

Review article

Natural hybridization within the genus *Quercus* L

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Summary — Hybridization within the genus *Quercus* L appears to be extensive and reports vary from sightings of individual hybrid trees to small numbers of individual hybrid trees within populations to populations with characteristics of small-scale (eg *Q robur* and *Q petraea* in Hurepoix, France) and large-scale introgression (eg *Q robur* and *Q petraea* in Scotland) and, in some cases, the occurrence of hybrid swarms (eg *Q douglasii* and *Q turbinella* subsp *californica* in California). This has persuaded some authorities to question the current formal species concept in the genus and to suggest alternatives.

The evidence supporting these cases of hybridization is examined in detail. The majority of the reports of hybrids between species of *Quercus* are based on an analysis of morphological data alone using a variety of univariate, bivariate and, more effectively, multivariate statistics, while other forms of evidence, such as estimates of fertility in the putative hybrids, resynthesis of hybrids, habitat characteristics of the putative hybrids and F_2 segregation of parental types, have only been used occasionally. Data from chemotaxonomic investigations of suspected *Quercus* hybrids (mainly isozymes and phenolic components) in some instances support the morphological evidence but in other instances are contradictory; chemical data are also shown to be variable and possibly related to environmental variation which will limit their usefulness.

It is concluded that, before any radical revision of the genus is attempted in which the specific limits are redefined, a wider application of the possible techniques for the study of hybrids be applied in order to clarify the true extent of gene flow between *Quercus* species.

natural hybridization / introgression / chemotaxonomy / morphology / *Quercus* L

Résumé — Hybridation à l'intérieur du genre *Quercus* L. L'hybridation à l'intérieur du genre *Quercus* L est très largement répandue. Les descriptions d'hybrides concernent soit des arbres isolés, soit un nombre limité d'arbres situés en peuplement (*Q robur* et *Q petraea* à Hurepoix, France), soit des zones d'introgression (*Q robur* et *Q petraea* en Écosse), soit de larges populations grégaires d'hybrides (*Q douglasii* et *Q turbinella* subsp *californica* en Californie). La notion même d'espèce à l'intérieur du genre a été mise en doute par les spécialistes, qui ont suggéré d'autres interprétations. Les différents cas d'hybridation sont examinés en détail dans cette contribution. La majorité d'entre eux se réfère à des données morphologiques interprétées sous forme univariée, bivariée ou multivariée. Par contre d'autres méthodes de mise en évidence telles que les estimations de fertilité des hybrides, les hybridations contrôlées, les ségrégations des types parentaux en F_2 , et la description de l'habitat des hybrides putatifs, ont été plus rarement utilisées. Les données chimiotaxonomiques relatives aux hybrides suspectés (essentiellement isozymes et composés phénoliques) corroborent les observations morphologiques dans certains cas, mais les infirment dans d'autres cas. Les

caractères biochimiques manifestent également des variations liées au milieu, qui limitent leur utilisation. En conclusion, il est recommandé d'utiliser l'ensemble des techniques disponibles pour l'étude de l'hybridation et des flux géniques avant de remettre en cause de manière radicale le genre Quercus.

hybridation naturelle / introgression / chimiotaxonomie / morphologie / Quercus L

INTRODUCTION

It is estimated that *Quercus* L, one of the largest genera of flowering plants, includes about 450 species (Jones, 1974), although the literature contains considerably more names and descriptions than this and variable estimates for the total number of species. Recorded hybrids between these would appear to be both common and widespread. The earliest record of a hybrid oak in America was the description of *x Q hispanica* by Michaux in 1812 (Palmer, 1948). In Europe, there are many similar early records (see Gardiner, 1974). The apparent abundance of hybrids in certain areas has caused taxonomic confusion (and "complete frustration"; Tucker, 1961) in the past and, in certain floras, has undoubtedly led to misidentification.

Population studies have indicated that the pattern of hybridization may follow 2 distinct paths: 1) the population shows evidence of hybrid swarm formation, where the majority of the population appears completely intermediate between the 2 suspected parental species; or 2) the population shows evidence of introgression (Anderson, 1953), where the population consists of one species and a series of F_1 and backcrossed hybrids. Wigston (1974) has reviewed the essential characteristics of introgression and how they apply to *Quercus*.

This paper reviews the evidence which has been utilized in the detection of hybrids and provides an evaluation, so far as current knowledge allows, of the different types of evidence.

THE DETECTION OF HYBRIDIZATION

Hybridization manifests itself in a number of ways, but the initial recognition of hybrids is by morphological intermediacy, the putative hybrids showing evidence of intermediate character states or a combination of suspected parental character states (Phipps, 1984). Indeed, as Gottlieb (1972) points out, in the absence of morphological intermediacy, hybridity would not be suspected. When the parental species are sufficiently distinct, morphology alone may be sufficient to establish a case for hybridity, but where, as is often the case in *Quercus*, the parental species show a wide range of natural variation and/or possesses few diagnostic characters, other criteria have to be used. These include (Gottlieb, 1972): 1) an additive biochemical profile for characters, such as flavonoids or proteins, which are present in one or other parent but not in both; 2) unusual amounts of interpopulational morphological variation (resulting from segregation of parental differences); 3) the occurrence of the putative hybrid in intermediate habitats and evidence that the putative hybrid has intermediacy for physiological characters; 4) the occurrence of the putative hybrid in areas where the 2 suspected parents are sympatric; 5) the occurrence of the putative hybrid in geological strata more recent than either of the 2 suspected parents; 6) the existence of at least partial fertility in F_1 hybrids between the parents to permit the possible production of segregant genotypes; and 7) experimental production of individuals that resemble the putative hybrid in segregants of hybrids between the parents.

