MORPHOLOGICAL AND GENETIC DIFFERENTIATION AMONG THE CENTRAL EUROPEAN WHITE OAKS [1]

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ABSTRACT

Differentiation of the Central European white oaks was studied on the basis of their morphology and genetics. Numeric-taxonomical analysis and isozyme gene markers were used in the investigation of separability of single oak taxa (*Quercus robur* L., *Q. pedunculiflora* C. Koch, *Q. petraea* (Matt.) Liebl., *Q. dalechampii* Ten., *Q. polycarpa* Schur, *Q. pubescens* Willd., *Q. virgiliana* Ten., *Q. frainetto* Ten., *Q. cerris* L.). Together, approx. 1800 trees sampled in 23 stands and 29 populations were analysed, 21 morphological characteristics were measured and 17 isozyme loci were involved in our experiments. Our attempt to differentiate oak species „*sensu stricto*" (all nine taxa) on the basis of chosen morphological traits was not successful. Much more we succeeded in the morphological and genetic discrimination of species „*sensu lato*". Results of clustering based on genetic distances are in accordance with taxonomic classification. The biggest differences in allelic frequences among species were observed in *Gludh-A, Pgm, Idh-B,* and *6-Pgd-B* loci.

Key words: *Quercus* subgenus *Lepidobalanus*, numerical taxonomy, allozymes, species discrimination.

INTRODUCTION

Although oaks belong to the most widespread and economically important broadleaved tree species in Central Europe, their taxonomy is still a matter of discussion. It is generally known that all taxonomic complications of oaks relate to their enormously high variability. Especially at the species level, taxonomic situation is unclear and controversial, and this is reflected in different numbers of species recognized by different authors. The Central European oak taxa except *Quercus cerris* (subgenus *Cerris*) belong to the subgenus *Lepidobalanus* (*Q. robur* L., *Q. petraea* (Matt) Liebl., *Q. pubescens* Willd.). The consensus about the status of these so-called „main species" is quite general, although controversies still exist, since they are interfertile and the frequency of individuals with intermediate morphology is high. In fact, these species *sensu lato* correspond to the sections *Robur*, *Roburoides* and *Dascia*, respectively, as defined by SCHWARZ (1936). However, related „microspecies" or species *sensu stricto* have been described within sections on the basis of morphological and ecological traits – *Q. pedunculiflora, Q. dalechampii, Q. polycarpa, Q. virgiliana* and *Q. frainetto*. In contrast to species *sensu lato*, forestry practice mostly ignores these microspecies. In many floras (Greece, Rumania, Serbia, etc., even in *Flora Europaea*; SCHWARZ, 1964), these taxa are listed as separate species, but there is no general agreement about their taxonomic status, since great intraspecific morphological variation makes them difficult to distinguish.

We investigated morphological and genetic differentiation of oaks using methods of numerical taxonomy and isozyme markers. The aim of the first part of this study was describing the morphological variability of oak taxa using numeric-taxonomical methods and finding morphological traits that are suitable for differentiation of single species *sensu lato* and *sensu stricto*. In the second part of study, genetic structures of oak populations were compared and the genetic differentiation among species *sensu lato* was investigated employing allozyme markers.

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MATERIALS AND METHODS

The material for the morphometrical analysis originated from two locations in western Slovakia, Cíbajky and Martinský les, where all nine oak taxa occur. The population Cíbajky represents a pasture covered by widely dispersed oak trees with well-developed crowns, aged 250–300 years, abundantly bearing fruits. Martinský les is a rather dense forest with a closed canopy, where trees have reduced crowns, and where fruits were not available during the sampling of material. From 400 trees in both stands, ten leaves from the light-exposed part of tree crown were taken. In Cíbajky, ten fruits per tree were sampled as well. Determination of single species was performed using detailed descriptions of taxa according to MAGIC (1974) and with the help of two identification keys of Slovak oak taxa (MAGIC 1975, POŽGAJ 1985). In total, 21 morphological traits were examined: 13 on leaves, 3 on buds, and 5 on fruits. Previous numeric-taxonomical studies on oaks (AAS 1993, DUPOUEY & BADEAU 1993, KREMER *et al.* 2002) indicate that some of the selected traits discriminate well among species.

Trees were characterized by arithmetic averages of the investigated traits. Principal component analysis (PCA) and canonical discriminant analysis (CDA) were used for the interpretation of morphological data.

