

Morphometric leaf variation in oaks (*Quercus*) of Bolu, Turkey

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Genus *Quercus* (Fagaceae) has a problematic taxonomy because of widespread hybridization between the infrageneric taxa. The pattern of morphological leaf variation was evaluated for evidence of hybridization in Bolu, Turkey, since previous studies suggested that in oaks leaf morphology is a good indicator of putative hybridization. Principal components analysis was applied to data sets of leaf characters from five populations to describe variation in leaf morphology. Leaf characters analyzed in this study showed high degrees of variation as a result of hybridization between four taxa (*Q. pubescens*, *Q. virgiliana*, *Q. petraea* and *Q. robur*) of subgenus *Quercus* while *Q. cerris* as a member of subgenus *Cerris* was clearly separated from the others.

Key words: hybridization, morphological leaf variation, principal components analysis, *Quercus*

Introduction

In the northern hemisphere oaks (*Quercus*) are conspicuous members of the temperate deciduous, broad leaved forests. The genus comprises 531 species, with 250 species found in the Americas, 125 species in Asia and Malesia and the remainder in Europe, North Africa and Macaronesia (Govaerts & Frodin 1998). The area including SE Asia and adjacent Pacific islands was suggested as the modern center of morphological diversity and the family's (Fagaceae) ancestral home, although the area does not contain the greatest number of *Quercus* species (Kaul 1985).

Axelrod (1983) suggested that the Fagaceae evolved and diverged into genera by the late Cretaceous period, followed by rapid evolution

in regions of mild and warm temperate climates. Fossil leaves indicate that today's several major oak groups are at least 40 million years old. General distribution of fossil ancestors supports the hypothesis that all major oak groups evolved at middle latitudes (Manos *et al.* 1999). *Quercus* became dominant in temperate forests in the Cenozoic Era (Axelrod 1983).

The Sierra Madre Occidental of Mexico and East and Southeast Asia are the areas of greatest diversity (Govaerts & Frodin 1998: 201). Turkey, with 18 species of oak, is one of the regions of high species diversity for *Quercus* (Yaltrık 1984). Most recently, Hedge and Yaltrık (1982) classified the species of *Quercus* in Turkey. Before Hedge and Yaltrık's classification the species concept of *Quercus* taxa was quite

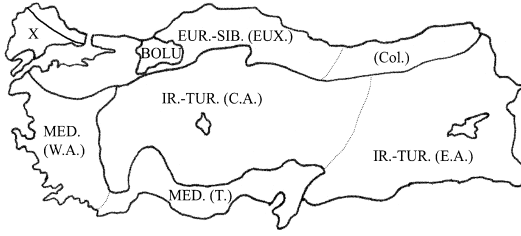


Fig. 1. Location of Bolu and approximate limits of the phytogeographical regions in Turkey. EUR.-SIB (EUX.): Euro-Siberian Region (Euxine province); Col.: Colchic sector of Euxine province. MED.: Mediterranean Region (east Mediterranean province); W.A.: west Anatolian district; T.: Taurus district. IR.-TUR.: Irano-Turanian Region; C.A.: central Anatolia; E.A.: east Anatolia.

narrow and many infra-specific taxa were classified as species. For example, *Q. petraea* has been split into fourteen taxa (Yaltrık 1984) and the total number of Turkish *Quercus* taxa was 35. Hedge and Yaltrık's (1982) classification reduced this number to 18. However, several nomenclatural and typification problems are still unresolved.

Oaks are geographically widespread, out-crossing, wind-pollinated species and exhibit the highest genetic variation among all woody plant species (Kremer & Petit 1993) or among all plant species (Hokanson *et al.* 1993). It is well known that reproductive barriers between oak species are weak (Bacilieri *et al.* 1996, Manos *et al.* 1999, Samuel 1999) and extensive hybridization may occur between species in the same major group or section within the genus. Many

oak species grow in mixed populations where hybridization seems common (Bacilieri *et al.* 1996). Therefore oaks are a taxonomically very problematic group.