These criteria are broadly the same as those proposed by Stace (1980) and Crawford (1985) and build on those already established in the earlier part of this century (see Stace, 1975). To this list may be added the possibility of reduced fertility shown by some hybrids and DNA polymorphism.

Within *Quercus*, few examples exist in which a thorough investigation using all the above criteria has been completed.

PATTERNS OF MORPHOLOGICAL VARIATION

Morphological intermediacy is the major, and often only, criterion used in assessing the status of putative oak hybrids. Characters are usually restricted to leaf and fruiting structures, though others (eg, buds: Jensen, 1988; bark: Dupouey, 1983) have been utilized. The comparative uniformity of floral structures within the genus (and possibly their ephemeral nature) has limited their use in population studies. Restriction of samples to only fruiting specimens inevitably underestimates levels of hybridity. In addition, differences in fruit production from year to year similarly bias sampling, if samples are restricted to only fruiting individuals.

Leaf morphology has been the most important discriminator for oak taxa, both at the level of the subgenus and the species (Muller, 1942), but clearly leaf morphology is subject to environmental modification. In the field, standardized collecting points (Cousens, 1963) have been used to overcome these effects. However, in a study of the influence of crown position on leaf characters of *Q palustris* and *Q velutina*, Ludlam and Jensen (1989) concluded that "leaves should be collected from several positions on each tree and these collections pooled for evaluating among-tree variation". One further result was that the 2

species could be more easily discriminated in one season than in another; the generality of this result needs to be confirmed (see also Blue and Jensen, 1988).

In the early population studies, the standard approach was to construct hybrid indices based on a limited range of morphological characters and display these data in the form of bivariate scatter diagrams in which the 2 axes of variation represented quantitative characters and each point on the scatter was usually a tree (Cousens, 1963, 1965). The points were annotated to show the variation in characters expressed in hybrid-index form to produce, for each point, a metroglyph which encapsulated the variation pattern (eg Brophy and Parnell, 1974). While this approach has much to commend it, since the full pattern of the variation is expressed together, the interpretation may be problematic because of the difficulties in choosing appropriate quantitative characters for the axes (Rushton, 1978).

Subsequently, with the advent of numerical taxonomic methods, multivariate methodologies were utilized and a wide range of these have now found application in analysis of morphological data from oak populations, including principal components analysis (Rushton, 1978, 1983; Dupouey and Le Boulter, 1989; Jensen, 1989, etc), discriminant function analysis (Ledig *et al*, 1969; Rushton, 1974; Wigston, 1975; Jensen *et al*, 1984) and cluster analysis (Rushton, 1978; Jensen, 1988). These methods have enabled a much more objective approach to pattern-seeking in morphological data and sophisticated shape-describing methods are now being evaluated (Jensen, 1990; Jensen *et al*, 1991) as a means of collecting objective morphological data from oak leaves.

One major disadvantage of these approaches (and earlier methods) is that of fixing known reference points to aid in in-

terpretation but this has been overcome by the use of reference populations (composed of natural populations showing no signs of hybridity or artificial populations of herbarium specimens) which are used in all analyses (see fig 1; and Rushton, 1978).

In some oak taxa, different groups of researchers have come to substantially different conclusions regarding the levels of hybridity using morphological data. This is particularly true of the 2 wide-ranging, common European species, *Q robur* and *Q petraea* (see below) and prompted Gardiner (1970) to describe the discrepancies as a "hybrid controversy". However, rarely are the data sets directly comparable with variation in sample sizes, numbers and types of characters, methods of scoring and analysis, use of reference material, etc. It must also be borne in mind that many species within the genus are extremely variable in morphological characteristics and are also likely to show variation in ability to cross, thus leading to differential hybridization levels in different areas.

Consideration of the use of morphological data to detect oak hybrids would indicate: 1) that considerably more attention be paid to within-tree variation and possibly between-season variation; and 2) that attempts should be made to standardize methods of scoring and data analysis. Undoubtedly, replicate samples from the same trees, combined with population samples and analyzed using multivariate methodologies would enable levels of phenotypic plasticity to be assessed alongside population variation, though the number of instances in which such intensive sampling has been coupled with extensive sampling is very small. Where morphological data have been collected alongside other data (see below), the correspondence between the different types of evidence may be poor, and it is difficult to

generalize about whether morphological data overestimate or underestimate levels of hybridity.

POLLEN VIABILITY

Stace (1975) provides cautionary advice concerning the use of fertility of putative hybrids as an indicator of hybrid status, since it has been shown that hybrids may be completely sterile, or show no significant reduction in fertility compared with the parents, or be intermediate. However, many hybrids have been shown to possess reduced pollen viability and correlation between morphological characteristics and pollen viability is supportive evidence for hybridity, eg *Cercidium* and *Parkinsonia* (Carter, 1974; Carter and Rem, 1974). Despite the extensive investigations of morphological variation in *Quercus* spp, detailed studies of pollen viability are scant and restricted to a very narrow range of species. However, in those studies in which extensive estimates have been made, the general conclusion is that reduced pollen viability can frequently be observed in putative *Quercus* hybrids (see also the discussion in Tucker, 1963; p 706–707). Of course, if substantive pollen sterility is a feature of *Quercus* hybrids, then this may limit gene flow between species and promote the maintenance of species identity.

