllabuk-do; **8**, Mt. Keroung, Yengi-gun, Chungcheungnam-do; **9**, Mt. Kaya, Hachen-gun, Gyeongsangnam-do; **10**, Mt. Chuyoang, Chungsong-gun, Gyeongsangbuk-do; **11**, Imha-myen, Andong-ci, Gyeongsangbuk-do; **12**, Mt. Odae, Yangyang-gun, Kangwon-do; **13**, Mt. Seuninbong, Ulreung-gun, Gyeongsangbuk-do; **14**, Mt. Seolak, Sokcho-ci, Kangwon-do; **15**, Sabuck-myen, Chunsung-gun, Kangwon-do.

leaf per plant) were sampled from each population (Fig. 1). To avoid including individuals from the same rhizome, the distance between the selected individuals was about 5 m.

The procedures for homogenization, starch gel electrophoresis, and enzyme assay were those described by Soltis et al. (1983). Leaves were homogenized by mechanical grinding to release enzymes from cell and organellar membranes, using a Tris-HCl grinding buffer-PVP solution. Electrophoresis was performed with an 11% starch gel. Twelve enzyme systems were assayed: acid phosphatase (ACP), fluorescent esterase (FE), leucine aminopeptidase (LAP), menadione reductase (MNR), and peroxidase (PER) were resolved on System 9 of Soltis et al. (1983); glucose phosphate isomerase (GPI), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), 6-phosphogluconate dehydrogenase (PGD), phosphoglucomutase (PGM), and shikimate dehydrogenase (SKD) on Soltis et al.'s System 10.

Data Analysis

For enzymes resolving in more than one zone of activity, the most anodal isozyme was arbitrarily designated '1' and subsequent isozymes were sequentially assigned higher numbers. Likewise, alleles were designated sequentially, with the most anodally migrating allozyme labeled 'a', and progressively slower forms 'b', 'c', etc.

A locus was considered polymorphic if two or more alleles were detected, regardless of their frequencies. Using a computer program developed by Loveless and Schnabel (personal communication), we estimated the following standard genetic parameters: percentage of polymorphic loci (P), mean number of alleles per locus (A), effective number of alleles per locus (A_E), number of alleles per polymorphic locus (A_P), and gene diversity (H_E) (Hamrick et al., 1992).

The observed heterozygosity (H_O) was compared with the Hardy-Weinberg expected value, using Wright's fixation index (F) or inbreeding coefficients (Wright, 1965). These indices were tested for deviation from zero by χ^2-statistics, following the guidelines of Li and Horvitz (1953). 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. The G_{ST} coefficient estimates relative population differentiation. In addition, the χ^2-statistics helped 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 ran a PC-SAS program (SAS Institute Inc., 1989) for 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 (1965) 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 all samples and within populations, respectively. Deviations of F_{IT} and F_{IS} from zero were tested with χ^2-statistics (Li and Horvitz, 1953). In the context of multiallelic

loci, F_{ST} was denoted as G_{ST} (Nei, 1973). The mating system of *C. breviculmis* was estimated using the equation Fe = (1-t)/(1+t) (Falconer, 1981), which assumes a mating system in equilibrium (Godt and Hamrick, 1993). The estimate of *Nm* (the number of migrants per generation) was based on G_{ST} (Wright, 1951). Absolute population differentiations (D_M) were calculated according to Nei's (1973) statistics. The correlation between geographical and genetic distance was tested with a modified Mantel's test (Smouse et al., 1986).

Table 1. Allozyme variation within 15 populations of *C. breviculmis*.

Pop[a]	N[b]	*P*	A_P	*A*	A_E	H_{POP}	H_{EP}
1	52	43.48	2.30	1.57	1.32	0.140	0.163
2	55	43.48	2.30	1.57	1.34	0.150	0.165
3	60	43.48	2.30	1.57	1.29	0.143	0.149
4	60	43.48	2.40	1.61	1.35	0.152	0.169
5	50	43.48	2.30	1.57	1.29	0.144	0.151
6	60	43.48	2.40	1.61	1.32	0.148	0.164
7	60	39.13	2.33	1.52	1.29	0.139	0.150
8	55	39.13	2.33	1.52	1.26	0.140	0.147
9	50	34.78	2.75	1.61	1.28	0.127	0.142
10	50	39.13	2.22	1.48	1.26	0.120	0.139
11	55	39.13	2.44	1.57	1.29	0.107	0.149
12	50	34.78	2.25	1.43	1.23	0.101	0.125
13	50	30.43	2.14	1.35	1.23	0.079	0.126
14	60	30.43	2.29	1.39	1.23	0.086	0.117
15	50	34.78	2.13	1.39	1.25	0.096	0.133
Mean		38.84	2.33	1.52	1.28	0.125	0.146
SD		2.61	0.15	0.09	0.04	0.003	0.012
Species		47.83	2.82	1.87	1.33	–	0.174