Within the genetic study, 29 natural oak populations growing in 23 stands (several stands contained more than one species) were investigated. Since the material was sampled during the winter when leaves and fruits are not available, the classification of sampled trees to species *sensu stricto* was not possible. A population was mostly represented by at least 50 non-adjacent trees. However, in some cases, fewer representatives of a species were present in a stand, in that case, the species population was sampled exhaustively. The location of the sampled populations is shown in Fig. 1.

Seventeen isozyme loci were used for the analysis: *Fest-A, Mnr-A, Idh-A, Idh-B, Mdh-A, Mdh-B, Mdh-C, Mdh-D, Pgm-A, Skdh-A, Got-A, Gdh-A, Pgi-A, Pgi-B, 6Pgd-A, 6Pgd-B,* and *Gludh-A* were used.

Table 1. Taxonomical classification of Slovak oak taxa according to SCHWARZ (1936).

Genus *Quercus* L.	– Subgen. *Lepidobalanus* (ENDL.) OERST.	– **Sect. *Robur* RCHB.**
		– *Q. robur* L.
		– *Q. pedunculiflora* C. KOCH
		– **Sect. *Roburoides* SCHWZ.**
		– *Q. petraea* (MATT.) LIEBL.
		– *Q. dalechampii* TEN.
		– *Q. polycarpa* SCHUR
		– **Sect. *Dascia* KY.**
		– *Q. pubescens* WILLD.
		– *Q. virgiliana* Ten.
		– *Q. frainetto* TEN.
	– Subgen. *Cerris* (SPACH) OERST.	– **Sect. *Eucerris* OERST.**
		– *Q. cerris* L.

Table 2 List of the examined characteristics.

1.	Lamina length (mm)	11.	Number of intercalary veins (number)
2.	Lamina width (mm)	12.	Basal shape of the lamina (score)
3.	Length of lamina from the base (mm) to the widest part	13.	Abaxial lamina pubescence (score)
4.	Lamina shape (index value)	14.	Dimension of buds (score)
5.	Petiole length (mm)	15.	Bud shape (score)
6.	Petiole pubescence (score)	16.	Bud pubescence (score)
7.	Lobe width (mm)	17.	Peduncle length (mm)
8.	Sinus width (mm)	18.	Acorn shape (score)
9.	Depth of sinus (index value)	19.	Grossness of scales (score)
10.	Number of lobes (number)	20.	Accrete of scales (score)
		21.	Number of acorns (number)

