Ann Sci For (1993) 50, Suppl 1, 166s-185s
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Review article

Intraspecific variation of growth and adaptive traits in European oak species

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Summary — According to various reports, 200–450 oak species including hybrid populations exist worldwide, with 24 of these – including 3 hybrid forms – having their natural range within Europe. They all belong to the subgenus *Lepidobalanus*. The most important section is *robur* with 21 species. The European species belong to both deciduous (15 species) and evergreen (9 species) oaks. Some difficulties in clear morphological and physiological definition of the species involved is caused by hybridization. Most studies into intraspecific variation exist for the species *Quercus robur* L and *Quercus petraea* (Matt) Liebl. Some information is available for *Quercus cerris* L, *Quercus virginiana* Ten (= *Q dalechampii* Wenz), *Quercus ilex* L and *Quercus suber* L, based on comparative plantations. In addition, a considerable number of morphological, physiological and biochemical studies based on natural populations exist which are not completely covered in this review paper. For most characters observed, oaks exhibit a wide variation. This is not only the case for morphological traits of pollen, seed, wood and plants but also for physiological traits and phenology which have great adaptive importance. Provenance experiments and progeny tests started as early as 1877. Most of these were only of local importance. This is partly due to the fact that acorns can only be stored for a limited period and flowering is irregular. However, the results available show that the choice of provenance can be important for the successful economic management of plantations. Variability of leaves, phenology, form, growth, wood and bark, roots, seed and flowering has been discussed separately. Improvement *via* selection and testing seems to be promising due to the considerable between-population and within-provenance variation. Vegetative propagation has been developed for some species by grafting, cutting propagation and *in vitro* propagation. Tree breeding approaches have also been discussed.

***Quercus* / morphology / provenance / progeny test / intraspecific variation / vegetative propagation**

Résumé — Variabilité intraspécifique des caractères de croissance et d'adaptation chez les espèces européennes de chênes. *Selon les auteurs, de 200 à 450 espèces de chêne, y compris les populations hybrides, ont été identifiées sur le globe. Vingt-quatre d'entre elles, comprenant 3 formes hybrides, ont été reconnues en Europe. Elles appartiennent toutes au sous-genre* Lepidobalanus. *La section la plus représentée est* robur, *avec 21 espèces. Les espèces européennes sont à feuilles caduques (15 espèces) ou persistantes (9 espèces). L'hybridation naturelle rend la classifi-*

cation difficile sur la base de critères morphologiques ou physiologiques. La majorité des études de variabilité intraspécifique concerne Quercus robur *L et* Quercus petraea *(Matt) Liebl. Des informations partielles, issues de plantations comparatives, sont disponibles pour* Quercus cerris *L,* Quercus virginiana *Ten (=* Q dalechampii *Wenz),* Quercus ilex *L et* Quercus suber *L. Par ailleurs, de nombreuses références relatives à des études de variabilité* in situ *de caractères morphologiques, physiologiques et biochimiques existent dans la littérature; elles ne sont qu'incomplètement évoquées dans cette revue. Pour la majorité des caractères, l'amplitude de variation est très grande. Il s'agit non seulement des caractères relatifs au pollen, à la graine, au bois, aux arbres, mais aussi aux caractères physiologiques et phénologiques, qui revêtent une grande importance adaptative. Les premiers tests de provenances et de descendances remontent à 1877. Ils ne comprenaient que les provenances locales, à cause de la difficulté à conserver les graines et l'irrégularité des fructifications. Les résultats de ces plantations montrent cependant que le choix de la provenance est primordial pour le succès économique du reboisement. La variabilité de la morphologie des feuilles, de la phénologie, de la croissance, de la forme, du bois et de l'écorce, des racines, des graines et de la floraison est également évoquée dans une partie séparée. L'amélioration dans des programmes de sélection peut aboutir à des gains élevés compte tenu de l'importance de la variabilité intraspécifique et individuelle. La multiplication végétative par greffage, bouturage et culture* in vitro *a été mise au point pour certaines espèces. Les méthodes d'amélioration génétique sont également mentionnées.*

Quercus / *morphologie / provenance / test de descendance / variabilité intraspécifique / multiplication végétative*

INTRODUCTION

The genus *Quercus* is represented by 200 (Neger and Münch, 1950), 320 (Krahl-Urban, 1959) or 450 (Krüssmann, 1978) species from the temperate to the tropical zones. The differences in the numbers are partly explained by the definition of hybrid forms as separate species (Krüssmann, 1978), partly by the species concept (binomial = classical or biological) and the subdivision of ecological forms into species. Species delineation is difficult if populations intermate and gene flow attains different degrees of intensity even with different subpopulations and individuals.

If we apply the biological species concept (Mayr, 1963) with the following definition: "Species are groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups", the number of oak species would be reduced considerably. One may even question whether *Q robur* and *Q petraea* are separate species in this sense, since intermating occurs frequently.

The oak population distribution appears to be related to ecological site types, *ie* taxonomic speciation and ecological segregation are closely linked (Grandjean and Sigaud, 1987). Species evolution is still underway in many cases and genetic isolation is not complete.

If we try to apply the biological species concept to oak, we find that the boundaries cannot be readily identified. So many classical species hybridize in *Quercus* that the genetically defined concept must be one of extraordinary complexity (Burger, 1975). The genetic (biological) species in oaks is simply too complex and too difficult to recognize to serve as the basis of a stable and functional system of nomenclature.

The genus is subdivided into 3 subgenera with 1–7 sections each (table I).

