northern Sweden. Royal College of Forestry, Dept. Forest Genetics. Research Notes 19, 132 pp. (1976). — Repo, T.: Rehardening potential of Scots pine seedlings during dehardening. Silva Fennica 25: 13–21 (1991). — Repo, T.: Seasonal changes of frost hardiness in *Picea abies* and *Pinus sylvestris* in Finland. Can. J. For. Res 22: 1949–1957 (1992). — Rummukainen, von U.: Die Haftfähigkeit von Kiefernnadeln. Allegemeine Forstzeitschrift 14: 416–418 (1982). — Sakai, A.: Freezing avoidance mechanism of primordial shoots of conifer buds. Plant and Cell Physiolgy 20: 1381–1390 (1979). — Stähl, E. G.: Variation in shoot growth phenology among clones and populations of *Pinus sylvestris* L.

Swedish Univ. Agricultural Sciences, Dept. Forest Yield Research, Garpenberg, 1984, ISBN 91-576-1942-5., 101 pp. (1984). — Sutinen, M.-L., Palta, J.P. and Reich, P. B.: Seasonal differences in freezing stress resistance of needles of *Pinus nigra* and *Pinus resinosa*: evaluation of the electrolyte leakage method. Tree Physiology 11: 241-254 (1992). — Timmis, R. and Worrall, J. G.: Translocation of dehardening and budbreak promotors in climatically split Douglas fir. Can. J. For. Res. 4: 229-237 (1974). — Weiser, C. J.: Cold resistance and injury in woody plants. Science 169: 1269-1278 (1970).

Multipurpose Gene Conservation in *Quercus suber* – a Portuguese Example

By M. C. VARELA1) and G. ERIKSSON2)

(Received 9th May 1994)

Summary

Quercus suber, the native forest tree of highest economic value to Portugal is continuously declining. Creating good conditions for future evolution is the most important gene conservation objective for Quercus suber. A simple breeding programme to improve the production of good cork is also included in the gene conservation objective. Gene conservation of species accompanying Quercus suber, or even dependent on Quercus suber, is a third objective. The suggested sampling of gene resource populations is mainly based on climatic, soil and management conditions of Quercus suber populations. Active selection of trees with good cork in small multiple populations growing over a broad array of site conditions is suggested to match the joint evolutionary and breeding objective in gene conservation. Management of large natural populations to create maximum habitat diversity is suggested to take care of the gene conservation of accompanying species. Knowledge of the genetic structure of Quercus suber and of gene flow is urgently needed and ought to be given priority in genetic research.

Key words: Quercus suber, cork oak, gene conservation objectives and methods, research needs.

FDC: 165.3; 165.4; 176.1 Quercus suber; (469).

Introduction

Quercus suber is the native forest tree of highest economic value to Portugal. The value of the export of cork amounts to approximately 200 million US \$ per year (Santos and Martins, 1993).

The actual range of the species is restricted to the western part of the Mediterranean area, in which the effect of summer drought is ameliorated by the wet Atlantic winds. The northernmost populations are found in southern France. The key climatic factors for the geographical limits of the species are essentially the annual precipitation and the winter temperatures whereas the species is not demanding with respect to soil conditions. The range of the annual precipitation of the

areas in which *Quercus suber* is growing varies between 400 mm and 2,500 mm although always with dry summers.

According to Natividade (1950) and Teixeira and Pais (1976) palaeobotanical data are insufficient to get a reliable picture of *Quercus suber* distribution during the Cenozoic or even during the beginning of the Quaternary when the Mediterranean region acquired its present orographic profile. Together with other species in the same genus it dominated the native forests in Portugal (Natividade, 1950; Teixeira and Pais, 1976). The prominent role of the *Quercus* genus is reflected in the ecological zonation of Portugal (Albuquerque, 1954).

Even if Portugal was outside the zone of ice cover during the glaciations, the climate turned cooler and became harsh to Quercus suber and other evergreen oak species. The compensatory effect of water and thermic balance on southern slopes with calcareous soil provided the microclimatic conditions under which Quercus suber could survive. From such refuges the species migrated and formed larger populations. During the xerothermic interglacial periods northern slopes housed the Quercus suber populations. As the climate turned cooler new migrations took place again. Today isolated populations are still to be found in spite of strong impact from anthropogenic factors. These vestiges of passed epochs reveal that the species is well able to cope with changed climatic conditions. Present observations lend further support for this. Whenever the human pressure is relaxed Quercus suber colonizes the freed areas within a few decades. This must be attributed to large genetic variation in adaptive traits and to its reproductive ability. This is certainly of great value for enabling the species to cope with the rapid change of the environmental conditions taking place today. However, it should be emphasized that the speed of the change now is higher than ever before (DAVIS and ZABINSKI, 1992).

In spite of a stable area of approximately 660 000 hectares (Anonymous, 1993) there has been a decline in *Quercus suber* owing to lower stocking accompanied by reduced production of high quality cork (Cabral and Sardinha, 1993). Climatic factors, pests and diseases as well as mismanagement were among the factors of greatest importance for the decline of *Quercus suber* during the recent decades. Cabral and Sardinha (1993) noted a relationship between extended droughts and

¹⁾ Estação Florestral Nacional, Tapada das Necessidadas, P-1300 Lisboa, Portugal

²⁾ Department of Forest Genetics, Swedish University of Agricultural Sciences, Box 7027, S-750 07 Uppsala, Sweden

mortality. Brasier (1992) mentioned that *Phytoftora cinnamomi*, which was found in some affected stands, might be another cause of the decline. Already 50 years ago PIMENTEL (1946) pointed out that the ink disease caused by *Phytoftora cambivora* occurred on cork oak trees.

In a historical perspective the area covered by Quercus suber has been reduced considerably by conversion into farm land. Still other areas are used for agroforestry with extremely low natural regeneration. When regeneration is allowed it is primarily based on spacing to fill gaps in the agroforestry population while selection for good cork quality is a secondary matter. During the recent century Quercus suber areas have been transferred to cultivation with other and faster growing tree species. Cities and towns have also claimed areas for urban development while the species was allowed to recover in other areas. Even extinction of some marginal populations of exquisite value has occurred as can be inferred by historic documentation and toponymic references (GIRAO, 1942). In summary man can be said to be the greatest threat to the distribution of Quercus suber, directly by his claim on land and indirectly by his pollution.

The decline of *Quercus suber* with its great economic value to Portugal calls for development of a gene conservation program for this species. Such a program has to be developed in the absence of the desired genetic knowledge. In this paper we describe principles in tree gene conservation and then how these principles can be applied to gene conservation of *Quercus suber* in Portugal.

