

A multivariate analysis of introgression between *Quercus robur* and *Q. petraea* in The Netherlands

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SUMMARY

Hybridization and introgression between *Quercus robur* and *Q. petraea* was investigated in 12 Dutch populations, using multivariate analysis. Compared with the reference groups, the differences between the two taxa are slight, but distinct. The *Q. petraea* types differ more from their reference group than the *Q. robur* types, possibly due to greater selection pressure. In most populations a range of specimens occurs between pure *Q. robur* and pure *Q. petraea*. The latter category is poorly represented, and actual F_1 - and F_2 -hybrids are most uncommon. Products of introgression between primary hybrids and *Q. robur* as well as *Q. petraea* constitute an important part of the populations. Hybridization and introgression is partly due to planting of *Q. robur* by man. In the natural population of the Meinweg a gradient is established between *Q. robur* in the lower, moist levels and *Q. petraea* in the higher, relatively dry levels.

Key-words: multivariate analysis, introgression, *Quercus robur*, *Q. petraea*.

INTRODUCTION

Relationship

In terms of macromorphology *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. are closely related taxa that belong to the subgenus and section *Quercus* (Schwarz 1964; Hedge & Yaltirik 1982). Only slight differences have been found in pollen morphology between the two taxa (van der Spoel-Walvius 1963; Dupont & Dupont 1972; Smit 1973). Brookes & Wigston (1979) established no significant differences between the two taxa in the major plant nutrients of the acorns for nitrogen, phosphorus, calcium, potassium and magnesium, and the minor element sodium. In most characteristics both taxa show a large infraspecific variation, particularly *Q. robur*, and for several characteristics the values overlap.

Differences and taxonomy

In spite of the above-mentioned similarities, *Q. robur* and *Q. petraea* are usually conceived as different species. A summary of the morphological differences between the Central-European populations of the two species is given in Table 1 (cf. Ascherson & Graebner 1911; Schwarz 1936–1937; Camus 1934–1948; Weimarck 1947a; Reching 1957; Cousens 1965; Jones 1968; Mátyás 1970; Olsson 1975a; Rushton 1979; Kissling 1980b). Subspecific

Table 1. Main discrimination characteristics for *Q. robur* and *Q. petraea*, as found in Central-European populations, from the literature

Characteristics	<i>Q. robur</i>	<i>Q. petraea</i>
Leaf shape	(Oblong) obovate; largest width at <i>c.</i> one-third from the top	(Oblong) ovate (to obovate) largest width at <i>c.</i> half
Leaf margin	Lobes asymmetrical, the lowest ones small, becoming larger towards the top; sinuses usually up to more than one-third of the leaf-half	Lobes symmetrical, all more or less equal; sinuses usually up to less than one-third of the leaf-half
Number of lobes per leaf-half	4-7(-8)	5-8(-10)
Intercalary veins in the leaf	Usually many present	Absent or a few present in the lower part
Leaf base	Auricles strongly (moderately) developed; base cordate	Auricles absent or weakly developed; base slightly cordate (or cuneate)
Indumentum on abaxial side of the leaf	Usually absent	Many (few) stellate hairs present
Petiole length	(2-)3-6(-7) mm	12-24(-30) mm
Peduncle length	30-60(-80) mm	(0-)2-10(-15) mm
Cupula scales	Imbricate, in spirals with free apex	Slightly bulged, but apex adpressed; not imbricate or spirally arranged

variation of the two species has been described in detail, including the formae-level, by Schwarz (1936-1937) and Camus (1934-1948). For *Q. robur* variation has been established in leaf and fruit characters, the ornamentation of the pollen wall (Dupont & Dupont 1972), the quantities of agglutinines in the leaves (Krahl-Urban 1955), and the peroxidase isoenzyme patterns (Olsson 1975c).

Geography and ecology

Q. robur can be considered as a temperate European flora element, and *Q. petraea* as a subMediterranean to Central-European mountain flora element (Rechinger 1957; Schwarz 1962). Krahl-Urban (1957) established differences between local populations of both *Q. robur* and *Q. petraea* for a number of ecophysiological characters, e.g. the occurrence of lammas shoots and the susceptibility to mildew. Schwarz (1936-1937) remarks that *Q. robur* shows its largest morphological variation along a line from Central-France to Hungary.

