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Original article

Allozyme variation in six native oak species in Korea

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Summary — Allozyme variation at 6 loci was studied in 28 populations of the 6 oak species native to Korea: *Quercus acutissima* Carruth, *Q aliena* Bl, *Q dentata* Thunb, *Q mongolica* Fisch, *Q serrata* Thunb, and *Q variabilis* Bl. The proportion of polymorphic loci per population (P) averaged over the 6 species was 74.6%. The average number of alleles/locus *(A/L)* was 2.26. The average observed and expected heterozygosities (H_o, H_e) were 0.302 and 0.298, respectively. Only a small amount (7%) of the observed genetic variation appeared to be interpopulational. Among the 6 species, *Q serrata* and *Q dentata* were genetically less variable than the others. Three loci could be used as markers for distinguishing *Q acutissima* and *Q variabilis* from the other 4 species. Based on genetic identity, the 6 oaks were also clustered into 2 groups. This approach yields results similar to the current taxonomic treatment by morphological characteristics.

allozyme / genetic variation / *Quercus* species

Résumé — Variabilité allozymique chez 6 espèces de chênes indigènes de Corée. *La variabilité allozymique a été étudiée dans 28 populations appartenant à 6 espèces de chênes indigènes de Corée à partir de données issues de 6 loci :* Quercus acutissima *Carruth,* Q aliena *Bl,* Q dentata *Thunb,* Q mongolica *Fisch,* Q serrata *Thunb et* Q variabilis *Bl. Le nombre moyen d'allèles (A/L) était de 2,26. Les hétérozygoties observées et théoriques* (H_o, H_e) *étaient de 0,302 et 0,298 respectivement. La variabilité entre populations ne représentait que 7% de la variabilité totale. Parmi les 6 espèces,* Q serrata *et* Q dentata *étaient les moins variables. Trois loci permettaient de distinguer* Q acutissima *et* Q variabilis *des 4 autres espèces. Le calcul des identités génétiques a permis de séparer les 6 espèces en 2 groupes.*

***allozyme / variabilité génétique* / Quercus**

INTRODUCTION

Quercus acutissima Carruth, *Q aliena* Bl, *Q dentata* Thunb, *Q mongolica* Fisch, *Q serrata* Thunb, and *Q variabilis* Bl are the 6 native deciduous oaks which are distributed throughout Korea (Lee CB, 1987; Yim, 1991). They grow abundantly as dominant trees both in pure stands and mixed with other species. This abundance is attributed mainly to vigorous sprouting ability and viability on poor sites. In addition to the important role in forest ecosystems, they are economically valuable especially for fuel and structural wood (Lee CB, 1987; Yim, 1991).

Due to indiscriminate exploitation of the wood and poor silvicultural treatments, most oak stands in Korea exhibit very poor growth and quality. In regard to their economic and ecological potential, it is likely that the importance of oak species will increase in the future. For these reasons, systematic genetic studies on oaks are now being carried out, but they are still at an early stage (Kim and Hyun, 1990; Lee, 1990; Park, 1991).

The objective of this study was to compare the genetic variation among the 6 oak species and also among populations in each species by means of isozyme analysis. Identification of marker genes that can be used to distinguish between the species and clarification of the systematic relationships among them were also points of interest.

MATERIALS AND METHODS

A total of 533 mature individuals from 28 populations of the 6 species were examined. From 5 to 30 individuals per population were assayed. Locations and the sample sizes are presented in table I.

For isozyme analysis, young leaves forced out of dormant twigs were homogenized in a drop of extraction buffer (50 ml of Tris–HCl buffer, pH 7.3, + 0.06 g of ethylenediaminetetraacetic acid (EDTA) + 0.05 ml of merceptoethanol + 5 g polyvinylpyrrolidone (PVP, mol wt 40 000)) and extracts were subjected to horizontal starch–gel (12.5%) electrophoresis using 2 buffer systems. System I was that reported by Poulik (1957) with slight modifications; an electrode buffer of 0.063 M sodium hydroxide titrated to pH 8.20 with 0.299 M boric acid and a gel buffer of 0.076 M Tris titrated to pH 8.7 with 0.0068 M citric acid. System II consisted of an electrode buffer of 0.07 M Tris titrated to pH 7.0 with 0.021 M citric acid and a gel buffer obtained from a 1:9 aqueous dilution of the electrode buffer. System I was used to resolve catalase (CAT), leucine aminopeptidase (LAP), menadione reductase (MNR) and phosphoglucoisomerase (PGI). System II was used to resolve aconitase (ACON). The Enzyme Commission numbers of analyzed enzymes and the number of loci

Table I. Location of populations and number of plants sampled for isozyme analysis.

