ISSN : 1225-9918
Journal of Life Science **2010** Vol. 20. No. 9. 1287~1293 DOI : 10.5352/JLS.2010.20.9.1287

Spatial Autocorrelation Analysis of *Carex humilis* on Mt. Giri by RAPD

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Received May 19, 2010 / Accepted September 3, 2010

The spatial distribution of alleles and geographical distances of a *Carex humilis* population on Mt. Giri in Korea were studied. A total of 102 DNA fragments (bands) were found among 107 plants. Among these 102 bands, 48 (47.1%) bands were polymorphic. In a simple variability of subpopulations by the percentage of polymorphic bands, distances I and V exhibited the lowest variation (16.7%). Distance VIII showed the highest variation (22.6%). The total genetic diversity (*H*) was 0.076 across species. Class VIII had the highest *H* (0.093), while class I had the lowest (0.063). Genetic similarity of individuals was found among subpopulations at up to a scale of 60 m distance, and this was partly due to a combination of alleles. Within the Mt. Giri population, a strong spatial structure was observed for RAPD markers, indicating a very low amount of migration among subpopulations and that the distribution of individual genotypes of a given population was clumped. The present study demonstrated that analysis of RAPD markers could be successfully used to study the spatial and genetic structures of *C. humilis*.

Key words : Genetic similarity, *Carex humilis*, spatial autocorrelation

Introduction

Ecologists and plant evolutionary biologists have recognized for a long time that plants are not distributed at random within communities but are rather clustered in distinct patches [7,9]. Environmental heterogeneity is usually cited as playing a critical role in determining the spatial structure, but colonization patterns and stochastic events affecting establishment and mortality are also important [5]. This nonrandom distribution of genetic variation is often referred to as the genetic structure of a population. The genetic structure is an integral part of the process of population genetics [8]. Population structure interacts with a number of factors: microenvironmental heterogeneity, mortality due to stochastic events [21], and mating systems that feature limited dispersal of seed or pollen [8]. Very important factors are gene flow and natural selection, both of which influence spatial patterns of the genetic structure [6,15].

In theory, genetic differentiation over short distances may occur either as a result of spatially variable selection or localized genetic drift, provided that gene flow is sufficiently restricted [5]. Indirect evidence for genetic correlations between neighboring plants has been obtained from data on mating systems [8]. Localized seed and pollen dispersals produce family clusters within these populations [6]. Several studies have revealed decreased seed set and seed survivorship from mating between genetically similar near-neighbors, which has been interpreted as inbreeding depression [20].

Carex humilis Leyss. (Cyperaceae) is a widespread herb occurring throughout cool and temperate regions of the Northern Hemisphere and is abundant in Korea [10]. The fibrous root system of this plant forms extensive networks in the soil. Thus, the species has become economically important in preventing soil erosion along slopes of new roads, deforested areas, and in places prone to mudslide. *C. humilis* can reproduce extensively by vegetative rhizomes and potentially by sexually produced seeds. Rhizomes are generally very short, prostate stems rooting at the nodes, and conversed with scale-like leaves. Continuous vegetative reproduction could act to retard the loss of genetic diversity and the risk of genet death within populations.

Random amplified polymorphic DNA (RAPD) assay has been useful in determining genetic relationships among closely related species [2,4]. RAPD is used widely owing in PCR development in stalk classification techniques because RAPD analysis is quick than other molecule creature school register techniques and an experiment is inexpensive than other techniques [18]. Therefore, we achieved a judged experiment to be useful analyzing population structure of *C. humilis* by RAPD analysis. This study could provide a dis-

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tance information among plants in order to avoid including individuals with a common genetic lineage when *C. humilis* is used for preventing soil erosion and mudslide.

The purpose of this paper was to describe a statistical analysis for detecting a species association which is valid even when the assumption of within- species spatial randomness is violated. Two questions are addressed: 1) is there a spatial genetic structure within this population? and 2) if so, what is the spatial pattern of variation and is it the same for all loci?