Although the two species are often found under the same ecological conditions (Jones 1959; Ellenberg 1968), the following differences in ecological preferences can be made. *Q. robur* requires 140 days per year with temperatures above 12°C and *Q. petraea* 230 days with temperatures of over 6°C, which means that the latter withstands a continental climate better (Gams 1924). *Q. petraea* grows best on dry, well-drained, stony soil which is relatively poor in minerals (Rechinger 1957; Jones 1959), at a pH of 4.7-5.1 (Weimarck 1947b). *Q. robur*, however, prefers a moist, loamy sand that contains more minerals, and has a somewhat higher pH (van den Burg 1981). Ninety-year-old *Q. robur* trees died on a sandy soil near Hannover when the ground water receded by approximately 1 m, the

Table 2. Mature fruits as a percentage of the number of fertilized flowers for self- and cross-fertilization of *Q. robur* and *Q. petraea* and hybridization of both (mean, minimum and maximum values). Dengler (1941) made observations for 7 years in Central Europe and Rushton (1977) for 3 years in England

	Dengler	Rushton
Self-fertilization <i>Q. robur</i>	1 (-)	19 (10-26)
Self-fertilization <i>Q. petraea</i>	1 (-)	40 (27-48)
Cross-fertilization <i>Q. robur</i>	45 (11-59)	51 (31-62)
Cross-fertilization <i>Q. petraea</i>	44 (20-100)	44 (26-59)
<i>Q. robur</i> × <i>Q. petraea</i>	4 (0-15)	0.7 (0.3-1.0)
<i>Q. petraea</i> × <i>Q. robur</i>	0.5 (0-5)	0.5 (0.1-0.7)

Q. petraea trees in the same area were undamaged (Oelkers & Meine 1923). The latter species is morphologically better suited to dry conditions having motile leaves with a thick cuticle and stellate hairs (Staf & Teerink 1936). A clear ecological differentiation between the two species is found in Yugoslavia, where *Q. robur* grows in moist river valleys and *Q. petraea* in the drier hills and mountainous areas (Jones 1959; Cousens 1965).

Detailed ecological studies on *Q. robur* and/or *Q. petraea* in The Netherlands and Belgium have been carried out by Vlieger (1935), Staf & Teerink (1936), Clason (1957), van Rompaey (1957), Smeets (1957) and Bakker (1969). The impact of pig herds on oak woods has been comprehensively described by ten Cate (1972).

Reproduction and hybridization

From the analyses of morphological characters, hybridization and introgression between *Q. robur* and *Q. petraea* has been shown for Thüringen and other parts of Central-Europe north of the Alps and Karpathians (Schwarz 1933, 1962), the Swiss Jura (Kissling 1980a, b), the Vosges (Becker 1972), southern Sweden (Gardiner 1970; Olsson 1975a, b), England (Wigston 1975; Rushton 1978), Scotland and Ireland (Cousens 1963, 1965). In southern Europe other species as well as *Q. robur* and *Q. petraea* are involved in hybridization, e.g. in Hungary *Q. dalechampii* Ten., *Q. frainetto* Ten., *Q. polycarpa* Schur, *Q. pubescens* Willd. and *Q. virgiliana* (Ten.) Ten., which all belong to the subgenus *Quercus* (Mátyás 1970). As a result, the taxonomy of these species is complex.

Hybridization and introgression is assisted by the fact that *Q. robur*, *Q. petraea* and the other *Quercus* taxa (mentioned above) are protandrous wind-pollinators.

In Table 2 the results are given of two pollination and hybridization experiments carried out by Dengler (1941) and Rushton (1977), from which it can be concluded that both species are virtually allogamous. However, poor results were obtained from artificial hybridization. In natural situations a number of abiotic factors, e.g. pH and moisture of the soil, rainfall and the lowest temperature in February (Becker 1972; Rushton 1977; Kissling 1980b), determine the hybridization pattern and the direction of introgression, through selection of genotypes in the seedling stage.