Objective

In a recent paper on gene conservation policy ERIKSSON et al. (1993) argued that a clear identification of the objectives for gene conservation must precede a decision on the methods for gene conservation. Finkeldey (1992) and Eriksson et al. (1993) also strongly emphasized the need for an evolutionary approach in gene conservation. We adopt this approach and regard the creation of good conditions for future evolution as the prime objective for the gene conservation of Quercus suber. This agrees well with the statement by Soulé and Mills (1992) that Conservation genetics exists for one reason only: To promote the fitness of targeted populations.

With the increased demand for good cork and the declining area of the species it is logical to try to combine breeding and gene conservation. Since financial support for sophisticated breeding is unlikely at present, we suggest a simple breeding programme to improve the amount of production of good cork to be included in the gene conservation objective. Therefore, the main objective of gene conservation in Portugal is to create good conditions for future evolution with a simultaneous improvement of the production of good cork.

Conservation of other species dependent on *Quercus suber* should be considered as well. However, it must be realized that we cannot expect stable conditions in any ecosystem. This is supported by a recent review of changes in ecosystems based on palaeoecological data by Huntley (1992) who concluded that migration was the fundamental means with which species had responded to rapid environmental changes. Moreover, species had responded individually and not as ecosystems. This means that the present-day species composition must be regarded as a transient stage in a geological time context. In such a time frame there are continuous changes in the species composition.

Finally genetically unique populations may be endangered for various reasons. This has to be considered before decisions are taken on sampling of gene resource populations (GRPs).

Methods

For the most developed gene conservation populations the methods involve sampling, plantation, management, and regeneration. It is selfevident that the methods suggested should match the objectives but this is frequently forgotten (cf Eriksson et al., 1993). Below a general discussion of sampling and management of GRPs is carried out. The tree species to be conserved will be referred to as target species.

Sampling

Sampling should be done such that genes with frequencies of 0.01 and higher will be conserved. As seen from figure 1 an effective population size (N_e) of 500 trees would satisfy that purpose. Concerns about the risks for erosion of genetic diversity have been raised repeatedly (e.g. YANG and YEH, 1992). It is inevitable that stochastic processes in small populations eventually lead to gene fixation and thereby reduce genetic variance. However, of still greater significance is that even in populations with less than 50 individuals the genetic variance can be kept at the initial level over many generations of selection (HILL and KEIGHTLEY, 1988). This must be attributed to occurrence of new mutations and/or to originally neutral genes becoming non-neutral as the environment changes over breeding generations. Therefore, the loss of genetic variance by fixation seems to be compensated for by either or both of these phenomena. Another condition that deserves to be stressed is that response to selection may be much faster in small populations, 20 to 50 individuals, than in one large population. Basics of population genetics imply that the response to selection of recessive genes is extremely slow at low gene frequencies. This also holds for genes with additive action but to a lesser extent. In small populations, < 25, there is no gene frequency less than 0.02 in a diploid plant. For that very reason the response to selection will be faster in such small populations than in one large population. This is important to consider when preparing populations for rapid change of the environmental conditions.

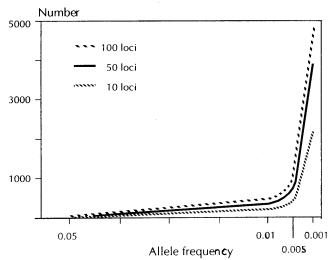


Figure 1. – Number of individuals needed to save alleles in different frequencies and with variable number of such alleles.

The disadvantage of inbreeding can be kept at an acceptable level if the effective population size is kept at 50. Such a population size will give an inbreeding coefficient, $F=1/2N_{\rm e}=0.01$, which will not cause any major reduction in the viability of the population concerned.

It is probable that natural selection has caused genetic differentiation of populations growing under different envi-

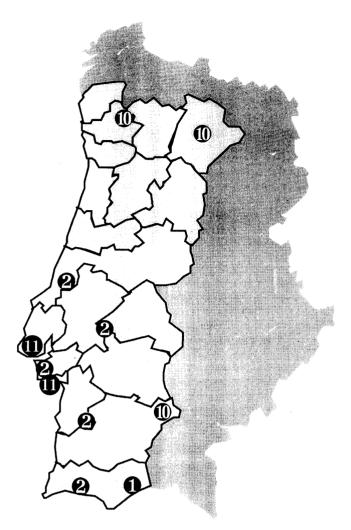


Figure 2. – The location of the Portuguese gene resource populations of *Quercus suber* and the suggested methods (numbers according to *Table 1*) for their management.

ronmental conditions. Even if this adaptation is far from a maximum in fitness it is useful to exploit this adaptation in gene conservation. Much effort has been devoted to the strategy of sampling, whether one large population or many small should be sampled. A general treatment for rare species was given by Brown and Briggs (1992) who suggested a sampling of some 5 populations with low numbers from each if the environmental differences were large. Recently Yang and Yeh (1992) had a useful discussion on sampling strategy based on allele distribution and allele frequency. When there is a significant differentiation among populations they recommended sampling of several populations. If the sampling covers several selective environmental neighborhoods in the sense of Brandon (1990) the approach becomes a combined gene and genotype conservation.

The existence of a considerable non-additive gene action will have a great impact on the sampling and management of gene resource populations (GRPs). If it occurs measures should be taken to avoid contamination by pollen from trees growing in other selective environmental neighborhoods. It has repeatedly been shown that adaptive traits in *Picea abies* and *Pinus sylvestris* mainly or even exclusively are regulated by genes with additive gene effects (EKBERG et al., 1991; SKRØPPA, 1993; NORELL et al., 1986). *Quercus suber* share many ecological features with those 2 conifers and few cases of coadaptation

have been observed in wild populations (cf Berry and Bradshaw, 1991). Therefore, we have assumed that the traits of adaptive significance in *Quercus suber* mainly show additive gene action.

Gene resource populations and their management

Gene conservation is frequently classified as ex situ or in situ (e.g. Namkoong et al., 1992) or sometimes as dynamic or static (ZIEHE et al., 1988; FINKELDEY, 1992). The introduction of the Multiple Population Breeding System (MPBS) according to NAMKOONG (1984) and its application in both ex situ or in situ gene conservation (ERIKSSON et al., 1993) call for a revision of this classification. Moreover, in situ gene conservation is related to plantations by many agricultural crop gene conservationists whereas such a plantation would be classified as ex situ by forest geneticists. The use of ex situ and in situ in forest genetics literature is at variance with the convention on biological diversity adopted in the Rio conference 1992 (Anonymous, 1992). Especially among layman in situ is mostly understood as a static means of gene conservation but may be rather dynamic depending upon how the GRP is managed. There is a continuous transition from dynamic to static gene conservation which makes classification with these terms as criteria somewhat equivocal.