Materials and Methods

Sampling procedure

The study was conducted from July to September 2009, at Daepo-ri, Samjang-myeon on Mt. Giri, Gyeongsangnam-do, and involved mapping and sampling of a total of 107 individuals from 12 subpopulations (Fig. 1). One leaves per plant was sampled. Tissues gathered from natural subpopulations were labeled and then refrigerated in plastic bags, until enzyme extraction was carried out. The distance between selected individuals was about 2.0 m, to avoid including those with a common lineage by vegetative reproduction.

RAPD analysis

RAPD analysis was performed using 60 different 10-base oligonucleotide primers (OPB-01~20, OPC-01~20, and OPD-01~20, series) purchased from Operon Technologies (Alameda, CA). A mixture contained 20 ng of template DNA, 0.5 pmol of a random primer, 10x PCR buffer (20 mM Tris-HCl pH 8.4, 50 mM KCl), 3.0 mM $MgCl_2$, 2.5 μM each dNTP, and 1.0 U *Taq* DNA polymerase. Amplification was performed in a Gene Amp PCR System 9700 (Perkin Elmer - Applied Biosystems), which was programmed for initially denatured at 94°C for 30 sec, followed by 30 cycles of 30 sec of denaturation at 94°C, 30 sec of annealing at 40°C and 60 sec of primer extension at 72°C, then finally incubated at 72°C for 7 min. The amplification products were separated by electrophoresis on 1.5% agarose gels, stained with ethidium bromide, and photographed under UV light using Polaroid 667 film. A 100 bp ladder DNA marker (Pharmacia) was used in the end of gels for the estimation of fragment size.

Statistical measures of genetic variation

All RAPD bands were scored manually and only unambiguously scored bands were used in the analyses. In addition, replicate samples were assayed in separate experiments to verify repeatability of results (Table 1). Because RAPD bands are dominant markers, it was assumed that each band corresponded to a single character with two alleles, presence (1) and absence (0) of the band.

The following genetic parameters were calculated using a POPGENE computer program (ver. 1.31) developed by Yeh *et al*. [22]: the percentage of polymorphic loci (P_p) mean numbers of alleles per locus (A), effective number of alleles per locus (A_E), and gene diversity (H).

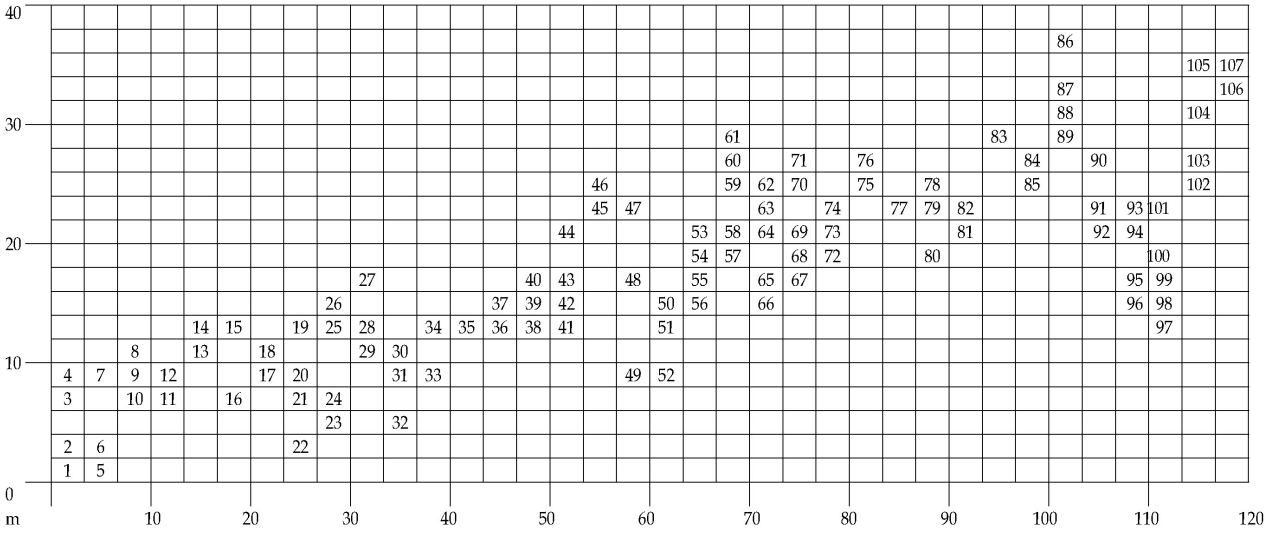

Fig. 1. Distribution of plants across patches within *Carex humilis* on Mt. Giri. All samples are designed with separate numbers. The collection classes are identified by code numbers.