Aim of this study

Hybridization between *Q. robur* and *Q. petraea* was investigated to establish whether the two taxa are distinct in The Netherlands and to determine what their status is compared with the situation in the central part of their area. This was carried out by comparing, on a



Fig. 1. Position of the Dutch *Quercus* populations studied. 1. Schoorlse Duinen, 2. Apeldoornse Kroondomeinen, 3. Ugchelse Bos, 4. Hoenderlose Bos, 5. Terletse Veld, 6. De Imbosch, 7. Loenense Bos, 8. Bergen Dal, 9. Meinweg, 10. Ravensbos, 11. Gerendal, 12. Savelsbos.

basis of morphological characters, 12 Dutch populations with one reference group for each species of Central- and South-European origin. For one Dutch population (Meinweg) the relationship between the hybridization pattern and the abiotic environment was investigated, because here a seminatural situation is encountered.

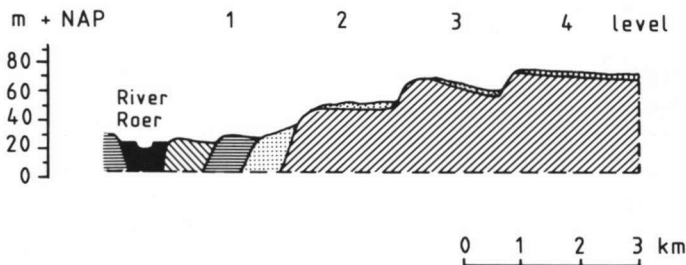
MATERIAL AND METHODS

Dutch populations

Figure 1 shows the location of the 12 Dutch *Quercus* populations studied, in Table 3 their co-ordinates according to the topographic maps of The Netherlands (1:25 000), altitude

Table 3. Co-ordinates, altitude and sample size for the Dutch *Quercus* populations studied. Population 9 comprises six subpopulations

Population number	Co-ordinate	Height above sea-level (m)	Number of trees sampled (n)
1	523.5/108.1	c. 30	17
2	473.5-474.0/187.5-188.8	70-90	72
3	465.5/188.5	c. 70	25
4	461.4/188.5	70-75	23
5	452.0/194.4	c. 75	17
6	453.2/195.6	90-95	26
7	457.1-457.8/196.7-197.2	50-70	23
8	425.5-426.0/192.2-192.6	45-80	19
9.1	352.0-355.0/204.0-208.5	c. 45	13
9.2		47-55	29
9.3		45-65	39
9.4		c. 70	29
9.5		58-75	16
9.6		c. 75	44
10	321.6/185.5	90-120	17
11	316.1-316.8/187.8-188.0	100-130	24
12	313.3-313.7/180.2-180.4	100-125	22

**Fig. 2.** Geological and pedological data for the *Quercus* population site 9 (Meinweg). (//) Mid-pleistocene sand and gravel, (•••) cover-/drift-sand, (||) loess, (≡) late-glacial clay, (≡) late-glacial sand, (■) holocene clay.

and sample size are given. In Fig. 2 geological and pedological data are presented for the site where the Meinweg population (9) grows: subpopulation 9.1 and 9.2 are found on level 2, 9.3 on a transition area of level 2-3, 9.4 on level 3, 9.5 on a transition area of level 3-4 and 9.6 on level 4.

Reference groups

Reference groups for both taxa were carefully taken from pure specimens, i.e. those that show the characteristics described in the literature; in particular in Schwarz (1936-1937).

