Ann Sci For (1993) 50, Suppl 1, 368s-383s

Review article

Tree improvement programs for European oaks: goals and strategies

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Summary — Most work concerned with the improvement of European oaks is concentrated on *Quercus robur* and *Q petraea*. Improvement is constrained by limited knowledge of the extent and pattern of genetic variation, the long period to reproductive maturity, levels of seed production relative to demand and difficulties in vegetative multiplication. The goals of improvement activities have focused on straightness, vigor and desirable branching; on wood anatomy, shrinkage, density and color, and susceptibility to problems such as frost cracks, shakes and defoliation. Three aspects of breeding are currently receiving attention: 1) *in vitro* methods for regeneration, flower induction and genetic manipulation; 2) technologies for clonal multiplication, and 3) elements of classical breeding programs. Recent conceptual and technological advances and greatly increased research activity have raised expectations of genetic progress, which will need to be accompanied by developments in associated topics such as silviculture, pathology and wood science.

oak / *Quercus* / breeding / genetic conservation / improvement

Résumé — Programmes d'amélioration des chênes européens : objectifs et stratégies. *La plupart des travaux concernant l'amélioration des chênes européens est concentrée sur* Quercus robur *et* Q petraea. *L'amélioration est rendue difficile du fait de la connaissance limitée des variations génétiques, de la longue période pour atteindre la maturité reproductive, de la quantité de graines produites par rapport à la demande et des problèmes rencontrés concernant la multiplication végétative. Les buts de l'amélioration ont été concentrés sur la rectitude, la vigueur et la ramification ainsi que l'anatomie du bois, le retrait, la densité, la couleur et la sensibilité à des problèmes tels que les gélivures, les fissures et la défoliation. Trois aspects de l'amélioration génétique sont actuellement abordés : 1) les méthodes de régénération* in vitro, *d'induction florale et de manipulations génétiques; 2) les techniques de multiplication clonale; et 3) les éléments de programmes d'amélioration classique. De récentes avancées technologiques et conceptuelles ainsi qu'une activité accrue de la recherche, ont apporté de nouveaux espoirs d'amélioration génétique qui devront s'accompagner de progrès en sylviculture, pathologie et science du bois.*

chêne /* Quercus */ reproduction / conservation génétique / amélioration

INTRODUCTION

Of the 27 European species of oak, only 3 are of major economic significance: *Quercus petraea, Q robur* and *Q suber*. The first 2 are important components of the forests of Europe north of the Mediterranean region, and their timber is highly valued. We concentrate on them in this paper. The third species, *Q suber*, produces most of the world's commercial cork and is the basis of an important industry, especially in Portugal.

Despite their economic importance, a comprehensive set of constraints — the long rotations, the delay in the onset of flowering, uncertainty as to the timing of heavy fruiting (good seed years occur at 2–10-yr intervals in most regions), impossibility of storing seed for extended periods, and difficulties in vegetative propagation — have made oaks relatively difficult subjects for geneticists and tree breeders, particularly in comparison to shorter-rotation, more promiscuous and more easily propagated species, such as poplars, eucalypts and many conifers.

At present, there are no large-scale oak improvement programs in Europe, due partly to the limited financial support for breeding long-rotation hardwoods. Consequently, the many seed stands which do exist will continue to provide the main source of reproductive material both for nursery production and direct sowing. They are considered by many to represent a considerable improvement over the previous situation when none existed because seeds are now harvested from well-adapted, phenotypically superior stands and, in France at least, seed transfers between regions are restricted. Even when seed orchards have been established, their contribution is limited under current silvicultural practice: a 1-ha seed stand or orchard will produce enough seed for the establishment of only between 2 and 7.5 ha/year of plantations at the typical German stocking of 10 000 trees/ha (Kleinschmit, 1986).

Goals: breeding objectives and selection criteria

Breeding objectives describe the goals of genetic improvement and selection criteria as the traits by which this improvement will be realized (Cotterill and Dean, 1990). In theory, breeding goals include all traits of economic importance; selection criteria usually comprise a more restricted set, chosen for their genetic control and relationship with the breeding objective. Typically traits which influence size and quality at harvest are included as breeding objectives and weighted according to their relative economic importance. Selection criteria are likely to include those juvenile growth, quality and resistance traits which can easily be assessed, and are known or expected to correlate well with mature performance.