Surveys of *Q robur* and *Q petraea* in England and Wales (see fig 2; and Rushton, 1978) and in Northern Ireland (Rushton, 1988) have shown that morphological intermediacy is accompanied by a tendency for reduced pollen viability and Olsson (1975a) has provided similar results for the same species. However, close examination of assumed F₁ hybrids indicated that they had an "unexpectedly high percentage of pollen stainability" (Olsson, 1975a),

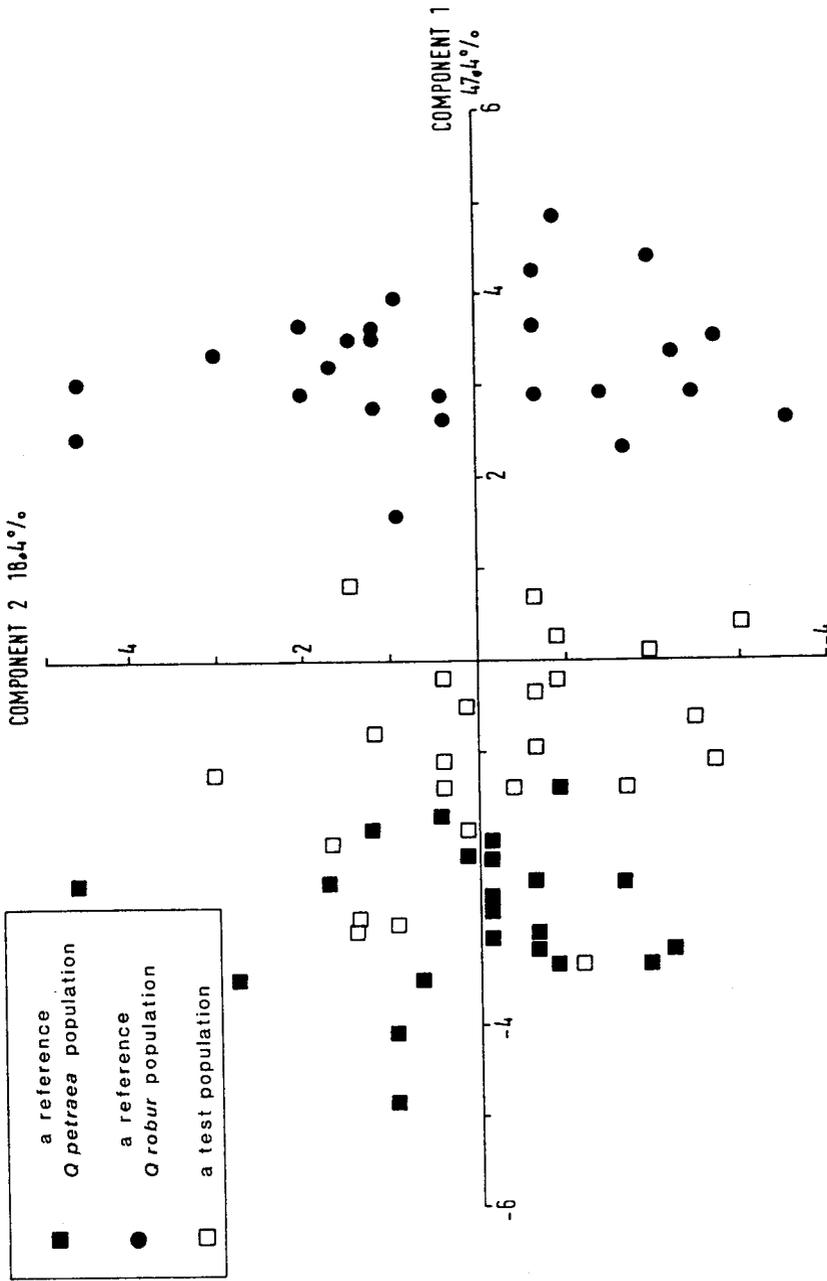


Fig 1. The use of 2 reference populations (*Q. robur* and *Q. petraea*) in principal components analysis as an aid to interpreting variation in a third population (the "test" population). The percentage of variation accounted for by each of the first 2 components is also given (from Rushton, 1978).