Table I. Systematic order or oak species – family Fagaceae, genus *Quercus* – according to Krüssmann (1978).

Subgenus	*Section*	*Species* [a]	
Cyclobalanopsis		8	
Erythrobalanus			
	Phellos	10	
	Nigrae	4	
	Rubrae	17	
	Stenocarpae	4	
Lepidobalanus			
	Cerris	15	
	Suber	8	
	Ilex	9	
	Gallifera	3	
	Robur	21	(most of the important European species)
	Albae	28	
	Dentatae	1	
			128 species (as compared to 450 mentioned by the same author)

[a] Number of species also including hybrids.

In this paper we follow the species definition of Krüssmann (1978). Twenty-four oak species and different hybrid forms exist in Europe, partly as introgression zones in the natural range. Fifteen species are deciduous, 9 species evergreen (table II). Only 8 of these are of economic importance.

Oak forests cover a considerable percentage of the total woodland area in most European countries. They exceed 30% in some countries (Greece and France), often cover 25% in others (*eg* UK, Romania, Hungary, Belgium) and only in a few cases do they comprise < 10% of the forest area (*eg* Germany, Czechoslovakia, The Netherlands).

The natural range of oak species has been drastically influenced by human activity. Since oak forests covered rich sites at low elevations, the majority of these have been converted into agricultural land. However, oak trees constituted a valuable base for human life in the past. The fruits served as a nutritional base for their animals and the wood was invaluable for construction, tools and shipbuilding. Oak was therefore extensively planted and *Quercus* silviculture was developed at an early date (Krahl-Urban, 1959; Thirgood, 1971). In France, oak silviculture for ship-construction was given active encouragement by Colbert as early as 1661; around 1700, Carl XII established oak stands in Sweden with seed imported from Poland (Krahl-Urban, 1959).

Nineteen oak species are natural to the former USSR. But more than 60 species have been introduced from different regions of the world; most have been successful, reproduce under plantation conditions (Trofimenko, personal communication) and hybridize with local populations.

Table II. European oak *(Quercus)* species (Neger/Münch, 1950; Mitchell, 1974; Krüssmann, 1978).

Name	*Also known as:*	*Natural range*	*Top height (m)*
Deciduous (15 species)			
Q robur L	*Q pedunculata* Erh	Europe, SW Asia, N Africa	50
Q pedunculiflora K Koch	*Q rhodopea* Vel	Balkans, E Romania, Asia Minor	45
Q virgiliana Ten	*Q robur* var *tenorei* DC; *Q dalechampii* Wenz non Ten	SE Europe	15
Q petraea (Matt) Liebl	*Q sessiliflora* Salisb	Europe, W Asia	45
Q dalechampii Ten		S Italy	10–15
Q cerris L		S Europe, SW Asia	35
Q pubescens Willd	*Q lanuginosa* Thuill	S Europe, W Asia, Caucasus	20
Q Frainetto Ten	*Q conferta* Kit; *Q hungarica* Hub; *Q Frainetto* Ten; *Q pannonica* Booth	S Italy, Balkans, Hungary	30–40
Q castaneifolia CA Mey		Caucasus, Iran, Algeria	25
Q pyrenaica Willd	*Q toza* DC; *Q tauzin* DC	S Europe	15
Q faginea Lam	*Q lusitanica* Webb non Lam	S Europe	20
Q pontica KL Koch		Caucasus	6
Q congesta Presl		S France	15
Q mas Thore		SW France, N Spain	
Q polycarpa Schur		SE Europe, Asia Minor	
Evergreen (9 species)			
Q ilex L		S Europe	20
Q suber L	*Q occidentalis*	S Europe, N Africa	20
Q coccifera L		Mediterranean coast	
Q infectoria Oliv		Greece, Asia Minor	5
Q macrolepis	*Q aegilops* Lam non L; *Q gracea* Kotschy	Greece, Asia Minor, S Italy	10–15
Q ballota Desj		Algeria, Spain, Portugal, Greece	
Q canariensis Willd	*Q mirbeckii* Durien	Spain, N Africa	25–35
Q lusitanica Lam	*non sensu* Webb	Spain, Portugal, Marocco	15
Q trojana Webb	*Q macedonica* A DC; *Q grisebachii* Kotschy	Yugoslavia, Greece	8
Hybrids (4 species)			
Q x *hispanica* Lam	nat hybr *Q cerris* x *Q suber*	S Europe	12–30
Q x *turneri* Willd	nat hybr *Q ilex* x *Q robur*	Originating from UK (Essex)	15
Q x *audleyensis* Henry	nat hybr *Q ilex* x *Q petraea*	Originating from UK (Essex)	
Q x *rosacea* Bechst	*Q hybrida* Bechst (nat hybr *Q petraea*) *Q robur*	Europe, SW Asia	45

The transfer of populations had occurred over considerable distances. Large quantities of oak seed (*eg*, up to 4 000 tonnes annually) were imported to Germany mainly from southeastern Europe during the last century (Lüdemann, 1962). These stands hybridized with local populations. Therefore the pattern of variation we find in the economically important oak species today may be far from natural. Studies of phenotypic variation in 'natural' populations generally exhibit a surprisingly high variability in all characters studied. Growth, stem form, crown morphology, formation of epicorms, wood characters, flushing, bud set, lammas shoot formation and attack by *Microphaera alphitoides* and *Tortix viridana,* for example, were found to differ from one population to another and quite often were even more variable within stands (Krahl-Urban, 1959; Weiser, 1964). Leaf number per branch unit and leaf size vary with location and stand age, *eg*, in *Q cerris*, *Q frainetto*, *Q pedunculiflora*, *Q petraea*, *Q pubescens* and *Q robur* (Dissescu and Coca, 1973). The variation in leaf characteristics decreases, however, with age (Semerikov, 1974). Pollen size and structure are different for species groups and for species. Smit (1973) divides *Quercus* pollen grains into 3 groups according to their morphology: 1) *Q robur/petraea* type; 2) *Q ilex/coccifera* type; and 3) *Q suber* type.