A classification of the methods for gene conservation of a species should have its starting point in their possibilities to capture existing adaptations and to promote future evolution. Both of these conditions depend on the number of gene resource populations, at least for species covering several selective environmental neighborhoods. Therefore, the number of populations is a useful classification criterion. One population in our case is equivalent to one selective environmental neighborhood in the sense of Brandon (1990). The coverage of several habitats is also a prerequisite for capture of present adaptations and for the maintenance of the existing genetic variation as well as for increasing among-population genetic variation. The classification according to this reasoning is shown in table 1.

The concept of the multiple population breeding system, MPBS, was first introduced by NAMKOONG (1976) for tree breeding. Later on he showed its potential for joint breeding and gene conservation (NAMKOONG, 1984). The MPBS means that the gene resource population is split into subpopulations each with some 50 genetic entries. The subpopulations according to the MPBS concept are always sampled to capture maximum among-population genetic variation. In its most elaborate form, method 1 in table 1, the subpopulations are planted over a broad array of site conditions and disruptive selection in future generations is carried out to increase the among-population genetic variation. Even plantations outside the present range of the species may be used (cf. Eriksson et al., 1993). The MPBS concept can also be used without any planting but with active management and selection to improve the genetic variation, method 2 in table 1. The potential to improve the genetic variation is smaller than for method 1 but this method benefits from its low costs. In method 3 only the capture of existing genetic variation only is exploited and this method is the one with least merits of the three MPBS methods.

Provenance and progeny trials (method 4) are sometimes overlooked as gene resources but they can readily be included in an account of genere sources. Their merits depend on the number of populations represented in the trials. If only few populations are represented they do not even keep the genetic variation of the species, whereas if they contain provenances from the entire distribution of the species they evidently fulfil

 $Table\ 1.$ – Methods for gene conservation based on a classification of gene resource populations with respect to population number, habitat diversity, and genetic variation in the target species as a whole.

Method, No.		Population number	Habitat diversity	Geneti kept	c variation improved ¹
Multiple populations MPBS; intentionally sampled to capture existing adaptation:					
planted and managed natural:	1	≈20	+	+	++
with management	2	≈20	+	+	+
without management	3	≈20	+	+	,
Provenance trials, progeny trials	4	a few - large	+	- to +	
Seedling seed orchard Clonal archives, clonal	5	a few - large	-	- to +	
seed orchards	6	a few - large	-	- to +	
Seed banks	7	large	-	+	
Pollen bank	8	large	-	+	
Tissue culture banks	9	large	-	+	
Single populations					
Large natural populations					
managed to create maximum		•			
habitat diversity	10	1	+	-	
Unmanaged natural population	11	1	-	-	
Botanical gardens	12	1	-		

¹⁾ Only potentials for improvement are indicated.

the requirement of maintaining the genetic variation. Generally provenance trials include more populations than progeny trials. Neither type of trial is designed to promote future evolution

A seedling seed orchard (method 5) may contain progenies from a few populations but these are mostly limited to populations originating from a limited part of the distribution of the species. At least for the traits selected for, the genetic variation is narrowed down by the culling of inferior families and inferior trees in good families. If there is a series of seedling seed orchards each with progenies from one population such a series comes close to planted small multiple populations.

Clonal archives, method 6, do not usually capture the total genetic variation in a tree species and the seed orchards even less often. Neither of them is intended to promote evolution.

The greatest merit of methods 7 to 9, seed banks, pollen banks, and tissue culture banks, is their preservation of the present genetic constitution. Since they are not space demanding they can house larger numbers of genotypes than all other gene conservation methods. For long-generation tree species these methods suffer from the long time it takes to subsequently obtain a new generation.

The greatest merit of method 10 as regards gene conservation is not for the target species itself but rather for the conservation of accompanying species. This is based on the knowledge that in all biosocieties there is a succession of species' appearances. Thus certain species are dependent on the young stages of succession of the climax species for their existence; even forest fires are required by some species. Others depend on the habitats available during the last stages in succession, *i.e.* habitats with snags and fallen logs. The specificity in habitat demands is evident from a recent Swedish study of factors critical for the sustained survival of endangered species (BERG et al., 1994). This study showed that habitat elements played a major role for cryptogams, vertebrates, and invertebrates whereas few vascular plants were demanding in this respect.

The plus sign under habitat diversity for this method in *table 1* is thus valid for the accompanying species while the minus sign under genetic variation is valid for both target and accompanying species.

A single unmanaged nature reserve, method 11, does not fulfil the requirements of conserving the present structure of the target species except for endemic species restricted to a single selective environmental neighborhood. Nor does it promote evolution. The role of unmanaged natural reserves in gene conservation would be a monitoring one to reveal changes in species composition that would indicate that large environmental changes had taken place.

Finally method 12, botanical gardens, rarely contains more than a few specimens of each species and their role as gene resource populations in such cases is of extremely limited value.

Methods for gene conservation of Quercus suber

ERIKSSON et al. (1993) recommended that the MPBS should be used for our objective of combining breeding and creation of the best conditions for future evolution. For economic reasons we suggest that method 2 in $table\ 1$ (small natural multiple populations with management) is applied for $Quercus\ suber$ in Portugal. For the simultaneous gene conservation of $Quercus\ suber$ and for the accompanying species dependent on the $Quercus\ suber$ ecosystem, we suggest that management of large natural populations (Method 10, $Table\ 1$) should be used.

Sampling must first of all be guided by the genetic variation in adaptive traits. Since there is no knowledge about genetic variation for such traits the sampling has to rely on educated guesses about possible genetic variation for these traits. Ecogeographical gradients were assumed to be one of the principal causes of genetic differentiation among populations (STERN and ROCHE, 1974). Climatic variables and soil type received special attention on the criteria for selection of stands for gene conservation (Table 2). Summer drought is believed to be a key

Table 2. – Climatic and ecological characterisation of Quercus suber GRPs in Portugal. P = annual rainfall in millimetres; $M^{\circ}C$ = mean of the maximum temperatures of the hottest month; $m^{\circ}C$ = mean of the minimum temperatures of the coldest month; Q_2 = climatic index of EMBERGER (1971); Ecological zone = after ALBUQUERQUE (1954). Suggested method No. according to classification in table 1.

GRP	Precipitation, mm	М°С	m°C	Q_2	Ecological zone ^a	Method suggested
Sobreiral da Ermida (Gerês)	2407.9	22 ^b	2 ^b	422.1	SA-AM	10
2. Sa de Bornes	1009.4	28 ^b	2 ^b	134.7	SA-SM	10
3. M.N. Mestras (Alcobaça)	945	25.8	4.8	156	AM	2
4. M.N. Cabeção	640.4	31	4.4	82.8	SM	2
5. Mª de Queluz	767.6	27.6	6.6	118.2	AM	11
6. Qa da Serra	764.4	29	5.6	109.8	AM	2
7. Sª Arrábida	764.4	29	5.6	109.8	AM	11
8. H. Loureiro	719.4	26.5	7.2	128.5	AM-SM	2
9 Sob. do Tio Sales M.N. Contenda	729.5	31.8	6.1	97.2	IM-SM	10
10. M.N. Conceição de Tavira	515.1	31	8.3	77.5	M	1
11. H. da Parra (Silves)	1076.9	30.5	7.5	160	SM	2

a) Explanation of the symbols used in the ecological zonation:

A Atlantic. Refers to climate always wet; moderate winters and mild summers. Indicative species: Quercus robur. M Mediterranean. Average pluviousity; mild winters; summers dry and hot Indicative species Priunus amygdalus, Ceratonia siliqua. I Iberian. Continental climate, low precipitation; very hot summers; warm winters. Indicative species Quercus rotundifolia.

