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Short Note: Genetic Control of Oak Shake; Some Preliminary Results

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Summary

The wood of ring porous oaks is frequently subject to a defect known as shake, which describes the development of extensive longitudinal fissures in the living tree. Previous work had suggested a relationship between the occurrence of shake and cross sectional area of earlywood vessels. This study investigated the degree of genetic control of vessel area in German *Quercus robur* and *Quercus petraea*, considered here as a single species. Ramets in a clonal seed orchard and open-pollinated progeny in an unreplicated trial were sampled. Heritability estimates for vessel area were high, ranging from 0.60 ± 0.25 (narrow sense, individual tree basis) to 0.93 ± 0.06 (broad sense, clonal mean basis). Interpretation of these results must acknowledge the limitations of the experimental material. However, the indication of strong additive genetic control of vessel area is consistent with information for other wood characteristics of other species, and suggests that simple selective breeding could be effective in reducing the frequency of shake in oaks.

Key words: Heritability, Quercus robur, Quercus petraea, shake, wood quality.

Introduction

The timber defect known as shake is described by PANSHIN and DE ZEEUW (1980) as "... longitudinal separations of the wood which appear in the standing tree". Shake occurs in nearly all British oak plantations, frequently affecting more than 50% of the trees. The roadside value of shaken timber may be as little as 20% of that of sound timber (BROWN, 1945; HENMAN, 1986).

An association betwen shake and soil has been proposed at least since 1679 when JOHN EVELYN observed that oak "... which grows in gravel is subject to be frow [shaken] and be brittle". There is now little doubt that soils greatly influence the frequency of shake. BROWN (1945) reported that sound oak is normally found on soils containing a reasonable proportion of clay; HENMAN (1986) reported that shake is most frequent on sites where water table levels are variable, particularly over drought-prone, light and sandy soils. HENMAN proposed that shake develops under the combined influences of "predisposing factors" and "triggers", suggesting that a predisposition results from weak or degraded wood which may be triggered to fracture by stresses such as those induced by droughts or gales.

The fact that even the most severely affected sites produce some sound stems implies that certain individuals are inherently less predisposed to shake than others. This encouraged SAVILL (1986) to examine wood samples for anatomical features that might be associated with shake. Of the many features investigated, only the mean cross sectional areas of the larger vessels in the earlywood, older than about 20 years from the pith, were found to be significantly correlated with shake: shaken trees possessed larger vessels than those in sound trees. This relationship between vessel size and shake conforms to findings by materials scientists, who have demonstrated that cracks are most easily propagated in cellular solids composed of large cells (ASHBY and GIBSON, 1983).

The working hypothesis upon which the studies described in this paper are based is that a predisposition to shake increases with vessel size. If this is so, then it would be of value to be able to recognise shake-prone trees in the field. This has been the subject of a separate investigation by SAVILL and MATHER (1990), which has indicated that trees with large vessels flush later in the spring. It might therefore be possible, for example, to remove shake-prone trees in early thinning operations, or to select only early flushing trees in breeding programmes. The latter approach could be complicated by the greater sensitivity of early flushing trees to attack by *Tortrix viridana*.

The objective of this associated study was to investigate the extent to which vessel size in oak is heritable, and therefore amenable to genetic manipulation. Many anatomical properties of wood in many species are known to be under relatively strong genetic control (BURLEY, 1982; ZOBEL and VAN BUIJTENEN, 1989). In oaks characteristics associated with vessel qualities, such as the width of the earlywood zone and wood density, have been shown to be highly heritable (NEPVEU, 1984a and b).

Materials and Methods

The material for which vessel size was examined is described in *Table 1*. Because of the limited availability of material, samples from both *Quercus robur* and *Quercus petraea* were pooled in subsequent analyses. This was regarded as legitimate because considerable hybridisation and introgression occurs between the two species and, as a result, there is an unresolved controversy about their status as two separate species (COUSENS, 1962 and 1965; GARDINER, 1970; VALEN, 1976).

The first available samples were radiographic images of 5 mm Pressler borer cores taken from a seed orchard of grafted clones near Hanover, Federal Republik of Germa-

Table 1. — Summary of experimental material.