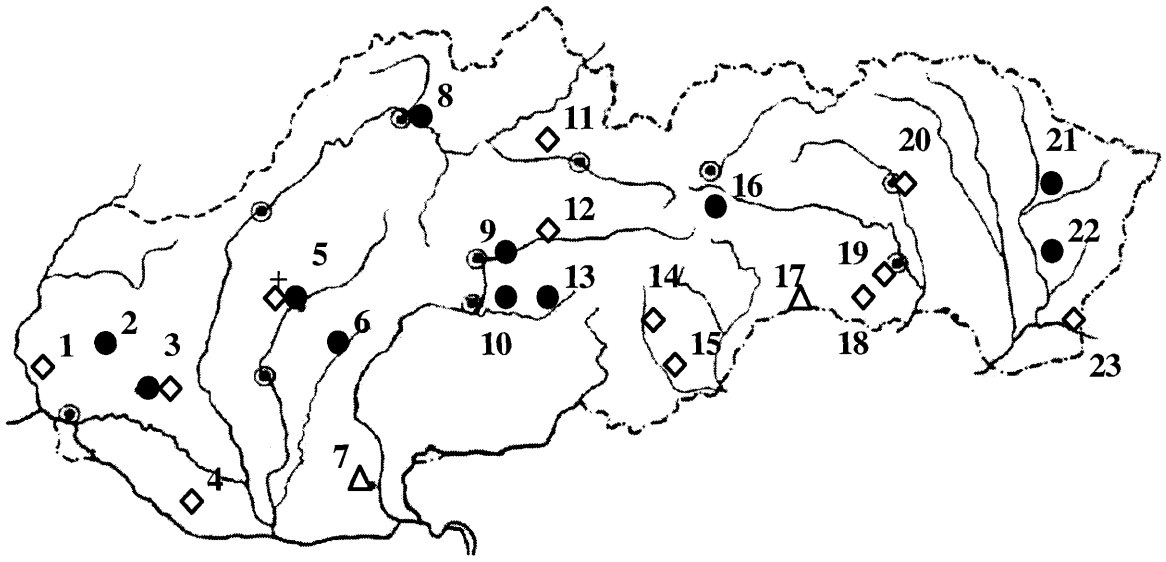

Figure 1. Location of the investigated oak populations (1 – Vysoká na Morave, 2 – Príboj, 3 – Martinský les, 4 – Číčov, 5 – Cibajky, 6 – Volkovce, 7 – Kováčovské kopce, 8 – Strečno, 9 – Príboj, 10 – Hrochoť, 11 – Turík, 12 – Valaská, 13 – Rohy, 14 – Hačava-Skálie, 15 – Kurinec, 16 – Kvetnica, 17 – Hrušov, 18 – Moldava, 19 – Dargov, 20 – Kvetnica, 21 – Hankovce, 22 – Vinné, 23 – Veľké Kapušany) (diamond – *Q. robur*, circle – *Q. petraea*, triangle – *Q. pubescens*, cross – *Q. cerris*).

Locus designation conforms with ZANETTO *et al.* (1996) and MÜLLER-STARCK *et al.* (1996), who proved the Mendelian inheritance of these isozyme systems except one. The Mendelian inheritance of the gene coding for a nonspecific NAD-dependent dehydrogenase (*Gludh-A*), able to utilise glucose and sorbitol as a substrate, was inferred from isozyme phenotypes (alternative occurrence of single-banded variants corresponding to putative homozygotes and triple-banded variants corresponding to putative heterozygotes for the case of a dimeric enzyme) and from the observation that putative genotype distributions correspond approximately to Hardy-Weinberg expectations (GÖMÖRY 2000). Because of technical problems, we were able to score this locus only in 16 out of 29 populations. However, as shown below, it contributes considerably to the species discrimination, therefore we decided to make most assessments of the genetic variation twice – once for a complete population set omitting *Gludh-A*, and second time for a set of 16 populations including this locus. Isozymes were separated by means of a horizontal 12% starch-gel electrophoresis using four buffer systems – tris-citrate pH 7.0, Li-borate pH 8.1/tris-citrate pH 8.1, Na-borate pH 8.0/tris-citrate pH 8.7, and tris-histidine pH 7.0. Alleles were designated by their relative migration rate as related to the most frequent one. Allelic frequencies at each locus were calculated based on diploid genotypes.

Genetic multiplicity was measured by mean number of alleles per locus and percentage of polymorphic loci. Expected Hardy-Weinberg heterozygosity was used to characterize genetic diversity. To quantify the among-population genetic differentiation, Nei's genetic distances (NEI 1973, 1978) were used. Principal coordinate analysis (PCoA) and cluster analysis (CA) were used for the interpretation of genetic distance matrix (SNEATH & SOKAL 1973).

RESULTS

Morphometric analysis

Our attempt to differentiate oak species *sensu stricto* (*Q. robur*, *Q. pedunculiflora*, *Q. petraea*, *Q. dalechampii*, *Q. polycarpa*, *Q. pubescens*, *Q. virgiliana*, *Q. frainetto*, and *Q. cerris*) in one step was not successful. This may be caused by the fact that data from acorn measurements, which are of relevance for distinguishing species *sensu stricto*, were not available for analysis.

Results of separation of oak species *sensu lato* by PCA are presented in Fig. 2. Because of incomplete data set (no information about fruits from trees in Martinský les) new axes were derived only from 16 parameters of leaves and buds. In the projection of trees into the first two axes, *Q. robur s. l.* is fairly well separated from the remaining three