We have assumed that quality timber production for veneer and sawn wood will continue to be the primary goal of breeding *Quercus robur* and *Q petraea*. Selection criteria are therefore likely to include fast growth, especially during the early stages of development, straightness and lack of forking in the stem, self-pruning, disease resistance and wood quality traits. The latter are probably the most difficult to nominate and include shrinkage and aesthetic appeal. Available genetic parameter estimates for oak are summarized in table I. They are generally consistent with expectations from more comprehensive studies in other species; specific results are discussed below and are dealt with more comprehensively elsewhere in this volume.

Table I. Heritability of various wood and growth characteristics in oaks.

Species	*Character*	*Heritability and comments*	*Reference*
Wood characteristics			
Q petraea and *Q robur*	Earlywood vessel area	Clonal ramets (broad sense, clonal mean basis); 0.87–0.93 Open-pollinated progeny (narrow sense; individual tree basis); 0.60 Open-pollinated progeny (narrow sense; family mean basis); 0.79	Kanowski *et al,* 1991
Q petraea	Basic density	Broad sense; 0.65	Nepveu, 1982
Q petraea/ Q robur	Basic density	Broad sense; 0.55/0.58	Nepveu, 1984b
	Axial shrinkage	Broad sense; –/0.24	
	Tangential shrinkage	Broad sense; 0.32/0.30	
	Radial shrinkage	Broad sense; 0.14/0.12	
	Volumetric shrinkage	Broad sense; 0.29/0.28	
	Shrinkage anisotrophy	Broad sense; 0.14/–	
Q robur	Width of earlywood	Broad sense; high	Nepveu, 1984a
	% of vessels in earlywood	Broad sense; intermediate	
	Width of latewood	Broad sense; very low	
	% of fibers in latewood	Broad sense; very low	
Q petraea/Q robur	Annual ring width	Broad sense; 0.25/0.21	
Growth and vigor characteristics			
Q robur	Straightness	Probably high	Irgens-Moller, 1955;
Q robur	Branch angle	Probably high	Zobel and Van Buijtenen, 1989
	Vigor	Probably low	McArdle and Santamour, 1985
Q petraea coppice	Shoots/ramet	Broad sense; 0.13	Nepveu, 1982
	Length of longest shoot/ramet	Broad sense; 0.58	
	Diameter of longest shoot	Broad sense; 0.66	
	Angle to vertical of longest shoot	Broad sense; 0.10	
Q petraea and *Q robur*	Epicormics	Open-pollinated progeny; (narrow sense); 0.38	Mather (personal communication)

–: non significant heritability.

Vigor, form and branching

Growth rate is usually under weaker genetic control than stem straightness, which is typically moderately heritable (see, for example, Zobel and Talbert, 1984). Both are usually sufficiently variable and genetically determined to allow substantial progress; the relationship between them has usually been of more concern to breeders. In some species, *eg Pinus caribaea,* adverse correlations between vigor and form have constrained simultaneous progress in both traits (Dean *et al,* 1986). However, it may be possible to achieve sufficient gains in straightness in the first generations of breeding to relax selection for this trait in subsequent generations, as with *P caribaea* (Kanowski and Nikles, 1989). Data for oak are quite limited. Significant improvement in stem form was reported by Irgens-Moller (1955) for *Q robur* selected in The Netherlands. Clonal variability in terms of vigor and form has been estimated in 1-year-old plants from coppice shoots (Nepveu, 1982) and is summarized in table I.

Many branch characteristics are more influenced by the environment than is stem straightness, and gains made through selection are generally much more modest. However, branch angle and, at least in the case of some tropical pines (RD Barnes, personal communication) branch diameter and distribution are highly heritable. There is some evidence that these generalities apply to oaks: many of the commonly propagated cultivars of *Q robur* are raised from seed collected from parents selected for, *eg,* branch angle characteristics (McArdle and Santamour, 1985). In their study, a very high proportion of the open-pollinated progeny exhibit the required branch angle trait: fastigiate trees tend to produce fastigiate offspring, and pendulous trees, pendulous offspring.

Wood properties

In general, wood properties are under relatively strong genetic control (*eg,* Zobel and Van Buijtenen, 1989). Their assessment and manipulation are likely to be important elements of programs directed at oak breeding and propagation.