Percentage of polymorphic loci (*P*), mean number of alleles per polymorphic population (A_P), mean number of alleles per locus (*A*), effective number of alleles per locus (Ae), observed heterozygosity (H_{OP}), and Hardy-Weinberg expected heterozygosity or genetic diversity (H_{EP}).
[a]Abbreviation codes as in Figure 1; [b]Number of individuals in the sample.

RESULTS

A high level of genetic variation was found in the 15 *C. breviculmis* populations. Eleven of the 23 loci (47.8%) showed polymorphism in at least one population, while the remaining 12 loci (*Acp, Fe-2, Gpi-1, Idh-1, Lap-2, Mdh-2, Mdh-3, Me, Mnr-1, Per-3, Pgd-1*, and *Pgm-2*) were monomorphic in all populations. An average of 36.0% of the loci was polymorphic within populations, with individual-population values ranging from 13.0 to 47.8% (Table 1). The majority of the polymorphic loci expressed two (*Gpi-2, Per-1, Per-2*, and *Pgm-1*) or three alleles (*Fe-1, Pgd-1, Idh-2, Mdh-1*, and *Lap-1*), whereas the remaining one expressed four (*Skd* and *Mnr-2*).

Across populations, the average number of alleles per locus (*A*) was 1.52, varying from 1.35 for the population with the lowest number of alleles to 1.61 for that with the highest number. The effective numbers of alleles per locus at the species and the population levels were 1.33 and 1.28, respectively. Numbers of alleles per polymorphic locus (A_P) were 2.33 across populations, varying from 2.13 for the population with the lowest number of alleles to 2.75 for that with the highest number. Mean genetic diversity within populations was 0.146. Population 4 had the highest expected diversity (0.169), Population 14 the lowest (0.117). In addition, genetic distance and geographic distance were highly correlated ($r = 0.66$, $p < 0.05$).

Table 2. Estimates of genetic diversity statistics and 11 polymorphic loci in *C. breviculmis*.

Locus	H_T	H_S	D_{ST}	D_M	F_{IS}	F_{IT}	G_{ST}
Fe-1	0.453	0.448	0.005	0.006	0.052	0.063	0.012
Per-1	0.128	0.109	0.020	0.021	0.292	0.401	0.154*
Per-2	0.425	0.414	0.011	0.011	0.120	0.142	0.025
Pgd-2	0.229	0.210	0.020	0.020	0.183	0.253	0.085
Idh-2	0.454	0.423	0.031	0.033	0.143	0.201	0.068
Mdh-1	0.015	0.013	0.002	0.002	0.484	0.542	0.113*
Skd	0.495	0.477	0.018	0.019	0.100	0.133	0.037
Mnr-2	0.331	0.295	0.036	0.039	0.377	0.445	0.109*
Lap-1	0.614	0.593	0.021	0.022	0.092	0.013	0.034
Pgi-2	0.318	0.294	0.024	0.026	0.512	0.549	0.076
Pgm-1	0.227	0.215	0.013	0.014	0.042	0.096	0.056
Mean	0.363	0.346	0.017	0.018	0.206	0.251	0.063

Total genetic diversity (H_T), genetic diversity within populations (H_S), among populations (D_{ST}), absolute population differentiation (D_M), deviations of genotype frequencies from Hardy-Weinberg expectations over all populations (F_{IT}), within individual population (F_{IS}), and proportion of total genetic diversity partitioned among population (G_{ST}).
* = $p < 0.05$.

Table 3. Wright's fixation indices for 15 populations of *C. breviculmis*.