Source and of material	Species	Replication	Data for estimation of heritabilities
Clonal seed orchard radiographic images	*Q. robur*	12 clones x 5 ramets	Mean area of 20 vessels per tree.
Clonal seed orchard 5 mm cores	*Q. robur* *Q. robur* *Q. petraea* *Q. petraea* Hybrid	4 clones x 5 ramets 1 clone x 4 ramets 3 clone x 5 ramets 1 clone x 4 ramets 1 clone x 5 ramets	Individual vessel measurements; 40 taken for each tree.
Half-sib progeny trial 5 mm cores	Q. robur	1 family x 3 progeny 1 family x 4 progeny 9 families x 5 progeny 5 families x 6 progeny 5 families x 7 progeny 7 families x 8 progeny 3 families x 9 progeny 1 family x 32 progeny *	Tree mean vessel area of 40 vessel area measurements per tree.

*) This was originally intended as a standard family for estimation of microsite variation, and had been planted in twelve sub-plots randomly allocated throughout the progeny trial.

ny. These were provided by Dr. G. Nepveu of Centre De Recherches Forestières de Nancy, who had previously used them in studies of genetic control of wood quality in oak (Nepveu, 1984a and b).

We sampled the same orchards with the permission of Dr. J. Kleinschmit and assistance of his colleagues at the Niedersächsische Forstliche Versuchsanstalt. Clones in the orchards were propagated from plus-trees selected throughout the Federal Republic of Germany, grafted and planted in the Forest Districts of Diekholzen and Lüss. The oldest orchard was a 1.0 ha stand of 41 *Quercus petraea* clones established in 1955. This was adjacent to a 0.85 ha seed orchard comprising 33 clones of *Q. robur* established in 1957. Ramets in both orchards had been randomly located and planted at 6 m x 6 m spacing.

A progeny trial, also under the jurisdiction of Niedersächsische Forstliche Versuchsanstalt, was located in the Bramwald Forest near Kassel in Lower Saxony. The experiment, of 0.62 ha established in 1950, consisted of 34 half-sib families planted in an unreplicated design. Progeny of one family had been planted in randomly allocated rows between family plots as a control for the purpose of evaluating microsite variation. However, because there were insufficient numbers of surviving control trees for reliable assessment of site variation, these were simply included as an additional family in our analyses.

Field and Laboratory procedures

Only unsuppressed trees with healthy crowns were sampled. Wood cores of 5 mm diameter were taken at breast height, avoiding any leaning stem surfaces, using a Pressler increment borer. Cores were subsequently dried and polished so that vessels were clearly exposed in cross section.

Vessel diameters were measured to the nearest μm, using a travelling binocular microscope equipped with an electronic incremental digitiser. Vessel cross sectional areas were calculated and expressed as μm^2. The diameters of four earlywood vessels in each of the five most recent rings of each radiographic image and each 5 mm core, were measured. In the case of the radiographic images rings corresponded to the years 1974 to 1978, and for the cores, 1984 to 1988. They therefore represented ages 17 to 21 years for the radiographs, and 27 to 31 years and 34 to 38 years for cores obtained from the clonal seed orchard and the progeny trial respectively.

Analyses

Data were analysed by the method of least squares, using Harvey's (1988) LSMLMW programme. The model fitted to the data from each trial is described by equation 1:

$$Y_{ij} = u + g_i + e_{ij} \quad (1)$$

where Y_{ij} is the observation on individual j of genotype i; u is the overall mean; g_i is the effect of genotype i; e_{ij} is the normally and independently distribution random deviation of individual j of genotype i, with a mean of zero.

In the clonal orchard, individuals were ramets of a clone; in the family trial, individuals were progeny in a family. Differences between clones or families were highly significant ($p < 0.001$) in all cases.

Variance components were estimated from analyses of variance by equating the appropriate mean squares to the expectations shown in *Tables 2, 3* and *4*. In these tables, σ^2_e is the variance component due to within-clone or within-family variation, σ^2_g is the variance component due to clone or family, and k is the appropriate coefficient described by Harvey (1988). In these analyses, $k_1 = 5.00$, $k_2 = 4.80$, and $k_3 = 7.13$.

Table 2. — Ecpected mean squares for analyses of variance of radiographic images of clonal material.

Source of variation	Degrees of freedom	Mean square	Expected mean squares
Family	31	3.1154×10^{10}	$\sigma^2_e + k_3\sigma^2_g$
Within-family	199	1.9969×10^{10}	σ^2_e

Table 3. — Expectations of mean squares for analyses of variance of core samples of clonal material.