Table 1. Lists of decamer oligonucleotides utilized as primers, their sequences, and associated fragments

Primer	Sequence (5′ to 3′)	No. of fragments detected	No. of *P*p
OPB-01	GTTTCGCTCC	8	4
OPB-02	TGATCCCTGG	7	4
OPB-15	GGAGGGTGTT	10	5
OPC-06	GAACGGACTC	12	4
OPC-11	AAAGCTGCGG	7	2
OPC-13	AAGCCTCGTC	10	3
OPC-18	TGAGTGGGTG	8	6
OPD-02	CGACCCAACC	6	2
OPD-07	TTGGCACGGG	14	5
OPD-09	CTCTGGAGAC	9	4
OPD-13	GGGGTGACGA	11	6
Total		102	45

Analysis of spatial structure

Numerical simulations of previous analyses were performed to investigate the significant differences at various distance scales, i.e., 2.0, 4.0 m, and so on. However, no significant population structure was found within the 10.0-m distance classes by means of Moran's *I*, and a significant population structure was revealed beyond 8.0-m. Thus, the distance classes are 0-10.0 m (class I), 10.0-20.0 m (class II), 20.0-30.0 m (class III), 30.0-40.0 m (class IV), 40.0-50.0 m (class V), 50.0-60.0 m (class VI), 60.0-70.0 m (class VII), 70.0-80.0 m (class VIII), 80.0-90.0 m (class IX), 90.0-100.0 m (class X), 110.0-110.0 m (class XI), and 110.0-120.0 m (class XII). The codes of classes are the same as in the distance classes and are listed Table 2.

The spatial structure of locus variations was quantified by Moran's *I*, a coefficient of spatial autocorrelation (SA) [16]. As applied in this study, Moran's *I* quantifies the genetic similarity of pairs of spatially adjacent individuals relative to the population sample as a whole. The value of *I* ranges between +1 (completely positive autocorrelation, i.e., paired individuals have identical values) and -1 (completely negative autocorrelation).

Pairs of sampled individuals [total number of pairs: (107x106/2=5,671] were classified according to the Euclidian distance, dij, so that class k included dij satisfying k-1<dij<k+1, where k ranges from 1 to 12. The interval for each distance class was 10 m. Moran's *I* statistic for class k was calculated as follows:

$I\ (k)=n\sum i\sum j(i\neq j)WijZiZj/S\sum Zi^2$

where Zi is *pi*-p (p is the average of *pi*); Wij is 1 if the distance between the *i*th and *j*th plants is classified into class k; otherwise, Wij is 0; n is the number of all samples and S is the sum of Wij $\{\sum i\sum j(i\neq j)Wij\}$ in class k. Under the randomization hypothesis, *I*(k) has the expected value u1=-1/(n-1) for all k. Its variance, u2, has been given in Sokal and Oden [16]. Thus, if an allele is randomly distributed for class k, the normalized *I*(k) for the standard normal deviation (SND) for the plant genotype, $g(k)=\{I(k)-u1\}/u2^{1/2}$, asymptotically has a standard normal distribution. Hence, SND g(k) values exceeding 1.96, 2.58, and 3.27 are significant at the probability levels of 0.05, 0.01, and 0.001, respectively.