Since both quantitative and qualitative morphological characters are easily recorded, intermediacy between putative parents is usually evaluated by means of morphological characters (Stace 1989). Applications of multivariate statistical methods to morphological data sets have demonstrated that such methods can support the hypothesis of hybridization and multivariate analyses are often used in studies of hybridization in oaks (Knops & Jensen 1980, Jensen *et al.* 1984, Jensen 1988, Jensen 1989, Jensen *et al.* 1993, Bacon & Spellengberg 1996, Bruschi *et al.* 2000).

In *Quercus* the leaf characters are the most important in classification (Stace 1989) and in oaks leaf characters may be especially valuable for delimiting species (Jensen *et al.* 1984). Most oak species can be readily identified by their leaf morphology which may also be a good indicator of putative hybridization. One characteristic of hybrids is that their leaves often have irregular and asymmetric shapes (Jensen 1995). Vegetative characters were used reluctantly in groups where reproductive characters are unhelpful in classification (Stace 1989) but it was concluded that quantitative leaf characters appear to be more susceptible to change as a result of hybridization than do quantitative fruit and bud characters (Jensen 1988, Jensen 1989). As a result of the common interspecific hybridization in oaks, hybrid individuals often exhibit intermediate

Table 1. Populations sampled.

Population	Sample no.	Location	Altitude (m)
Gölköy	100	40°42' 857''N, 31°30' 527''E	820
	54	40°39' 483''N, 31°23' 682''E	945
Mudurnu	11	40°35' 627''N, 31°24' 215''E	1037
	10	40°34' 605''N, 31°16' 046''E	1075
	6	40°34' 635''N, 31°16' 348''E	1110
	11	40°35' 053''N, 31°16' 138''E	1183
	9	40°35' 137''N, 31°15' 847''E	1273
Göynük	18	40°19' 064''N, 30°53' 321''E	825
	10	40°20' 234''N, 30°51' 049''E	900
	22	40°23' 130''N, 30°38' 875''E	896
	12	40°30' 896''N, 31°03' 923''E	750
Düzce	28	40°54' 204''N, 31°10' 821''E	617

morphological features between parent taxa although there may be putative hybrids that are not intermediate and intermediacy may occur in many degrees and appearance. Therefore sometimes it is not possible to identify an oak tree to a species, and oak species exhibit such high morphological variation that single characters often fail to allow recognition and discrimination of species or infraspecific entities (Jensen 1988).

It is well known that most tree species produce leaf sizes in a wide range depending upon seasonal and positional effects. Light density influences leaf morphology. For example, the leaves on outer branches have broader, deeper sinuses and a narrower lamina than inner leaves. This shade effect is common in oaks. Therefore it is recommended that leaf collection in taxonomic and systematic studies should be on the same date and after leaf growth has stopped and from the same height and location to avoid taxonomical errors (Blue & Jensen 1988).

This study has two primary goals. First, to evaluate morphological variation in the populations sampled in Bolu, Turkey. Second, to determine if multivariate studies of quantitative morphological variation in these populations would support the hypothesis of hybridization. Finally, results of this study will be compared with similar studies done elsewhere.

Material and methods

Locations and sampling

The populations sampled are located in the province of Bolu, Turkey. One population is located in Düzce, which was a district of Bolu before the earthquake on 12 November 2000 (Fig. 1 and Table 1). Bolu is located in the Euro-Siberian phytogeographical region in Turkey. The climatic regimen of the Black Sea coastal region, which is characterized by fairly mild winters and moderate summers, is dominated by the SE European variant (Zohary 1973). The mean annual temperature of Bolu is 10.1 °C and the mean annual precipitation is 545.6 mm.