Locality	Quercus acutissima	Quercus aliena	Quercus dentata	Quercus mongolica	Quercus serrata	Quercus variabilis
Chunsung, Kangwon-Do	11	22	19	25	7	12
Mt Chiri, Chollanam-Do	0	0	0	12	0	10
Puyo, Chungchongnam-Do	0	8	7	28	5	12
Taegu, Kyngsangpuk-Do	24	30	6	20	28	24
Mt Wolak, Kyungsangpuk-Do	9	0	20	14	0	0
Yangpyung, Kyunggi-Do	30	30	30	30	30	30

scored are listed in table II. Enzyme activity staining protocols were those of Conkle *et al* (1982) with slight modification.

The inheritance pattern of observed enzymes has already been reported by Kim and Hyun (1990). The genotypes were scored in the following manner: the fastest migrating locus was assigned A and the next locus B and so on; the fastest allozyme at a given locus was designated '1' and the slower forms were '2', '3' etc.

Allele frequencies, percent of polymorphic loci, the mean observed and expected heterozygosities, genetic identities (Nei, 1978), and the phenogram drawn by the UPGMA clustering technique (Sneath and Sokal, 1973) were calculated and produced using the BIOSYS-1 program of Swofford and Selander (1989).

The amount of interpopulational genetic variation within *Quercus* species and populations was determined by analyzing genetic diversity measures (H_T, H_S, D_{ST} and G_{ST}) (Nei, 1973, 1975).

RESULTS AND DISCUSSION

Allele frequencies for the 6 loci studied are presented in table III. Five loci (ACON-A, LAP-A, MNR-A, PGI-A, PGI-B) were polymorphic in all 6 taxa, although not in every population. Three loci, CAT-A, MNR-A and PGI-B, served as allozyme markers for discriminating *Quercus acutissima* and *Q variabilis* from the other 4 oak species. At CAT-A, allele 1 was present in *Q acutissima*, allele 2 in *Q acutissima* and *Q variabilis* and allele 4 was observed in the other 4 species. Among the 4 alleles at MNR-A, allele 4 was found only in *Q acutissima* and *Q variabilis*, but allele 1 was observed in the other species, while alleles 2 and 3 were displayed in all 6 species. Among the 5 alleles at PGI-B, allele 5 was observed in *Q acutissima* and *Q variabilis*, but alleles 1 and 2 were found in the other 4 species, whereas alleles 3 and 4 were in all 6 species.

Measurements of the genetic variability of the 6 *Quercus* species are presented in table IV. The percent of polymorphic loci ranged from 66.7 *(Q serrata)* to 84.5% *(Q acutissima)*. The amount of polymorphic loci averaged over the 6 oak species was 74.6%. The mean number of alleles/locus *(A/L)* averaged over all loci ranged from 2.03 *(Q serrata)* to 2.65 *(Q mongolica)* and the mean number averaged over the 6 species was 2.26. The mean observed heterozygosities within species ranged from 0.293 *(Q mongolica)* to 0.307 (*Q aliena* and *Q serrata*). The mean expected heterozygosities ranged from 0.276 *(Q dentata)* to 0.325 *(Q acutissima)*. The overall means of the observed and expected heterozygosities for the 6 species were 0.302 and 0.298, respectively.

Table II. Enzymes assayed, their abbreviations, Enzyme Commission (EC) designations, and number of loci scored.

Enzyme	*Abbreviation*	*EC designation*	*No of loci scored*
1. Aconitase	ACON	4.2.1.3	1
2. Catalase	CAT	1.11.1.6	1
3. Leucine aminopeptidase	LAP	3.4.11.1	1
4. Menadione reductase	MNR	1.6.99.2	1
5. Phosphoglucoisomerase	PGI	5.3.1.9	2

Table III. Allele frequencies at the 6 loci in 6 species of *Quercus*.