Nepveu (1984a) determined for *Q robur* that the width of the earlywood is under strict genetic control and the percentage of vessels in the earlywood under moderate control. In contrast, environmental effects — both of individual tree and year — largely determine the width of the latewood and the percentage of fibres within it. Broad-sense heritabilities of wood density and shrinkage have been estimated by Nepveu (1984b) for *Q robur, Q petraea* and *Q rubra.* In all 3 species, they are high for density, medium for volume shrinkage and low for the ratio of tangential to radial shrinkage, as detailed in table I. Shrinkage characteristics are further discussed by Nepveu (1982, 1990), Deret-Varcin (1983), Eyono Owoundi (1991), Huber (1991a) and Nepveu and Huber (1991). Wood basic density varies greatly between trees, as do the numbers of rays; these variations could, it is thought, account for differences in shrinkage.

In the more continental parts of Europe, frost crack in *Q robur* and *Q petraea* becomes a serious problem and susceptibility may have some genetic component. Cinotti (1987, 1989a,b, 1990a,b; and manuscript in preparation) and Cinotti and Tahani (1988) support this contention. In comparison with sound trees, and amongst other factors, frost-cracked individuals tend to have different grain angles, specific gravities, radial and tangential shrinkages, moisture contents, rays, proportions of earlywood and a differing proportion of vessels in the early-wood. Many of these characters are known to have high heritabilities and so might eventually be used as selection criteria, but correlations with other mature traits are not yet sufficiently determined to make their immediate application possible.

Another defect to which *Q petraea* and *Q robur* are peculiarly susceptible is ring and star shake. This has been investigated by Henman (1984) and at the University of Oxford where Savill (1986) found that trees with large vessel cross-sectional areas are particularly predisposed to shake; Kanowski *et al* (1991) reported vessel size to be under relatively strong genetic control and therefore amenable to genetic improvement; and Savill and Mather (1990) discovered that large vessels are often associated with late flushing trees, providing a relatively easy way of determining shake-prone trees at the time of leaf emergence in the spring. The prospects for breeding against shake therefore seem reasonable.

To those less skilled than the French and Germans at growing clean stems of oak, the problem of controlling epicormic shoot growth can be serious. This characteristic has been found by Mather (personal communication) to be under reasonably strong genetic control (table I), and therefore amenable to selective breeding.

The significance of wood aesthetics has been investigated by Flot (1988), Mazet (1988), Janin *et al* (1989, 1990a,b), Framond (1990), Klumpers (1990), Mazet and Janin (1990) and Janin and Eyono Owoundi (1991). Studies by several of these authors and others such as that by Scalbert *et al* (1989), provide more basic information on wood chemistry. Early studies established that light-colored oak is particularly valued by most professional users. Investigations of the wood itself indicated that there are significant correlations between color, basic density and volumetric shrinkage. Results suggest that color characteristics might be used as indicators of basic and technological properties of the wood of oak, and the work now underway to address this topic should be most useful.

The breeder's interest in juvenile–mature correlations, in terms of the relationship between selection criteria and breeding objective, is complicated in the case of wood properties by their changes from juvenility to maturity. Studies to investigate the feasibility of juvenile selection for specific wood characteristics in mature trees by F Huber (1991b; and manuscript in preparation) and Nepveu and Huber (1991) suggest a high level of variability between trees for several characteristics, *eg,* vessel diameter, superimposed on a substantial increase with age for about the first 20 years. The amount of earlywood changes with age; fiber percentages decrease with age and, in adult wood, seem to be affected by climate. The proportion of rays is relatively constant within a tree, but varies greatly between trees. The authors stress the preliminary nature of these results, and note that further work will be necessary before any strategies for juvenile selection can be formulated.

Gebhardt *et al* (1989) have suggested that it should be possible to screen aseptic shoot cultures for resistance to various pests and diseases; however, to our knowledge, no successful applications of such work have yet been demonstrated. Toscano Underwood and Pearce used tissue explants to screen for fungal invasions in *Picea sitchensis* and their results suggested genetic differences in resistance (Toscano Underwood and Pearce, submitted); although the screening was empirical without presupposing any mechanisms, it may serve as a model for work with oak.

In an attempt to reduce defoliation of *Q robur* by insect larvae, Roest *et al* (1991) have attempted to develop an *Agrobacterium*-mediated transformation procedure with the aim of transferring *Bacillus thuringiensis* toxin genes and, consequently of increasing resistance. They achieved an apparently induced transformation which, in principle, indicates that the species is amenable to *Agrobacterium* gene transfer for the ultimate production of transgenic plants. To date, however, they have been unable to achieve regeneration of shoots and plantlets.