Zones with transitional profiles: The symbol S stands for sub, which means that the region has an attenuated profile of the second symbol. When 2 symbols are used together, the second is the dominant factor. Example: AM is a region of Mediterranean profile smoothed by Atlantic influence.

Linked zones: Zones of mixed characteristics where influence of the indicate ecological zones is balanced. Example: SA-SM means a balance Subatlantic and Submediterranean profiles.

b) Estimations based on DAVEAU (1985)

climatic variable (cf Cabral and Sardinha, 1992). To get some neutral characterization of the GRPs selected, climatic and ecological data are given in $table\ 2$.

Summer drought and winter minimum temperatures are the key climatic parameters of Mediterranean climates. Drought is difficult to estimate and various methods have been suggested. In Mediterranean climates the evaporation is proportional to the difference between the extreme temperatures (hottest month – coldest month). When this variable is related to the total precipitation, an index \mathbf{Q}_2 (EMBERGER, 1971) is obtained which constitutes a successful combination of temperature and drought that matches the ecological zonation of Mediteranean formatics.

 $Q_{o} {=}\, 2000 P {/}\, (M{+}m{+}546.4)\, (M{-}m)$ in which

P- annual precipitation in mm;

M- average maximum temperature of the hottest month in $^{\circ}C$; m- average minimum temperature of the coldest month in $^{\circ}C$. Values of Q_{\circ} :

 $\begin{array}{lll} 10 \leq Q_2 \leq 12 & \text{Lower limit of the arid Mediterranean climate;} \\ 25 \leq Q_2 \leq 27 & \text{Upper limit of the arid Mediterranean climate;} \\ Q_2 = 50 & \text{Upper limit of the semi-arid Mediterranean climate:} \end{array}$

 ${\bf Q}_2$ =100 Upper limit of the sub-humid Mediterranean climate:

 Q_2 = 200 Upper limit of the humid Mediterranean climate.

The Emberger \mathbf{Q}_2 index as well as soil characterisation, aspect and phytoassociations constituted the main basis for ecological zonation for Portugal elaborated by Albuquerque (1954). The ecological classification for each GRP is also shown in table 2.

Management and isolation were also considered as important factors for genetic differentiation among populations. All GRPs except population 10 have a natural regeneration origin. As seen from $table\ 2$ we have tried to select as many different combinations as possible among the factors considered. The annual variation in precipitation and monthly temperatures are illustrated in $figures\ 3$ to 6 as ombrothermic diagrams, in which summer drought can be estimated by the shaded area.

Brief characterisation of the cork oak GRPs

Population 1- Sobreiral da Ermida, Gerês

This is a natural population of odd site conditions for *Quercus suber*. The winters are cold, precipitation is extremely high, summer drought is light and soils are poor with huge granite formations. It is considered by NATIVIDADE, 1950 a relic grove when the species migrated northwards. It is now an isolated population in a region where *Quercus pyrenaica* and *Pinus syl-*

 $Table\ 3.-A$ summary of the objectives for gene conservation of $Quercus\ suber$ in Portugal and the methods suggested to match the objectives.

Objective	Method			
Saving of all genes with a frequency of 0.01 and higher	Multiple populations over a broad array of site conditions			
Creation of good opportunities for future evolution	Managed multiple populations over a broad array of site conditions			
Inclusion of existing adaptedness	Multiple populations over a broad array of site conditions			
Combined breeding and gene conservation	Managed small multiple populations			
Threat of extinction	Nature reserves			
Gene conservation of associated species	Management to create maximum habitat diversity in large natural populations			
Preparedness for rapid environmental change	Establishment of transferred populations, mainly from a warmer and dryer climate			

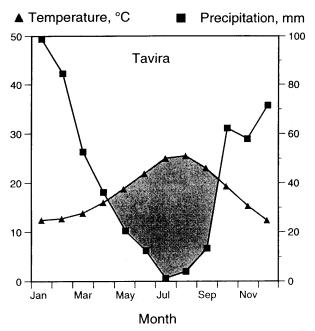


Figure 3. – Ombrothermic diagram for GRP 10, MN Conceição de Tavira, based on meteorological data from this locality. The main feature of this locality is the long and dry summers, where the water availability is at the threshold for $Quercus\ suber$. The pattern showed holds to some extent for GRPs 4 and 9 too.

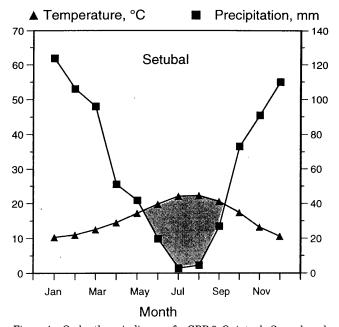


Figure 4. – Ombrothermic diagram for GRP 6, Quinta da Serra, based on meteorological data from Setubal. Summer drought is considerable but always above the threshold for the species. The pattern showed holds to some for GRPs 7 and 11 too.

vestris used to dominate but is now invaded by Pinus pinaster and exotic forest tree species. It is a population in great jeopardy. It is submitted to intensive grazing by goats which is responsible for the old age status of the population. Although showing profuse levels of natural regeneration the browsing pressure is so intense that all seedlings and young plants are destroyed in a short time. Measures to restore an even ageclass distribution are urgently needed but will be hard to

accomplish owing to the ownership of the land. Besides its qualities for gene conservation this GRP is of great importance for studies of the levels of genetic differentiation of *Q. suber* populations and for studies on gene flow.

Population 2- Serra de Bornes

The main feature is the contrast between the hot dry summers and the cold winters. The species reaches one of its

Table 3. – A summary of the objectives for gene conservation of Quercus suber in Portugal and the methods suggested to match the objectives.

