

## Allozyme Variation and Population Structure of *Carex okamotoi* (Cyperaceae), a Korean Endemic Species

Man Kyu Huh\* and Joo Soo Choi

Department of Molecular Biology, Dong-eui University, Busan 614-714, Korea

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The genetic diversity and population structures of fourteen *Carex okamotoi* (Cyperaceae) populations in Korea were determined using genetic variation at 25 allozyme loci. The *Carex okamotoi* species is native to Korea. It is endemic to three mountains (Mt. Taebak, Mt. Sobak, and Mt. Noreong) where it is found at 700~1,500 m above sea level. The percentage of polymorphic loci was 40.0%. Genetic diversity at the species level and at the population level was low ( $H_{ES}=0.106$ ;  $H_{EP}=0.094$ ), and the extent of the population divergence was relatively low ( $G_{ST}=0.082$ ). Measurement of deviation from random mating ( $F_{IS}$ ) within the 14 populations was 0.238. An indirect estimate of the number of migrants per generation was 2.78 ( $Nm=2.78$ ). Analysis of fixation indices revealed a substantial heterozygosity deficiency in some populations and at some loci. Mean genetic identity between populations was 0.986.

**Key words** : *Carex okamotoi*, genetic diversity, population structure

### Introduction

Many plant populations consist of small groups of genetically related individuals rather than randomly arrayed entities of related and unrelated individuals [17]. Genetic variation of plant populations is also distributed nonrandomly, which has many important consequences for the evolutionary dynamics of these species [23].

Species that occur as small isolated patches scattered over large geographic areas may experience significant genetic drift and high levels of population divergence. In contrast, species with large, interconnected populations are expected to maintain higher levels of genetic variation within their populations [7]. However, various studies have shown that asexually reproducing plants can be maintained by variation in the extent of the diversity [3,11]. 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 for plant species which reproduce both sexually and asexually.

The genus *Carex* is a widespread perennial herb occurring throughout the world, in moist temperate habitats [19]. It

is notable that although the Korean species (*C. okamotoi*) is endemic species, this species has much high within-population genetic diversity and much lower genetic differentiation among populations compared with all *Carex* species of North America. *C. okamotoi* reproduces extensively by vegetative rhizomes and potentially by sexually produced seeds. This species is native to Korea. It is endemic to Taebak, Sobak, and Noreong Mountains where it is found at 700~1,500 m above sea level. Leaves of this species are evergreen, basal, 3 ranked, and linear. Flowers are monoecious. Clonal species of *C. okamotoi* is wind-pollinated outcrossing [16]. No specialized seed dispersal mechanisms were known this species. Bracts subtend each flower. The male flower is surrounded with 1 bract and female flower is surrounded with 2 bracts. The pistil is compound of 3 united carpels. Rhizomes are generally horizontal elongated underground or prostrate stem rooting at the nodes, covered with scale-like modified leaves, and upturned at the apex. Buds in the axils of the scales may grow into aboveground stems. Stems of *C. okamotoi* are made into mats, straw ropes, and materials for mud brick. Fibrous root systems of this plant form extensive networks in the soil. Recently, the species has become economically important as a protectant of washout. The objectives of this study are to estimate how much allozyme diversity is maintained in the species and to describe how genetic variation is distributed within and among populations of *C. okamotoi*.

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#### \*Corresponding author

Tel : +82-51-890-1529, Fax : +82-51-890-1521

E-mail : mkhuh@deu.ac.kr

## Materials and Methods

## Sampling procedure

*Carex okamotoi* (Cyperaceae) was collected from fourteen populations in Korea (Fig. 1). Populations of *C. okamotoi* are composed four major groups of the western (GL1 and GL2), southern (PS1~5), central (YO1~3), and eastern (TU1~4) regions. The elevations of the sampling sites were estimated to be: GL 763~822 m, YO 1,054~1,440 m, PS 1,430~1,915 m, and TU 721~1,236 m. In southern below GL1 and northern above TU4 areas, we failed to find the species. Young leaves from more than 35 plants were collected from each population (Table 1). The distance between the selected individuals was about 5 m to avoid inclusion of individuals emanating from the same rhizome. Sampled leaves were stored in plastic bags for several days in a refrigerator until electrophoresis was carried out.