Another approach to reducing defoliation by insects soon after leaf flush in the spring is to desynchronize the emergence of leaves and larvae, and this has been investigated by Leffef (1988). It should be possible to select and propagate trees, perhaps the latest-flushing ones (Jovanović and Tucović, 1975), to minimize this risk and that of late spring frost damage. However, as noted above, such trees are more likely to be susceptible to shake; different breeding populations may be necessary to address these potentially conflicting breeding objectives.

A few investigators (*eg,* Harmer, this volume) are working on aspects of the physiology and phenology of oaks. None of this work has yet been framed in strict genetic terms, but it is providing information which may eventually be of value to oak breeders.

STRATEGIES

The extent and pattern of genetic diversity

Recent advances in allozyme and molecular technologies (see, for example, reviews by Brown *et al,* 1990; Soltis and Soltis, 1990; Neale and Williams, 1991) have revolutionized our ability to investigate the extent and pattern of genetic diversity within a taxon. The definitive work to date on northern European oaks is that reported by Kremer *et al* (1991) who had as one of their aims the development, for seed identification purposes, of a large-scale genetic map based on variation in both allozyme and chloroplast DNA markers. In some regions of Europe, at least, this might be difficult because of the long history of planting and sowing with imported seed which must have confused patterns of natural variation. Nevertheless, Kremer *et al* (1991) found that these 2 species maintain levels of allozyme diversity that are among the highest of any woody species so far studied, but that little differentiation is evident at the molecular level.

The results of their work led them to describe *Q robur* and *Q petraea* as "broadly sympatric species occupying distinct ecological niches with extensive potential gene flow between them". Natural introgression occurs between *Q robur* and *Q petraea* to the extent that van Valen (1976) has questioned "the reproductive species concept" among some oaks. Hybridization has been reported in many studies, as described by Rushton (this volume).

The existence of triploids has been recorded (Johnsson, 1946; Jones, 1959) in polyembryonic individuals. These exhibit superior growth to that of diploid trees (Butorina *et al,* 1983, 1986). Both hybrid and non-diploid types may offer possibilities for breeding and propagation. Activity in artificial hybridization of oaks is discussed elsewhere in this volume.

Provenance and progeny tests

Substantial differences have been observed between provenances of *Quercus petraea* and *Q robur* in terms of growth, flushing and flowering times, lammas and epicormic shoot growth, and bud set

(Krahl-Urban, 1957; Kleinschmit, 1986). Some of these traits are linked to susceptibility to frost damage and defoliation by insect larvae. Differences in stem form, variation in susceptibility to mildew and other factors have also been found. However, no obvious geographical (clinal) trends have been apparent at any test site (Jovanović and Tucović, 1975), probably reflecting — at least in part — the long history of planting and artificial sowing of oaks in parts of Europe. In Germany, at least, human intervention has been sufficiently strong to lead Kleinschmit (1986) to conclude that oaks should be tested by stand rather than by region.

Progeny trials have only been established relatively recently and results from them are therefore more limited. Plus-tree selection and the establishment of seed orchards began in Germany in 1949 (Kleinschmit *et al*, 1975a,b) and progeny tests were subsequently installed with open-pollinated families of selected trees. Given the long rotation period of oaks, information from progeny trials on juvenile–mature correlations will be of particular importance to breeding strategies.

Seed orchards

Clonal seed orchards have been established in many locations; the earliest substantial ones were those in Germany, progressively established since 1949 (Kleinschmit, 1986). Seed orchards are established primarily for the production of seed for use in operational forestry; however, the low rate of seed production of oak and the limited supply of seed from all sources relative to demand have limited the utility of seed orchards. There are also the usual problems of different clones contributing differentially to the seed crop, due to their different flowering patterns, of graft incompatibilities; and of the small number of clones used in most seed orchards restricting further selection (Kleinschmit, 1986). These limitations, and the relative inflexibility of clonal orchards compared to other propagation options, have prompted a reassessment of their role in many breeding programs, including those with oak. We consider below the conceptual framework of genetic improvement as a necessary background to the exploration of alternative breeding and multiplication options.

