

Original article

**Taxonomical impact of morphological variation
in *Quercus robur* and *Q. petraea*:
a contribution to the hybrid controversy**

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Summary — Numeric - taxonomical analysis of the complex *Quercus robur*-*Q. petraea* showed that variability within each of the 2 species is so wide that none of the features considered is suitable for clear distinction. By using multivariate statistical analysis, it was possible to differentiate 2 distinct groups and thus to locate intermediate individuals. However, designating such morphologically intermediate individuals as hybrids remains questionable because it is not possible to find the exact limits of each group. For practical reasons, such limits have often been defined more or less arbitrarily without taking into account the wide variability of the 2 species. This explains the widely accepted view that they hybridize frequently, a view that cannot be supported by the findings of this project.

***Quercus robur* / *Quercus petraea* / taxonomy / morphological variation / hybridization**

Résumé — Impact taxonomique de la variation morphologique chez *Quercus robur* et *Q. petraea* : une contribution à la controverse sur les hybrides. L'analyse taxonomique numérique du complexe *Quercus robur*-*Q. petraea* montre que la variabilité à l'intérieur de chacune des 2 espèces est si grande qu'aucune des caractéristiques considérées ne permet une claire démarcation. En utilisant les statistiques multivariées, il a été possible de différencier 2 groupes distincts et ainsi de localiser les individus intermédiaires. Pourtant, désigner de tels individus morphologiquement intermédiaires comme hybrides reste contestable, parce qu'il n'est pas possible de définir une limite exacte pour chaque groupe. De telles limites ont souvent été définies, pour des raisons pratiques, de manière plus ou moins arbitraire. Elles ne tenaient pas compte de la grande variabilité des deux espèces. Cela explique l'opinion répandue selon laquelle elles s'hybrident fréquemment, opinion qui ne peut être soutenue par les résultats de cette étude.

***Quercus robur* / *Quercus petraea* / taxonomie / variation morphologique / hybridation**

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INTRODUCTION

Pedunculate and sessile oak (*Quercus robur* L. and *Q. petraea* (Matt) Liebl) can hybridize, a fact proved by numerous crossing experiments (Dengler, 1941; Rushton, 1977; Aas 1991). However, deductions on the frequency of hybridization under natural conditions are a different matter. Investigations on this subject revealed different results (see review in: Gardiner, 1970; Olsson, 1975; Wigston, 1975; Rushton, 1978, 1983; Dupouey, 1983; Kissling, 1983; Grandjean and Sigaud, 1987).

It is quite possible that there are regional differences in the occurrence of hybrids. In any case, conclusions are linked to the method: the designation of a particular individual or of parts of a population to a clearly defined group ('pure' species / hybrid) depends greatly upon which part of the variation observed is attributed to hybridization, and which part to the variation of the 'pure' species. Since these designations have been arrived at by different means it is not surprising that the results vary.

The aim of the study was to describe the morphological variability of the complex *Quercus robur-petraea* using numeric-taxonomical methods. The focal point was to find out how far morphological characteristics are suitable for identification of hybrids. How abundantly hybrids occur in different regions was of minor importance.

MATERIALS AND METHODS (for details see Aas, 1988)

Oaks were chosen from 30 different stands in Germany and Poland (stands of pedunculate oak, sessile oak and mixed stands; the number of specimen trees per stand varied between 5 and 20). The majority of the trees were sampled randomly. Of special interest were intermediate

trees, *ie*, trees that at the time of sampling could not be assigned to the respective species. For this reason, some stands were examined specifically for such trees, and 33 of them (12%) were included in the total of 279 trees.

For each tree the following 10 characteristics were examined: 1) length of petiole (mm); 2) length of lamina (mm); 3) width of lamina (mm); 4) shape of lamina (width at 0.25 length of lamina / width at 0.75 length); 5) depth of sinuses (index value); 6) leaf base (5 shape values ranging from 0=extremely cordate to 4= tapering); 7) number of lobes; 8) sinus-veins (relative frequency of lateral veins running to sinuses in the middle portion of the leaf; values obtained ranged from 0 to 1.0 = absent on all leaves, 1 = present on all leaves, 0.3 = present on 3 out of 10 leaves examined); 9) clustered hairs (occurrence on lower leaf surface: 0 = none, 1 = few, 2 = many); 10) length of peduncle (mm).

For each tree, 10 leaves and 10 infructescences were analyzed. The statistical analyses (carried out with BMDP, Bollinger *et al*, 1983) were based on the arithmetic means of each tree. For the multivariate statistical analysis, the variable length of peduncle was not included, because the respective values were not available for all trees.