Colombo *et al* (1983) were able to differentiate between the species of the Mediterranean area on the basis of pollen morphology and size. However, individual variability is considerable and sampling has to be extensive.

Kissling (1977) studied the hairs on the lower side of the leaves of *Q pubescens*, *Q petraea*, *Q robur* and *Q cerris* and found that these were a good character for differentiating the 4 species. The hybrid forms had heteromorphous hairs which were intermediate between those of the parent species. The variability in all characteristics observed was considerable within the species.

For the *Quercus* species with extended natural ranges, such as *Q robur* and *Q petraea* (fig 1) certain geographical trends can be observed with latitude, longitude and elevation. Since all these studies of phenotypic variation within and between stands do not enable separation of genetic and environmental components, only a few are discussed in more detail in this paper.

INTRASPECIFIC VARIATION

The intensity of research into intraspecific variation is largely dependent upon the economic importance of the species. Variability is greatly influenced by the extent of the natural range. Extreme differences exist between the oak species. Since almost no provenance or progeny studies have been carried out with oak species other than *Q robur* and *Q petraea*, these will be discussed first. I am aware that not all the literature can be covered by our central system and I am grateful to those colleagues who have provided me with additional information on provenance and progeny tests which have not yet been published.

Quercus cerris *and* Quercus dalechampii

A comparative plantation with 9 oak species was established in 1982 in Levice Forest Enterprise in West Slovakia. Leaf area (Masarovicova and Pozgaj, 1988) was followed for 3 of these species. Variability in individual trees within the species *Q cerris* and *Q dalechampii* was larger than between the species.

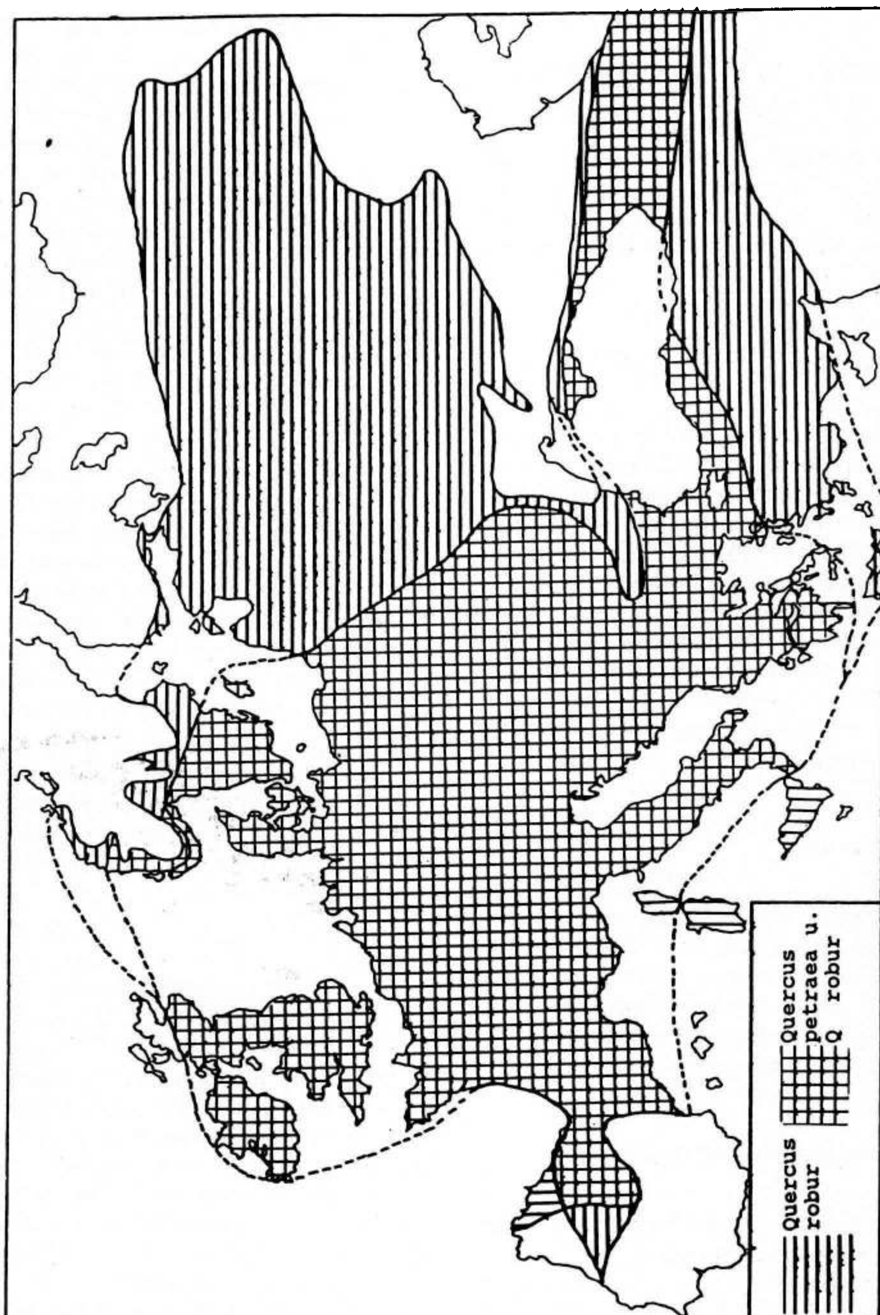

Fig 1. Natural range of *Quercus robur* and *Quercus petraea*.