Herbarium specimens, additional leaves and fruits samples for identification and statistical analyses were collected from 291 trees in 12

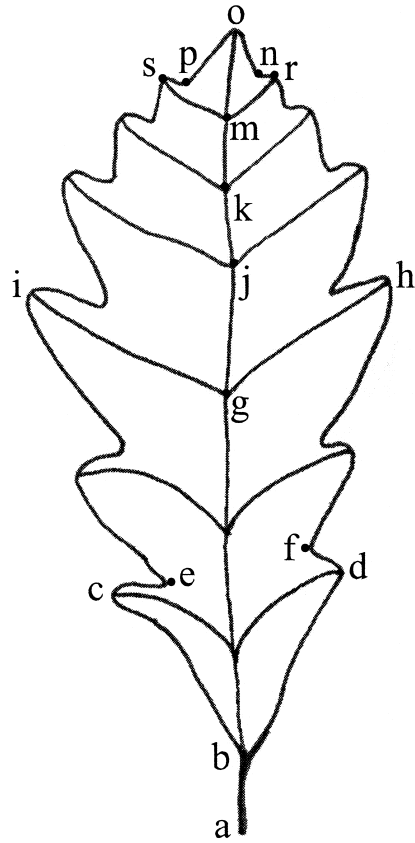


Fig. 2. Definition of oak leaf characters used in PCA. The figure should be consulted in conjunction with Table 2.

populations. For each tree five leaves were collected from different branches to avoid statistical errors. All materials were collected between 20 September and 20 October in 1999 and 2000. All leaf samples were collected at approximately the same level and location after leaf growth had stopped to avoid seasonal and positional variations reported by Blue and Jensen (1988). All samples were pressed in standard presses.

Scoring of leaf characters

Data for 16 morphological leaf characters were measured manually on five leaves from each tree (Fig. 2 and Table 2). Arithmetic means for each tree were recorded to evaluate the variation in each population. Most oak leaves are not perfectly symmetric and not morphologically

uniform on every leaf to the extent that it is easy to locate the reference points (a, b, etc.) shown in Fig. 2, in which a morphologically symmetric leaf is illustrated as an aid for interpretation of the measurements. All leaves were measured in the same orientation and all measurements were taken with the leaf in adaxial view. The measurements (bh, gj, km and cn) were made at the right side on every leaf.

Multivariate analysis

Analysis of variation in leaf characters was carried out by using principal components analysis (PCA) using MVSP version 3.12. Multivariate techniques are particularly useful in taxonomy because the techniques allow comparing samples of organisms taken from different localities or from what are believed to be different taxa. The main purpose of PCA is to describe the total variation in a sample in a few dimensions (Rohlf 1971).

The data matrices consisting of the mean value of each variable for each tree were used to produce variable by variable correlation matrices which were analyzed by PCA. The data matrices were ln-transformed and standardized. Transfor-

mation is desirable to stabilize the variance over their range to prevent conventional standard errors and transforming data can reduce its skewness, resulting in a more interpretable analysis (Sneath & Sokal 1973). A transformation, such as taking the logarithm or square root of the variable, eliminates the undesirable characteristic and improves the symmetry about the mean and the approximation to a normal distribution to provide more natural expressions of the characteristics being studied (Hair *et al.* 1998, Johnson & Wichern 2002).

PCA is a method of partitioning a resemblance matrix into a set of orthogonal axes or components. The basic data matrix was first standardized, which is useful if the variables were measured on different scales or are of different orders of magnitude. The observed variables were standardized to have a mean of zero and a variance of one; each observed variable contributes one unit of variance to the total variance in the data set. The principal components of matrix are computed by its eigenvalues and eigenvectors, which describe the relationship between operational taxonomic units (OTUs) (Sneath & Sokal 1973, Ludwig & Reynold 1988).

Each principal component is proportional to the variance of variables along its axis. Geometrically, the first principal component (accounts for the greatest amount of variance) has a minimum of squared perpendicular projections of all variables on to it; the second (accounts for second largest amount of variance), orthogonal to the first, minimizes the sum of perpendicular distances remaining; and so on for the succeeding axes. Quite often a few principal components will be responsible for most of variance. In other words, not all principal components are needed to summarize the data adequately. In practice, only the first few components that account for the major patterns of variation are retained. Thus, principal component analysis is widely used as a method for summarizing data in a few dimensions while retaining most of the essential information in the sample (Sneath & Sokal 1973).

Table 2. Morphological leaf characters used in principal components analysis. Compare with Fig. 2.