The reference group of *Q. robur* contains 61 specimens, of which 53 were selected from the collections made by J. Cousens in 1963 from populations in Yugoslavia (River Sava area in Slavonia). To this were added eight specimens, selected from other herbaria. They

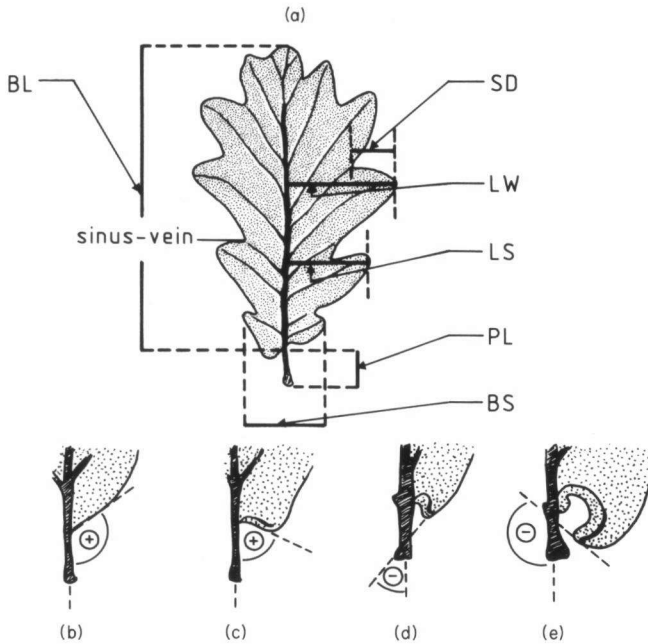


Fig. 3. *Quercus* leaf characters: (a) whole leaf, (b-e) leaf bases (for further explanation see section 'Character choice').

originated from Rumania, Yugoslavia, Hungary, Austria, West Germany, France and Poland (2x).

Of the 53 specimens that formed the reference group of *Q. petraea*, 15 were sampled by the second author in Austria (Weiner Wald). The other 38 were selected from herbarium specimens and originated from Albania (1x), Rumania (2x), Hungary (3x), Yugoslavia (10x), Italy (1x), Austria (5x), Czechoslovakia (2x), Poland (2x), East Germany (2x), West Germany (7x), Luxembourg (1x), and France (2x).

Sampling methods

Because leaves can vary considerably in shape and size within a tree, depending on the position, exposure and season (Cousens 1962, 1965), samples (collected by the authors) were taken in June or July, from the southeastern side of a tree-top, and from the middle part of a branch.

In the Dutch populations and the Wiener Wald, five leaves were analysed per sample. From each herbarium specimen one to five leaves were studied depending on their availability. For Cousens' material this number was two. If present, one peduncle per sample was measured.

Character choice

In the first instance, 15 characteristics of the leaf and one of the fruit stalk were chosen. They are summarized below and illustrated in Fig. 3.

PL = Length of the petiole (Fig. 3a).

PC = BL/PL , length of the petiole correlated to that of the leaf-blade (lamina).

BL = Length of the leaf-blade (Fig. 3a).

- BS = Size (= width) of the leaf-blade at the lowest pair of lobes (Fig. 3a).
 LN = Number of lobes per leaf-blade.
 VN = Number of sinus-veins per lamina; only those that reached the sinus-margin were counted (Fig. 3a).
 VC = VN/LN, number of sinus-veins correlated to the number of lobes per leaf-blade.
 AT = Auricle type, expressed as the angle between the leaf-base (auricle) and the petiole (Fig. 3b-c).
 HN = Number of stellate hairs on the abaxial side of the leaf per 4 mm².
 LW = Width of the broadest lobe (Fig. 3a).
 SD = Depth of the sinus above the broadest lobe (Fig. 3a).
 SC = SD/LW, sinus depth correlated to the width of the broadest lobe.
 BC₁ = LS/LW, in which LS is the size (= width) of the lobe below the broadest lobe (Fig. 3a); a measure for the shape of the leaf-blade.
 BC₂ = (SD - LS)/LW, another measure for the shape of the leaf-blade.
 BC₃ = BS/(LW_l + LW_r) in which l refers to the left and r to the right half of the leaf-blade; also a measure for the shape of the leaf-blade.
 PDL = Length of the peduncle.

Weighting of analysis methods

Four methods were tested for their utility in detecting hybridization and introgression.

Hybrid-indices and pictorialized scatter diagrams according to Anderson (1949, 1953) were considered. Although successfully demonstrated, e.g. Kwak (1980; *Rhinanthus*) and Cousens (1965; introgression path between *Q. robur* and *Q. petraea*), this method appeared to be inappropriate for the simultaneous examination of 17 characters.