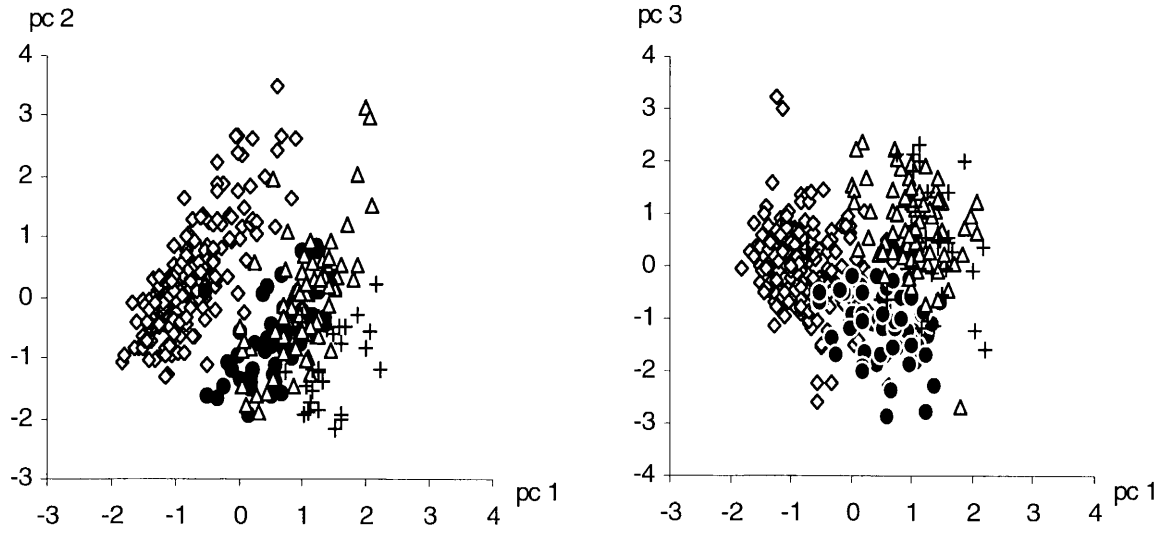

Figure 2. Separation of oak species *sensu lato using PCA* – the projection into first three axes (diamond – *Q. robur*, circle – *Q. petraea*, triangle – *Q. pubescens* and cross – *Q. cerris*).

Table 3. List of the best discriminating characteristics of four oak sections (*F*-values of the univariate analysis of variance indicating degree of difference and mean values).

Characteristics	*F*-test	*Q. robur*	*Q. petraea*	*Q. pubescens*	*Q. cerris*
Intensity of abaxial lamina pubescence	713 (***)	1.10	2.56	3.74	5.36
Petiole pubescence	409 (***)	1.14	1.47	2.95	2.46
Petiole length	348 (***)	7.04	16.87	17.29	15.06
Basal shape of the lamina	251 (***)	6.86	3.95	4.85	3.28
Number of intercalary veins	120 (***)	3.31	0.58	1.96	0.95
Bud pubescence	91 (***)	1.71	2.11	2.92	3.56

taxa (Fig. 2, left). *Q. petraea s.l.* and *Q. pubescens s. l.* appear well differentiated in the projection into the first and third axis (Fig. 2, right), although some overlapping (perhaps caused by the above mentioned reason) is visible. We did not succeed in reaching a good separation of *Q. cerris* from the remaining species employing the PCA. Certainly, if we applied acorn parameters, the overlapping between pubescent and Turkey oak would not be so complete, because of a typical shape of Turkey oak acorn cupules. Among the leaf traits used, the following ones proved to be those with the biggest discriminatory power: intensity of abaxial lamina pubescence, petiole pubescence, petiole length, basal shape of the lamina, number of intercalary veins, and bud pubescence (Table 3).

Among the investigated oak taxa, *Q. robur* and *Q. petraea* belong to the most widespread and important European forest tree species from economical as well as from ecological point of view. Using the CDA, the species represented by 206 investigated specimens were clearly separated along the first canonical axis based on 21 measured leaf and acorn traits, without any overlapping (Fig. 3). As shown in Table 4, the best distinguishing characteristics between pedunculate and sessile oaks were the basal shape of the lamina, petiole length, the intensity of the abaxial lamina pubescence, peduncle length and the number of intercalary veins, which are the traits, commonly used in the systematical diagnosis.