Objective	Method
Saving of all genes with a frequency of 0.01 and higher	Multiple populations over a broad array of site conditions
Creation of good opportunities for future evolution	Managed multiple populations over a broad array of site conditions
Inclusion of existing adaptedness	Multiple populations over a broad array of site conditions
Combined breeding and gene conservation	Managed small multiple populations
Threat of extinction	Nature reserves
Gene conservation of associated species	Management to create maximum habitat diversity in large natural populations
Preparedness for rapid environmental change	Establishment of transferred populations, mainly from a warmer and dryer climate

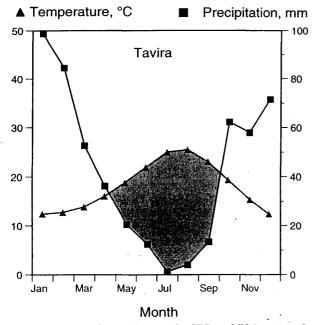


Figure 3. – Ombrothermic diagram for GRP 10, MN Conceição de Tavira, based on meteorological data from this locality. The main feature of this locality is the long and dry summers, where the water availability is at the threshold for Quercus suber. The pattern showed holds to some extent for GRPs 4 and 9 too.

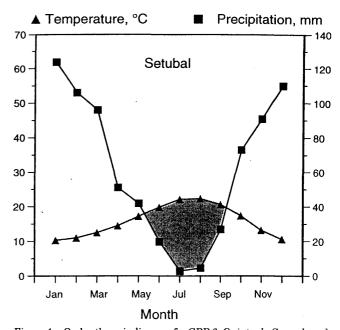


Figure 4. – Ombrothermic diagram for GRP 6, Quinta da Serra, based on meteorological data from Setubal. Summer drought is considerable but always above the threshold for the species. The pattern showed holds to some for GRPs 7 and 11 too.

vestris used to dominate but is now invaded by Pinus pinaster and exotic forest tree species. It is a population in great jeopardy. It is submitted to intensive grazing by goats which is responsible for the old age status of the population. Although showing profuse levels of natural regeneration the browsing pressure is so intense that all seedlings and young plants are destroyed in a short time. Measures to restore an even ageclass distribution are urgently needed but will be hard to

accomplish owing to the ownership of the land. Besides its qualities for gene conservation this GRP is of great importance for studies of the levels of genetic differentiation of Q. suber populations and for studies on gene flow.

Population 2- Serra de Bornes

The main feature is the contrast between the hot dry summers and the cold winters. The species reaches one of its

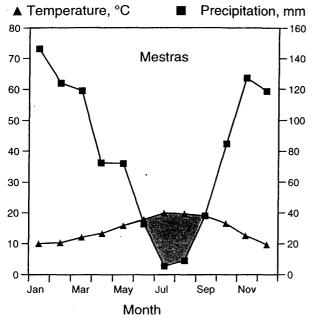


Figure 5. – Ombrothermic diagram for GRP 3, MN des Mestras, based on meteorological data from Alcobaça. Summer drought is mild with satisfactory water availability during the summer. The pattern showed holds to some extent for GRPs 5 and 8 too.

highest altitudes in Portugal, more than 1000 m. Along with GRP 1 it is considered by NATIVIDADE (1950) a living relic population for the actual distribution of the species.

Population 3- MN. das Mestras, Alcobaça

This is a relict of the once dominating species in the center of Portugal. The site exhibits average climate conditions for the species but the soil is of good fertility. The region has suffered from human pressure for more than a millenium. The good conditions for agriculture and human settlement are the reason for the destruction of the stands of *Quercus suber* in this region. Presently the income from cork oak is not competitive.

Population 4- MN do Cabeção

The population occupies a region of poor soils, arenits with pebbles, with low capacity for water retention, which probably aggravates the summer drought. The population is surrounded by private stands where management is often wrong and where worrying rates of death occur. The Portuguese Forest Service practices a careful management which probably explains the healthy performance of this population. The contrasting appearance of this GRP strengthens the interest for its gene conservation.

Population 5- Matinha de Queluz

This natural reserve has been included in the gene conservation since it constitutes a relic population from the originally widespread area of the species in the Lisboa region, now almost eradicated owing to agriculture in the past and urban activities presently. The population is situated along a highway and should be monitored for the effects of pollution from the intensive road traffic.

Population 6- Quinta da Serra. Setubal

This is a population of natural origin submitted to intensive, but correct, economical and agroforestry management with temporary grazing. The philosophy of sustained production

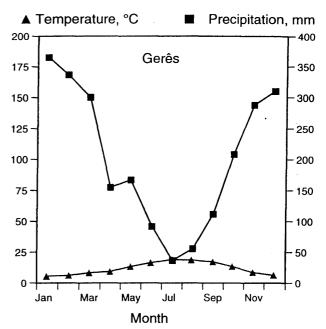


Figure 6. – Ombrothermic diagram for GRP 1 Sobreiral da Ermida, Gerês based on precipitation from Ermida meteorological station and temperature estimations from DAVEAU (1985). The summer precipitation is extremely high for Portuguese conditions and the climate of this locality is unique for Quercus suber.

guides the human intervention. It is a pure stand without inter- or intra-specific competition. Tree spacing is uneven and age classes are roughly zoned to a few hectares each. The soil is fertile, of good water retention, and cork quality is excellent.

Population 7- Serra da Arrábida

In spite of being situated close to GRP No. 6 the Arrábida population No. 7 differs dramatically from No. 6, justifying its selection as a GRP. The flora of Arrábida mountains is considered by RIBEIRO (1988) the most precious remnant of a pristine Mediterranean forest, a typical maqui of evergreen plants that reach outstanding dimensions. Chodat (quoted by RIBEIRO, et al., 1988) classified Arrábida as one of the last vestiges, if not the last, of a pre-glacial forest in the South of Europe. This GRP is a nature reserve where, contrary to GRP 6, there is no kind of human intervention nor is there any grazing. Quercus suber trees coexist in mixtures of other Mediterranean tree and shrub species, facing intense competition. Nowadays Quercus suber is only found on the north slope on which the trees are less exposed to the hot summer sunshine. The Emberger index showed in table 2 for this site is probably somewhat underestimated since it is plausible that maximum temperatures are lower on the north slopes of Arrábida than those of Setubal, the nearest meteorological station.

Population 8- Herdade do Loureiro

This is a population in a mild site for the distribution of the species in Portugal. It gathers its interest for gene conservation because intensive management for breeding purposes can be performed, it is situated in a region where abnormal rates of death for the species in Portugal occur (CABRAL et al., 1993) and because for the last 2 decades it has been on the route for industrial pollution from the Sines industrial complex.

Population 9- MN da Contenda

This is a population of natural profile where the main features of the region is stands of man-made sowing. Climate is

harsh for the species with heavy summer drought in adverse soils which probably aggravate the low water availability.

Population 10- MN Conceição de Tavira

This GRP originates from an artificial sowing around 1930. Nowdays it coexists with *Quercus rotundifolia* which dominates whenever the intense summer drought, the main feature of this locality, is stressed by the geographical aspect. There was no *Quercus suber* neither *Quercus rotundifolia* in this region before, both species thus being introduced. Since this GRP shows an extremely good adaptation with abundant regeneration we include it in the gene conservation in spite of its being a non-natural population. Moreover, this GRP grows in a part of the country with extremely low precipitation. The good adaptation under these adverse conditions suggest that it may contain genotypes not existing in other GRPs.