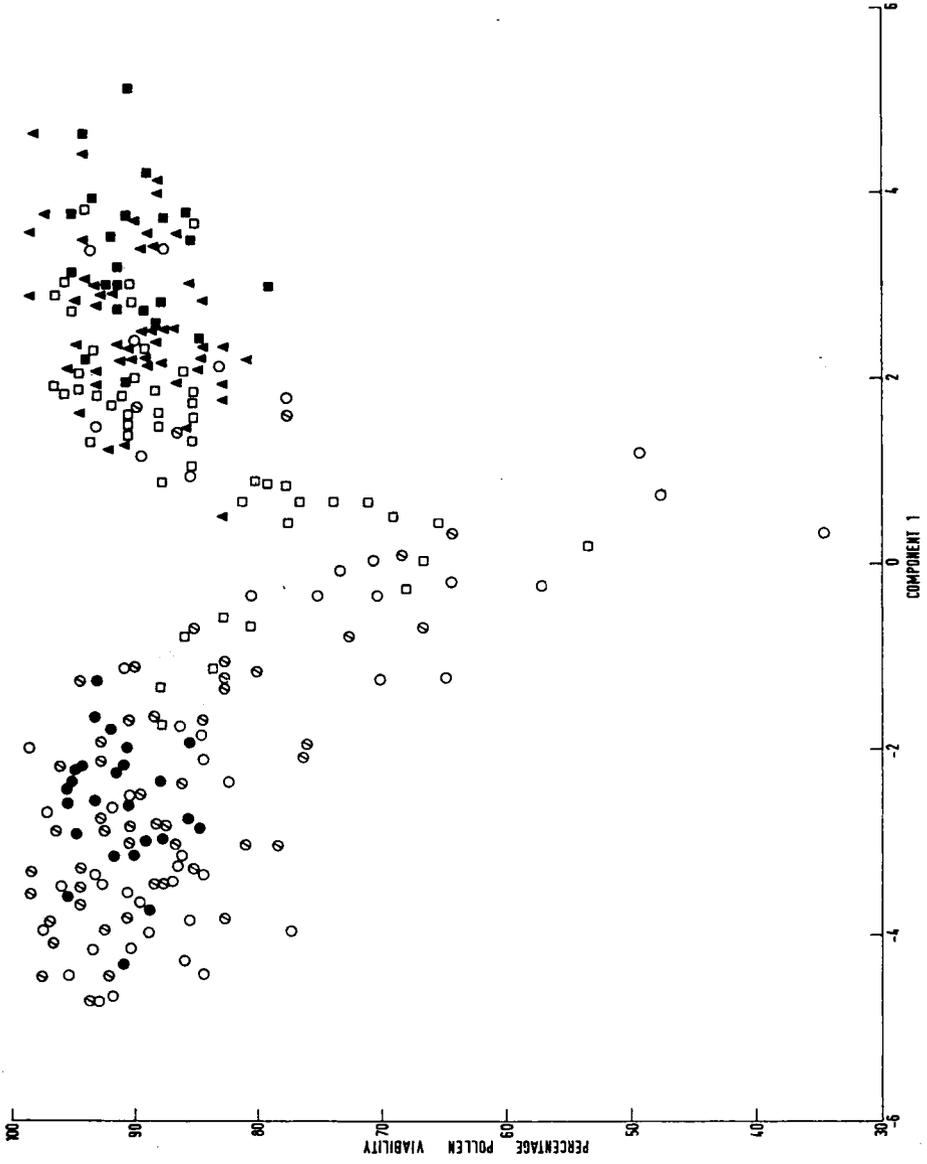


Fig 2. Percentage pollen viability in trees of 6 *Quercus* populations ordinated along a morphological component derived from a principal components analysis. *Q. petraea* ▲ and ■; *Q. robur* ●; introgressed *Q. robur* populations ○ and ◊; introgressed *Q. petraea* population ◻ (from Rushton, 1978).

similar to that recorded in some intermediate trees observed by Rushton (1978) and Minihan and Rushton (1984), and this was tentatively ascribed to cryptic structural hybridity.

CHEMOTAXONOMIC STUDIES

Electrophoretic evidence

Crawford (1985) has pointed out that allozymes offer several advantages over other types of evidence when assessing hybrid origin, since it is possible to examine the products of a number of genes without the problem of character intermediacy or additivity which is sometimes the case with morphological characteristics; that is, the allelic products of specific genes in the putative hybrid are either the same or different from those of the suspected parental species. Despite this considerable advantage, examination of *Quercus* spp by chemotaxonomic methods is restricted to a small number of reports and often these are not specifically concerned with the occurrence or incidence of hybridization but with variation between species (eg, Bellarosa *et al*, 1990) or genetic diversity within species (eg Yacine and Lumaret, 1988, 1989). Several reports are mentioned here to focus attention on their potential or because their results relate to hybridization within the genus generally.

Perhaps the most wide-ranging enzyme study was that of Santamour (1983) who surveyed cambial peroxidase isoenzymes in over 90 taxa. Major bands enabled subgeneric differences to be highlighted, but there was variability within the subgenera *Quercus*, *Cyclobalanus* and *Erythrobalanus* so that individual species could not be assigned to these subgenera on the basis of isoenzyme patterns alone. There was

also variation between individual trees, though detailed data on the extent of this were not provided. Guttman and Weigt (1989) examined leaf material from 10 species of subgenus *Erythrobalanus* and 8 species of subgenus *Quercus* and were able to resolve 18 loci which represented 12 different enzyme systems. Subgeneric differences were re-enforced by the allozymes and species relationships compared well with other data, though there were differences. For example, *Q nigra* and *Q laurifolia* were found to be closely related using morphological data analyzed by cladistic and phenetic means (Jensen, 1983), but isozymic results (Guttman and Weigt, 1989) suggested they were more distantly related and in different groups within the subgenus. One interesting conclusion of Guttman and Weigt (1989) was that the rather small genetic distances estimated between the oak taxa (especially within subgenus *Erythrobalanus*) may reflect the extensive interspecific hybridization and introgression that has taken place within the genus. Manos and Fairbrothers (1987) studied 6 species of the subgenus *Erythrobalanus*, and obtained similar results and thus concluded that, within the subgenus, evolution may have taken place by morphological divergence accompanied by little electrophoretically detectable genetic differentiation.