Pop.	*Fe-1*	*Per-1*	*Per-2*	*Pgd-2*	*Idh-2*	*Mdh-1*	*Skd*	*Mnr-2*	*Lap-1*	*Pgi-2*	*Pgm-1*
1	0.105	0.252	0.406*	0.059	–	0.489***	–0.048	0.086	0.174	0.208	–
2	0.114	0.363*	0.413**	–0.139	0.109	–	–0.033	0.205	0.130	0.278	–0.057
3	0.125	0.269	0.083	–0.117	0.042	–	–0.053	0.292	0.079	0.364	–0.015
4	0.141	0.195	0.029	0.127	0.012	–	–0.038	0.228	0.125	0.369*	–0.073
5	0.029	0.240	0.146	0.055	–0.049	–	–0.192	–0.047	0.075	0.313	–0.039
6	–0.053	0.457**	0.172	0.164	0.039	–	–0.018	0.307	0.081	–0.009	–0.031
7	0.064	–	–0.010	0.081	0.083	–	–0.044	0.244	0.232	–0.080	0.035
8	0.093	–	–0.037	0.017	0.069	–	–0.170	0.209	0.058	0.308*	0.077
9	–0.065	–	0.171	–0.076	0.194	–	–0.042	0.675***	–0.021	0.292**	–
10	0.006	–	–0.188	0.027	0.141	–	0.129	0.655***	–0.072	0.778***	0.299*
11	0.027	–	0.047	0.225	0.092	–	0.446***	0.592***	0.215	0.601***	0.194
12	0.089	–	0.094	0.184	0.185	–	0.036	–0.047	0.221	0.651***	–
13	0.208	–	0.163	0.170	0.441**	–	0.549	–	–	0.775***	0.212
14	0.015	–	0.120	0.229	0.276	–	0.190	–	0.126	1.000***	–
15	0.029	–	0.222	0.044	0.164	–	0.437	–	0.141	1.000***	0.342*

Note: A dash indicates fixed loci. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

F_{IS}, a measure of the deviation from random mating within the 15 populations, was 0.206, ranging from 0.042 for *Pgm-1* to 0.512 for *Gpi-2* (Table 2). The observed significant and positive F_{IS} value (0.206) indicated a significant deficit of heterozygotes in the populations. Analysis of fixation indices, calculated for all polymorphic loci in each population, showed a slight deficiency of heterozygotes relative to Hardy-Weinberg expectations (Table 3). Assuming mating-system equilibrium, the estimated outcrossing rate (t) was 0.658, as calculated from the mean F_{IS} value.

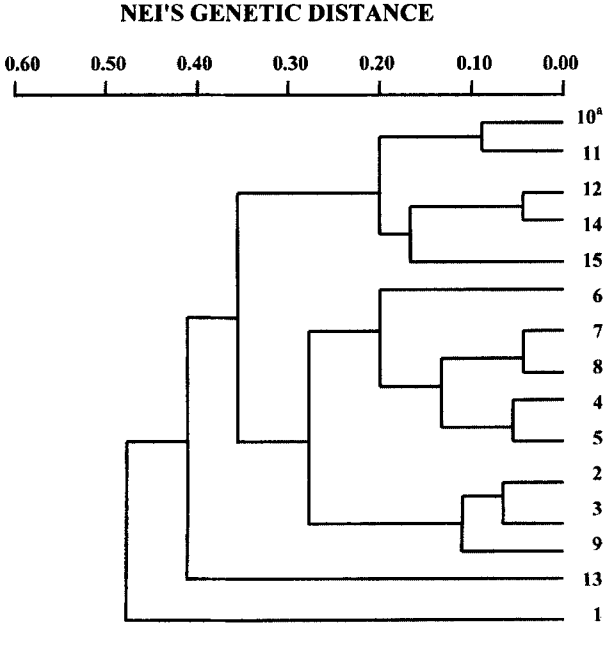

Figure 2. Dendrogram showing the genetic similarity among 15 populations of *C. breviculmis*, based on data of genetic distance obtained by starch gel electrophoresis.
[a]Abbreviation codes as in Figure 1.

Total genetic diversity values (H_T) varied between 0.015 (*Mdh-1*) and 0.614 (*Lap-1*), for an average over all polymorphic loci of 0.363. Interlocus variation in the within-population genetic diversity (H_S) was high (0.346), but the absolute measure of genetic differentiation among populations (D_M) was very low (0.018). On a per-locus basis, the proportion of total genetic variation due to differences among populations (G_{ST}) ranged from 0.014 for *Pgd-2* to 0.154 for *Per-1*, with a mean of 0.063. This indicated that about 6.0% of the total allozyme variation was among populations. The estimate of gene flow, based on G_{ST}, was slightly high among Korean populations of *C. breviculmis* ($Nm = 3.69$). Values of genetic distance (D) were below 0.045. Genetic-identity values among pairs of populations ranged from 0.956 to 0.999. The similarity among *C. breviculmis* populations was evident in the UPGMA dendrogram, where total populations clustered below a genetic distance of 0.490 (Fig. 2).