Population 11- MN Herdade da Parra

It is a population that well represents the *Quercus suber* stands of the Algarve hill range where the cork quality attains some of the highest qualities in Portugal. Winters are mild, summers are dry. In spite of being situated in a region where annual precipitation exceeds the average for the Algarve hills the summer drought still constitutes a limiting factor. This GRP has the typical appearance of the *Quercus suber* populations of the Algarve hills.

Management of the gene resource populations

There is a large phenotypic variation among trees in their ability to produce cork of high value (Carvalho, 1989). So far there is no knowledge of whether this phenotypic variation is genetically conditioned. However we assume that part of the phenotypic variation can be attributed to genetic differences among trees. The selection in the GRPs to improve the yield of good cork can be done by:

- 1) active selection in the parental population;
- 2) selection among the trees in the progeny generation which allows a higher selection intensity;
- 3) a combination of the 2 methods.

Since the GRPs vary from an intensively managed forestry or agroforestry type (GRPs 2, 3, 4, 6, 8, and 11) to natural forests of *Quercus suber* (GRPs 1, 5, 7, and 9), different methods have to be used for different GRPs. The two natural reserves, GRPs 5 and 7, will not be managed.

Agroforestry gene resource populations

We suggest method 2 to match the 2 objectives, creation of good conditions for future evolution and the combined gene conservation and breeding.

For the managed cork producing populations with their large spacing and the absence of any regeneration the first measure to take is to create conditions for regeneration. Therefore, we suggest that an area containing 120 to 150 mature trees, centrally located within the GRP, is fenced to lock out cattle from feeding on acorns and from browsing on young seedlings of Quercus suber. A census number of 120 to 150 corresponds to an No of 50 (VARELA, 1994). Such a population size will allow for good natural regeneration. This means that more than 50 trees are primarily used for the regeneration. Altogether more than 500 trees will be included in the Portuguese combined breeding and gene resource population. A selection by culling of some of the parental trees does not seem meaningful since the selection intensity will be extremely low. Therefore we suggest a culling in the new stand during the course of its development. If there are any previously selected plus trees from the same ecogeographic zone, a supplementary sowing with acorns from these trees can be done. Finkeldey (1992) suggested that the progenies from individual trees should be kept separate to improve the potential for evolution. Although we support this view, we find it, for the time being, economically impossible to carry out.

Managed natural populations

We suggest method 10 to match the objective of joint gene conservation of *Quercus suber* and accompanying species. During the scrutiny of different gene conservation methods we argued that the prime management undertaking would be to create different age classes of the target species. Accordingly we suggest that some GRPs are managed to cover the whole range from young seedlings of *Quercus suber* to overmatured *Quercus suber* trees. Until knowledge becomes available about the specific demands of associated species we cannot prescribe detailed protocols for creation of important habitats for those species. However, a management that maximizes habitat number seems to be most sensible. Forest fires constitute integrant elements of the Mediterranean forests (PIUSSI, 1992). It is conceivable that forest fires create specific habitats. Therefore forest fires should be allowed or even controlled burning be applied.

Since the global change may lead to a warmer and dryer climate a few *ex situ* plantations with material from hotter and more arid climates would be useful to include in the gene conservation program if financial support is available.

Research needs

Research is needed to make the previously described program more efficient and useful. The above described work lays the foundation by establishing a base that will take care of almost any existing structure of variation. Research can now both clarify the actual structure as well as indicate how it can be used.

The genetic structure probably varies with the traits studied. For gene conservation purposes the utility of different traits has been discussed many times (e.g. LIBBY and CRITCH-FIELD, 1987; ERIKSSON, 1994). It has repeatedly been shown that adaptive traits and markers (isozymes, DNA fragments) result in different structure. Therefore, there is an urgent need to initiate studies on the genetic structure of adaptive traits in Quercus suber. This agrees with a recent statement by CAIN and Provine (1991) in their review of the history of genecology. No molecular technique can ever provide a quick fix to the basic problems of ecological genetics. However, Petit et al., (1993) recently showed that chloroplast DNA could be used to distinguish populations both in Quercus petrea and Q. robur. In the forefront, genetic variation in drought tolerance during the growth period ought to be studied. It can be speculated that some of the cork properties would improve the drought tolerance. Their relationships with drought tolerance would be useful to study. Knowledge on gene flow mechanisms is also absent for Quercus suber. Since gene flow may play a crucial role for the species to cope with environmental change such studies should also be undertaken. Acorn production is another adaptive trait that ought to be studied. The same is true for cold tolerance, and pest and disease susceptibility.

The studies on genetic structure ought to be designed as long-term combined among- and within-population studies with trials located along an ecological gradient. If there are potentials for evaluation in short-term tests, such should be utilized. Drought tolerance is a trait that advantageously might be studied in growth chambers. If the trials are designed

in such a way that they will give useful information on the heritabilities of the traits, their genetic correlations as well as the genotype x environment interaction.

Recently d'Alpuim and Roldão (1993) presented a program for breeding *Quercus suber*. In addition to what they stated we should like to make some further suggestions. Thus the studies presented in the previous paragraphs are useful for breeding, too. As regards the reliability of phenotypic selection for cork formation we stress that this is best studied by testing a representative sample of offspring from one naturally regenerated population. If selected trees only are included in the study this will reduce the possibilities of revealing a strong parent-offspring correlation.

Studies of mating pattern must be carried out to be able to improve the acorn production of superior trees in a coming breeding program. This is especially important for a future breeding that has to rely on acorn production in any form of seed orchards.

An artificial reforestation technique is needed for any intensive form of breeding. Therefore studies covering the path from identification of phenotypically superior trees to planting must be carried out (Fig. 7). Since seeding or planting is critical for any implementation of gains from breeding, research related to that part of the regeneration should be given priority.

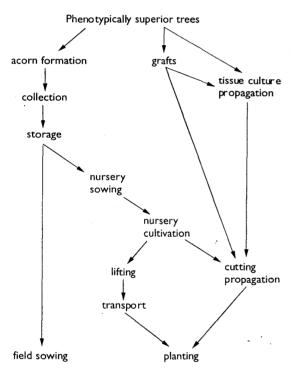


Figure 7. – Flow chart illustrating research needs related to referestation.

Conclusion

For Portugal we have identified several objectives for gene conservation of *Quercus suber* besides the overriding one of saving all genes at a frequency of 0.01 and higher. We argue for inclusion of the adaptedness that may be the result of natural selection under different site conditions. This does not mean that we consider them as maximally adapted to the site conditions they live under. We have also included a breeding objective to improve the production of good cork. Of great concern is also to include the gene conservation of associated

species in the *Quercus suber* ecosystem. Inclusion of some populations which are under a strong threat of extinction is also suggested. Finally the preparation for a possible rapid change of the climatic conditions is another objective.