RESULTS

Cluster analysis (City-block distance, centroid linkage; BMDP 2M) allows the 279 trees to be divided into two large (1 and 2) and one small group (3) (fig 1). In table 1, the mean values are indicated for each of the 3 groups, and the F-values of the variance-analytical comparison of groups 1 and 2 (Welch-Test, BMDP 7D) are included. None of the analyzed features allows these 2 groups to be separated without overlap (fig 2). The best distinguishing feature is 'sinus-vein', which has a very small overlap; almost complete overlap can be observed for 'length of lamina'. A good differentiation between the 2 groups can be achieved with the variable 'clustered hairs' (fig 3): this characteristic can be observed on all trees of group 2, but only on few

Table I. Comparison of the 3 groups (grouping by cluster analysis): mean values and *F*-values of the analysis of variance between groups 1 and 2 (*F*-values indicate the degree of difference between these 2 groups).

<i>Variable</i> ^a	<i>Group 1</i> (<i>n</i> = 138)	<i>Group 2</i> (<i>n</i> = 127)	<i>Group 3</i> (<i>n</i> = 14)	<i>F-value</i>
Sinus-veins	0.93	0.15	0.43	2255
Clustered hairs	0.14	1.86	0.71	1254
Length of petiole (mm)	6.5	15.8	9.1	742
Length of peduncule ^b (mm)	28.7	4.3	–	443
Leaf base	1.8	3.0	3.5	334
Number of lobes	4.6	6.0	6.2	243
Shape of lamina	0.69	0.84	0.66	180
Depth of sinuses	2.36	1.74	1.77	157
Length of lamina (mm)	95.2	99.3	94.3	7
Width of lamina (mm)	57.8	59.1	52.8	2

^a For details concerning these variables, see *Materials and Methods*. ^b $n_{\text{group 1}} = 87$; $n_{\text{group 2}} = 72$.

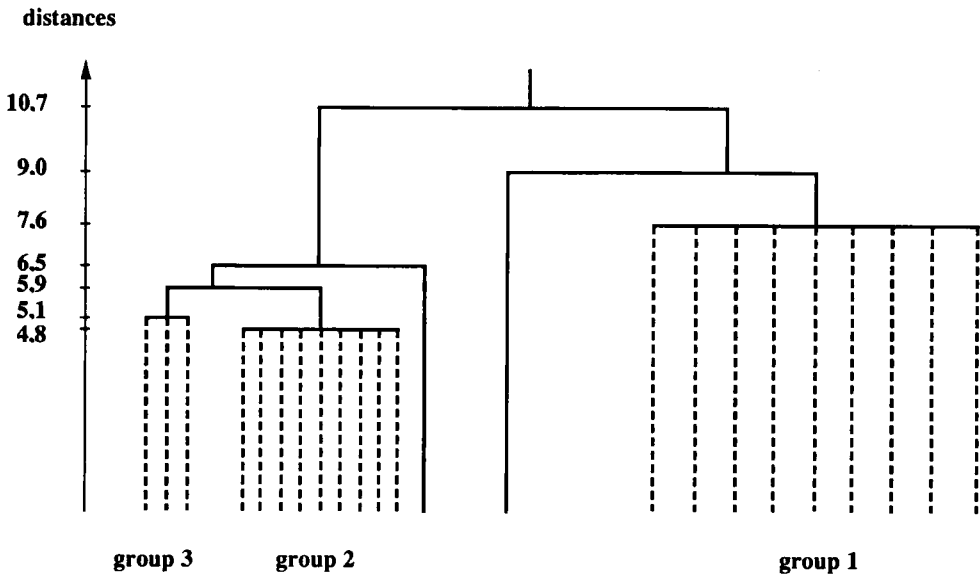


Fig 1. Dendrogram of the cluster analysis revealing 3 groups of morphologically similar oaks. The broken lines indicate the further differentiation of the 3 groups.