OPTIONS FOR OAK BREEDING

The tree breeding cycle

The process of genetic improvement is best represented as a cycle; figure 1 presents one such depiction. The selection of genetically superior trees and the recombination of their genes in mating are

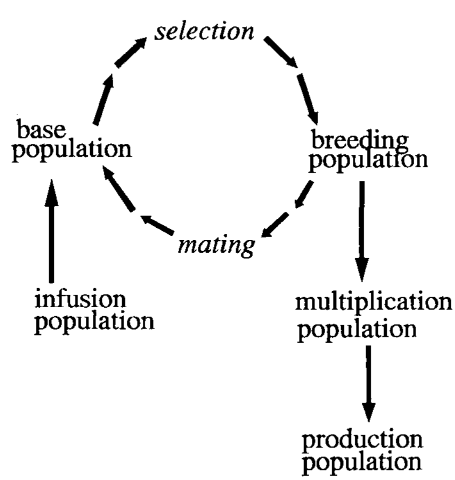

Fig 1. The tree breeding cycle (adapted from White, 1987). Although not explicit in this depiction, genetic testing of populations is fundamental to successful breeding.

the essential elements of any breeding program. The means by which the gains realized in breeding are transferred to operational production are also critical in the practical application of genetic improvement. Each of these activities results in the assembly of particular groups or populations of trees. Although not explicit in figure 1, genetic testing of these populations is fundamental to successful breeding.

There are a number of choices for each of these key elements of genetic improvement and its operational implementation. Selection may be based on either phenotype or genotype: the former is essentially subjective and relatively imprecise; the latter is accurate but demands some genetic information. Mating between selected trees may be unrestricted or limited to particular crosses. While the latter can be expected to produce greater gains, it is more expensive and usually takes longer to accomplish. Multiplication of genetically superior material to an operational scale may be based on seed production, clonal reproduction or a combination of the two.

The particular combination of selection, mating and multiplication options, and the physical arrangement of populations and genetic tests is described by the breeding strategy. The optimum breeding strategy for a particular species and circumstances will depend upon the biology of the species, its genetic characteristics, the level of resources available and the objectives of breeding. An objective implicit in most tree improvement programs is the maximization of genetic gain, usually for a number of traits, per unit of time and resources. As Cotterill (1986a) noted, tree breeding programs have tended to emphasize complicated mating designs, which are theoretically advantageous but practically difficult and expensive, at the cost of efficient selection. Further, Cotterill (1986a,b) demonstrated that a combination of genetically effective selection and simple, open-pollinated mating returns optimum genetic gains per unit of time and resources. Open-pollinated mating is easily achieved and effective where the selected trees can be isolated from outside sources of pollen. Efficient selection requires information from genetic tests and the development of a selection index; the necessary genetic information is easily obtained from genetic tests and the requisite computer software is easily available and readily applicable.

Evidence from breeding programs with tropical and subtropical species demonstrates that simple, robust and cost-effective means of genetic improvement are applicable to temperate species, and we contend that their use is long overdue. We now discuss options for the major elements of breeding programs, and their potential application in oak breeding.

Selection, mating and genetic testing

We suggest that for each region, whether defined on a genetic or geographical basis, the elements of efficient breeding described above may best be integrated into a single physical population, described by Barnes (1986) as the "breeding seedling orchard". The implementation of this concept in the breeding of various species, in environments as diverse as Australia, Florida and Zimbabwe (Reddy *et al,* 1986; Barnes and Mullin, 1989; Cameron *et al,* 1989) has demonstrated it to be simple, robust and genetically- and cost-efficient. Kanowski and Savill (1989) proposed its extension to temperate species and estimated costs only marginally greater than those incurred in routine woodland establishment and management.

In essence, application of the breeding seedling orchard methodology involves the establishment of genetic tests of the species of interest, the assessment of these tests for genetic information, the use of that information to select genetically superior trees and progressive thinning of the test to form an orchard for the production of improved seed. Efficient and effective selection, using index (*eg,* Baradat, 1989; Cotterill and Dean, 1990) or BLUP (best linear unbiased predictor) methodologies (White and Hodge, 1989) and relatively short generation intervals are essential to its success because of the smaller genetic gains made with each selection cycle when using simple mating designs. Although Barnes' original concept was based on the establishment of seedlings, vegetative propagules could be used if necessary. Similarly, the outstanding individuals or genetically improved families generated by breeding may be vegetatively propagated; this may be particularly important for many oak species, in which seed production is limited. Details of management regimes for breeding seedling orchards of subtropical species are well documented elsewhere (*eg,* Barnes, 1986; Barnes and Mullin, 1989); adaptation for temperate conditions should not be too problematic, as Cameron *et al* (1989) have demonstrated. In summary, the breeding seedling orchard methodology offers the advantages of genetic improvement for little more than the cost of woodland establishment. Indeed, we are currently establishing such orchards of *Fraxinus excelsior* in Britain on this basis.