## Enzyme electrophoresis

Enzyme extraction, starch gel electrophoresis and enzyme assay were conducted by following the procedures of Soltis *et al.* [25]. Leaves were homogenized by mechanical grinding to release enzymes from cell and organellar membranes with Tris-HCl grinding buffer-PVP solution as described in Soltis *et al.* [25]. Electrophoresis was performed with a 12.0% starch gel. Twelve enzyme systems were assayed: acid phosphatase

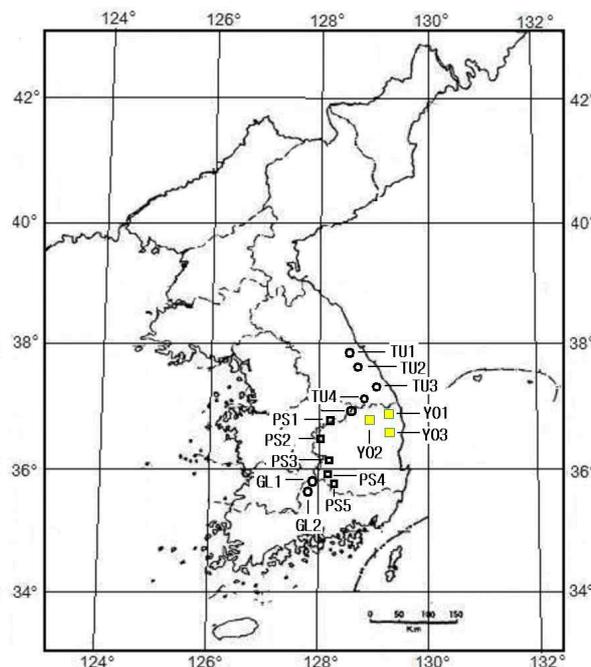


Fig. 1. Collection localities for populations of *C. okamotoi* as source for isozyme analysis. GL1: Bancheon-ri, Sancheong-gun; GL2: Buchun-ri, Hadong-gun; PS1: Goseong-ri, Geesan-gun; PS2: Unheung-ri, Sangju-si, PS3: Sanggeum-ri, Gimcheon-si; PS4: Jisan-ri, Geochang-gun; PS5: Banpo-ri, Hapcheon-gun; TU1: Daechi-ri, Yangnag-gun; TU2: Imgok-ri, Gangneung-si; TU3: Icheon-ri, Samcheok-si; YO1: Geumcheon-ri, Uljin-gun; YO2: Dongmyeon-ri, Bonghwa-gun; Yeong-ri, Yeongdeok-gun.

Table 1. Summary of allozyme variation within fourteen populations of *C. okamotoi*

Pop <sup>a</sup>	N <sup>b</sup>	<i>P</i>	<i>A</i>	<i>A<sub>P</sub></i>	<i>A<sub>E</sub></i>	<i>H<sub>OP</sub></i> (SD)	<i>H<sub>EP</sub></i> (SD)
GL1	35	28.0	1.28	2.00	1.11	0.057 (0.008)	0.079 (0.028)
GL2	35	28.0	1.28	2.00	1.12	0.060 (0.008)	0.080 (0.028)
PS1	35	40.0	1.44	2.10	1.17	0.085 (0.010)	0.113 (0.031)
PS2	36	40.0	1.44	2.10	1.21	0.101 (0.010)	0.130 (0.035)
PS3	39	40.0	1.48	2.20	1.20	0.096 (0.010)	0.125 (0.034)
PS4	37	40.0	1.48	2.20	1.18	0.096 (0.010)	0.121 (0.033)
PS5	38	40.0	1.56	2.40	1.20	0.101 (0.010)	0.125 (0.035)
TU1	37	20.0	1.20	2.00	1.11	0.053 (0.008)	0.069 (0.030)
TU2	36	28.0	1.28	2.00	1.12	0.059 (0.008)	0.080 (0.029)
TU3	35	32.0	1.32	2.00	1.10	0.057 (0.008)	0.073 (0.024)
TU4	35	32.0	1.32	2.00	1.12	0.062 (0.008)	0.083 (0.027)
YO1	36	28.0	1.32	2.14	1.11	0.064 (0.008)	0.076 (0.028)
YO2	35	28.0	1.32	2.14	1.13	0.067 (0.009)	0.083 (0.029)
YO3	35	24.0	1.28	2.17	1.11	0.063 (0.008)	0.073 (0.027)
Mean		32.0	1.36	2.10	1.13	0.073 (0.008)	0.094 (0.008)
Species		40.0	1.60	2.50	1.16	-	0.106

Percentage of polymorphic loci (*P*), mean number of alleles per polymorphic population (*A<sub>P</sub>*), mean number of alleles per locus (*A*), effective number of alleles per locus (*A<sub>E</sub>*), observed heterozygosity (*H<sub>OP</sub>*), and Hardy-Weinberg expected heterozygosity or genetic diversity (*H<sub>EP</sub>*).