Genetic analysis

Despite a rather high intraspecific variation, the investigated white oak species differ both in allelic frequencies at several allozyme loci and in the levels

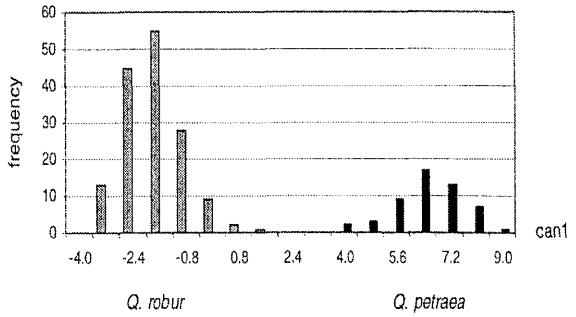

Figure 3. Canonical discriminant analysis of the complex *Q. robur – Q. petraea sensu lato.*

of the genetic diversity. Although the genetic differentiation at most loci is rather low, apparent differences in the frequencies of common alleles ($p > 0.05$) were observed in *Idh-B, Pgm-A, 6Pgd-B* and *Gludh-A* (Fig. 4).

The *Gludh-A* locus appears to be the most interesting from the point of view of species discrimination.. Frequency of the allele *100* was nearly 100 % in most *Q. robur* populations, whereas in *Q. pubescens,* it was the allele *117*, which was predominating. In *Q. petraea,* the share of the alleles *100* and *117* was roughly equal. At the same time, species seem to differ also by the presence of rare alleles, allele *83* was found only in *Q. robur*, whereas allele *133* only in *Q. petraea*. Obviously, no reliable final conclusions can be made about the presence of rare alleles on the basis of the sample sizes used.

Common characteristics of genetic multiplicity and diversity for pooled populations of the investigated white oak species are presented in Table 5.