For the Portuguese gene conservation program of *Quercus suber* we have suggested 11 gene resource populations, each with at least 50 trees. Any single method, if used exclusively, would either not achieve some objectives or would be very costly if made to accomodate all objectives. The selection shows that an efficient set of methods can be chosen and combined in a strategy. For other situations, a wide choice of methods is available that may be put together in a strategy. The gene conservation program suggested has been designed for Portugal but may easily be extended to other countries in which this species grows. If this is done, the gene conservation of *Quercus suber* will be well taken care of. The program suggested may be utilized for other tree species sharing the ecological features of *Quercus suber*.

Since genetic knowledge is absent for *Quercus suber* we have suggested several research activities to be initiated. Of primary concern is to start genetic research on traits of adaptive significance, among which drought tolerance should be given priority. Knowledge on mating pattern in natural populations is urgently needed. Research to develop techniques for artificial regeneration is also urgently needed for any future breeding program.

Acknowledgements

We thank professors GENE NAMKOONG, Vancouver, Canada, RAÚL SARDINHA, Lisboa, Portugal, for their valuable comments on our manuscript as well as for useful discussions on gene conservation, and Dr. DAVID CLAPHAM for revision of the English text. Thanks are also due to the Camar Project Improvement of quality and productivity of cork oak ecosystem, Contract No. 8001, Ct 91-0-11 (PL 900653) (CEE-RTD-CAMAR-1989-1993), Instituto Florestal, and Instituto de Conservação da Natureza in Portugal.

References

ALBUQUERQUE, J. P. M.: Carta Ecólogica de Portugal Min. da Economia, Direcção Geral dos Serviçoa Agrícolas. Lisboa. 58 pp. (In Portuguese) - Anonymous: Convention on biological diversity. United Nations Environment Programme. 24 pp. (1992). — Anonymous: Distribuição da floresta em Portugal continental. Estudos e Informação No. 303. 30 pp. (In Portuguese). (1993). — d'Alpium, M. and Roldão, M. I.: Quercus suber breeding strategy for cork quality. Ann. Sci. For. 50, Suppl 1, 444-447 (1993). — Berg, Å., Ehnström, B., Gustafsson, L., HALLINGBÄCK, T., JONSELL, M. and WESLIEN, J.: Threatened plant, animal and fungus species in Swedish forests - distribution and habitat associations. Conserv. Biol., In press (1994). - BERRY, R. J. and BRAD-SHAW, A. D.: Genes in the real world. In: Genes in Ecology. 33rd Symp. Brit. Ecol. Soc., Univ. East Anglia. Eds. R. J. BERRY, T. J. CRAWFORD, and G. M. HEWITT. Blackwell Scient. Publ., London, Edinburgh, Boston, Melbourne, Paris, Berlin, Vienna. 431-449 (1991). — Brandon, R. N.: Adaptation and environment. Princeton Univ. Press., Princeton, New Jersey. 214 pp (1990). — Brasier, C. M.: Phytophtora cinnamomi as a contributory factor in European oak declines. In: Recent Advances in Studies on Oak Decline. Proc. Int. Congr. Selva di Fasano, Italy. Sept 13 to 18, 1992. Eds. N. Luisi, P. Leirario, and A. Vannini. 49–57 (1993). Brown, A. H. D. and Briggs, J. D.: Sampling strategies for genetic variation in ex situ collections of endangered plant species. In: Genetics and Conservation of Rare Plants. Eds. D. A. FALK and K. E. HOLSINGER. Oxford Univ. Press, New York. 99-119 (1991). — CABRAL, M. T., LOPES, F. and SARDINHA, R. A.: Determinação das causas de morte do sobreiro nos concelhos de Santiago do Cacém, Grândola e Sines. Relatório síntese. Silva Lusitana 1, 7-24. (In Portuguese, English summary). (1993). — CABRAL, M. T. and SARDINHA, R. M. A.: Prespectiva integrada do declino dos montados de sobro. 2º Encontro sobre os montados de sobre e azinho, Évora. Junho 1992. Soc. Port. Ciên. Florest., Évora, Portugal. 217-231. (In Portuguese). (1992). - CAIN, A. J. and PROVINE, W. B.: Genes and ecology on history. In: Genes in Ecology. 33rd Symp. Brit. Ecol. Soc., Univ. East Anglia. Eds. R. J. BERRY, T. J. CRAWFORD and G. M. HEWITT. Blackwell Scient. Publ., London, Edinburgh, Boston, Melbourne, Paris, Berlin, Vienna. 3-28 (1991). — CARVALHO, A.: Considerações sobre silvotecnologia em subericulturra. In: identificação de prioridades

e recursos de I&D sobre cortica. Workshop da Fundação Luso-Americana para o Desenvolvimento, Lisboa, Julho, 1988, (In Portuguese). (1989). — DAVEAU, S.: Mapas climáticos de Portugal. – Nevoeiro nebulusidade e contrastes térmicos. Memórias do Centro de Estudos Geográficos, n°7, Lisboa. 66 pp. (In Portuguese, English summary). (1985). — DAVIS, M. B. and ZABINSKI, C.: Changes in geographical range resulting from greenhouse warming: Effects on biodiversity in forests. In: Global Warming and Biological Diversity. Eds. R. P. Peters and T. E. Lovejoy. Yale Univ. Press, New Haven and London. 297-308 (1992). - EKBERG, I., ERIKSSON, G. and NILSSON, C.: Consistency of phenology and growth of intra- and interprovenance families of Picea abies. Scand. J. For. Res. 6, 323-333 (1991). — EMBERGER, L.: Travaux de Botanique et d'Écologie. Masson et C., Paris. 465 pp (1971). - ERIKSSON, G.: Which traits should be used to guide sampling for gene resources. Proc. Int. Symp. Pop. Genet. Gene Cons. For. Trees, Carcans Maubison Aug. 24 to 28, 1992. In press. (1994). — Eriksson, G., Namkoong, G. and Roberds, J.: Dynamic gene conservation for uncertain futures. For. Ecol. Managem. 62, 15-37 (1993). — FINKELDEY, R.: Auswahlskriterien und Anlage genetischer Resourcen bei der Fichte (Picea abies [L.] KARST.). Forstarchiv 63, 25-32 (1992). — DE GIRÃO, A.: Distribuição antiga do sobreiro em Portugal. Bol. Junta Nac. Cortiça, Ano IV (44), 5-7, (In Portuguese), (1942). — HILL, W. G. and KEIGHTLEY, P. D.: Interrelations of mutation, population size, artificial and natural selection. In: Proc. 2nd Intern. Conf. Quant. Genet.. (Eds. B. S. Weir, E. J. Eisen, M. M. GOODMAN and G. NAMKOONG). Sinnauer Ass. Inc. Publ., Sunderland, MA, 57–70 (1988). HUNTLEY, B.: How ecosystems respond to environmental change: evidence from late-Quarternary palaeoecological records. In: Responses of forest ecosystems to environmental changes. Commission of the European Communities. Elsevier Applied Science, London, 45-54: (1992). LIBBY, W. J. and CRITCHFIELD, W. B.: Patterns of genetic architecture. Ann. Forest. (Zagreb) 13, 77–92 (1987). — Namkoong, G.: A multiple index selection strategy. Silvae Genet. 25, 199–201 (1976). — Nam-KOONG, G.: Strategies for gene conservation in forest tree breeding. In: Plant Gene Resources: A conservation imperative AAAS Selected Symp. 87. Eds. C. W. YEATMAN, D. KAFTON and G. WILKES. Westview Press, Boulder, Co.79-89 (1984). — Namkoong, G., Bawa, K., Burley, J. and Shen, S.: Managing Global Genetic Resources. Forest trees. Natl. Acad. Press, Washington, DC. 229 pp. (1991). — NATIVIDADE, J. V.: Subericultura. 2nd edition. Ministério da Economia, Pescas e Alimentação, Direcção Geral das Florestas et Aquicolas. 387 pp. (In Portuguese,