<sup>a</sup>: Abbreviation codes as in Fig. 1.

<sup>b</sup>: Number of individuals in the sample.

(ACP), leucine aminopeptidase (LAP), and menadione reductase (MNR), were resolved on System 9 of Soltis *et al.* [25]; glucose phosphate isomerase (GPI), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), 6-phosphogluconate dehydrogenase (PGD), and phosphoglucomutase (PGM) were resolved on System 10 of Soltis *et al.* [25]; fluorescent esterase (FE), peroxidase (PER), and shikimate dehydrogenase (SKD) were resolved on System (morpholine-citrate, pH 6.1) of Clayton and Tretiak [2]. Gels were run in a refrigerated chamber at 4°C. The systems 9 and 10 were run at 150 V for 4.5 hr and at 100 V for 5.5 hr, respectively. Morpholine buffer system was run at 200 V for 4.0 hr. For enzymes resolving in more than one zone of activity, the most anodal isozyme is arbitrarily designated '1' and subsequent isozymes were sequentially assigned higher numbers. Likewise, alleles were designated alphabetically with the most anodally migrating allozyme designated 'a'.

#### Analysis of data

Various standard genetic parameters were estimated using a computer program developed by Loveless and Schnabel (personal communication); percentage of polymorphic loci ( $P$ ), mean number of alleles per locus ( $A$ ), effective number of alleles per locus ( $A_E$ ), the number of alleles per polymorphic locus ( $A_P$ ), and gene diversity ( $H_E$ ) [9]. 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]. 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. In addition,  $\chi^2$ -statistics were used to detect significant differences in allele frequencies among populations for each locus [28]. Nei's genetic identity was calculated for each pairwise combination of populations [20].

The genetic structure within and among populations was also evaluated using Wright's  $F$ -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 [29]. In the context of multiallelic loci  $F_{ST}$  is denoted  $G_{ST}$  [21]. The mating system of *C. okamotoi* was estimated using the equation  $Fe=(1-f)/(1+f)$  [10] which assumes mating system in equilibrium. Two indirect estimates of gene flow were

calculated. One estimate of  $Nm$  (the number of migrants per generation) was based on  $G_{ST}$  [29] and the other estimate was based on the average frequency of rare alleles found in only one population [23]. Correlation between geographical and genetic distance was tested using Mantel's test as advocated by Smouse *et al.* [24].

A phenetic relationship was constructed by the neighbor-joining (NJ) method [22] using the NEIGHBOR program in PHYLIP version 3.57 [4].

## Results

#### Genetic diversity

Ten of the 25 loci (40.0%) showed detectable polymorphism in at least one population, while the remaining fourteen loci (*Acp*, *Fe-2*, *Gpi-1*, *Idh-1*, *Lap-1*, *Lap-2*, *Mdh-2*, *Mdh-3*, *Mdh-4*, *Me*, *Mnr-1*, *Per-3*, *Per-4*, *Pgd-2*, and *Pgm-2*) were monomorphic in all populations (Table 1). Significant differences were found in allele frequencies between regions for 3 loci (*Fe-1*, *Per-2*, and *Mdh-1*). In YO region, *Fe-1* is monomorphic while others are polymorphic. In GL and TU regions, *Per-2* locus is also the same trend. In PS region, *Mdh-1* was shown polymorphic. An average of 32.0% of the loci was polymorphic within populations, with individual population values ranging from 20.0% to 40.0%. The average number of alleles per locus ( $A$ ) was 1.36 across populations, varying from 1.20 for the population with the lowest number of alleles and 1.56 for the population with the highest number of alleles. The effective number of alleles per locus ( $A_E$ ) was similar at the species and the population level ( $A_{ES}=1.16$ ;  $A_{EP}=1.14$ ). The number of alleles per polymorphic locus ( $A_P$ ) was 2.10 across populations, varying from 2.00 for the population with the lowest number of alleles and 2.40 for the population with the highest number of alleles. The mean genetic diversity within populations was 0.094. The Population PS2 had the highest expected diversity (0.130), while the Population TU1 the lowest (0.069). In addition, the correlation between genetic distance and geographic distance was low ( $r=0.51$ ,  $p<0.05$ ), and indicated that geographically close populations tended to be genetically similar and about 74% of the variation in genetic distance was caused by unknown factors other than distance.