The distance diagram was considered in its original form (Wells, 1980), as well as in its improved version, i.e. the F₁ weighted Wells' distance diagram (Adams 1982). Although useful results have been obtained with this method, e.g. Ietswaart *et al.* (1983), the two analyses techniques mentioned below proved to be more suitable to solve the special problems connected with this *Quercus* investigation.

Principle component analysis combined with cluster analysis has been successfully applied to unravel several hybrid-complexes, e.g. *Q. robur*-*Q. petraea* complex (Rushton 1978, 1979), *Q. rubra* complex (Jensen 1977), and *Solanum* species complex (Schilling & Heiser 1976). With these methods a first segregation of the *Quercus* matrix may be obtained. However, with this approach, no character weighting can be carried out.

For this reason our final choice fell on discriminant analysis based on Fisher's discriminant function (Nie 1975) as applied to *Picea* (Taylor & Patterson 1980). This method is particularly appropriate for situations where the parental taxa overlap in most features, as it uses several weighted characters (Jolicoeur 1959).

We first investigated whether the values of the characteristics showed a normal distribution for both reference groups in terms of kurtosis and skewness, and via a normality test from 'MINITAB' (Ryan 1981). The characters were further tested for their usefulness via univariate analysis, using the reference group values, directly or after a log transformation. Modus, median, minimum and maximum value, standard deviation, variance and coefficient of variation were calculated using one-way ANOVA (Nie 1975). *F*-ratio's were established to determine the diagnostic value of the characters. After selection of the most efficient characters the group-centroids were calculated for both the *Q. robur* and *Q. petraea* reference groups. All individuals in reference groups as well as in the investigated populations were plotted along an axis determined by the first discriminant

Table 4. Selected *Quercus* characteristics with their standardized canonic discriminant coefficient (left) and pooled within groups correlation (right)

Characteristic	Coefficient	Characteristic	Correlation
AT	+0.64335	AT	+0.61077
VN*	+0.41152	PC	-0.56538
PC	-0.41008	VN*	+0.45284
PDL*	+0.29685	PDL*	+0.34467
LN	-0.27309	BC ₃ *	-0.25427
BC ₃ *	-0.19609	BC ₁	-0.21427
BC ₁	-0.13554	SC	-0.21071
SC	-0.11894	LN	-0.12229

*Indicates a log transformation (for explanation of codes see section 'Character choice').

function. On this axis the limits were computed between the following five categories: typical *Q. robur* plants (qr), products of introgression between *Q. robur* and primary hybrids (ir), F₁ and F₂-phenotypes (hy), products of introgression between *Q. petraea* and primary hybrids (ip) and typical *Q. petraea* plants (qp), (Goodman 1966). We also calculated the place of the exact intermediates (ii).

Investigating chromosome number, as used in a study on *Potentilla* (Ietswaart & Kliphuis 1985) or chromosome morphology, demonstrated by a study on *Scilla* (Ietswaart *et al.* 1983), was not considered because the small chromosomes of *Q. robur* and *Q. petraea* are reported to be equal in number (tetraploids with $2n = 24$) as well as in shape (Sax 1930; Fouarge 1974; Federov 1974).

RESULTS

The reference framework

After character selection eight characteristics appeared to have sufficient discriminating power (Table 4). With the aid of these characteristics a primary discriminant axis was calculated, on which the category limits of pure species and different hybrid types were computed (Fig. 4a). By ordinating the values for the specimens of the two reference groups along this axis it becomes evident that *Q. robur* and *Q. petraea* are clearly separate taxa (Fig. 4a).