All pairwise comparisons of geographic and genetic distances among the analyzed individuals were used for the definition of the so-called Fr function [19]. Like Moran's *I*, this function provides a method for investigating spatial autocorrelations, i.e., the correlation between geographic and genetic distances under isolation by the distance model. For every distance class, r, the relative frequency of individuals with an identical haplotype to x is calculated as {Ir(r)}. Then we calculated values of the Fr function as:

$Fr(r)=\{Ir(r)-\sum pi^2\}/(1-\sum pi^2)$

where pi is the relative frequency of haplotype i for the entire populations [3].

Results

Diversity among classes and population structure

The 12 subpopulations were studied with 60 oligonecleotide primers for RAPD analysis. Of the 60 primers, some primers did not give any clear-cut bands, or showed only smeared bands. Seven primers were all monomorphic bands which did not contributed entirely to analyze population structure. Therefore, the data on these primers are omitted from "Results" and "Discussion" in this paper. Amplified 11 primers were analyzed. The number of bands generated by each primer varied from 6 (OPD-02) to 14 (OPD-07), with an average of 9.3 bands per primer. The size of the amplified DNA fragments varied from 320 bp to 2.8 kbp. Totally 102 DNA fragments (bands) were found among 107 plants (Table 1). Among these 102 bands, 48 (47.1%) bands were polymorphic. In a simple variability of intra-subpopulations by the percentage of polymorphic bands, the distances I and V exhibited the lowest variation (16.7%) (Table 2). The distance VIII showed the highest (22.6%) (Table 3). Mean number of alleles per locus (*A*) ranged from 1.167 to 1.226 with a mean of 1.186. The effective number of alleles per locus (A_E) ranged from 1.107 to 1.159. The phenotypic frequency

Table 2. Measurements of genetic variation for *Carex humilis*

Subpopulation	*N*p	*P*p	*A*	A_E	*H*	*I*
I	17	16.67	1.167	1.107	0.063	0.094
II	18	17.65	1.177	1.148	0.079	0.112
III	18	17.65	1.177	1.132	0.073	0.106
IV	19	18.63	1.186	1.132	0.077	0.113
V	17	16.67	1.167	1.118	0.067	0.098
VI	19	18.63	1.186	1.131	0.074	0.109
VII	18	17.65	1.177	1.125	0.073	0.107
VIII	23	22.55	1.226	1.159	0.093	0.136
IX	21	20.59	1.206	1.145	0.082	0.120
X	20	19.61	1.196	1.141	0.079	0.116
XI	19	18.63	1.186	1.126	0.072	0.107
XII	19	18.63	1.186	1.132	0.077	0.113
Mean	19.00	18.63	1.186	1.133	0.076	0.111

The number of polymorphic loci (*N*p), percentage of polymorphism (*P*p), mean number of alleles per locus (*A*), effective number of alleles per locus (A_E), gene diversity (*H*), and Shannon's information index (*I*).

of each band was calculated and used for estimating genetic diversity (*H*) with in 12 subpopulations. The *C. humilis* maintained a low level of genetic diversity for polymorphic primers. The total *H* was 0.076 across species. Class VIII had the highest genetic diversity (0.093), while class I had the lowest (0.063). Shannon's index of phenotypic diversity (*I*) of *C. humilis* ranged from 0.094 to 0.136 with a mean of 0.111.

Analysis of spatial autocorrelation

The spatial autocoefficient, Moran's *I*, for polymorphic loci is presented in Table 3. Moran's *I* of *C. humilis* was positive in 63 of 132 cases (47.7%) and 52.3% was negative. Figs. 2, 3, and 4 showed the distribution of Moran's *I* for *C. humilis* across the distance classes. Most OPB, OPC, and OPD except OPD-13 showed positive Moran's *I* values within distance class VI. Seven primers except four primers (OPB-15, OPC-06, OPD-07, and OPD-09) had negative Moran's *I* values with positive beyond class VII. In *C. humilis*, the population structure of the distribution of alleles consists of a scale of 60.0 m intervals. As a matter of course, All primers had negative Moran's *I* values at classes from VIII to XII. Thus, genetic dissimilarity among pairs of individuals could be found by more than 80 m.

However, no spatial structure of alleles was found for one marker (OPD-09) within the natural population of *C. humilis*.