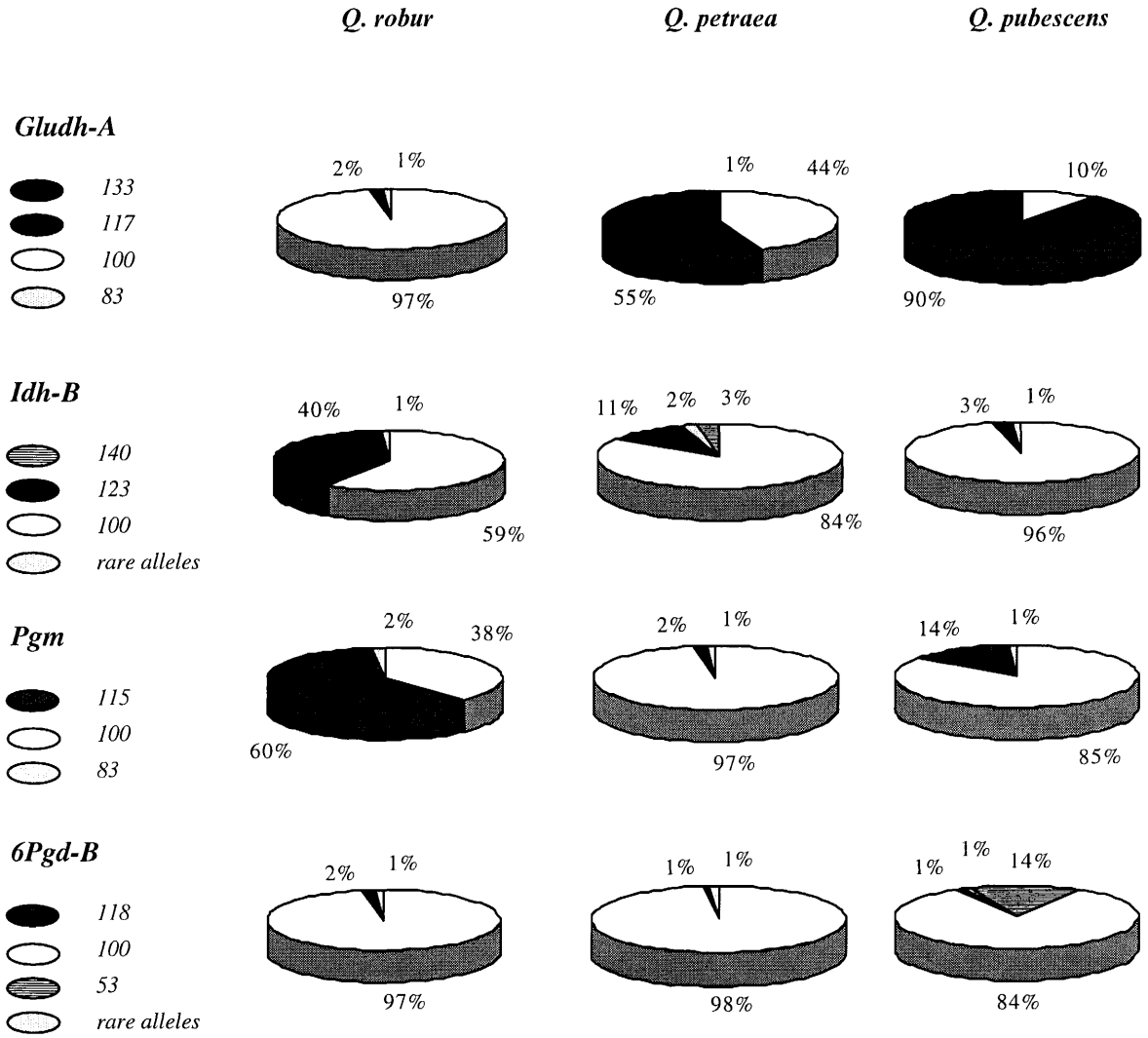

Figure 4. Interspecific differences in allelic frequencies at *Gludh-A* (nonspecific NAD-dependent dehydrogenase), *Idh-B* (isocitrate dehydrogenase), *Pgm-A* (phosphoglucomutase), and *6Pgd-B* (6-phosphogluconate dehydrogenase) loci.

Table 4. List of the ten best discriminating characteristics in the *Q. robur* – *Q. petraea* complex (*F*-values of the univariate analysis of variance and mean values).

Characteristics	*F*-test	*Q. robur*	*Q. petraea*
Basal shape of the lamina	756 (***)	6.94	3.92
Petiole length	628 (***)	7.06	16.85
Intensity of abaxial lamina pubescence	456 (***)	1.12	2.57
Peduncle length	345 (***)	51.52	3.74
Number of intercalary veins	288 (***)	3.34	0.56
Depth of sinus	107 (***)	1.98	2.88
Accreteness of scales	69 (***)	1.69	1.06
Grossness of scales	68 (***)	2.36	3.17
Number of acorns	67 (***)	1.54	2.10
Number of lobes	65 (***)	3.34	11.40

Table 5. Standard characteristics of the genetic variation in Slovak white oak populations (16 loci).

Species	N	n_a	PP	H_O	H_E
Q. robur	649	4.8	84.6	0.139	0.159
Q. petraea	471	4.7	100.0	0.107	0.121
Q. pubescens	164	3.8	84.6	0.151	0.179

N – total sample size, n_a – mean number of alleles per locus, PP – proportion of polymorphic loci, H_O – mean observed heterozygosity, H_E – mean expected heterozygosity.

Divergent trends of allelic richness and diversity among species were observed: *Q. pubescens* exhibits the highest diversity (as measured by the expected Hardy-Weinberg heterozygosity), but at the same time, the lowest level of allelic richness (only 3.8 alleles per locus on average). In the pooled *Q. petraea* sample, all investigated loci were found to be polymorphic, and the allelic richness was almost the same as in *Q. robur*, but genetic diversity was clearly the lowest in this species. Table 5 presents the results for the whole population set, so that the *Gludh-A* locus could not be considered. However, inclusion of this locus would not change substantially the pattern of distribution of diversity values among species.

Nei's genetic distances were used to reveal the multilocus pattern of genetic differentiation. Since the *Gludh-A* locus contributed considerably to the interspecific differentiation, separate calculations were performed for 16 populations, where this locus was scored, and subsequently for all 29 populations based on the remaining loci. When *Gludh-A* was excluded, the interspecific genetic distances were only slightly bigger than intraspecific distances (Table 6). Despite a smaller number of populations, interspecific genetic distances based on the complete set of allozyme loci (including *Gludh-A*) increased considerably, mainly between *Q. robur* and *Q. pubescens*. On the other hand, only a slight differentiation was observed between *Q. petraea* and *Q. pubescens*.

Matrix of genetic distances based on the set of 16 populations in which the *Gludh-A* locus was examined, is interpreted employing cluster analysis (Fig. 5). Outcomes of clustering fit perfectly with the taxonomical classification, as well as with the results of the morphometric analysis. *Q. robur* appears to be the genetically most homogeneous species, clearly most differentiated from the remaining two taxa. Despite the highest number of analysed populations, the cluster of pedunculate oak is the most consistent one. Intraspecific differentiation within *Q. petraea* and *Q. pubescens* is much more distinct.