A similar conclusion was reached by Chechowitz *et al* (1990) who showed that oak populations in South Dakota and Wyoming could not be distinguished electrophoretically from *Q macrocarpa*, whilst morphologically they showed extensive introgression between *Q macrocarpa* and *Q gambelii*. They argued that such disparity reflected natural selection operating differently on morphological and electrophoretic characters. Some species (eg *Q rubra*; Houston, 1983) have been shown to possess extensive isoenzyme variation, which would also preclude the use of isoenzymes

in studies of their hybrids, whilst other morphologically very similar species can be resolved electrophoretically (eg *Q ilex*, *Q rotundifolia*; Afzal-Rafii, 1988). Isozyme variation has also been used to show considerable gene flow between island populations of red oaks (Hokanson *et al*, 1991).

Discrepancy between morphological and chemical characters has been interpreted very differently by Cristofolini (1985), who assessed seed and leaf proteins of a number of species. Whilst each species gave characteristic protein patterns, morphologically intermediate plants nearly always produced protein patterns corresponding to one or other of the suspected parental species. The conclusion drawn was that morphological variation may be due to phenotypic plasticity rather than to hybridization. An earlier investigation of some of the same species (Olsson, 1975b) indicated that leaf peroxidase isozymes showed high interspecific variation in *Q robur* and *Q petraea* and that introgressed populations had more affinities with *Q petraea*.

Because of the conflicting results already shown by isoenzyme studies, it is unlikely that isoenzyme investigations will generally provide accurate estimates of the levels of natural hybridization, though they may be useful in establishing individual cases of hybridization.

Variation in phenolic compounds

An extensive study of phenols of American oaks by Li and Hsaio (eg 1973) provided the basis for our knowledge of phenolic variation in *Quercus*. Leaf phenols of 49 species were studied and, generally, the phenolic pattern allowed differentiation of the subgenera *Quercus*, *Protobalanus* and *Erythrobalanus*, though the authors indicated that no one chromatographic spot was diagnostic for any subgenus. Two hy-

brids in the survey yielded somewhat different results. *Q x bebbiana*, thought to be a hybrid between *Q alba* and *Q macrocarpa*, was shown to possess a largely additive phenolic profile. The parentage of *Q comptonae* was thought to be *Q lyrata* x *Q virginiana*, but chromatographically it was generally very similar to that of *Q virginiana* and lacked the most prominent spot of *Q lyrata*.

One of the most elegant studies of oak hybridization using leaf phenols was that of Knops and Jensen (1980) involving 3 species, *Q ilicifolia*, *Q marilandica* and *Q velutina*; morphological data indicated that hybridization was restricted to *Q ilicifolia* x *Q marilandica* and *Q marilandica* x *Q velutina*. The 3 species had distinctive phenol patterns which allowed detection and confirmation of the putative hybrid parentages and confirmed the lack of hybrids between *Q ilicifolia* and *Q velutina*. Cottam *et al* (1982) also used anthocyanidins and catechins to confirm the status of artificially raised hybrids.

Like isozymes, phenol can, however, be variable within species and this variation may be related to the environment. McDougal and Parks (1984) showed that foliar phenols of *Q rubra* varied with elevation (fig 3) and it was subsequently shown (McDougal and Parks, 1986) that the differences in phenols between different elevations was largely under genetic control.

As argued above for isoenzyme studies, it is also unlikely that the use of phenolic compounds will prove particularly useful in estimating levels of natural hybridization in oak populations.

DNA

Organellar DNAs show a high degree of potential for assessing levels of hybridity in natural populations (Whittemore and