Separate counts for each type of joined alleles and for each distance class of separation were tested for significant deviation from random expectations by calculating the SND. SND for Moran's *I* of *C. humilis* significantly differed from the

Table 3. Spatial autocorrelation coefficients (Moran's *I*) of 11 loci among 12 subpopulations of *Carex humilis* for twelve distance classes

Primer	Distance classes											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
OPB-01	0.418***	0.379***	0.313***	0.066	0.039	0.059	-0.011	-0.137	-0.156*	-0.191**	-0.352***	-0.298***
OPB-02	0.318***	0.239*	0.172*	0.120	0.068	0.034	-0.026	-0.061	-0.010	-0.207*	-0.221**	-0.467***
OPB-15	0.334***	0.261**	0.192**	0.140	0.049	0.089	0.052	-0.054	-0.102	-0.206*	-0.237*	-0.386***
OPC-06	0.350***	0.153*	0.185*	0.170*	0.131	0.077	0.036	-0.029	-0.079	-0.173*	-0.364***	-0.196**
OPC-11	0.224**	0.183**	0.019	0.084	0.018	0.125	-0.033	-0.101	-0.184**	-0.208**	-0.213***	-0.379***
OPC-13	0.452***	0.358**	0.248*	0.107	0.048	0.079	-0.137	-0.205	-0.233**	-0.370***	-0.505***	-0.267**
OPC-18	0.470***	0.439**	0.194*	0.237*	0.144	-0.009	-0.037	0.023	-0.117	-0.407***	-0.298**	-0.510***
OPD-02	0.388***	0.369***	0.244*	0.045	0.008	0.094	-0.068	-0.019	-0.034	-0.155*	-0.196**	-0.242**
OPD-07	0.277**	0.138*	0.187*	0.231**	0.108	0.104	0.095	-0.083	-0.037	-0.292**	-0.300***	-0.382***
OPD-09	0.116	0.202*	0.057	0.026	0.054	0.039	0.017	-0.031	-0.013	-0.253**	-0.017	-0.131*
OPD-13	0.428***	0.386***	0.102	0.079	0.044	-0.005	-0.055	-0.061	-0.156*	-0.193*	-0.227**	-0.375***

*p<0.05, **p<0.01, ***p<0.001

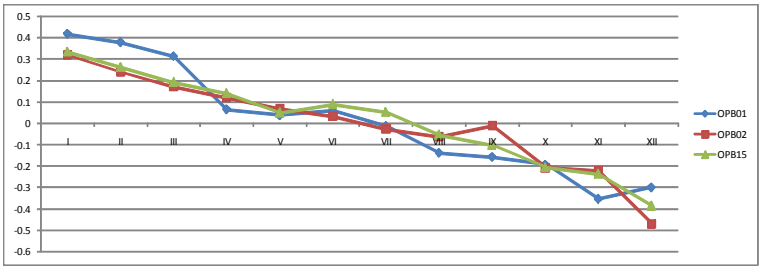

Fig. 2. Correlograms of *C. humilis* on Mt. Giri using values of Moran's *I* for OPB primers.

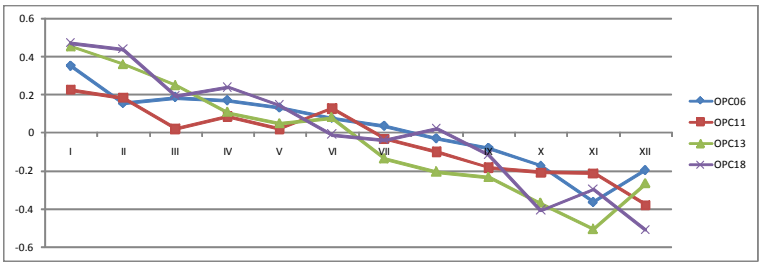

Fig. 3. Correlograms of *C. humilis* on Mt. Giri using values of Moran's *I* for OPC primers.