Quercus conferta

Morphological variability of *Q conferta* within the Strandsha Mountains has been studied by Garilov and Stojkov (1978). Thirty-five morphological forms have been described and 3 ecological forms differentiated. The stem form is better in the mesophillous form and worse in the xerophytic form.

Quercus ilex

The growth of 2-year-old seedlings of 46 provenances was correlated with acorn size but not with site parameters or geographic variables of the location of origin (Bonani *et al,* 1988). Local provenances were slow growing. Pollination occurred between individuals which flower synchronously (Yacine and Lumaret, 1988). Variability in phenology was found to be considerable both between individuals within a stand and between populations (Yacine and Lumaret, 1989).

Quercus suber

The species is subdivided into 4 intraspecific taxa depending upon the lifespan of leaves and duration of acorn development (1 or 2 years), (Globa-Mikhailenko, 1973). The high variability of these characters in the species is demonstrated.

Quercus petraea *and* Quercus robur

The variability of these species is affected by environmental and genetic factors. The environment of the habitat of both species is very variable. Within its natural range (fig 1), *Quercus petraea* covers an elevational range from sea level up to 600 m in the Harz mountains, 975 m in the Black Forest, 1 185 in the Central Alps and 1 600 m in the French Alps (Rameau *et al,* 1989). *Q robur* remains about 200–300 m lower in the mountains. According to Krahl-Urban (1959), *Q petraea* has its optimum in France between the Seine and the Loire, in Germany in Spessart, the Pfälzer Forest, the Mosel region, the north-eastern plains of Lower Saxony, Mecklenburg, Pommern, and Brandenburg, and also in Croatia and Bosnia. *Q robur* grows best in the Rhine valley, in the Danube–Drau–Save (Slavonia) lowlands and in northern Germany. The genetic component is influenced by the species itself.

Q robur has a sequence of subspecies and Menitzky (1971) concluded that *Q pedunculiflora* Koch, *Q longipes* Stev and *Q erucifolia* Stev are not autonomous species, but form the southern subspecies of *Q robur*. Their formation was substantially influenced by introgressive hybridization with xerophytic oaks, especially *Q pubescens* and to a lesser degree *Q petraea*.

Q virgiliana Ten is an intermediate form between *Q robur* and *Q pubescens*. *Q pedunculiflora* and *Q virgiliana* are listed as separate species here following Krüssmann (1978) (table II), in spite of the fact that they could also be ranked as subspecies.

For *Q petraea*, 4 subspecies have been described (Jovanović and Tucović, 1975): *Q petraea* Liebl ssp *petraea* Menits, *Q petraea* Liebl ssp *iberica* (Stev) Krassil, *Q petraea* Liebl ssp *dshorchensis* (Koch) Menits and *Q petraea* Liebl ssp *medwediewii* (Camus) Menits. *Q dalechampii* Ten is an intermediate form between *Q pubescens* and *Q petraea* in the contact zones of both species; it is however, kept separate here too. Studies on intrapopulation variability of *Q petraea* show differences in leaf shape and size, such as platyphyllous, laciniate and longifoliate (Schwarz, 1936–1939), which have been separated into different varieties.

For *Q robur* and *Q petraea*, a number of provenance experiments have been established since the beginning of this century (table III). The information obtained from these experiments is the basis of the following sections of this paper.

Hybridization

A discussion of variability in these species is not possible without looking into their hybridization. Since this topic has been treated by Rushton and others (this volume) I will present here only some major results. Experiments with controlled pollination demonstrate that hybridization of *Q robur* and *Q petraea* is easier with *Q robur* as the mother (Dengler, 1941; Aas, 1988, 1990). Considerable differences in crossability exist on an individual level, covering the whole range from infertility to full fertility as compared to the within-species crosses.

It is of interest that isolation seems to be more developed in *Q petraea* as compared to *Q robur*. One could speculate that adaptation to the more specific site conditions of *Q petraea* (dry, fewer nutrients) needs higher specialization and that this can only be maintained by better protection against introgression. *Q robur*, on the other hand, usually grows under more optimal ecological conditions and thus can maintain a broader gene pool.

Morphological studies show that in addition to pure and mixed stands of both species, there are also stands with hybrid forms and stands in which the latter forms prevail (Burger, 1921; Seitz, 1923; Oppermann, 1932; Krahl-Urban, 1959; Cousens, 1965; Gardiner, 1970; Olsson, 1975a; Rushton, 1978, 1983; Dupouey, 1983, Spethmann, 1986b; Lower Saxonomy Forest Research Institute, Escherode, 1986–1991) (fig 2). Depending upon the ecological conditions of the site, one or the other can be dominant. On rich, humid sites, *Q robur* usually prevails and on warm, dry sites *Q petraea* is dominant. On sites with a mosaic pattern of dry and wet areas as in the mountainous regions of Germany, both species are sympatric and show intensive introgression.

Leaves

Numerous studies have compared leaves of both species (*eg* Oelkers, 1913; Rushton, 1976, 1978; Staszkievicz, 1970). Some characteristics are typical of the species; however, a continuous variation exists from one species to the other. Willkomm (1875–1887) considered that *Q robur* had the highest variability of all broad-leaved tree species, mainly in the size of the leaves, their shape, crenature, structure and leaf color.