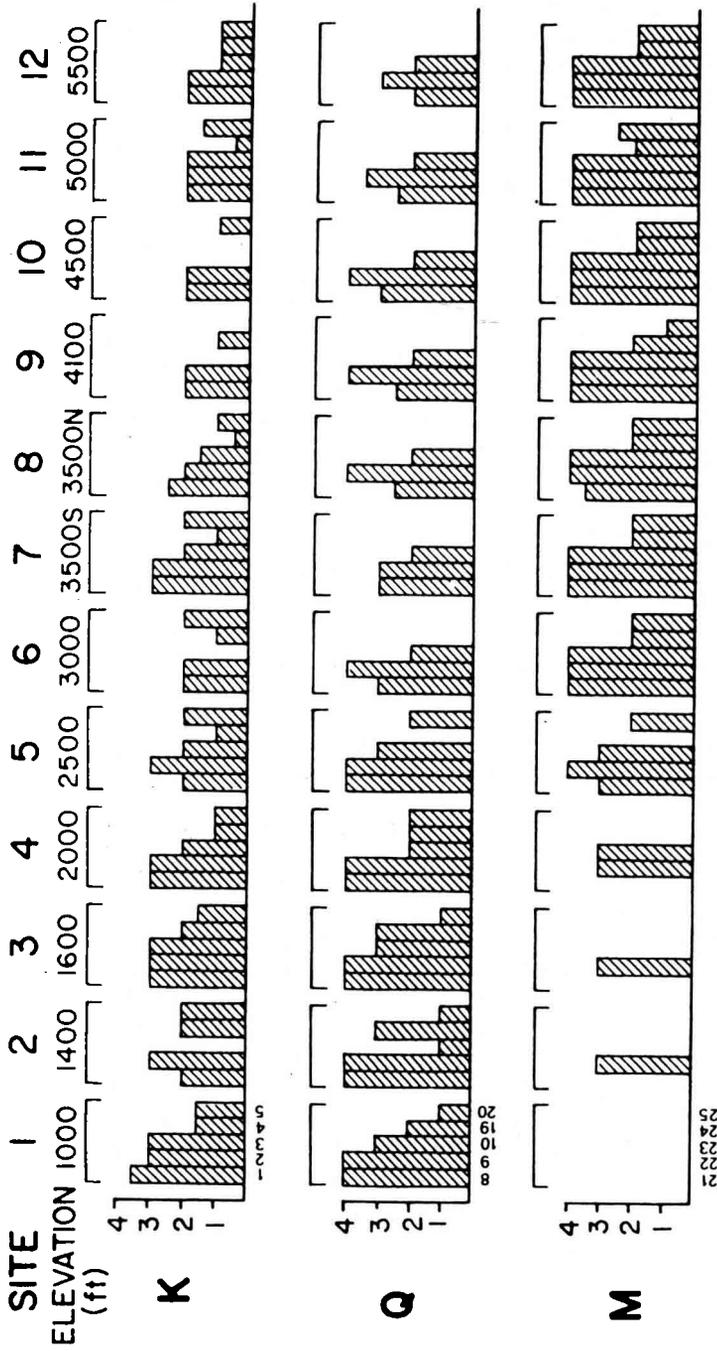


Fig 3. Elevational distribution of the average concentration (0-4 arbitrary scale) of 15 major *Q rubra* flavonoids at 12 sites. The flavonoids are arranged in 3 groups, kaempferols (K), quercetin (Q) and myricetin (M) (from McDougal and Parks, 1984).

Schaal, 1991), though their use in *Quercus* has so far been very limited. Whittemore and Schaal (1991) used variation of chloroplast DNA and nuclear ribosomal DNA extracted from winter buds and expanding leaves of 5 species of American white oak which differed in many morphological characters but which had different but overlapping geographical ranges and ecological tolerances. Using obviously non-hybrid individuals (assessed on morphological data), they were able to conclude that there were "... several clear cases of localized gene exchange between species, showing that there is appreciable gene flow between sympatric species in this group." The recognition that gene flow occurs in this group without apparent morphological intermediacy suggests that hybridization may be more common than other data types indicate, and there is little doubt that further investigations along these lines will assist in assessing levels of gene flow in *Quercus*.

HYBRIDITY RELATED TO THE HABITAT

The importance of the habitat in controlling natural hybridization has been examined by Anderson (1948). He argued that the F_1 hybrid should be uniform in its habitat requirements and that these are likely to be intermediate between those of the 2 parental species (the "hybrid habitat"). For example, edaphic restriction of hybridization is seen in *Q. harvardii*, which is restricted to deep, coarse sands, and *Q. mohriana*, which occurs on exposed limestone. Where erosion creates a mixture of sand and limestone fragments, hybrids are common (Muller, 1952). In other species, it may be climate which restricts hybridization, as is the case of *Q. harvardii* and *Q. stellata* (Muller, 1952).

Tucker (1961) showed that *Q. turbinella* and *Q. gambellii* are ecologically separated, the former living in semi-arid areas compared to the more mesic habitats at higher altitude of the latter, but where they are sympatric, in certain forest types, they hybridize. Neilson and Wullstein (1985) reported that the differential drought response of the 2 species is primarily due to anatomical/morphological leaf differences but, unfortunately, no hybrids were studied. Rushton (1979) demonstrated that populations, which were composed largely of hybrids between *Q. robur* and *Q. petraea* and which may have been hybrid swarms, were found along coastal river valleys in Wales where they occupied intermediate habitats between the better drained, siliceous, nutrient-poor hill-tops and the wetter, more poorly drained nutrient-richer valley floors.

Disturbance may also be a factor in promoting hybridization. For example, Silliman and Leisner (1958) showed that a mixed population of *Q. alba* and *Q. montana* on a stable, undisturbed site had no hybrids, whilst hybrids were common on a site subject to successive disturbance by fire and forestry.

In an F_2 generation, segregation and recombination would suggest that the individuals should be more heterogeneous in their habitat requirements compared to either the F_1 generation or the original parental species. Conversely, backcrossed F_2 trees might be expected to show habitat preferences similar to those of the backcrossed parental species (Grant, 1971; Rushton, 1979). Benson *et al* (1967) have provided a clear example of such ecological segregation, though the method of data collection may be suspect. Hybrid populations between *Q. douglassii* and *Q. turbinella* subsp. *californica* were examined and the composition of each population related to the degree of site exposure; on south-west facing slopes, the populations were

more like *Q turbinella* subsp *californica*, while *Q douglasii*-like populations were more prominent on north-east facing slopes. Thus selection among the F₂ generation for different recombinant types had occurred as a result of exposure differences. Evolutionary sorting in this instance must be very rapid (Benson *et al*, 1967).