Locus	Quercus acutissima				Q aliena				Q dentata				
	CS	*YP*	*TG*	*WL*	*CS*	*PY*	*YP*	*TG*	*CS*	*PY*	*WL*	*YP*	*TG*
ACON-A													
(N)	10	30	25	8	22	7	30	29	19	6	18	30	6
1	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.000
2	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.026	0.083	0.000	0.000	0.000
3	0.850	0.950	0.978	0.875	0.773	0.857	0.783	0.741	0.816	0.917	0.833	0.950	0.917
4	0.150	0.050	0.022	0.125	0.182	0.143	0.217	0.259	0.132	0.000	0.139	0.050	0.083
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.028	0.000	0.000
CAT-A													
(N)	10	30	22	8	22	7	30	29	19	6	19	30	6
1	0.000	0.067	0.159	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	1.000	0.933	0.841	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.000	0.000	0.000	0.977	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LAP-A													
(N)	10	25	23	7	22	7	30	29	19	6	18	21	6
1	0.000	0.000	0.000	0.000	0.318	0.714	0.000	0.741	0.632	0.583	0.528	0.548	0.750
2	0.000	0.000	0.022	0.214	0.091	0.000	0.000	0.000	0.000	0.083	0.000	0.024	0.000
3	0.850	0.860	0.935	0.500	0.568	0.286	0.883	0.259	0.211	0.250	0.417	0.405	0.250
4	0.000	0.000	0.043	0.071	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5	0.150	0.140	0.000	0.214	0.023	0.000	0.117	0.000	0.158	0.083	0.056	0.024	0.000
MNR-A													
(N)	8	28	12	7	21	5	30	29	15	6	19	30	6
1	0.000	0.000	0.000	0.000	0.119	0.100	0.067	0.000	0.033	0.000	0.000	0.000	0.000
2	0.063	0.000	0.000	0.000	0.881	0.900	0.933	1.000	0.967	1.000	0.921	0.983	1.000
3	0.875	0.714	0.792	0.643	0.000	0.000	0.000	0.000	0.000	0.000	0.079	0.017	0.000
4	0.063	0.286	0.208	0.357	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGI-A													
(N)	10	30	23	7	21	7	30	28	18	6	19	29	6
1	0.000	0.000	0.000	0.000	0.405	0.286	0.017	0.375	0.278	0.417	0.474	0.534	0.500
2	0.450	0.167	0.565	0.500	0.595	0.714	0.983	0.625	0.722	0.583	0.526	0.466	0.500
3	0.550	0.833	0.435	0.500	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGI-B													
(N)	9	30	18	8	22	7	30	29	19	6	19	30	6
1	0.000	0.000	0.000	0.000	0.159	0.143	0.000	0.224	0.026	0.000	0.000	0.000	0.000
2	0.000	0.000	0.000	0.000	0.545	0.357	0.700	0.362	0.158	0.333	0.053	0.317	0.167
3	0.111	0.317	0.083	0.063	0.295	0.429	0.283	0.414	0.737	0.667	0.947	0.683	0.833
4	0.278	0.167	0.306	0.125	0.000	0.071	0.017	0.000	0.079	0.000	0.000	0.000	0.000
5	0.611	0.517	0.611	0.813	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

CS : Chunsung; JR: Jiri; PY: Puyo; TG: Taegu; WL: Wolak; YP: Yangpyung.