#### Genetic structure

$F_{IS}$  a measure of the deviation from random mating within the 14 populations, was 0.238, and ranged from 0.081

(*Per-2*) to 0.428 for *Pgd-1* (Table 2). The observed significant and positive  $F_{IS}$  value (0.238) 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 slight deficiency of heterozygotes relative to Hardy-Weinberg expectations (Table 3). For example, on an individual locus level, 92.0% of fixation indices were positive (103/112), and 28 of those departed significantly from zero ( $p < 0.05$ ). Eight of indices were negative, indicating an excess of heterozygotes, but none departed significantly. Assuming mating system equilibrium, the outcrossing rate ( $\hat{t}$ ) which calculated from the mean  $F_{IS}$  value was estimated to be 0.616. Total genetic diversity values ( $H_T$ ) varied between 0.076 (*Per-1*) and 0.449 (*Fe-2*), giving an average over

all polymorphic loci of 0.265. The interlocus variation in within population genetic diversity ( $H_S$ ) was high (0.240). On a per locus basis, the proportion of total genetic variation due to differences among populations ( $G_{ST}$ ) ranged from 0.007 for *Pgi-2* to 0.341 for *Fe-1* with a mean of 0.082, indicating 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. okamotoi* ( $N_m = 2.78$ ). Values of genetic distance (D) were below 0.033. Genetic identity values among pairs of populations range from 0.967 to 0.999. The similarity among *C. okamotoi* populations can be seen in the NJ dendrogram, where total populations cluster at a genetic distance below 0.032 (Fig. 2). Four major clusters of *C. okamotoi* regions, corresponding to

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

Locus	$H_T$	$H_S$	$D_{ST}$	$F_{IS}$	$F_{IT}$	$G_{ST}$
<i>Fe-1</i>	0.449	0.296	0.153	0.256	0.510	0.341***
<i>Per-1</i>	0.076	0.068	0.008	0.290	0.364	0.104
<i>Per-2</i>	0.185	0.165	0.020	0.081	0.179	0.107*
<i>Pgd-1</i>	0.234	0.212	0.022	0.428	0.481	0.092
<i>Idh-2</i>	0.339	0.330	0.010	0.180	0.204	0.029
<i>Mdh-1</i>	0.207	0.201	0.007	0.348	0.369	0.033
<i>Skd</i>	0.172	0.164	0.008	0.302	0.335	0.047
<i>Mnr-2</i>	0.291	0.287	0.005	0.218	0.230	0.015
<i>Pgi-2</i>	0.394	0.392	0.003	0.094	0.101	0.007
<i>Pgm-1</i>	0.298	0.284	0.015	0.185	0.223	0.049
Mean	0.265	0.240	0.025	0.238	0.300	0.082

Total genetic diversity ( $H_T$ ), genetic diversity within populations ( $H_S$ ), among populations ( $D_{ST}$ ), 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 ( $G_{ST}$ ).

\*  $p < 0.05$ ; \*\*  $p < 0.001$ .