NPLB:	total number of primary leaf lobes
NSLB:	total number of secondary leaf lobes
LBL:	leaf blade length (bo)
LBW:	leaf blade width (at widest point) (jh)
DBW:	the distance between the widest point and the leaf base (bh)
BLW:	basal lobe pair width (cd) ALW: apical lobe pair width (rs)
DAB:	the distance between the apical lobe and basal lobe (cn)
ICVI:	interval between central vein intersections (gj)
IAVI:	interval between apical vein intersections (km)
IBPS:	interval between basal pair of sinuses (ef)
IAPS:	interval between apical pair of sinuses (np)
PTL:	petiole length (ab)
LBL/LBW:	leaf blade length/leaf blade width (bo/jh)
BLW/IBPS:	basal lobe pair width/interval between basal pair of sinuses (cd/ef)
ALW/IAPS:	apical lobe pair width/interval between apical pair of sinuses (rs/np)

Results

Identification of each tree sampled was based on Hedge and Yaltrık's (1982) taxonomic iden-

Fig. 3. OTU projections of PCA for the Abant population. The symbols represent *Quercus pubescens* (open circles), *Q. petraea* (open triangles), *Q. virgiliana* (open squares) and *Q. robur* (crosses).

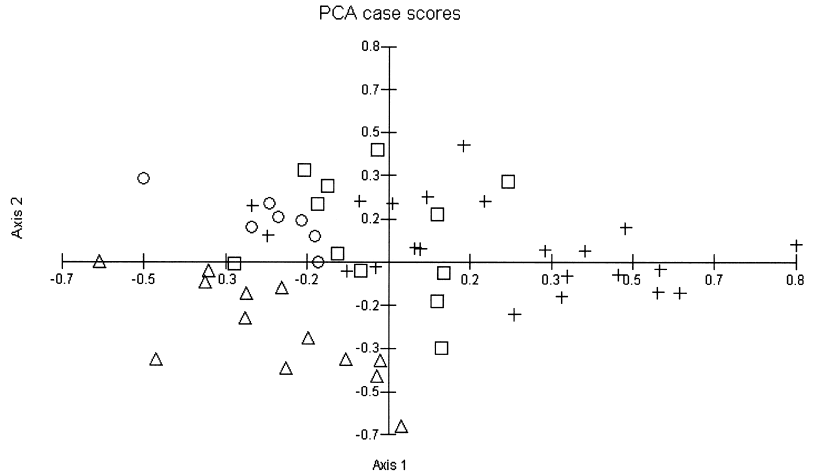
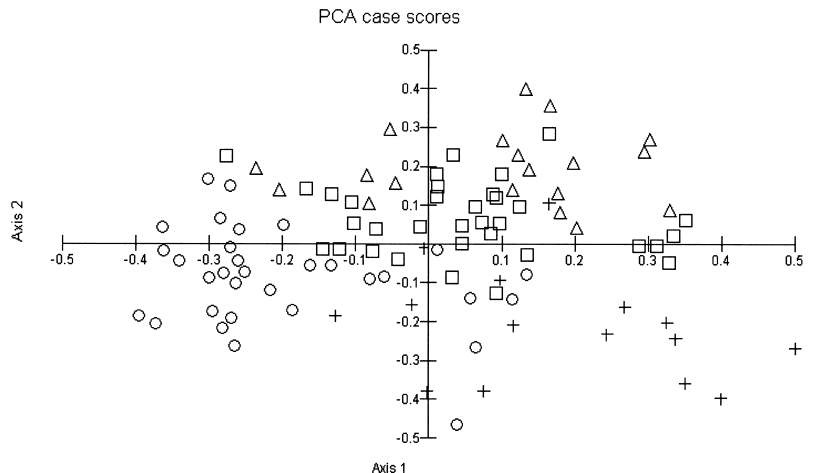


Fig. 4. OTU projections of PCA for the Gölköy population. The symbols represent *Quercus pubescens* (open circles), *Q. petraea* (open triangles), *Q. virgiliana* (open squares) and *Q. robur* (crosses).



tification key for *Quercus*. It was difficult to assign each tree sampled to a given species and the presence of some misplaced OTUs on PCA graphs may be explained by backcross or segregation products, which are similar to one of the parent species (Knops & Jensen 1980).