Table III. Continued

Locus	Q mongolica						Q serrata				Q variabilis.				
	CS	*JR*	*PY*	*WL*	*YP*	*TG*	*CS*	*PY*	*YP*	*TG*	*CS*	*JR*	*PY*	*YP*	*TG*
ACON-A															
(N)	24	11	27	14	26	16	5	4	30	28	12	9	11	29	24
1	0.021	0.000	0.000	0.036	0.000	0.063	0.000	0.375	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	0.188	0.045	0.130	0.107	0.077	0.063	0.000	0.000	0.183	0.446	0.083	0.000	0.045	0.000	0.063
3	0.750	0.955	0.870	0.857	0.885	0.844	0.700	0.500	0.783	0.518	0.625	0.778	0.864	0.741	0.500
4	0.042	0.000	0.000	0.000	0.038	0.031	0.300	0.125	0.033	0.036	0.292	0.222	0.091	0.259	0.396
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.042
CAT-A															
(N)	24	12	28	14	14	20	5	4	30	28	12	10	11	30	24
1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000
3	0.000	0.000	0.000	0.000	0.036	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.000	0.000
4	1.000	1.000	1.000	1.000	0.964	1.000	1.000	1.000	0.933	1.000	0.000	0.000	0.000	0.000	0.000
LAP-A															
(N)	24	12	28	14	27	20	5	4	24	28	12	10	11	28	24
1	0.208	0.250	0.089	0.071	0.130	0.050	0.300	0.125	0.229	0.357	0.000	0.000	0.000	0.125	0.021
2	0.021	0.125	0.018	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.042
3	0.667	0.542	0.857	0.821	0.870	0.875	0.500	0.875	0.604	0.268	0.667	0.700	0.727	0.839	0.646
4	0.021	0.000	0.000	0.036	0.000	0.000	0.100	0.000	0.000	0.000	0.208	0.000	0.045	0.000	0.000
5	0.083	0.083	0.036	0.071	0.000	0.075	0.000	0.000	0.167	0.375	0.083	0.300	0.227	0.036	0.292
MNR-A															
(N)	24	12	28	14	30	20	4	4	30	28	10	10	9	28	21
1	0.021	0.000	0.018	0.036	0.033	0.150	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000
2	0.958	0.917	0.911	0.929	0.967	0.850	1.000	0.625	0.950	1.000	0.000	0.000	0.000	0.000	0.048
3	0.021	0.083	0.071	0.036	0.000	0.000	0.000	0.375	0.000	0.000	0.950	0.950	0.889	0.982	0.952
4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.050	0.111	0.018	0.000
PGI-A															
(N)	24	12	26	8	28	19	5	4	30	28	12	10	10	30	24
1	0.479	0.500	0.462	0.813	0.125	0.289	0.400	0.375	0.000	0.018	0.000	0.000	0.000	0.000	0.000
2	0.521	0.500	0.538	0.188	0.839	0.711	0.600	0.625	1.000	0.982	0.375	0.250	0.550	0.583	0.771
3	0.000	0.000	0.000	0.000	0.036	0.000	0.000	0.000	0.000	0.000	0.625	0.750	0.450	0.471	0.229
PGI-B															
(N)	24	12	27	14	30	20	5	4	30	28	12	10	9	30	24
1	0.042	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000
2	0.354	0.250	0.389	0.286	0.350	0.250	0.200	0.000	0.033	0.089	0.000	0.000	0.000	0.000	0.000
3	0.375	0.667	0.481	0.500	0.450	0.550	0.800	1.000	0.950	0.911	0.125	0.050	0.000	0.083	0.146
4	0.229	0.083	0.130	0.214	0.200	0.175	0.000	0.000	0.000	0.000	0.167	0.050	0.333	0.017	0.000
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.708	0.900	0.667	0.900	0.854

The mean values of 74.6% polymorphic loci, 2.26 alleles/locus and 0.298 mean expected heterozygosity (table IV) are larger than those for red oaks in northeastern America (P = 29.7%, A/L = 1.37, H_e = 0.081; Manos and Fairbrothers, 1987). These values are also somewhat larger than those obtained over long-lived perennial woody plants (P = 64.7%, A/L = 2.19, H_e = 0.177; Hamrick and Godt, 1989).

Although the enzymes investigated tend to be biased towards the polymorphic enzymes, these results show that Korean oaks have a great deal of genetic variation. By increasing the number of isozymes to be investigated, more reliable data will be obtained.

The mean values for the differentiation between populations (G_{ST}) of the 6 oak species (table V) were from 0.040 *(Q dentata)* to 0.115 *(Q serrata)*, and the overall value for the 6 oak species was 0.073. In other words, about 7% of the observed genic diversity appears to be interpopulational. This result is similar to that for American red oaks (G_{ST} = 0.086; Manos and Fairbrothers, 1987).

Mean genetic identities among the 6 species (table VI) ranged from 0.295 to 0.956. This wide range seems to be due to the presence of different alleles at 3 marker genes in the 6 species. The genetic identity between *Q acutissima* and *Q variabilis* was 0.956, and those among the other 4 species ranged from 0.885 to 0.933. But the genetic identities between the species from each group were very low, ranging from 0.295 to 0.434. Mean identities among populations within species ranged from 0.937 to 0.995.

Two species, *Q dentata* and *Q serrata* displayed less genetic variation (P, A/L and H_o) than the other oaks and *Q acutissima* had the most genetic variation. It appears that these results are related to the different ecological characteristics of the species and agree with the general rule that the wider the range of species, the greater the expected genetic polymorphism. *Q acutissima* is the most abundant species with the widest ecological range.

Table IV. Genetic measurement of variability for 28 populations in 6 oak species: percentage of polymorphic loci *(P)*, mean number of alleles/locus *(A/L)*, mean observed (H_o) and expected (H_e) heterozygosities.

Species	P [a]	A/L	H_o	H_e [b]
Q acutissima	84.5	2.30	0.306	0.325
Q aliena	75.0	2.20	0.307	0.310
Q dentata	70.0	2.16	0.305	0.276
Q mongolica	75.0	2.65	0.293	0.304
Q serrata	66.7	2.03	0.307	0.280
Q variabilis	76.7	2.28	0.295	0.291
Total	74.6	2.26	0.302	0.298

[a] A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95. [b] Unbiased estimate (Nei, 1978).