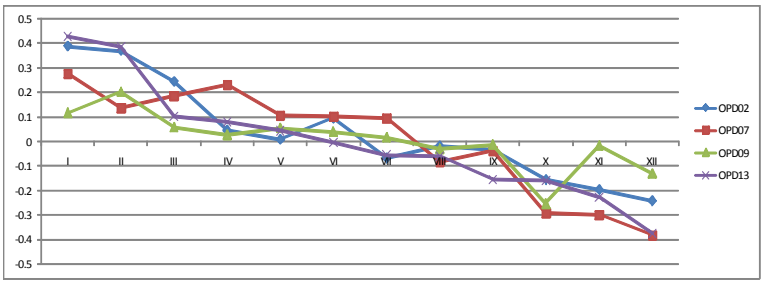

Fig. 4. Correlograms of *C. humilis* on Mt. Giri using values of Moran's *I* for OPD primers.

expected value in only 68 of 132 cases (51.5%). Thirty-six of these values (52.9%) were negative, indicating a partial genetic dissimilarity among pairs of individuals in the 12 distance classes. Thirty-two of the significant values (47.1%) were positive, indicating genetic similarity among individuals in the first 4 distance classes except for three loci (OPC-06, OPC-18, and OPD-07), i.e., pairs of individuals can be separated by more than 30 m. Namely significant aggregations of an identical allele were partially observed at eight markers (72.7%) except for the three markers within these III classes.

The significantly negative SND values indicate an excess of different allelic pairs at loci for the X~XII distance classes. This suggests that neighboring patches in which there are different alleles are predominantly 100 to 120 m apart, on average.

Pairs of individuals with positive value can separate by more than 90.0 m (Fig. 5). It is almost consisted the result of Moran's *I*. The comparison of Fr values to a logistic regression indicated that a highly significant percentage of genetic variation in the Mt. Giri population could be explained by isolation by distance.

Discussion

A significant positive value of Moran's *I* indicated that pairs of individuals separated by distances that fell within distance class k had similar genotypes (gene frequencies), whereas a significant negative value indicated that they had dissimilar genotypes. The overall significance of individual correlograms was tested using Bonferroni's criteria [14]. The results revealed that genetic similarity was shared among individuals within up to a scale of a 60 m distance. Mixed genetic similarity and dissimilarity was shown among individuals between 60~70 m distance scale. Similar genets were not found in more than 80 m, Thus we directly looked

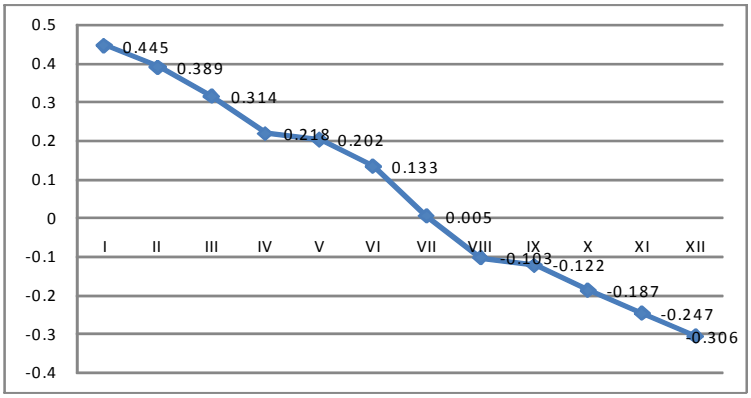

Fig. 5. Genetic versus geographic distances on Mt. Giri population in Korea. Values of the Fr function are given.

for the presence of genetic correlations between neighbors at this scale.