Figures 3, 4 and 5 show the PCA graphs of Abant, Gölköy and Mudurnu populations where only four taxa of subgenus *Quercus* are found and these PCA graphs do not depict clear separation of the four taxa. In Figs. 3 and 4 some *Q. robur* taxa tend to form more discrete groups while other *Q. robur* individuals are located in mixed groups with other *Quercus* taxa. Cumulative percentages and morphological leaf character loadings on axis 1 and axis 2 for each analysis are listed in Table 3.

Trees of *Quercus virgiliana* did not form discrete groups in any of the analyses (Figs. 3, 4, 5 and 6). *Quercus virgiliana* OTUs are located in mixed groups, with *Q. petraea* in Mudurnu population (Fig. 5), with *Q. pubescens* Göynük population (Fig. 6) and with *Q. pubescens*, *Q. petraea* and *Q. robur* in Abant (Fig. 3) and Gölköy (Fig. 4) populations. The mean leaf measurements of *Q. virgiliana* show that its leaves are usually larger than in *Q. pubescens* and smaller than in *Q. petraea* and *Q. robur*.

Quercus pubescens individuals formed a discrete group in the PCA graph of Mudurnu population (Fig. 5). However, in the PCA graphs of Gölköy and Göynük populations only some *Q. pubescens* individuals formed discrete groups, while other *Q. pubescens* individuals were located

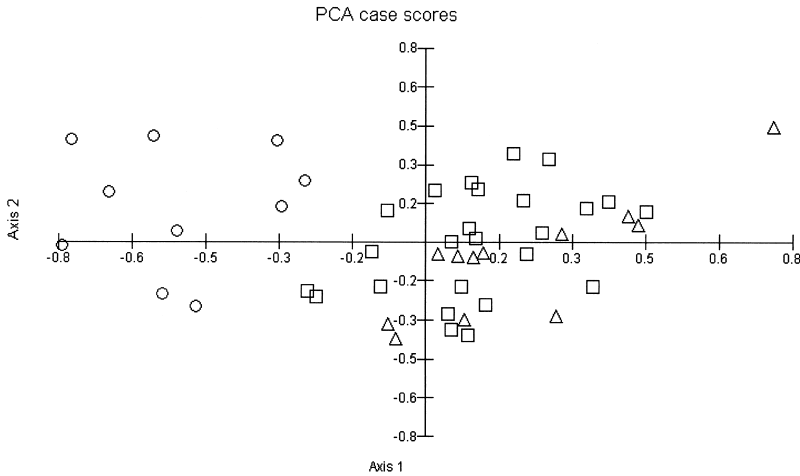


Fig. 5. OTU projections of PCA for the Mudurnu population. The symbols represent *Quercus pubescens* (open circles), *Q. petraea* (open triangles) and *Q. virgiliana* (open squares).

in mixed clusters (Figs. 4 and 5). The distinction between *Q. pubescens* and others is primarily size-related. *Quercus pubescens* leaves are relatively smaller with short petioles and few primary lobes. Four members of subgenus *Quercus* (*Q. pubescens*, *Q. virgiliana*, *Q. petraea* and *Q. robur*) also tend to form a morphological continuum from typically smaller *Q. pubescens* leaves to relatively larger *Q. virgiliana*, *Q. petraea* and *Q. robur* leaves (Fig. 4).

In PCA projections for Göynük and Düzce populations identified as *Quercus cerris*, a

member of subgenus *Cerris*, the individuals showed good separation from *Q. frainetto* (Fig. 7), *Q. pubescens* and *Q. virgiliana* (Fig. 6). Subgenus *Cerris* and subgenus *Quercus* are very different on the basis of morphological leaf characters and distinction in the PCA graph (Fig. 6) is size-related. *Quercus cerris* leaves are typically larger than those of *Q. pubescens* and *Q. virgiliana*. However, *Q. cerris* leaves are smaller than *Q. frainetto* leaves, which have more primary and secondary lobes and a smaller petiole length.