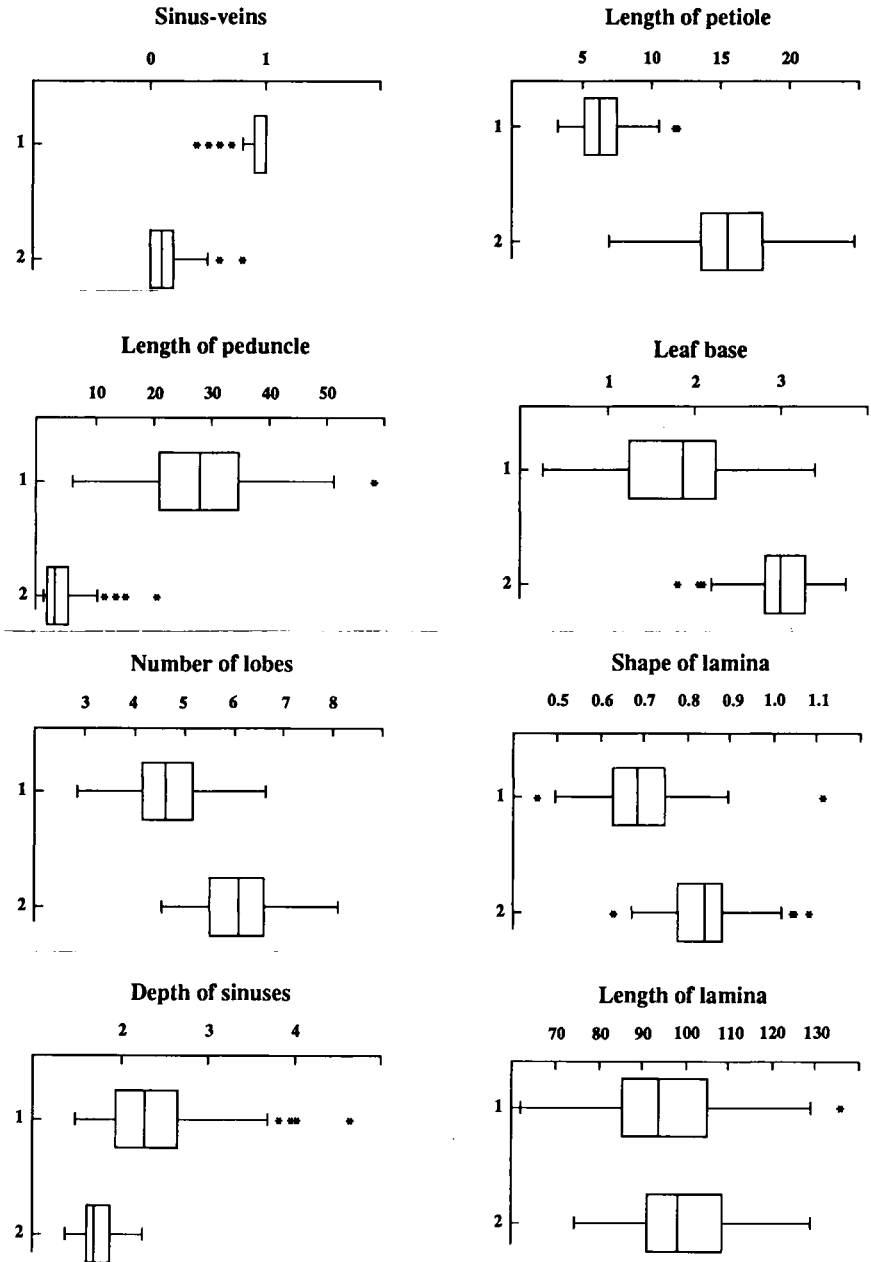


Fig 2. Comparison of groups 1 and 2 (1 and 2 on the ordinate) using box plots of 8 of the characteristics examined. The box is the interquartile range (Hspread), the median the centre vertical line in the box. The lines emanating from each box extend to the smallest and largest observation that are less than 1.5 Hspread from the end of the box. Observations outside this range are marked with asterisks.

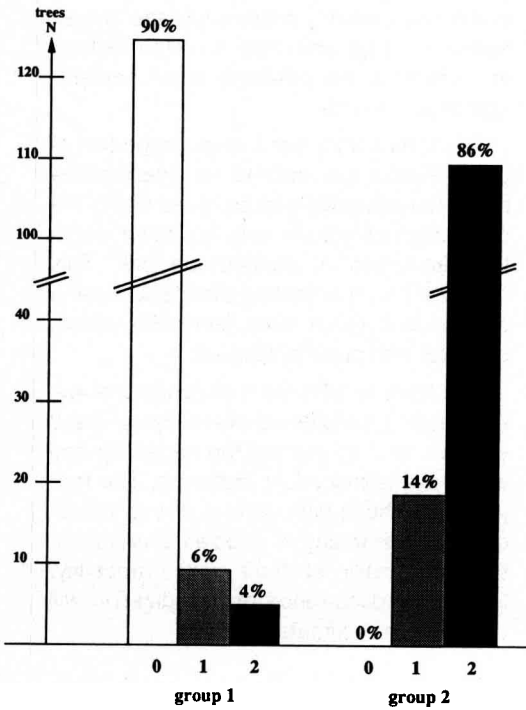


Fig 3. Comparison of groups 1 and 2 : histogram of the variable 'clustered hairs' (0 = none, 1 = few, 2 = many clustered hairs on the lower leaf surface).

oaks of group 1. A separation without any overlap is possible with a discriminant function (Stepwise Discriminant Analysis, BMDP 7M) (fig 4) using the following variables (between parentheses respective discriminant coefficients): sinus-veins (4.57); clustered hairs (-1.15); (length of petiole) (-0.88); (leaf base)2 (-0.20); shape of lamina (-5.10); number of lobes (-0.42); length of lamina (0.01); constant 7.66.