Semerikov (1974) suspected a stabilizing selection for leaf characteristics of isolated populations. The first statistical analysis for the separation of *Q robur* and *Q petraea*, using leaf and fruit characteristics, was made by Oelkers (1913), who regarded both species as subspecies. He also observed the phenological variation within and between the species. He found considerable variation in all characters observed and an overlap in all characteristics. Burger (1914) summarized the knowledge of morphological differences in both species and established a provenance experiment in the nursery.

Phenology

Under the same site conditions, *Q robur* has a longer vegetative period with earlier flushing and later bud set. However, extreme provenance differences exist (Krahl-Urban, 1959). Provenances from regions with shorter vegetative periods flush earlier (Oppermann, 1932), but this trend is not consistent (Cieslar, 1923).

Table III. Provenance (prov) experiments with *Quercus robur* and *Quercus petraea*.

Reference	*No of prov/species*	*Year planted*	*Country*	*Origin*
Kienitz (1879)	8 / *Q petraea*	1877	Germany	Germany
	57 / *Q robur*	1877	Germany	Germany
Cieslar (1923)	1 / *Q petraea*	1905 mostly	Austria	Europe
	21 / *Q robur*	1905 single progenies	Austria	Europe
Hauch (1909, 1915, 1916, 1925)	13 / *Q robur*		Denmark	Europe
Oppermann (1932)	90 / *Q robur*	1911 + single trees and provenances	Denmark	Europe
Burger (1921, 1949)	3 / *Q robur*	1922	Switzerland	Switzerland
	6 / *Q petraea*	1922	Switzerland	Switzerland
	3 / *Q robur*	1926	Switerland	Switzerland
	2 / *Q petraea*	1926	Switzerland	Switzerland
	7 / *Q robur*	1935	Switzerland	Switz + Yg
	3 / *Q petraea*	1935	Switzerland	Switz + Hung
Johnsson (1952)	15 / *Q robur*	1940 (81 progenies)	Sweden	Sweden
Krahl-Urban (1959)	7 / *Q petraea*	1939–1942	Germany	Germany
	2 / *Q robur*	1939–1942	Germany	Germany
	3 / *Q petraea*	1941	Germany	Germany
	1 / *Q robur*	1941	Germany	Germany
	50 / *Q petraea*	1950	Germany	Germany
	50 / *Q robur*	1950	Germany	Germany
	9 / *Q petraea*	1952	Germany	France, UK, Sweden, Denmark
	23 / *Q petraea*	1955	Germany	Germany
	11 / *Q robur*	1955	Germany	Germany
	29 / *Q petraea*	1956	Germany	Germ + Yug
	10 / *Q robur*	1956	Germany	Germ + Yug
Kostov (1968)	9 / *Q robur*		Bulgaria	Bulgaria
Fober (1968)	2 / *Q petraea*		Poland	Poland
	7 / *Q robur*		Poland	Poland
Patlai and Boiko (1977)	20 / *Q robur*		Ukraine	Former USSR
Rachwal (1982)	1 / *Q petraea*	1976	Poland	Poland
	14 / *Q robur*	1976	Poland	Poland
Kleinschmit [a]	22 / *Q robur*	1983	Germany	France / Germ
	17 / *Q petraea*	1984	Germany	France, UK, Germ
Madsen [a]	19 / *Q petraea*	1989	8 countries	8 countries
Kleinschmit [a]	183 / *Q petraea*	1990	Germany	Germany
	198 / *Q robur*	1990		

[a] Not published.

Burger (1921) compared *Q robur* and *Q petraea* from the same region around Zurich for flushing and bud set. Earlier flushing at a young age was found in *Q petraea*, while at advanced ages there were no differences between the species. After germination, leaf color is red in *Q robur.* Flowering and seed ripening were synchronous with considerable individual differences within species.

Hauch (1909) found late flushing provenances from Slavonia and Galicia, early flushing provenances from Hungary and other southern sources.

The differences between the results of Krahl-Urban (1959) and Burger (1921) can easily be explained by ecotypic variation and sampling. We studied 198 *Q robur* stands and 183 *Q petraea* stands from northern Germany in the nursery. The frequency distribution for provenance mean flushing is given in figure 3. From this figure, it is obvious that the 2 species do not differ significantly in flushing time. *Q robur* is more represented at the extremes. As early as 1923, Cieslar found considerable ecotypic variation in flushing but a more clinal pattern with bud set with continental

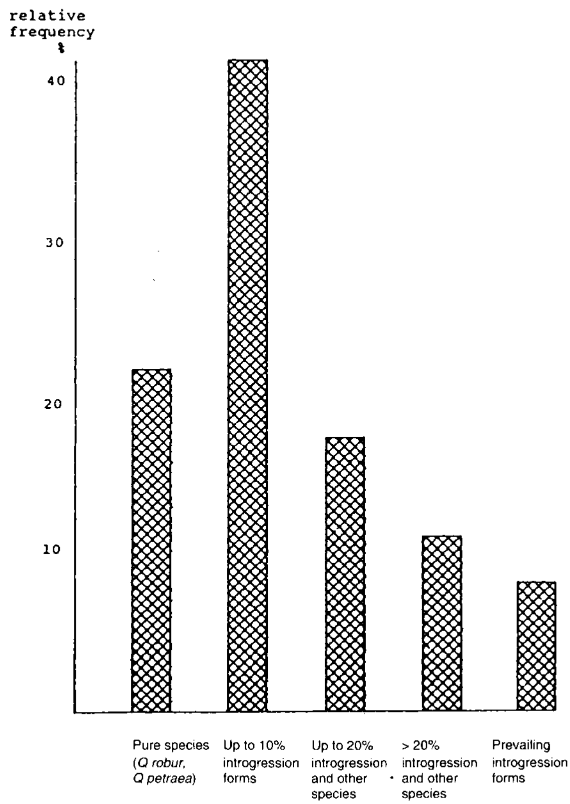

Fig 2. Distribution of oak stands in northern and western Germany.