Table 3. Cumulative percentages and morphological leaf character loadings on axis 1 and axis 2 for each analysis.

Population	Abant		Gölköy		Mudurnu		Göynük		Düzce	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Cum. percentage:	30.92	49.71	27.16	45.85	34.86	50.94	47.56	62.58	50.7	66.8
Character										
NPLB	0.066	-0.108	0.21	0.298	0.09	-0.558	0.275	-0.294	0.338	-0.077
NSLB	0.164	0.383	0.058	-0.357	-0.034	-0.145	0.31	-0.231	0.328	0.03
LBL	0.342	-0.282	0.332	0.078	0.393	-0.162	0.349	0.008	0.284	0.278
LBW	0.327	-0.153	0.396	0.035	0.385	-0.118	0.349	0.038	0.305	0.23
DBW	0.333	-0.11	0.386	-0.019	0.198	-0.17	0.316	0.059	0.289	0.251
BLW	-0.249	-0.268	0.156	0.269	0.278	-0.002	0.274	0.216	-0.304	0.007
ALW	0.226	-0.106	0.257	-0.203	0.23	0.462	0.035	0.587	-0.182	0.452
DAB	0.346	-0.201	0.408	0.04	0.341	-0.298	0.349	-0.065	0.314	0.195
ICVI	0.365	-0.092	0.317	-0.275	0.317	0.084	0.341	0.025	-0.206	0.278
IAVI	0.315	-0.073	0.289	-0.307	0.303	0.1	0.292	0.016	-0.212	0.395
IBPS	-0.205	-0.427	0.126	0.39	0.263	0.271	0.147	0.092	-0.243	-0.05
IAPS	0.152	-0.274	0.258	0.052	0.276	0.382	-0.028	0.59	-0.138	0.429
PTL	-0.2	-0.332	0.031	0.383	0.217	-0.161	0.191	0.238	-0.319	0.037
LBL/LBW	0.012	-0.184	-0.071	0.15	-0.03	-0.086	-0.098	-0.131	-0.13	-0.194
BLW/IBPS	0.021	0.212	-0.016	-0.268	-0.025	-0.06	0.091	-0.153	-0.11	-0.032
ALW/IAPS	0.254	0.379	-0.085	-0.31	-0.128	0.152	0.085	0.074	-0.035	0.312

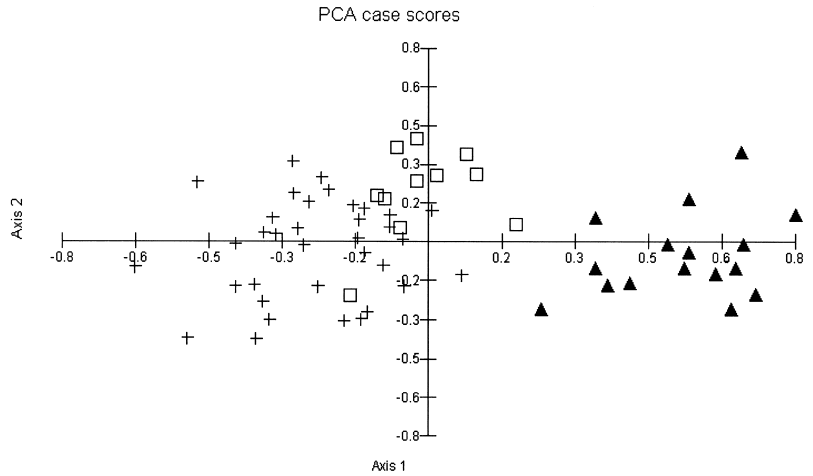


Fig. 6. OTU projections of PCA for the Göynük population. The symbols represent *Quercus pubescens* (crosses), *Q. virgiliana* (open squares) and *Q. cerris* (solid triangles).