Consequently, the successful outcome of a hybridization event in *Quercus* depends crucially upon the habitat conditions, and the level of hybridity reported under field conditions may be a reflection more of the habitat restriction on establishment than other factors.

ARTIFICIAL HYBRIDIZATION

There have been 2 major research programmes aimed at producing artificial hybrids, one led by Piatnitsky, started in 1937 in Russia, and the other reported by Cottam *et al* (1982). The work of Piatnitsky was summarized in Piatnitsky (1960). In all, over 200 000 pollinations were made representing 47 different interspecific crosses, and 24 of these from 9 species were considered successful (it should be noted, however, that *Q fastigiata* was considered a separate species rather than a variety of *Q robur*). Many of the successful crosses were between species in the subgenus *Quercus* but there were a number of

successful intersubgeneric crosses. Jovanović *et al* (1973) also reported some success in attempted hybridization between *Q robur*, *Q alba*, *Q pubescens* and *Q pedunculiflora*. Whilst most interspecific crosses gave very low success rates (usually less than \approx 1.5%) compared with intraspecific crosses, the *Q pedunculiflora* x *Q robur* cross was highly successful (30.7%). However, Cottam *et al* (1982) have viewed much of the work done in eastern Europe as dubious: "Most American tree geneticists have tended to be sceptical about the work done in eastern Europe." Wright (1976) stated that "... the authenticity of some is in doubt because the 'hybrids' resembled the female parent only". This criticism is mild compared to some opinions and comments made (not for publication) at geneticists' gatherings.

The work of Cottam *et al* (1982) is well documented and, in cases of doubt regarding the suspected hybrid, supplementary data of F₂ segregation, phenolic compounds and epidermal characters (as seen under the scanning electron microscope) were all utilized. The only data not provided are the absolute success rates for each cross made – the number of acorns and subsequent seedlings are reported from the number of pollination 'sacks' but no indication is given of the number of female flowers in each sack. Nevertheless, the programme was successful (table I) and resulted in 43 hybrid combinations. Inter-

Table I. A comparison of the results of 2 programmes of artificial hybridization in *Quercus*.

Number of:	Cottam <i>et al</i> (1982)	Schreiner (1962)
Interspecific hybridization attempts	241	Not comparable
Different interspecific hybrid combinations attempted (total)	137	62
Attempts resulting in <i>bona fide</i> hybrid seedlings	75	1
Different interspecific hybrid combinations represented	\approx 43	1
Definite intergeneric hybrid combinations	3	0

estingly, data given by Cottam *et al* (1982) for another programme (Schreiner, 1962) show an almost complete absence of success (table I), resulting, according to Cottam *et al* (1982), from a different pollination method that may have "overpollinated" the stigmas.

In addition to these 2 major research programmes, there are numerous reports of more limited crossing experiments (*eg*, Dengler, 1941; Gegel'skii, 1975; Rushton, 1977). One general point to emerge from some of these studies is that certain species show a degree of self-incompatibility.

Artificial resynthesis has therefore been achieved in a number of cases. However, the lack of success in some instances where extensive natural hybridization has been reported (*eg Q robur* and *Q petraea*) remains for further investigation. It should be recalled that the inability to resynthesize hybrids artificially does not in itself invalidate the case for natural hybridization events. One other line of investigation would be to examine the frequency of occurrence of hybrids in natural populations of those species shown to have a high potential for successful artificial hybrid production.

KARYOTYPE ANALYSIS

Karyotype analysis has yielded little information that can be of value in hybridization studies; the chromosomes are very small and, although differences between species have been shown (*eg* Rushton, 1974; Wang, 1986), the karyotype is very uniform in those species examined.

F₂ SEGREGATION

Theoretically, the F₂ should show a range of types including the recovery of forms re-

sembling the parental species. Two different approaches have been used: 1) F₂ segregation to determine the parental species of natural hybrids (*eg* Allard, 1949; Tucker and Bogert, 1973); and 2) the examination of the inheritance patterns in artificial hybrids (see fig 4; and Yarnell, 1933). Where F₂ generations were raised by Cottam *et al* (1982), there was a clear segregation of parental characters and, potentially, this would appear to be a most useful tool in establishing parentage (see also Burk, 1965).

LEVELS OF HYBRIDIZATION IN NATURAL POPULATIONS

It is not possible to generalize on the levels of hybridization in natural populations; instances are recorded of individual hybrid trees (Tucker and Boger, 1973), barely introgressed (*eg* Dupouey, 1983) to highly introgressed populations (*eg* Cousens, 1963) and hybrid swarms (Benson *et al*, 1967). What is apparent is that, in some species pairs that have been investigated over a wide geographical range, the levels of hybridity vary considerably (see table II) though some of the differences could be due to different methodologies of investigation.