Our approach is consistent with Kleinschmit's (1986) proposed revision of classical breeding methods as applied to oak. He concluded that more efficient propagation techniques are needed if genetic gains are to be transferred to field application and advocated a number of strategies to overcome the limitations of clonal seed orchards as the multiplication population. He therefore proposed the establishment of seedling seed orchards with families of orchard origin, using 200–500 trees per breeding population to enlarge the base of existing seed orchards. He also suggested the development of both macro- and micro-propagation technologies for clonal production, and it is to these elements of operational genetic improvement that we now turn.

In vitro *regeneration and clonal multiplication*

Propagation *via in vitro* plantlets or cuttings allows the multiplication of superior individuals or families; it provides an essential means of multiplication in circumstances such as those commonly found in oak, where seed production is inadequate for operational requirements. Successful vegetative propagation of most trees, including oaks, must be cheap and depends upon the development of the right growing medium and the degree of juvenility of the material used. As with many woody species, propagation from trees more than 6–8 years old from seed is difficult, necessitating rejuvenation. Large differences between clones in terms of rooting success and subsequent growth exist. Coppice and epicormic shoots are the most amenable sources of material (Harmer, 1988; Harmer and Baker, 1991).

Although micropropagation has the advantage of high multiplication rates over short periods, it has a high requirement for relatively skilled labor and micropropagated plants can be very expensive in comparison to those produced from seed or cuttings. A degree of automation is therefore desirable, especially for inducing branching in embryo cultures and for replenishing nutrients without subculturing. Systems have been developed in The Netherlands by Vermeer and Evers (1987a,b), which are successful both with *Populus* and *Quercus* cultures, and these have the potential for wider commercial application.

Regardless of the propagation methodology, maintenance of genetic diversity is essential; relevant considerations have been well summarized by Burdon (1989). The risks of limiting production to relatively few genotypes are accentuated by the long rotations under which oaks are grown, and emphasize the need for multiplication of a minimum of around 20 genotypes from each breeding population (Libby, 1982; Burdon, 1989).

Flower induction, grafting and gene transfer

Attempts at artificial induction of flowering — which have worked well in many other species — are being developed in Germany. They involve treatment with growth regulators or grafting to selected rootstock genotypes. Gebhardt and Goldbach (1988) think that, as with, for example, apples and cherries, it should be possible to find rootstock genotypes which induce early fruiting and cause dwarf growth in grafted seed orchards.

The establishment of clonal orchards or conservation banks requires development of reliable grafting techniques, which are now reasonably established, and have been described by Chalupa and others in this volume. The technique of micrografting shoots *in vitro* from shoot-tip cultures onto seedlings, and *vice versa* (Gebhardt and Goldbach, 1988) could be valuable if it is successful with oaks.

The rapid development of techniques in molecular genetics suggests that they could, in time, be used in oak breeding programs. In the short term, it seems likely that the focus of such work will remain on pest and disease resistance. As our knowledge and understanding of the oak genome increases, the prospects for wider application will become apparent, as Peacok (1989) has discussed in general terms.

Seed production and storage

In most parts of Europe, oak seed production is characterized by occasional years of surplus, interspersed by several years with little or no seed. Until recently, few attempts at storing acorns for long periods have come to much. Acorns are recalcitrant seeds which lose their capacity to germinate if too dry and do not survive very low temperatures. However, Evers *et al* (1990), Muller and Bonnet-Masimbert (1984), and Suszka and Tylkowski (1980) have demonstrated that they can be stored with acceptable levels of germination over 3 winters (*ie* 30 months) if they are maintained at a temperature of –1 °C and at a moisture content of not less than about 40%. They require soaking in water at 41 °C for 3 h before storage to prevent damage by the fungus *Ciboria batschiana*.