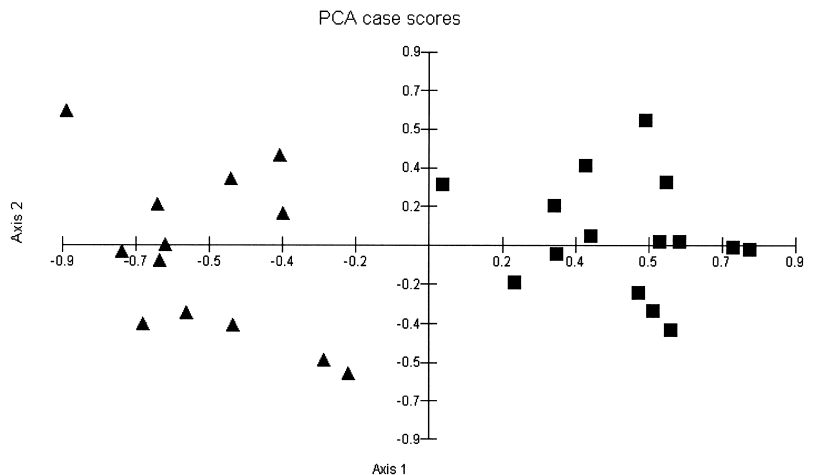


Fig. 7. OTU projections of PCA for the Düzce population. The symbols represent *Quercus frainetto* (solid squares) and *Q. cerris* (solid triangles).

Discussion

In this study, PCA analyses could not separate clearly the four taxa belonging to subgenus *Quercus* and in Fig. 4 the species tend to form a morphological continuum instead of separate or clear clustering. However, some individuals of the three taxa (*Q. pubescens*, *Q. petraea* and *Q. robur*) locate out of the mixed groups (Figs. 3, 4 and 5). Among European oaks, the greatest taxonomic discrimination problems occur in the subgenus *Quercus*, especially the complex of *Q. robur*–*Q. petraea*–*Q. pubescens* (Bruschi *et al.* 2000) and it is well known that they frequently hybridize (Bussotti & Grossoni 1997). The high intraspecific variation also does not allow clear separation of the taxa.

Three PCA projections (Figs. 3, 4 and 5) show that *Quercus virgiliana* taxa locate in the mixed groups with *Q. pubescens*, *Q. petraea* and *Q. robur* taxa. The continuum of leaf size extending from relatively smaller *Q. pubescens* leaves to relatively larger *Q. petraea* leaves supports the hypothesis of hybridization between these two species. Bussotti and Grossoni (1997) studied the European and Mediterranean oaks' abaxial leaf surface micromorphology by scanning electron microscope and reported that *Q. pubescens* could not be separated from *Q. virgiliana*. Hedge and Yaltrık (1982) separated *Q. virgiliana* from *Q. pubescens* by a larger petiole, larger, flat leaves, often rounded lobes, a rounded base and often shortly pedunculate fruits (Davis 1982). Yaltrık (1984) treated the similarities between

Q. pubescens and *Q. virgiliana*. Because of the taxonomic problems, some systematists accept that *Q. virgiliana* is a doubtful species. A close affinity between *Q. pubescens* and *Q. virgiliana* has also been reported in Austria and the specific status of the latter was questioned (Samuel *et al.* 1995). According to Samuel *et al.* (1995), Bussotti and Bruschi (2000) and Bussotti and Grossoni (1997), *Q. virgiliana* might be a hybrid between *Q. pubescens* and *Q. petraea*. This suggestion is supported by our study.

In the Abant and Gököy populations (Figs. 3 and 4), some *Quercus robur* individuals formed discrete groups at the right side of the graphs while other individuals of the same taxon located in mixed groups with *Q. virgiliana*, *Q. petraea* and *Q. pubescens*. Therefore, it can be suggested that leaf characters employed in this study are successful for classifying *Q. robur* by using a multivariate approach. However, *Q. robur* individuals located in the mixed clusters with other *Quercus* taxa may be hybrids. It is not possible to find out the other parent taxon of these hybrid *Q. robur* individuals because multivariate analyses do not allow identification of segregation or hybridization products or OTUs as F_1 's, F_2 's, etc. If hybridization has taken place for a long time and as a result of introgression, backcross or segregation products will often be quite similar to one of the parental taxa (Knops & Jensen 1980). Dumolin-Lapegue *et al.* (1999) reported that the significant cy(mt/cp)DNA differentiation between *Q. pubescens* and *Q. robur* and the rarity of morphologically intermediate individuals between these species indicate a more limited introgression than for the other species pairs. It was reported that *Q. robur* and *Q. petraea* show complete absence of cpDNA differentiation at a continental (Europe) scale and it was argued that interspecific gene flow might have happened after a prolonged contact in glacial refugia (Ferris *et al.* 1993). *Quercus robur* and *Q. petraea* are completely outcrossing, closely related species with a wide sympatric distribution over Europe and the genetic contribution of *Q. petraea* to *Q. robur* was estimated to vary from 17% to 47% depending upon the populations used as reference while the genetic contribution of *Q. robur* was estimated to be negative. However, *Q. petraea* can more easily hybridize with *Q. robur*