Source of variation	Degrees of freedom	Mean square	Expected mean squares
Clone	11	1.1359×10^{10}	$\sigma^2_e + k_1\sigma^2_g$
Within-clone	48	4.8455×10^{9}	σ^2_e

Table 4. — Expectations of mean squares for analyses of variance of core samples of progeny material.

Source of variation	Degrees of freedom	Mean square	Expected mean squares
Clone	9	9.1130×10^{11}	$\sigma^2_e + k_2\sigma^2_g$
Within-clone	470	4.7024×10^{11}	σ^2_e

The clonal data were used to estimate broad-sense heritabilities on a clonal mean basis, following Russell and Libby (1986), as described by equation 2:

$$h^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_e/n) \quad (2)$$

where n is the number of ramets per clone. Standard errors of these heritabilities were estimated by adapting Wright's (1976, p. 248) procedure. Wright noted that the standard errors thus estimated were likely to underestimate the true standard errors.

The progeny data were used to estimate narrow-sense heritability on both an individual tree and family mean basis. Progeny within families were assumed to be half-sibs, and heritability on an individual tree basis was estimated according to equation 3:

$$h^2 = 4\sigma^2_g / (\sigma^2_g + \sigma^2_e) \quad (3)$$

The standard error of this heritability was estimated according to Swiger et al. (1964). Heritability on an individual tree basis was converted to that on a family mean basis following Falconer (1981, *Table 13.4)*, and the standard error of this heritability estimated as for the clonal data.

Heritabilities and associated standard errors are presented in *Table 5*. Phenotypic and additive genetic correlations between vessel cross sectional area and stem diameter were calculated on an individual tree basis from the progeny trial data. The genetic correlation and its standard error were estimated following, respectively, the procedures of Hazel et al. (1943) and Tallis (1959). The value of the phenotypic correlation was 0.53, and that of the genetic correlation 0.60 ± 0.44.

Discussion

Discussion of these results must acknowledge the limitations of the experimental material; the effects of stock plant on vessel area of the scion are unknown, and unreplicated clonal or progeny trials are not a good basis for the estimation of genetic parameters. Nevertheless, material from replicated trials, from which more soundly based estimates can be made, will not be available in the next decade. In the interim, these results may offer some guidance at a time when broadleaved afforestation including *Quercus robur* and *Quercus petraea* is being strongly encouraged in Britain (Forestry Commission, 1989).

Table 5. — Heritabilities and associated standard errors for vessel area of *Quercus robur.*

Basis of estimate	Heritability ± standard error	Comments
Clonal ramets; radiographs	0.87 ± 0.10	broad sense; clonal mean basis
Clonal ramets; cores	0.93 ± 0.06	broad sense; clonal mean basis
Open-pollinated progeny; cores	0.60 ± 0.25	narrow sense; individual tree basis
Open-pollinated progeny; cores	0.79 ± 0.21	narrow sense; family mean basis

Although the heritability estimates presented in *Table 5* should be treated with caution, they do suggest that vessel area in *Q. robur* and *Q. petraea* is under strong additive genetic control. This result is consistent with results reported for many other wood characteristics in many other species (Zobel and van Buijtenen, 1989), and with conclusions drawn by Nepveu (1984a) from the radiographs used here. They suggest, for example, that simple selective breeding will be effective in manipulating vessel area, and that clonal propagation of selected individuals could be used to produce populations with vessel areas tending towards those of the ortets. Both of these approaches have been proposed by Kleinschmit (1986) for German oak populations.

The relationship between vessel area and other parameters, e. g. growth rate, also needs to be established on a firmer basis than was possible from these studies. Although there is a suggestion from the progeny trial data that larger vessels are associated with faster growth, other results from sawmill-based studies currently underway on unreplicated material have not suggested any adverse relationships between the date of growth and the occurrence of shake. According to our working hypothesis, the progeny of populations or ramets of individuals selected for smaller vessel area would be less prone to shake. However, these suggestions can be little more than informed speculation until they are confirmed by results from trials already established in many European countries. Our own work continues to investigate the relationship between wood anatomical characteristics and occurrence and severity of shake in oaks.

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