Table 3. Wright's fixation indices for fourteen populations of *C. okamotoi*

Pop.	<i>Fe-1</i>	<i>Per-1</i>	<i>Per-2</i>	<i>Pgd-1</i>	<i>Idh-2</i>	<i>Mdh-1</i>	<i>Skd</i>	<i>Mnr-2</i>	<i>Pgi-2</i>	<i>Pgm-1</i>
GL1	0.205	-	-	0.460**	0.100	0.463**	0.440**	0.228	0.162	-
GL2	0.120	-	-	0.497**	0.125	0.307	0.444**	0.156	0.181	-
PS1	0.206	0.427*	0.211	0.528**	0.215	0.263	0.218	0.256	0.074	0.433*
PS2	0.232	0.357	0.153	0.508**	0.252	0.205	-0.062	0.352*	-0.006	0.217
PS3	0.263	0.367*	0.234	0.335	0.226	0.163	0.252	0.184	0.294	0.201
PS4	0.217	0.228	0.292	0.433*	0.155	0.372*	0.361*	0.189	0.123	0.115
PS5	0.274	-0.027	-0.180	0.360**	0.124	0.430**	0.372*	0.193	-0.023	0.310
TU1	0.359	-	-	-	0.446	-	-	0.274	0.027	0.263
TU2	0.317	-	-	0.534**	-0.061	-	0.280	0.261	0.106	0.263
TU3	0.415*	-	-	0.358*	0.438	0.356	0.218	0.216	0.034	0.015
TU4	0.311	-	-	0.278	0.344	0.533***	0.444**	0.165	0.004	0.201
YO1	-	-	-0.024	-	0.028	0.278	0.367*	0.120	0.224	0.296
YO2	-	-	0.112	-	0.213	0.438*	0.278	0.256	0.201	0.120
YO3	-	-	0.034	-	0.189	0.372	-	0.348*	0.120	-0.024

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

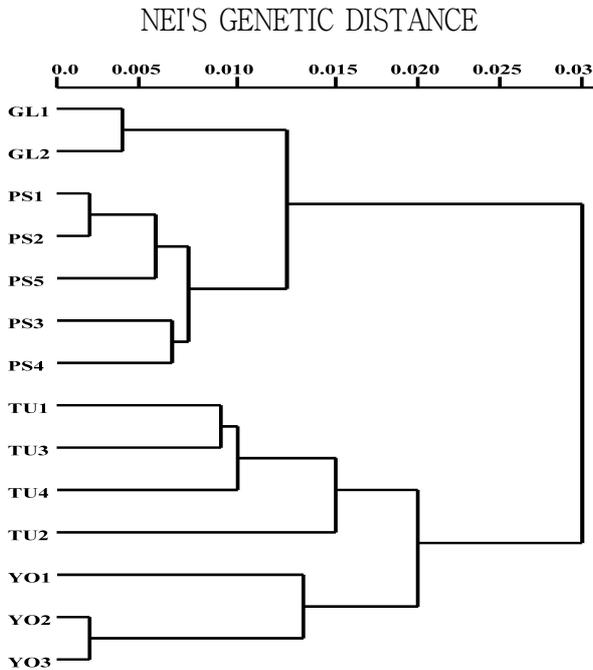


Fig. 2. A dendrogram showing the genetic similarity among the fourteen populations of *C. okamotoi*, based on data of genetic distance obtained by starch gel electrophoresis.

groups of the western, southern, central, and eastern regions, revealed by the tree. Within the four major clades, associated between distance and genetic divergence were somewhat more tenuous, the two spatially closest pairs of regions (central and eastern regions) exhibited the highest genetic identities. Within the four east populations, TU2 forms a long cluster with three populations. The same trend is observed in the YO region.

### Discussion

#### Genetic diversity and genetic structure in *Carex* complex

*C. okamotoi* maintains lower diversity in populations than the average plant species. For example, its genetic diversity at 0.106 is lower than that of temperate-zone species (0.146), species with a reproduction mode that is sexual and asexual (0.138), and species are short-lived herbaceous perennials (0.116) [9]. Other genetic diversity parameters of *C. okamotoi* were also lower than those of species with similar ecological and history traits. These comparisons suggest that genetic diversity levels of *C. okamotoi* are lower than that of its associates, the temperate-zone species. In addition, among three Korean *Carex* species for which there are allozyme data (Table 5), *C. okamotoi* had the lowest total genetic diversity ( $H_T$ ). Rare and/or endemic species may become genetically

depauperate, historically or prehistorically, owing to small population size, to strong directional selection for specialized niches, or to a combination of these factors [27]. Karron [14] reported that widespread species had a greater number of polymorphic loci than restricted congeners. For all 9 genera cited by Karron where number of alleles polymorphic loci was calculated, widespread species had more alleles than restricted species. The differences in genetic variability among *Carex honoensis*, *Carex humilis* var. *nana*, and *C. okamotoi* are consistent with these trends (Table 5).

*Carex* species of North America except *Carex lasiocarpa* have much lower genetic diversity compared with the tree Korean species (Table 5). That is due at least in part to low abundance and the ranges of collecting populations. For example, in *C. rariflora*, the range of western population and eastern population is more than 1500 km. But, in this study, the distance between the two most distinct populations is only 250 km (Fig. 1). Vellend and Waterway [26] suggest that geographic separation is more important than local selection in determining the pattern of genetic diversity in *Carex rariflora*.