QUERCUS SUBER, MEDITERRANEAN AND OTHER OAKS

There is little in the forestry literature on European oaks other than *Q robur* and *Q petraea; Q suber* and *Q ilex* are the other species which have received more than passing attention.

Quercus suber

Despite its importance and several exhortations as to the necessity of research, genetic improvement of cork oak received little attention until 1988 (Sardinha, personal communication). Natividade (1954, 1958) described cork oak as exceedingly variable in terms of vigor, form and the characteristics and production of cork tissue. It therefore appears well suited to selective breeding; Natividade (1954) proposed a breeding program, detailing traits which should be sought or discouraged, both for the production and technical properties of cork, and the acorns, which were much valued as animal feed. He suggested the establishment of clonal seed orchards, investigations into vegetative propagation and other now familiar methodologies for improvement. Current work aims to develop breeding methodologies, particularly those which will take account of genotype–environment interactions. This approach has involved characterization of the trees and selection of plus trees (especially for cork quality) in selected stands; investigations into the genetics of cork production; estimation of the correlations between cork quality and leaf enzyme systems and the development of grafting and macro- and micropropagation techniques. Several papers have already emerged from this work, including those by Nobrega *et al* (1990) on isozymes, and Roldao (1990) and Roldao *et al* (1990) on vegetative propagation. Current research in Portugal reveals that many of the issues implicated in the genetic improvement of cork oak are similar to those of *Q robur* and *Q petraea* described above.

Quercus ilex

Yacine and Lumaret (1988, 1989) used allozyme markers to investigate genetic diversity in *Quercus ilex* over various parts of France, including Corsica, and North Africa. They found substantial between-population, but little within-population, diversity, which they suggested resulted from a number of evolutionary and anthropogenic factors. They also studied the species' mating system and found that trees were not necessarily pollinated by neighboring individuals, but by those which are phenologically synchronous and which are predominantly pollen producers. As this temporal isolation reduces the effective population size, they proposed that it also contributed to the current population structure.

CONSERVATION OF GENETIC RESOURCES

The consequence of erratic seeding and inability to store seed has, for centuries, been a major reliance on planting with imported stock, with the associated risks of genetic erosion. An extreme case is that of Great Britain, where it is now virtually impossible to be certain that any oak is of native origin. In areas less contaminated with foreign seed, such as the Pyrenees (Cantegrel, 1984), strong concerns have been expressed about the possible degeneration of local races and the need for their conservation. Both methodologies for seed storage or plant preservation and identification of the nature and pattern of genetic variation are necessary for effective conservation measures.

The results of recent work on conventional seed storage have been described above. Jörgensen (1990) reported results of attempts to find a means of conserving genetic resources at very low temperatures. Gebhardt *et al* (1989) proposed the conservation of shoot-tip cultures at low temperatures, but no such work has yet been reported.

Early results of the INRA-Bordeaux program, which is investigating oak genetic diversity, have been reported by Kremer *et al* (1991); this program should provide much of the information necessary for effective genetic conservation.

CONCLUSION

It is apparent that any program for the genetic improvement of oaks is likely to be of a much more long-term nature than similar work for shorter rotation, less recalcitrant species such as poplars. However, both techniques and understanding have advanced considerably in recent years and the immediate challenge is to continue the initial research work and consider the means by which it can integrate with practical forestry.

Given the resource constraints of most agencies and individuals involved in forestry, the practical application of tree breeding depends upon simple, robust, cost-efficient means of genetic improvement. Fortunately, genetic theory is consistent with these 2 requirements. We believe that the two keys to this synthesis are: 1) the integration of all key elements of the breeding cycle in a single physical population, which serves as a genetic test, selection base, and source of improved seed and propagules, and; 2) the use of resource-efficient multiplication methodologies. The breeding seedling orchard approach is ideally suited to address the first requirement and we think that it can be successfully adapted to oaks. Its adoption adds few costs to those of conventional woodland establishment but can be expected to deliver substantial genetic gains. The considerable work already under way on propagation techniques gives us confidence that satisfactory multiplication technologies will soon be widely available. Progress towards the more widespread and effective implementation of oak genetic conservation and improvement therefore depends, in part, upon continuing research efforts, but equally upon our ability to communicate its prospects and promise to forest managers.

ACKNOWLEDGMENTS

We thank the many respondents to our request for information on current work in Europe; were it not for their helpful responses, this paper could not have been written. We also thank two anonymous reviewers for their constructive comments.

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