reediting 1990). (1950). — NORELL, L., ERIKSSON, G., EKBERG, I. and DORMLING, I.: Inheritance of autumn frost hardiness in Pinus sylvestris L. seedlings. Theor. Appl. Genet. 72, 440-448 (1986). — Petit, R. J., KREMER, A. and WAGNER, D. B.: Geographic structure of chloroplast DNA polymorphisms in European oaks. Theor. Appl. Genet. 87, 122-128 (1993). — PIMENTEL, A. A. L.: O sobreiro também é parasitado pela Phytophtora cambivora (PETRI) BUIS., agente da "doença da tinta do castanheiro. Publicação da Direcção Geral dos Serviços Florestais e Agricolas 13, 45-49. (In Portuguese), (1946). - Piussi, P.: Environmental changes in forests: Exemples from the South of Europe. In: Responses of forest ecosystems to environmental changes. Commission of the European Communities. Elsevier Applied Science, London, 298-309 - RIBEIRO, O., LAUTENSACH, H. and DAVEAU, S.: Geografi de Portugal, Vol II. O ritmo climàtico e a paisagem. Ed. João Sá DA COSTA. 337-623, (In Portuguese) (1988). — Santos, M. N. D. S. and Martins, A. M. M.: Cork oak decline. Notes regarding damage and incidence of Hyploxylon mediterraneum. In: Recent Advances in Studies on Oak Decline. Proc. Int. Congr. Selva di Fasano, Italy. Sept. 13-18, 1992. Eds. N. LUISI, P. LEIRARIO and A. VANNINI. 115-121 (1993). - SKRØPPA T.: Variation and inheritance in diallel crosses within natural populations of Norway spruce. Proc. IUFRO Meet. Norway Spruce Prov. Breed., Jurmala, Latvia. Sept. 13 to 17, 1993. Abstract, 240 (1993). - Soulé, M. E. and MILLS, L. S.: Conservation genetics and conservation biology: a troubled marriage. In: Conservation of Biodiversity for Sustainable Development. Eds. O. T. SANDLUND, K. HINDAR and A. H. D. BROWN 55-69 (1992). - STERN, K. and ROCHE, L.: Genetics of Forest Ecosystems. Springer Verlag, Berlin, Heidelberg, New York. 330 pp. (1974). TEIXEIRA, C. and PAIS, J.: Introducção à paleobotânica, As grandes fases da evolução dos vegetais. Lisboa. 199 pp. (In Portuguese) (1976). VARELA, M. C.: Overview on ongoing research in Q. suber in Portugal. Workshop on inter and intraspecific variation in European oaks: Evolutionary implications and practical consequences. Brussels, 15, 16 June 1994. In press (1994). - YANG, R.-C. and YEH, F. C.: Genetic consequencies of in situ and ex situ conservation of forest trees. For. Chron. 68, 720–729 (1992). — Ziehe, M., Gregorius, H.-R., Glock, H., Hattemer, $H.\ H.\ and\ Herzog\ S.:$ Gene resources and gene conservation in forest trees: General concepts. In: Genetic Effects of Air Pollutants in Forest Tree Populations. Eds. F. Scholz, H.-R. Gregorius and D. Rudin. Springer Verlag Berlin, Heidelberg, New York, London, Paris, Tokyo, HongKong. 173-186 (1989).

Effects of Inbreeding on Growth, Stem Form and Rust Resistance in *Pinus elliottii*

By A. C. Matheson $^{1)}$, T. L. White $^{2)}$ and G. R. Powell $^{2)}$

(Received 14th September 1994)

Abstract

Effects of relatively low levels of inbreeding were studied in a slash pine (*Pinus elliottii* Engelm. var. *elliottii*) experiment established over 4 test sites in 1980 and 1981. There were 3 levels of inbreeding: outcrosses (F=0), half-sib (F=0.125) and backcrosses (F=0.25). Measurements of growth, rust incidence, stemform and forking were taken in 1982, 1983, 1986, 1988 and 1993. Grandparental contribution to the progeny of each crossing type was not the same, i.e. there were some grandparents included in outcrosses that were not included in backcrosses. For this reason, adjustment to growth measurements based on a priori prediction of volume growth breeding value was carried out through covariance analysis. Adjustment for rust breeding value to rust scores had no effect.

Inbreeding depression was found to be linearly related to the inbreeding coefficient F with no significant quadratic effects for

any trait. Inbred families were shorter and had smaller diameters and volumes than those that were outcrossed. On the other hand, analysis of the standard deviations and coefficients of variation of the traits showed significant quadratic effects, such that inbred families had higher variance than those that were outcrossed, but backcrosses did not necessarily have higher variances than half-sib crosses.

Inbreeding depression for plot volume was not the same for families derived from 2 grandparents of similar breeding value.

The implications of these results on inclusion of relatives in wind-pollinated seed orchards were investigated. It was better to include parent-offspring pairs than either full-sib or half-sib families because the proportion of related matings was less. Fewer siblings in the full-sib or half-sib families together with more families would have the same effect of reducing related matings. It was better to include half-sibs than full-sibs because the increased number of half-sib survivors was outweighed by the greater depression exhibited by full-sibs.

 $\it Key\ words:$ inbreeding depression, slash pine, growth, stem form, rust resistance.

FDC: 165.41; 181.6; 174.7 Pinus elliottii.

I) CSIRO Division of Forestry, PO Box 4008, Queen Victoria Terrace, Canberra, ACT 2600, Australia

²⁾ Department of Forestry, University of Florida, Gainesville, FL 32611-0420 USA