Most northern *Carex* species usually occur in the relatively narrow transition zone between wetland and forest or tundra [26]. Thus, the sizes of populations are relatively small. Thus, low gene flow among isolated populations due to genetic drift and genetic differentiation among populations [7].

These *Carex* are mostly species with relatively large ranges in the North Temperature zones of Asia, North America, and Europe. The northern North American regions were heavily impacted by Pleistocene glaciation, with much of their areas covered by ice [26]. Four regions of *C. okamotoi* are isolated, which might result from life history traits and historical events (e.g. the Holocene Paleoclimatic history) of the species. Holocene uplifts created the present Sobak-Noreong Mountains [15]. When North Korea was covered with glaciers throughout the Pleistocene, the South Korea did not experience strong glaciation history period at that time. It is highly probable that the glacial remnants of these *Carex* species after the glacial warm to the warm Southern Korea Peninsula [15]. Population bottlenecks regulating from founder effects during postglacial colonization may explain the lower genetic diversity in *C. okamotoi* compared with *C. honoensis* and *C. humilis* var. *nana* in Korea.

Genetic differentiation among populations is principally a function of natural selection, genetic drift, and gene flow among populations via pollen and seed dispersal [23]. Of

Table 4. Estimates of gene flow and genetic diversity within regions

Region	P(I) <sup>a</sup>	Nm(S) <sup>b</sup>	Nm(W) <sup>c</sup>	H <sub>T</sub>	H <sub>S</sub>	G <sub>ST</sub>
GL	0.000(0)	1.00	7.26	0.409	0.407	0.009
PS	0.083(2)	0.61	6.54	0.432	0.429	0.035
TU	0.049(1)	1.46	2.15	0.418	0.418	0.029
YO	0.032(1)	2.98	5.56	0.408	0.408	0.014

<sup>a</sup>: P(I) is the mean frequencies of 'private' allele.

<sup>b</sup>: Estimates based on Slatkin's equation.

<sup>c</sup>: Estimates based on Wright's equation.

Table 5. Measures of genetic variability for all previously studied northern rhizomatous *Carex* species

Species	A	P	H <sub>S</sub>	H <sub>T</sub>	G <sub>ST</sub>	Nm	Data set	Data source
<i>C. saxatilis</i>	1.6	45	0.146	0.182	0.198	1.01	Ramet	Ford <i>et al.</i> [5]
<i>C. membranacea</i>	1.6	44	0.162	0.199	0.183	1.12	Ramet	Ford <i>et al.</i> [5]
<i>C. rotundata</i>	1.6	44	0.120	0.148	0.184	1.11	Ramet	Ford <i>et al.</i> [5]
<i>C. lasiocarpa</i>	1.6	48	0.226	0.266	0.151	1.41	Genet	McClintock and Waterway [19]
<i>C. pellita</i>	1.6	44	0.203	0.248	0.181	1.13	Genet	McClintock and Waterway [19]
<i>C. bigelowii</i>	1.8	49	0.167	0.180	0.072	3.22	Genet	Jonsson <i>et al.</i> [13]
<i>C. limosa</i>	1.5	42	0.137	0.146	0.063	3.72	Genet	Waterway and McClintock (unpublished data)
<i>C. paupercula</i>	1.2	19	0.068	0.151	0.553	0.20	Ramet	Waterway and McClintock (unpublished data)
<i>C. hondoensis</i>	1.6	42	0.315	0.326	0.043	5.51	Ramet	Huh [12]
<i>C. rariflora</i>	1.4	32	0.071	0.134	0.467	0.29	Ramet	Vellend and Waterway [26]
<i>C. humilis</i> var. <i>nana</i>	1.4	48	0.256	0.274	0.068	3.42	Ramet	Huh [12]
<i>C. okamotai</i>	1.6	40	0.240	0.265	0.082	2.78	Ramet	This study
Mean	1.5	41	0.171	0.210	0.187	2.24		

the total variation observed in *C. okamotai* about 6.0% was due to differences among populations ( $G_{ST}=0.082$ ). Predominantly wind-pollinated outcrossing species have on an average less than 10 % of the genetic variation between populations [9]. This low level of genetic differentiation also suggests that gene flow among population is high ( $Nm=2.78$ ). The indirect outcrossing estimate reported in this paper ( $t=0.616$ ) suggests a mixed-mating system in *C. okamotai*.