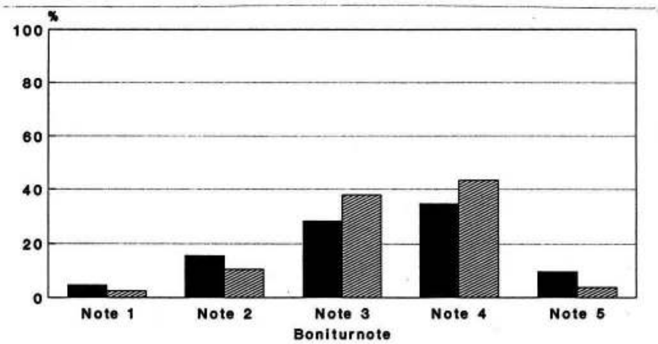

Fig 3. Flushing of oaks provenances (21 May 1991). Frequency distribution of provenances means. ■ *Quercus robur*, ▨ *Quercus petraea*; 1: not flushed; 5: leaves fully developed.

and northern provenances occurring early, southern and oceanic provenances occurring late. Menitsky (1971) stated that clinal variation was hardly noticeable in oak. Variation in flushing of mother trees is clearly inherited by their progenies, but there was no correlation between growth and flushing in Oppermann's studies (1932).

Different provenances from all over Europe of the same species show greater differences in flushing than between individuals of the different species at the same location (Burger, 1949). For German provenances, the individual variability in phenological traits is larger than between provenance means (Cieslar, 1923).

Bud set is earlier in *Q petraea* at the same location. Considerable differences in leaf yellowing and fall were observed between individuals of *Q robur* at the northeastern limit of the natural range (Danilov *et al*, 1972). Late yellowing leaves have higher transpiration rates and lower soluble carbohydrate contents.

Phenological characteristics of *Q robur* were also studied by Jevlev (1972a,b,c) and compared in provenance plantations. Henrik (1973) found a 7-day difference in flushing and a 3-day difference in bud set in stands of *Q robur* in Poland. These were not correlated with wood characters. Krahl-Urban (1959) described provenance differences in flushing of 3 weeks between Slavonian (*Q robur tardissima*) and German provenances.

In the Voronezh region, late flushing oaks show higher resistance to late frost and are therefore recommended for cultivation (Verchenko, 1975). On the other hand, late flushing provenances have a maximum water demand in July and transpiration exceeds early provenances by 31%; therefore Silina (1951) recommended planting early flushing provenances on elevated areas where little water is available.

Southern provenances set buds later and are more sensitive to early frost (Cieslar, 1923). Provenances from central France and the UK, for example, are less resistant to winter frost in central Germany and Denmark than local provenances (Oppermann, 1932; Krahl-Urban, 1959). Northern provenances set buds earlier (Kienitz,

1879) and are more resistant to early frost (Cieslar, 1923); however, they do not use the growth potential of southern regions (Oppermann, 1932).

Lammas shoot formation is more frequent in *Q robur* (Krahl-Urban, 1959; Jovanović and Tucović, 1975) and thus susceptibility to *Microsphaera alphitoides* is higher (Rack, 1957). But again, provenance differences and individual variability are considerable. Late bud-setting provenances have a high incidence of lammas shoots and thus high susceptibility to *Microsphaera alphitoides* and early frost.

Summarizing the research on phenology one can state: clinal and ecotypic patterns of variation exist side by side. Bud set shows a clearer clinal variation pattern than flushing. Individual variation is considerable and exceeds variation between provenances of limited areas.

Form

There are some general species descriptions showing the typical differences between *Q robur* and *Q petraea* (Burger, 1921; Krahl-Urban, 1959; Jovanović and Tucović, 1975). Crowns of *Q robur* are usually irregularly forked with widely spaced, vigorous, crooked branches mainly in a horizontal plane. Monoaxiality is rare. *Q petraea*, on the other hand, has a more regular crown with thinner branches, which are more evenly distributed and at a more acute angle.

This general description excludes the high variability within populations, between provenances and the introgression problem. Both species show high variabilities in crown types, as demonstrated by Oppermann (1932) and Krahl-Urban (1959); these are inherited. Koloszar (1987) demonstrated that the excellent form of *Q robur tardissima* from Slavonia is maintained under a variety of plantation conditions. Narrow-crowned oaks are especially adapted to urban conditions and selected for this purpose (Thompson, 1986). Extreme variability in form can occur, as described by Oppermann (1932), like pendula, fastigiata, pyramidalis and creeping, straight or crooked trunks. Hauch (1916-1921), Cieslar (1921), Oppermann (1932) and Krahl-Urban (1959) found a close relationship between the shape of the crown and the trunk of the mother trees and their progenies. The same was true for stands with good and bad form. Oppermann gave the frequency distribution for progenies of good and bad stands at age 17 years: good stands had 10 good, 3 medium and 2 bad progenies; bad stands had 0 good, 1 medium and 5 bad progenies. Including stand– and single tree – progenies in the comparison, Oppermann found that: good mother trees had 61% good, 25% medium and 14% bad progenies; bad mother trees had 15% good, 26% medium and 59% bad progenies.