DISCUSSION

The morphological discontinuity of the investigated oaks could be shown by using cluster analysis. Groups 1 and 2 are distinct subunits of the complex, which can be separated without overlap with the help of several morphological characteristics. The features of each group (see table I) indicate that group 1 represents pedunculate oak and group 2 sessile oak. For group 3, such an assignment is not possible.

Pedunculate and sessile oaks, grouped in this way, show an extremely wide variation. Since all respective values of both species overlap, none of the characteristics considered are suitable for a clear dis-

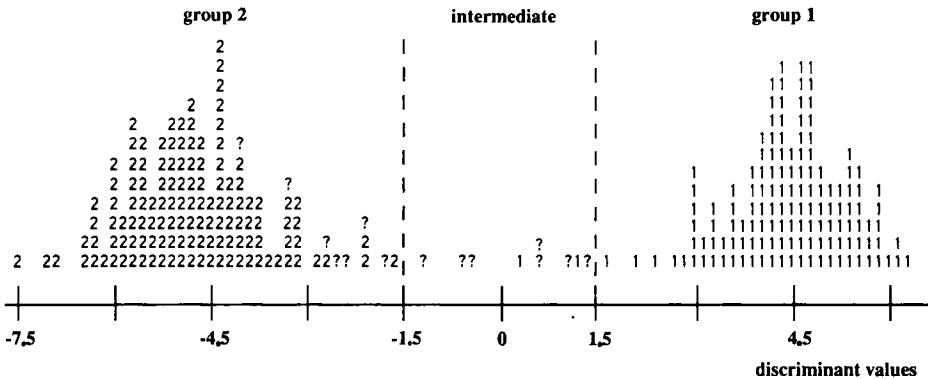


Fig 4. Distribution of the discriminant values of all 279 oaks (grouping by cluster analysis: 1 = oak from group 1, 2 = oak from group 2, ? = oak from group 3).

inction. A characteristic regarded as intermediate can always be assigned to at least one of the 2 species and is thus not sufficient proof for hybrid origin. The degree of overlap varies greatly depending upon the characteristic considered. Unlike the commonly used diagnostic features — 'length of petiole', 'shape of lamina' or 'length of peduncle' — the 'sinus-veins' and 'clustered hairs' show a small overlap and therefore have more diagnostic value.

In literature (reviewed in Aas, 1988), the distinction between pedunculate and sessile oaks is usually based on a much smaller intraspecific variation. This can be demonstrated with the example 'length of petiole', commonly considered a reliable distinctive feature. According to *Flora Europaea* (Tutin *et al*, 1964), it is up to 5 mm in pedunculate oak and between 18 and 25 mm in sessile oak. This variation covers about 60% of the trees classified here as pedunculate oaks and only 30% of the sessile oaks.

The question arises as to whether the variation in pedunculate and sessile oaks found as described is really species-related or if it could have been influenced by gene exchange between the 2 oaks. The morphology of the trees in each of the two groups (1 and 2) is so similar that within them no distinct subunits can be detected in either the dendrogram (cluster analysis, fig 1) or the distribution of the discriminant values (fig 4). We cannot discount the possibility that trees of hybrid origin (*eg*, backcrosses) are included in groups 1 and 2. However, such individuals cannot be identified morphologically. Thus they have to be treated taxonomically as either pedunculate or sessile oak.

The 2 species can be separated without any overlap by using multivariate statistics (discriminant analysis). Therefore, it is possible to locate intermediate individuals. Oaks with discriminant values close to 0 are hybrids with a high probability. Howev-

er, the problem remains, where to draw the limits of the 2 species and the intermediate status. By defining subjectively the values between -1.50 and 1.50 as intermediate, we arrived at the relatively small percentage of 3% hybrids.

It is remarkable that a large proportion of group-3-oaks (*ie*, defined as intermediate by cluster analysis) can be found within the distribution of sessile oak, but none within the distribution of pedunculate oak. This may well be an indication that backcrossing of hybrids is much more likely with sessile oak than with pedunculate oak.

We have to assume that occasional hybridization promotes introgression of the 2 species, thus increasing the variability and with it the taxonomical problems. The major part of these difficulties is due to insufficient understanding of species characteristics, especially of their wide variability. Hence the occurrence of hybridization will often be overestimated.

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