Dutch populations without Meinweg

The data for all the Dutch populations with the exception of the Meinweg are summarized in Fig. 4c, using the framework mentioned above. It appears that the clusters of both *Q. robur* and *Q. petraea* take positions that differ from the reference group; this is strongest for *Q. petraea*. Despite this the taxa remain distinct from each other in the Dutch situation. *Q. robur* phenotypes (qr) occur frequently and *Q. petraea* phenotypes (qp) are rarely found, while products of introgression (ir and ip) are common; F₁- and F₂-hybrids (hy) are

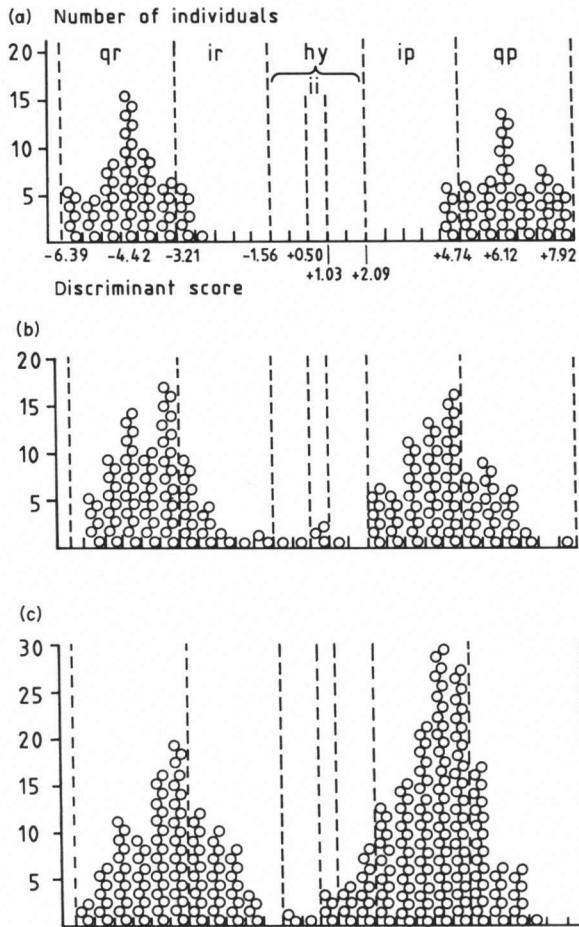


Fig. 4. Plot of the *Quercus* specimens along the primary discriminant axis: (a) the two reference groups, (b) the Meinweg subpopulations, (c) the other Dutch populations. The width of each class is 0.53. The numbers along the axis of Fig. 4a refer to: -6.39 to -3.21 pure *Q. robur* (qr), with centroid -4.42; -3.21 to -0.56 introgression products (ir); -1.56 to +2.09 pure hybrids (hy), with +0.50 to +1.03 as centre; +2.09 to +4.74 products of introgression (ip); and +4.74 to +7.92 pure *Q. petraea* (qp), with centroid +6.12 (for further information see section 'Weighting of analysis methods').

rarely encountered. It is clear that the hybrids (hy) blend into the *Q. petraea* cluster (ip and qp), and not into *Q. robur*. From Table 5 in which the data are given for each population separately, the following additional conclusions can be made. Most populations are dominated by *Q. robur*-like plants (qr + ir), but in populations 2, 4, 5, 6 and 10 the majority is formed by *Q. petraea*-like specimens (qp + ip). In population 13, and particularly in 7, the share of hybrids (hy) is relatively large.

Meinweg population

The data for the Meinweg population (9) as a whole are presented in Fig. 4b, and detailed for its subpopulations in Table 6. The picture resembles that for the other Dutch populations studied, given the understanding that the *Q. petraea* cluster (qp + ip) shows less

Table 5. Number of specimens (%) in each *Quercus* category for the Dutch *Quercus* populations studied, without the Meinweg population (9) one (for abbreviations see section 'Weighting of analysis methods' and Fig. 4)

Population number	<i>Quercus</i> category				
	qr	ir	hy	ip	qp
1	82	18	0	0	0
2	9	8	4	50	29
3	24	40	8	20	8
4	13	4	0	61	22
5	29	0	6	53	12
6	8	4	4	76	8
7	13	13	30	35	9
8	16	16	5	52	11
10	12	12	6	29	41
11	54	12	13	21	0
12	41	14	4	9	32
Mean	27	13	7	37	16

Table 6. Number of specimens (%) in each *Quercus* category for the Meinweg subpopulations (see Table 5)