Within more limited geographically defined regions, there is a clear indication that stem form and crown form are under strict genetic control.

Krahl-Urban (1959) found high heritability for forking, multiple leader and stem straightness in progeny tests.

The transfer of provenances from a milder climate with associated frost damage is reflected in worse stem form and slower growth. But there are some broadly adaptable provenances. Early flushing can be associated with late frost damage and the resultant form defects. Generally, *Q robur* provenances from Lipovljana in Croatia and from South Bohemia had the best stem form (Cieslar, 1923; Oppermann, 1932; Krahl-Urban, 1959) under different growing conditions.

Krahl-Urban (1959) found 50–70% straight *Q robur* trees in progenies of stands in the Save Valley, 25–30% in *Q petraea* from Slavonia, 20% in *Q pe-*

traea from the Spessart Mountains and 0% in *Q robur* from Haste in Lower Saxony.

The general opinion is that crown form and stem form are better with acute branch angles than with broad crowns (Cieslar, 1921; Hauch, 1916-1921), but timber quality may be inferior with acute branches. Oak from The Netherlands had exceptionally good form in Denmark, but growth was somewhat slower (Oppermann, 1932).

Davidova (1970) reported that phenotypic selection gave satisfactory results in form among > 313 trees tested.

Growth

Juvenile growth of oak is influenced by acorn weight. This may be one of the reasons for the better early growth of *Q robur* (Burger, 1921; Krahl-Urban, 1959; Jovanović and Tucović, 1975). Influence of seed weight only disappears after 12–15 years (Cieslar, 1923). There is no clear geographic trend in growth potential, but the climate of the location of origin is reflected in the progenies (Cieslar, 1923). Variation in leaf size seems to be weakly correlated with growth, with oceanic origins having smaller leaves (Cieslar, 1923).

Provenance variation can be extraordinary. Krahl-Urban (1959) found > 100% differences in height growth at age 6 years. These differences may continue at later ages. Late flushing *Q robur* provenances from Slavonia were not only better in stem straightness and in lack of epicorms but also 40% superior in volume growth compared with local German provenances at age 69 years (Hesmer, 1958). These provenances are not susceptible to attack by *Tortrix viridana*. In their natural range in Slavonia, considerable variation exists in stem form over short distances. The percentage of forking is especially low in Lipovljana and high in Otok and Krstovi (Krahl-Urban, 1959).

Northern provenances usually display a slower growth rate (Oppermann, 1932; Naidenova and Kostov, 1979). Good stem form is correlated with good growth over limited areas (Oppermann, 1932). In Bulgaria, early flushing trees within provenances displayed better growth (Kostov, 1983). Among German provenances, volume production may differ by as much as 100% at age 35 years. Non-indigenous provenances may be included in the comparison. Similar differences have been described by Oppermann (1932) for Danish provenance experiments. Growth potential shows more ecotypic than clinal variation. Quite often, phenological characteristics seem to be correlated with growth characteristics.

Wood and bark

As early as 1893–1894 Hartig studied the variability of oak wood characters and the effect of environmental influences on them. There are some minor differences between *Q robur* and *Q petraea* wood characteristics (Huber *et al*, 1941). *Q robur* has darker and more compact heart- and sapwood as compared to *Q petraea* (Jovanović and Tucović, 1975). To what degree these differences are due to the variations in humidity and nutritional levels of the respective sites remains questionable. Krahl-Urban (1959) provided a good summary of the earlier studies in oak wood characters and their variability.

Most recent studies have been concentrated on within-population variation. Polge (1984) detected considerable variability between trees in most wood characters studied and considered, like Lanier (1985), that genetic improvement was possible. Birot *et al* (1980) found significant individual differences in spiral grain. Nepveu *et al* (1981) studied infradensity, early wood percentage, percentage of vessels, fibers and rays in *Q robur* and *Q petraea* using clones and described high heritabilities for infradensity and earlywood percentage. In a study of *Q robur* grafted clonal material, Nepveu (1984a,b) reported high variability. Early wood percentage was under more strict genetic control than vessel percentage. Basic density showed high heritability and shrinkage low heritability. Savill (1986) studied shake in *Q robur* and *Q petraea* and described high variability. Early wood vessel size was significantly correlated with shake. Nikolov *et al* (1981) detected significant correlations between wood density and flushing in *Q robur*. Early flushing trees with rough bark had the highest basic density and widest rings with maximum latewood percentage. Similar results were reported by Jevlev (1972a,b,c). The mechanical properties of early flushing forms of *Q robur* have 10–14% higher values than those of late flushing forms.

Bark structure of *Q robur* is coarser than that of *Q petraea* (Klepac, 1957; Krahl-Urban, 1959; Jovanović and Tucović, 1975). However, a high variability exists on individual tree levels within populations. Significant influences of tree age and competition on bark structure were observed (Krahl-Urban, 1959). No correlation between bark structure and wood characteristics could be detected by Schulz (1954). Jevlev (1972a,b,c) studied different bark types in the Voronezh reserve and described 6 different forms, 2 of which showed differences in wood characteristics.

Wood quality is negatively influenced by epicorms. Late flushing oak (*Q robur tardissima*) forms fewer epicorms, harder and more durable wood and narrower sapwood. Within provenances, there also seems to be considerable variability in the potential to form epicorms.

R Kleinschmit has selected trees free from epicorms for a seed orchard since 1960. This seed orchard is flowering and included in progeny testing.