Although no distinct spatial structure of allelic frequencies was found for either of the one primer (OPD-06) within the natural subpopulations of *C. humilis*, many significant aggregations of an identical allele were partially observed at the 10 markers for some classes. The results from this study are consistent with the supposition that a plant population is subdivided into local demes, or neighborhoods of related individuals [3,14]. Previous reports on the local distribution of genetic variability suggested that microenvironmental selection and limited gene flow are the main factors causing substructuring of alleles within a population [6,8]. Local genetic differentiation at RAPD or other marker loci caused by microenvironmental heterogeneity has been observed in a variety of plant species [7]. Those loci showed significant aggregation of an identical allele, which persists for generations, as long as the same microenvironmental conditions continue. This persistence was demonstrated, for example, in the *Got-1* locus in lodgepole pine [8] and for the genetic variation in quantitative traits of *Impatiens capensis* [1]. In the present study, most loci (90.9%) showed significant aggregation in the Korean *C. humilis* population. This aggregation, however, did not persist at all loci, thereby excluding microenvironmental selection as being the main cause for allelic aggregation.

It is important to infer the genetic patch width because it defines the spatial scale within which individuals have similar genetic backgrounds. The distance at which mean Moran's *I* values first intercept the u1 value provides a measure of the shortest diameter of irregularly shaped patches [17].

In simulations, Ohsawa *et al*. [13] and Epperson [6] showed that local genetic differentiation is very sensitive to the degree of actual gene dispersal. An indirect estimate of gene flow, based on the mean Gst (the proportion of total genetic diversity partitioned among populations), was low (*Nm*=0.302) in Korean classes. Levels of gene flow calculated in the present study are of insufficient magnitude to counterbalance genetic drift or weak selection, thus playing a major role in shaping the genetic structure of *C. humilis* [21]. Clonal colonies are common in many genus *Carex* species [10]. Although *C. humilis* reproduces sexually through the production of seed, some plants reproduce by underground stolons or rhizomes. Above ground these plants appear to be distinct individuals, but underground they remain interconnected and are all clones of the same plant. The ordered sampling of ramets permitted an examination of the spatial structure in some of the smaller *C. humilis* populations. This study indicated that the distribution of individual genotypes of a given population was clumped.

If drift was the only force structuring genetic variation, we would not expect all of the markers to produce similar correlograms, or to decline with increasing distance classes, with the patch size for positive autocorrelation determined by the neighborhood area, although the actual spatial patterns would be uncorrelated among markers [17]. If the observed differences in spatial structure among markers are significant, these cannot be explained by drift alone. Unfortunately, no precise statistical procedures exist for testing the significance of differences among Moran's *I*-correlograms [1]. Moreover, since different markers displayed different amounts of genetic determination, the power or precision of the *I*-statistic may differ among markers. Nevertheless, most correlograms showed significance at a scale of 50～60 m.

Within the Mt. Giri population, a strong spatial structure was observed for RAPD markers, indicating a very low amount of migration among subpopulations. Neighboring patches of *C. humilis* are predominantly 50 to 60 m apart on average. The present study demonstrates that a spatial structure in the Mt. Giri population could be explained by isolation by distance, limited gene flow, and topography.

Acknowledgement

This work was supported by Dongeui University Research Grant (2010AA100).

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초록 : RAPD에 의한 지리산 내 산거울 집단의 공간적 상관관계 분석

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RAPD에 의한 지리산 내 산거울 집단의 유전자 빈도와 지리적 거리에 따른 공간적 상관관계를 분석하였다. 전체 102 DNA 분절(밴드)이 107 개체에서 탐지되었다. 102 밴드 중 48(47.1%)개 밴드는 다형성을 나타내었다. 분집단간 다형성의 비교에서 거리 구간 I와 V가 가장 낮은 변이(16.7%)를 나타내었고, 거리 구간 VIII이 가장 높은 변이를 나타내었다(22.6%). 전체 다양도는 0.076이었다. 구간 VIII이 가장 높은 다양도(0.093)를 나타내었고, 구간 I가 가장 낮았다(0.063). 구간 사이의 유전적 유사도는 60 m 거리까지는 유사하였다. 지리산 집단에서 산거울은 강한 공간구조를 나타내고 있음이 RAPD 마커로 알 수 있었다. 이는 지리산 집단에서 낮은 이주자수와 개체들이 덩어리 모양의 분포를 나타내기 때문으로 판단된다. 본 연구에서 RAPD 마커로 산거울의 공간구조와 유전적 구조를 파악하는데 유용하게 이용될 수 있음을 입증하였다.