DISCUSSION

The separation of oak species *sensu lato* (or sections of the subgenus *Lepidobalanus sensu* SCHWARZ 1936) using methods of numerical taxonomy was demonstrated in this study. *Q. robur, Q. petraea*, and *Q. pubescens* can be separated using multivariate statistics (BOROVICS & MÁTYÁS 2000). The results are in agreement with those reported by DUPOUEY & BADEAU (1993) who stated that whit

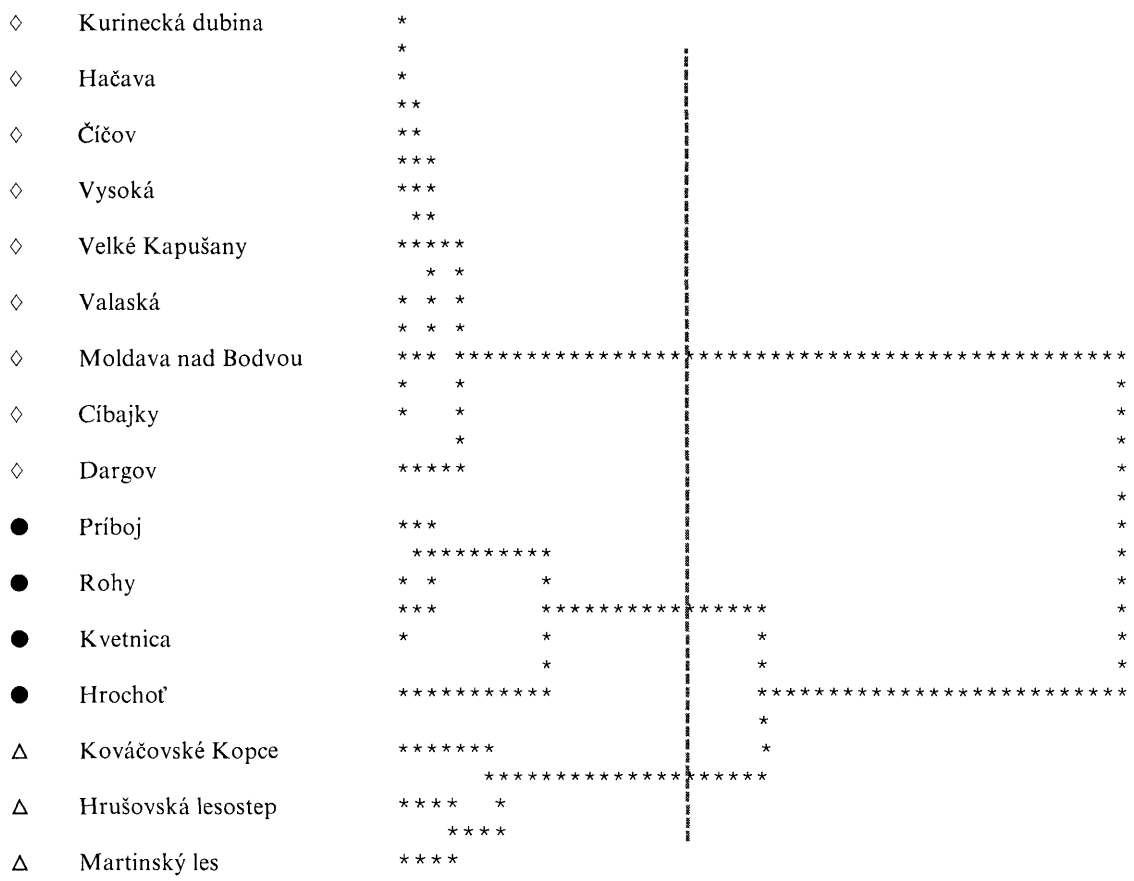

Figure 5. UPGMA dendrogram of 16 populations in which *Gludh-A* locus was examined (diamond – *Q. robur*, circle – *Q. petraea*, triangle – *Q. pubescens*).

Table 6. Ranges of inter- and intra-specific Nei's genetic distances among the investigated whit oak populations.