#### Genetic variation among regions

Plants cannot move to more favorable patches. New genets by break of physically connections among ramets occur in near parental plants. Some genets move considerably with collapse of cliffs. But gene flow by clonal spread may only occur in short distance. Although many of sampled *C. okamotai* populations were small and appear to be relatively isolated, indirect estimates of gene flow for the four regions were moderate.  $Nm$  ranged from 2.15 for TU region to 7.26 for GL region (Table 4). The estimate of gene flow might be an overestimate for the species as a whole because two of the sampled populations (GL1 and GL2) were consisted of many subpopulations within 25 km. Only two pop-

ulations of region GL had the fixed allele on the *Pgm-1* locus. Because two populations of region GL found along the same side (East) of the Sobak Mountain, the Mountain is not acted as a barrier of gene flow of two populations. Other regions are same trend. *C. okamotai* can be found growing erratically anywhere from the top of the mountains to valley from elevations of 700 m to 1,500 m. Physical barriers are always possible between populations. The  $G_{ST}$  ranging from 0.009 to 0.035 indicates the physical barrier does not restrict gene flow between populations within regions (Table 4).

In any case, the main agent of gene flow in this species is probably seed or pollen dispersal by wind. Perigynia possess an eliasome-like body, suggesting that species may be ant dispersal [8]. Plants are frequently found on slopes, often in association with streams. In these areas perigynia may fall downslope and could be carried some distance by snow or water. Morphological adaptations, such as perigynia with long serrated beaks, could favor long-distance by small mammals [5,6].

Fragmentation of historically contiguous populations is expected to lead to genetic drift and increased levels of population divergence as population sizes become smaller and gene flow decrease [18]. However, the low allelic diversity

and heterozygosity within populations and the low  $G_{ST}$  estimates show that genetic drift has not yet had a major influence on Korean *C. okamotoi* populations. Species with naturally isolated, patchy distributions might be expected to exhibit similar genetic structure. In this regard, the pattern of genetic divergence between *C. okamotoi* regions is notable. Analyses of subpopulation structure within four of the regions indicated that, on an average, 2.2% of the total genetic diversity for each region was found between subpopulations (Table 4).

Although *C. okamotoi* maintains low level of genetic diversity, the small isolated populations that currently characterize the Korean populations of *C. okamotoi* coupled with the recent increased destruction of natural habitats for the construction of skiing grounds. It may result in further species extinction of rare species as well as erosion of genetic variation in the future. Thus, environmental factor (a basin between two high mountains) plays a role as an endemic species. The basin is a region of heavy snow in winter and very hot in summer owing to high mountains. In addition, for a student of adaptive evolution it is natural to seek out an extreme environment with strong selection pressures where conspicuous adaptations are likely to be found, such as alpine habits [1,13]. *C. okamotoi* is endemic to three ranges of mountains (Fig. 1), plants must withstand the full force of the winter gales and the abrasive action of drifting snow. Therefore, *C. okamotoi* has sparsely herbaceous stems each terminated by a leaf rosette and strong roots.

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초록 : 한국 내 국부적으로 분포하는 지리사초의 알로자임 변이와 집단구조

허만규\* · 최주수

(동의대학교 분자생물학과)

한국 내 국부적으로 분포하는 지리사초(*Carex okamotoi*)의 14집단에 대해 유전적 다양성과 집단구조를 실시하였다. 이 식물은 세 산맥(태백산맥, 소백산맥, 노령산맥)의 고지대(700~1,500 m)에 제한적으로 자생한다. 다형성을 나타내는 대립유전자좌위는 40.0%였다. 종 수준과 집단 수준에서 유전적 다양성은 낮았으며( $H_{ES}=0.106$ ;  $H_{EF}=0.094$ ), 집단간 분화도 낮았다( $G_{ST}=0.082$ ). 14집단에 대한 임의 교배로부터 산출한 편차는 0.238이었다. 간접적으로 산출한 세대간 이주하는 개체들의 수는 2.78이었다( $N_{m}=2.78$ ). 고정지수 분석에서 이형접합체의 실질적 결핍이 일부 집단과 대립유전자좌위에서 나타났다. 집단간 유전적 동질성은 평균 0.986이었다.