Cousens (1965) believed that there was an increasing cline of introgression between *Q robur* and *Q petraea* northwards in England and Scotland. Rushton (1979) has shown a similar cline of increasing introgression from east to west in England and Wales. The presence of suitable habitats for hybrid and backcross establishment may be a factor here, and planting of important amenity and forestry species like these may have accelerated hybridization in some areas. In Scotland, the shorter growing season may also allow a greater

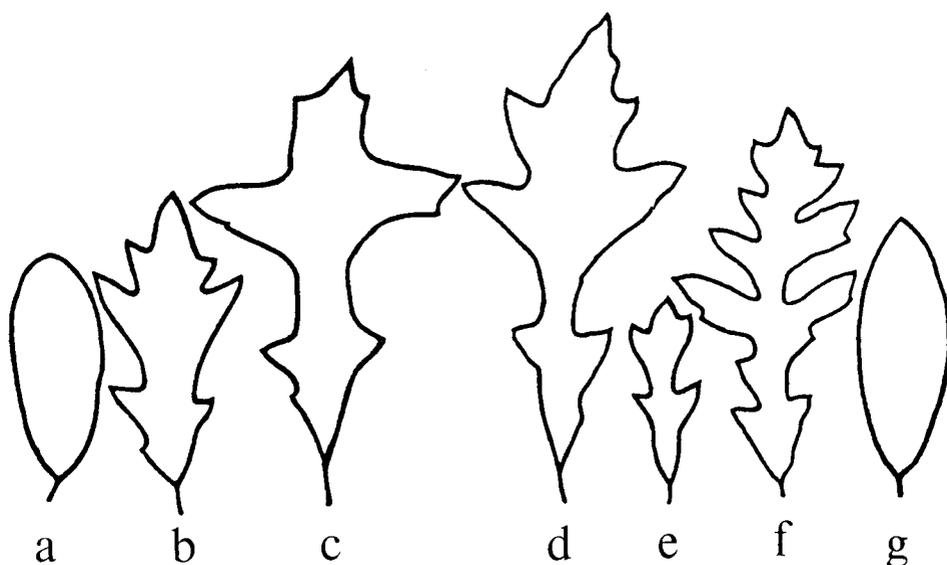


Fig 4. Segregation in an oak hybrid. Leaf silhouettes of a: *Q virginiana*; b: the F_1 hybrid; c: *Q lyrata*; d-g: F_2 plants (from Yarnell, 1933).

overlap of flowering period which would enhance hybrid formation.

It should be clearly emphasized, however, that the view of widespread hybridization in *Quercus* is not shared by all researchers (eg, Jones, 1959), who have indicated that oaks are very plastic and that the great range of variation in (largely) foliage characters with tree age, crown position, growing conditions *etc.*, results in misinterpretations of patterns of variation. To some extent this view is supported by the low percentage of success rates in many artificial hybridization studies compared to intraspecific crosses (eg Rushton, 1977; Ostrolucka, personal communication); whilst it has been possible to produce numerous artificial hybrids, the actual percentage of success rates is usually extremely low.

CONCLUSION

The extensive occurrence of hybrids within the genus is now well documented; Hardin (1975) has observed that gene exchange "occurs or at least has the potential for taking place among nearly all species of subgenus *Quercus* in eastern North America (albeit to a very limited extent in most cases), and the species can be thought of as comprising the most inclusive breeding group or syngameon." This has led some authorities, such as Burger (1975), to question the traditional species concept within *Quercus* and for some to suggest alternatives, such as the multispecies (Van Valen, 1976), a concept very like that of the syngameon (Grant, 1971). It must be recalled, however, that a large proportion of recorded hy-

Table II. Estimates of the levels of hybridization between *Q. robur* and *Q. petraea* in natural populations in northwestern Europe.

<i>Survey</i>	<i>No of populations</i>	<i>No of trees</i>	<i>Overall level of hybridity</i>
Cousens (1963) ^a Scotland	55	821	29% "truly intermediate" 49% intermediate
Cousens (1965) ^a Eire	12	329	2% "truly intermediate" 10% intermediate
Scotland	19	241	8% "truly intermediate" 19% intermediate
Eastern England	6	108	22% "truly intermediate" 41% intermediate
South and Eastern England	11	249	26% "truly intermediate" 50% intermediate
Dupouey (1983) ^b France	2	44	5%
Ietswaart and Feij (1989) ^c The Netherlands	11	285	7% F ₁ s and F ₂ s, 50% "products of introgression"
	1	170	3% F ₁ s and F ₂ s, 39% "products of introgression"
Olsson (1975a) ^d Sweden	17	239	15% "truly intermediate" (Cousens, 1965) 22% intermediate
Rushton (1978, 1979) ^e England and Wales	135	6 673	8% (mean)
Rushton (1983) ^f Northern Ireland	35	1 087	13% (mean), 0–50% (range)

Levels of hybridity assessed as follows: ^a bivariate scatter diagram and metroglyphs; ^b bivariate scatter diagram, hybrid index and reciprocal averaging analysis; ^c discriminant function analysis using reference material; ^d bivariate scatter diagram, metroglyphs and pollen viability; ^e cluster analysis and principal components analysis using reference material and pollen viability; ^f cluster analysis and principal components analysis using reference material. *NB.* In some cases, the original papers did not provide full details of all populations studied; the data above refer only to those results fully reported.

brids have been determined on morphological grounds alone and that the percentage of success rates for artificially raised hybrids is usually quite low. Re-evaluation of the systematic organization of the genus in terms of species relationships must await the more extensive application of alternative lines of evidence. As Whittemore and Schaal (1991) state: "Sympatric oak species are able to remain distinct despite considerable introgression, so that species concepts that rely on total genetic isolation between species to explain their distinctness clearly are not applicable in *Quercus*." It will only be by the application of a wide range of different techniques that the levels of gene flow between *Quercus* species and the limits of individual species will be accurately assessed.

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