Table V. Gene diversity for 6 loci in populations of the *Quercus* species.

Species	H_T	H_S	D_{ST}	G_{ST}
Q acutissima	0.336	0.311	0.025	0.072
Q aliena	0.341	0.299	0.041	0.089
Q dentata	0.274	0.263	0.011	0.040
Q mongolica	0.319	0.296	0.022	0.052
Q serrata	0.310	0.271	0.039	0.115
Q variabilis	0.304	0.280	0.024	0.070
Total	0.314	0.287	0.027	0.073

H_T: total diversity; H_S: diversity within populations; D_{ST}: diversity between populations; G_{ST}: differentiation between populations.

Table VI. Mean genetic identities for pair-wise comparisons of populations in *Quercus* species by hierarchical design (Nei, 1978).

Species	*1*	*2*	*3*	*4*	*5*	*6*
1. *Q acutissima*	0.972					
2. *Q aliena*	0.368	0.939				
3. *Q dentata*	0.345	0.933	0.995			
4. *Q mongolica*	0.434	0.925	0.926	0.974		
5. *Q serrata*	0.382	0.885	0.929	0.910	0.937	
6. *Q variabilis*	0.956	0.330	0.295	0.371	0.349	0.973

This species is distributed throughout the Korean peninsula and also in China and Japan (Krüssmann, 1986; Lee CB, 1987; Yim, 1991).

The dendrogram produced by the UPGMA clustering technique based on Nei's identity (1978) is depicted in figure 1.

The 6 oaks were clustered into at least 2 groups: group I is composed of *Q acutissima* and *Q variabilis* and the other species constitute group II. These results are similar to those provided by morphological characteristics (Ma, 1974; Kim and Kim, 1987). According to Krüssmann (1986),

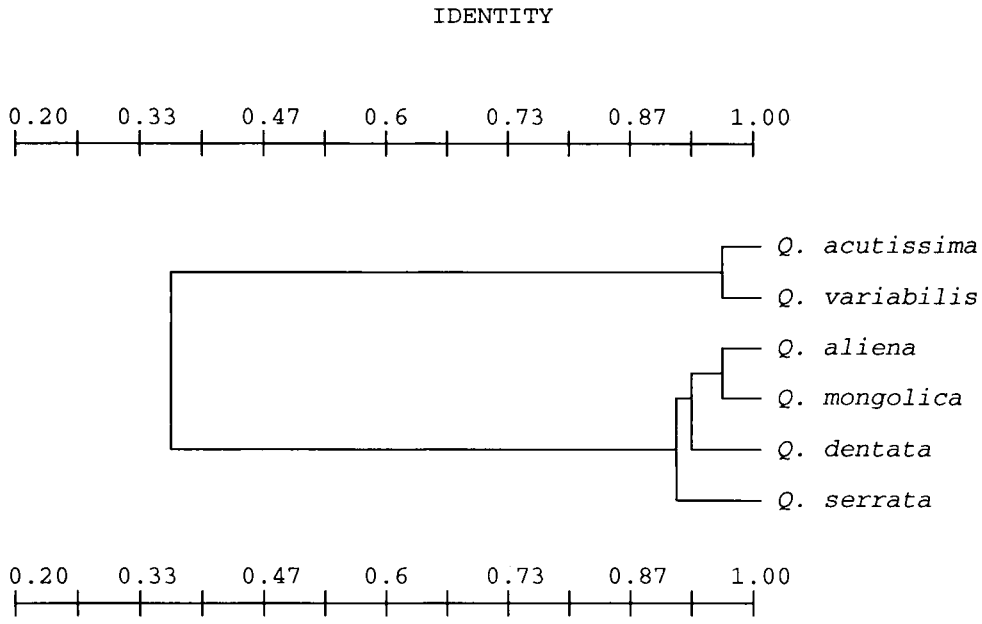

Fig 1. UPGMA-derived phenogram based on Nei's (1978) genetic identity measured in *Quercus* species. Cophenetic correlation is 0.995.

Q acutissima and *Q variabilis* are classified into the section *Cerris* of the subgenus *Lepidobalanus*, *Q aliena*, *Q mongolica* and *Q serrata* into the section *Alba* of the subgenus *Lepidobalanus*. *Q dentata* is classified into the section *Dentatae* of the subgenus *Lepidobalanus*.

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