Roots

Root systems have been studied for young plants under comparable conditions. Burger (1921) and Krahl-Urban (1959) found more intensive root systems for *Q petraea* with a considerable variability in root percentage and structure within species. Jovanović and Tucović (1975) reported that young plants of *Q robur* have a superior root system to that of *Q petraea*. *Q robur* roots were found to be less sensitive to waterlogging than other oak species (Colin-Belgrand *et al*, 1991) and photosynthesis is less influenced by waterlogging. *Q robur* roots can penetrate compacted soil and improve it (Oppermann, 1932).

Seed and flowering

On average, the seed of *Q robur* is bigger than that of *Q petraea* (Oelkers, 1913; Burger, 1914, 1921), but there is a wide overlap between the species. The best characteristics for species differentiation are the dark longitudinal strips on *Q robur* seed (Oelkers, 1913) and the relationship between length and diameter of acorns, which is > 1.6 for *Q robur* (Burger, 1914). Provenance differences in size are bigger than species differences (Krahl-Urban, 1959). The 1 000-seed weight ranges from 2 900 to 4 200 g for *Q petraea* and from 3 000 to 5 450 g for *Q robur* on a provenance mean level. Seed size has an influence on initial growth.

Seed shape in *Q robur* can be quite different even between neighboring trees (Kienitz, 1879). Southern sources were found to have higher variability than northern sources. Petrov (1975) described considerable variability in all seed characters studied in 117 trees of the Alma Ata region. Peduncle length was most variable; length, diameter and form were the most stable. But a high variability among acorns also exists in terms of size and shape of the same tree (Oppermann, 1932; Kleinschmit, 1976), which is dependent upon the time of ripening, the year and the position.

Q petraea seed germinates earlier. It can germinate on the tree in autumn. Germination capacity rapidly decreases with length of storage (Szczotka, 1978; Tylkowski, 1982; Suszka and Tulkowski, 1983).

The pollen grains of *Q robur* and *Q petraea* have very similar exine and intine structures. The pollen grains have a regular oval form with 3 longitudinal scars symmetrically arranged and are 30–45 µm in size (Jovanović and Tucović, 1975). Intraspecific variation is higher than interspecific variation. Pollen dimensions are greater in *Q petraea* (Olsson, 1975b). Trees with abnormal leaf forms show pollen which may be of a hybrid nature. Rushton (1976) compared pollen of *Q robur*, *Q petraea* and suspected hybrid trees and described a broad overlap in both species but with a higher variability in the putative hybrids.

One male catkin contains > 550 000 pollen grains which can be transported 60–70 km at elevations up to 3 000 m (Pianitzky, 1954). The maximum pollen concentration is, however, within 100–200 m (Jovanović and Tucović, 1975). Since protandry is common, self-fertilization is reduced. Pollen germination is better on the stigma of other genotypes than on that of the parent trees.

Usually flowering starts at 50–70 years. Early and late flowering trees exist in populations. We found fertile seed on trees as young as age 7 years in plantations. Population differences in flowering are also described for *Q robur* var *praecox* Czern var *tardiflora* Czern (Jovanović and Tucović, 1975).

Flowering is irregular with 3- to 10-year intervals between good seed years, depending upon climate. Some trees bear seed at more frequent intervals (Litsharev, 1969). Flower variability was used for classification into several types (Kravtsova, 1968). Abnormal flowers occur with bisexual or female flowers on male catkins (Piatnitsky, 1954). Numbers of acorns are low in relation to flowers formed with high individual variabilities ranging from 0 to 30%.

DISCUSSION

European oak species are not strict biological species but hybridize naturally in the contact zones with other species. This increases natural variability considerably and makes it difficult to draw clear boundaries. From a practical point of view, it is nevertheless meaningful to maintain the binomial system, as discussed by Burger (1975) for the North American oaks. Evolutionary differentiation parallels ecological differentiation and this is reflected in the patterns of variation. This variation is a combination of clinal variation (*eg* for bud set) and ecotypic variation (*eg* flushing, growth, form). Ecotypic variation prevails, however. Adaptation to climate is not only reflected in phenological traits but also in survival. Southwestern provenances in particular show high losses when planted in northern or eastern countries and may exhibit extreme growth depressions due to frost damage. These injuries in return are reflected in the shape of the trees. Therefore phenotypic selection only makes sense if the material is grown under similar climatic conditions. If environmental conditions are changed drastically, lack of phenological adaptation has a series of negative consequences. However, broadly adaptable provenances exist which perform well even under different climatic conditions of the plantation site. *Q robur* from certain locations in Slavonia seems to constitute such provenances.

The natural pattern of variation in oaks is superimposed by a man-made artificial pattern due to provenance transfer, plantation activities and subsequent hybridization. This considerably complicates the description of oak variability and sometimes makes it impossible to trace what was natural variation and what was artificial.

For a practical approach, intensive testing and selection of populations and single trees seems worthwhile due to the considerable variation available in growth and quality traits. The possibilities for genetic improvement of oaks have been discussed elsewhere (Gathy, 1969; Beuschel, 1975; Kelinschmit *et al*, 1975a,b; Davidova, 1977; Kleinschmit and Svolba, Molotkov and Davydova, 1979; Mol'chenko, 1982; Tishchenko, 1982; Spethman, 1986a; Meier-Dinkel, 1987; Harmer, 1989).

Studies on susceptibility of European oaks to oak wilt disease and the relationship between growth and timber quality for veneer production are important topics for future research.

The long rotations of oak trees make it particularly important to choose well-adapted, fast-growing reproductive material of high quality when plantations are established.

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