DISCUSSION

C. breviculmis maintains moderate or greater diversity in populations than does the average plant species. For example, its genetic diversity of 0.174 is higher than that for species with a sexual and asexual reproduction mode (0.138) or for temperate-zone species (0.146). However, its diversity is lower than that of long-lived herbaceous perennials (0.205; Hamrick and Godt, 1989). The percentage of polymorphic loci at the species level was 47.8%. Although

Table 4. Measures of genetic variability for all previously studied northern rhizomatous *Carex* species.

Species	*A*	*P*	H_S	H_T	G_{ST}	*Nm*	Data set	Data source
C. saxatilis	1.6	45	0.146	0.182	0.198	1.01	Ramet	Ford et al., 1991
C. membranacea	1.6	44	0.162	0.199	0.183	1.12	Ramet	Ford et al., 1991
C. rotundata	1.6	44	0.120	0.148	0.184	1.11	Ramet	Ford et al., 1991
C. lasiocarpa	1.6	48	0.226	0.266	0.151	1.41	Genet	McClintock and Waterway, 1993
C. pelllita	1.6	44	0.203	0.248	0.181	1.13	Genet	McClintock and Waterway, 1993
C. bigelowii	1.8	49	0.167	0.180	0.072	3.22	Genet	Jonsson et al., 1996
C. limosa	1.5	42	0.137	0.146	0.063	3.72	Genet	Waterway and McClintock (unpublished data)
C. paupercula	1.2	19	0.068	0.151	0.553	0.20	Ramet	Waterway and McClintock (unpublished data)
C. hondoensis	1.6	42	0.315	0.326	0.043	5.51	Ramet	Huh and Huh, 1998
C. willdenowii	1.5	23	0.148	0.177	0.167	1.25	Ramet	Ford et al., 1998
C. basiantha	1.5	37	0.138	0.156	0.114	1.94	Ramet	Ford et al., 1998
C. superata	1.3	18	0.071	0.072	0.011	22.48	Ramet	Ford et al., 1998
C. rariflora	1.4	32	0.071	0.134	0.467	0.29	Ramet	Vellend and Waterway, 1999
C. breviculmis	1.9	48	0.346	0.363	0.063	3.69	Ramet	Current study
Mean	1.6	38	0.166	0.196	0.175	3.43		

this value is higher than average for species with a reproduction mode that is sexual and asexual (43.8%) and for long-lived herbaceous perennials (39.6%), it is similar to that for temperature-zone species (48.5%; Hamrick and Godt, 1989). In addition, among the northern rhizomatous *Carex* species (Table 4), *C. breviculmis* had the highest H_T value. These comparisons suggest that genetic diversity levels of *C. breviculmis*, as well as *C. hondoensis*, are higher than those of the North American *Carex* species.

The relatively high level of genetic variation found in *C. breviculmis* is consistent with several aspects of its biology. First, the breeding system of a species is an important determinant of variability at both the species and population levels. Typical of the species, flowers of *C. breviculmis* are monoecious and highly reduced (Lee, 1997; Ford et al., 1998), apparently making it a species that is primarily wind-pollinated. Predominantly outcrossing species maintain higher levels of intrapopulation genetic variation than do predominantly inbreeding species (Gottlieb, 1981; Brown, 1989). Second, a perennial species such as *C. breviculmis* generally maintains relatively higher levels of variation than do annuals (Loveless and Hamrick, 1984).

Finally, the reproduction modes of *C. breviculmis* play an important role in genetic variability. Vegetative reproduction and spread can affect the genetic structure of populations (Murawski and Hamrick, 1990). Cook (1983) contended that clonal growth could retard the loss of genetic diversity within populations. *C. breviculmis* can regenerate from fibrous roots when plants are harvested for firewood or otherwise destroyed. Species with independent ramets could spread the risk of mortality, thereby reducing the probability of genet death and preserving genetic diversity (Huh et al., 1999). Hartnett and Bazzaz (1985) have also argued that physiological independence among ramets may maintain genetic diversity by buffering clones against localized, patch-specific selection forces. Sexual reproduction could enhance and maintain genetic variation (Bayer, 1990). *C. breviculmis* reproduces by seed or by vegetative spread. Asexual reproduction assures the stabilization and persistence of a phenotype that is well adapted to the immediate environment (Huh et al., 1996; Huh, 1999).