than with *Q. pubescens*. *Quercus petraea* ovules are preferentially fertilized by other extreme *Q. petraea* genotypes while *Q. robur* can be easily fertilized by *Q. petraea* resulting in more different progenies from *Q. robur* (Bacilieri *et al.* 1996). Because of extensive introgressive hybridization and reticulate evolution between infrageneric taxa in *Quercus*, it is possible that *Q. virgiliana* is the extensive introgressive hybridization product of *Q. robur*, *Q. petraea* and *Q. pubescens*. Hybridization between these three oak species is well known and their hybrid progenies may produce new backcross or segregation products. In Austria, allozyme study of nine enzyme systems showed that *Q. robur*, *Q. petraea* and *Q. pubescens* are genetically closely related and there is no diagnostic character that would allow clear discrimination among the three taxa (Samuel *et al.* 1995). The existence of species-specific alleles was reported between *Q. petraea* and *Q. pubescens*, but only at a low frequency in nuclear microsatellite analysis (Bruschi *et al.* 2000). By the nuclear genome studies of *Q. robur* and *Q. petraea* the estimated extremely low level of nucleotide divergence between these species is 0.5% on average, but up to 3.3% in the most discriminating regions (Bodenes *et al.* 1997).

Quercus cerris, a member of subgenus *Cerris*, was clearly separated from the three taxa (*Q. pubescens*, *Q. virgiliana* and *Q. frainetto*) of section *Quercus* in the PCA projections of Göknyük and Düzce populations (Figs. 6 and 7). Subgenus *Cerris* and section *Quercus* are very distinct on the basis of morphological variables and this fits well with the significant cpDNA differentiation (Manos *et al.* 1999) and allozyme differentiation (Samuel *et al.* 1995).

Our PCA findings allow some conclusions. First, it appears that there is hybridization involving four taxa of subgenus *Quercus* (*Q. robur*, *Q. pubescens*, *Q. virgiliana* and *Q. petraea*). This is evident in the high degree leaf variation in Gököy, Mudurnu, Göknyük and Abant populations. Morphological variation and field observations suggest that there is gene flow among the four taxa of the subgenus *Quercus* in the populations sampled in this study. Gene flow is an important factor in population genetics, shaping the diversity of species (Jensen *et al.*

1993, Dumolin-Lepague *et al.* 1999). This study suggests that in the four populations sampled (Gölköy, Mudurnu, Göynük and Abant) inter-specific gene flow occurs and is associated with great morphological variation. The maintenance of genetic diversity in sympatric *Quercus* species is associated with complete out-crossing (Bacilieri *et al.* 1996) and it seems clear that the evolution and long-term management of the sympatric *Quercus* species should not be considered independently (Jensen *et al.* 1993). Second, in this study, quantitative leaf characters appear to be susceptible to change as a result of hybridization. Leaf characters analyzed in this study demonstrated a morphological continuum (Fig. 4) and high degree leaf variation as a result of hybridization. Third, results of this study are quite similar with those of other related studies that were done in other countries. The findings of intermediate individuals and a morphological continuum (Fig. 4) were accepted as evidence of the hypothesis of hybridization, as reported by other workers (Jensen 1988, Jensen 1989, Dupouey & Badaeu 1993, Jensen 1995, Bacilieri *et al.* 1996).

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