Species	*Q. robur*		*Q. petraea*		*Q. pubescens*	
Q. robur	0.000–0.042	**0.000–0.008**				
Q. petraea	0.000–0.045	**0.030–0.084**	0.000–0.008	**0.000–0.014**		
Q. pubescens	0.014–0.064	**0.079–0.144**	0.004–0.030	**0.016–0.036**	0.003–0.007	**0.003–0.008**

Note: normal script – *Gludh-A* locus excluded, bold script – *Gludh-A* locus included.

oak species are morphologically different, and also they differ widely in their degree of separation from one another. *Q. robur* appears to be more homogenous whereas *Q. petraea* and *Q. pubescens* form a continuum and exhibit much more intraspecific morphological variability. The delimitation between these two species is more difficult than between sessile and common oak. According BREZNIKAR *et al.* (2000), the hairiness of the lower leaf lamina is the main differential characteristic between these taxa.

Morphological analysis of the complex *Q. robur s. l.* and *Q. petraea s. l.* showed that in spite of interspecific gene flow, both species are morphologically distinct. Their morphological divergence was fully confirmed by the use of canonical discriminant analysis based on several traits. The two species show clear differences in leaf and fruiting structures (RUSHTON 1983). Characteristics of leaves and fruits, which proved to be the most reliable in the

discrimination between pedunculate and sessile oaks, are commonly used as diagnostic traits. AAS (1993), DUPOUEY & BADEAU (1993) and BREZNIKAR *et al.* (2000) found the greatest differences between these two species in the length of petiole, intercalary veins, hairiness of leaf lower lamina, and the shape of the leaf base. It is very surprising that intermediate forms between pedunculate and sessile oak reported as frequent in a number of publications (KLEINSCHMIT *et al.* 1993, 1995, KLEINSCHMIT & KLEINSCHMIT 2000) were rarely found during the field sampling both for genetic morphometric analyses. In fact, in both stands where samples for morphometry were collected, just a single oak tree with intermediate traits occurred.

Among the 17 studied loci significant differences in allelic frequencies among species exhibited four of them – *Pgm-A, Idh-B , 6Pgd-B*, and *Gludh-A. Pgm-A* and *Idh-B* showed important species differentiation also in previous studies (ZANETTO *et al.* 1994, MÜLLER-STARCK *et al.* 1993). In *Gludh-A,* the magnitude of differentiation and a relative consistency of allelic profiles within species suggest that the observed differentiation at this locus is characteristic for sessile and pedunculate oaks (GÖMÖRY *at al.* 2001). Unfortunately Slovakia is the sole region where this locus was analysed for more than one oak species.

The levels of the genetic diversity and allelic richness are opposite among the investigated species. At the geographic level, such diverging trends were observed in several species and at different scales (COMPS *et al.* 2000, GÖMÖRY *et al.* 1999, 2001). This study indicates that they may diverge also on the level of species.

According to some authors (KLEINSCHMIT *et al.* 1993, 1995; STEINHOFF 1997; KLEINSCHMIT & KLEINSCHMIT 2000), limited genetic differentiation and different ecological requirements indicate that pedunculate and sessile oak are ecotypes or subspecies of the same composite species *Q. robur.*

Although a major part of both nuclear and cytoplasmic genetic variants is widely shared by all white oak taxa, there are indications of differentiation based on genetic markers in some studies. BORDÁCS & BURG (1997) and COART *et al.* (2002) demonstrated the existence of species-specific RAPD markers. The study of MUIR *et al.* (2000) demonstrated that *Q. robur* and *Q. petraea* are separate taxonomic units, which can be distinguished by nuclear microsatellites.

It is possible to conclude that the results of morphological analysis are in accordance with the results of genetic analysis in our study. European white oak species *s. l.* were successfully separated by means of numerical taxonomy and isozyme gene markers. *Q. petraea* is morphologically more similar to *Q. pubescens* than to *Q. robur.* Interspecific genetic distances indicated that *Q. petraea* and *Q. pubescens* are related, whereas *Q. robur* is a more distinct taxon (MUELLER & AAS 1997). This fits well with the significant differentiation found between *Q. robur* and *Q. pubescens* and low level of differentiation found between *Q. pubescens* and *Q. petraea* for cpDNA (DUMOLIN-LAPÈGUE *et al.* 1999). Therefore, the theory of a composite species *Q. robur* L. seems to be premature. As RUSHTON (1993) concluded, a wider range of techniques should be involved in the study of *Quercus* L. before any radical revision of this genus.

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