Compared with the two Korean species, most *Carex* species in North America have much lower within-population genetic diversity and much higher genetic differentiation among populations (except for *C. bigelowii* and *C. limosa*) (Table 4). That is at least partially due to their low abundance and the range of collecting populations. For example, western and eastern populations of *C. rariflora* are more than 1500 km apart. In contrast, the distance between our two most distinct populations was only 500 km (Fig. 1). The correlation between genetic distance and geographic distance was about 56.4% (1- r^2) of the total genetic variations, which further demonstrates that geographically close populations tend to be genetically similar.

Genetic differentiation among populations is principally a function of natural selection, genetic drift, and gene flow via pollen and seed dispersal (Loveless and Hamrick, 1984). For *C. breviculmis*, about 6.3% of the total variation was due to differences among populations (G_{ST} = 0.063). In contrast, the genetic variation in predominantly outcrossed wind-pollinated species averages <10% between populations (Hamrick and Godt, 1989). This low level of genetic differ-

entiation also suggests that gene flow among the population is high ($Nm = 3.69$). Ford et al. (1998) reported that seed dispersal in the *Carex* section contributed more to gene flow than did pollen dispersal, namely because (1) perigynia possess eliosome-like bodies; (2) plants are frequently found on slopes; and (3) morphological adaptations, such as perigynia with long beaks, could favor long-distance dispersal by small mammals (Ford et al., 1998).

Artificial action, such as harvesting materials for mats, straw ropes, and mud brick, is one of the factors that affect high gene flow in Korean *Carex*. Although formal analyses of the mating system of *Cyperaceae* are not available, the floral architecture and the fixation index of *C. breviculmis* suggest that populations of this species typically outcross. A small deficit of heterozygotes was found for *C. breviculmis*, indicating that some selfing or biparental inbreeding may occur, or that plants are intermating and dispersing over a smaller scale than was sampled (i.e., the Wahlund effect).

Ford et al. (1991) reviewed the literature on the genetic structure in the *Carex* complex and presented two contrasting groups. Group 1 is characterized by low levels of intrapopulation genetic variation, such as is found in *C. criticana*, *C. viridula*, *C. gynodynama*, *C. mendocinensis*, and *C. pachystachya* (Bruederle and Fairbrothers, 1986; Waterway, 1990; Bruederle and Jensen, 1991; Whitkus, 1992). Fixation indices are highly positive, suggesting high levels of selfing. Group 2 species, which comprise *C. saxatilis*, *C. membranacea*, *C. rotundata*, *C. lasiocarpa*, and *C. pelllita*, possess similar levels of interspecific variation, but this is apportioned within, rather than between, populations (Ford et al., 1991; McClintock and Waterway, 1993). Their *F* values are close to 0, suggesting higher levels of outcrossing (Ford et al., 1998).

These two patterns of genetic variability might be related to differences in life-history strategies (Ford et al., 1991). Group 1 is characterized by multiple hermaphroditic species or staminate species that are overlapped at the lateral pistillate spikes. They have a casespitose growth habit. Thus, Group 1 is usually self-pollinating. Group 2 species are rhizomatous, with relatively few, unisexual spikes that are widely separated from each other. Culms of this group can be spaced far apart along an elongated rhizome. Therefore, the nearest neighbor may not be from the same individual, thereby increasing the chances for outcrossing (Ford et al., 1998).

In the present study, high levels of variation within populations and low interpopulational differentiation were found in *C. breviculmis*. Short culms within the florescence are crowned in the many long leaves of the same plant. Although it can sprout at the rhizomatous culms, this species never produces long rhizomes. Thus, *C. breviculmis* is more closely related morphologically to the species in Group 2 than in Group 1 (Naczi et al., 1998). However, it should not be included in either group on the basis of genetic variation. For *F* values, 83.7% of fixation indices were positive (Table 3), and 34 (22.8%) of these departed significantly from zero ($p < 0.05$). Twenty-nine of the indices were negative; none was significant.

Genetic diversity in the Korean *Carex* species is the highest of all the *Carex* complexes (Table 4). Therefore, one of our most interesting results was that genetic features in the Korean complex were clearly different from those of the North American species. However, more evidence is needed before the real phenology of *Carex* can be classified.

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