Subpopulations of Meinweg number	<i>Quercus</i> category				
	qr	ir	hy	ip	qp
9.1	77	23	0	0	0
9.2	59	24	0	10	7
9.3	23	16	3	43	15
9.4	21	3	3	45	28
9.5	60	6	6	13	15
9.6	18	4	7	48	23
Mean	43	13	3	26	15

shift with respect to the centroid of the reference group (+6:12), moreover the cluster is more symmetrically divided when compared with Fig. 4c. The number of hybrids (hy) is somewhat smaller than in the other Dutch populations (3 against 7%). An important phenomenon is that with the increasing altitude of the subpopulations the number of *Q. petraea*-like specimens (qp + ip) grows, with the exception of subpopulation 9.5.

Multivariate identification formula

The status of an unknown specimen belonging to the *Q. robur*-*Q. petraea* complex can be ascertained by calculating its score with the aid of the formula given below, and then

plotting this value along the primary discriminant axis (Fig. 4). The formula is based on the non-standardized discriminant coefficient of the characters (see Table 4; the character PDL*, is omitted, because it is not always measurable). Logarithmic transformation must be carried out as follows:

$$BC_3^* = \log BC_3 \text{ and } VN^* = \log (VN + 1).$$

Score =

$$17.60PC + 2.07SC + 1.70BC_1 + 1.13BC_3^* + 0.23LN + (-1.61)VN^* + (-0.035)AT.$$

DISCUSSION

In The Netherlands, *Q. robur* and *Q. petraea* are distinct species, with the understanding that the differences between them are comparatively slight. That they are small is most probably due to hybridization, introgression and selection. These processes would have begun as the taxa dispersed from their ice-age refuges into West- and North-Europe. Thus slightly altered taxa may have arrived in western Europe. In addition, the *Q. robur* types have an advantage over the *Q. petraea* types in The Netherlands because the optimal conditions of the first, i.e. moist, summer-cool soils within reach of ground water, are more common than the dry, summer-warm hills favoured by the latter (Gams 1924; Schwarz 1933; Jones 1959; Cousens 1963). This results in a selection pressure on *Q. petraea* types in the direction of *Q. robur*. To this should be added the fact that man has preferred to plant *Q. robur* to obtain a better acorn harvest, even in places where originally *Q. petraea* occurred, e.g. in the Dutch Veluwe area (Staf & Teerink 1936; Buis 1985).

In the Meinweg site the lower areas (level 1 and 2, Fig. 2) are reasonably wet, while the higher ground (level 3 and 4) is generally drier. The preponderance of *Q. robur* types in the lower and *Q. petraea* in the higher levels harmonizes with this trend. The high percentage of *Q. robur* characteristics in subpopulation 9.5 is most probably caused by seepage water and accumulation of loess in the steep border area between level 3 and 4 (Engelen 1984, and personal communication).

ACKNOWLEDGEMENTS

The authors are very grateful to the Directors of the Naturhistorisches Museum (Wien), Botanisches Institute der Universität (Wien), Rijksherbarium (Leiden) and the Institute für Spezielle Botanik und Herbarium Haussknecht (Jena) for their kind permission to have on loan a number of their herbarium specimens, and to the curators of these institutes for the selection and shipment of the sheets. We are indebted to Dr J. Cousens (Edinburgh) for the loan of his extensive *Quercus* material from Yugoslavia and to S. van der Werff (Bennekom) and J.A.A. van Schendel (Roermond) for their comprehensive information on *Quercus* populations in the Veluwe and Meinweg area, respectively. We thank the Staatsbosbeheer, the Nederlandse Vereniging tot Behoud van Natuurmonumenten and the Provinciaal Waterleiding Bedrijf Noord-Holland for their kind permission to study *Quercus* populations in nature reserves administered by them. Mrs A. Schooneboom-Giele is thanked for computer assistance, Mrs D.H.M. Hoonhout for typing the manuscript, Mr L. Sanna for drawing the figures, and Miranda Aldham-Breary MSc for correcting the English. Finally we thank Professor W.H.O. Ernst for his critical remarks concerning the draft of this paper.

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