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Original article

Genetic determination of vessel area in oak (*Quercus robur* L and *Q petraea* Liebl): a characteristic related to the occurrence of stem shakes

RA Mather, PJ Kanowski, PS Savill

Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

Summary — The term "shake" describes the presence of longitudinal separations in the wood of living trees. Predisposition to shake in *Quercus robur* and *Q petraea* increases with the cross-sectional areas of earlywood vessels. Investigations suggest that vessel area is under strong genetic control, and is related to provenance and to the timing of leaf emergence in the spring. These results are promising for those concerned with selecting oak varieties less prone to shake or wishing to recognize and remove shake-prone trees early in rotations.

heritability / *Quercus* / shake / wood quality / phenology

Résumé — Déterminisme génétique du diamètre des vaisseaux du bois chez le chêne (*Quercus robur* et *Q petraea* Liebl) : une caractéristique liée à la sensibilité aux fentes internes du tronc. *Le terme de «fente» désigne la présence de séparations longitudinales dans le bois des arbres vivants. La prédisposition aux fentes chez* Quercus robur *et* Q petraea *augmente avec la surface de la section transversale des vaisseaux du bois initial. Des recherches suggèrent que la surface des vaisseaux est soumise à un contrôle génétique fort (niveau intraspécifique et niveau génétique individuel), ainsi qu'à la période d'apparition des feuilles au printemps. Ces résultats sont prometteurs pour ceux qui s'intéressent à la sélection des variétés de chêne peu sensibles aux fentes du tronc ou qui souhaitent repérer et éliminer précocement les arbres sensibles aux fentes lors d'éclaircies.*

héritabilité /* Quercus */ fente du tronc / qualité du bois / phénologie

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". Ring porous oaks are frequently affected by shake. Savill (1986) found that the mean cross-sectional area of the large earlywood vessels was significantly greater in shaken trees than in sound ones. Additionally, Cinotti (1991) has shown that the incidence of frost-cracking in oak, a condition that is similar to shake, also increases with vessel size. With the information that large vessels predispose oaks to shake, our objectives were to: 1) determine provenance variations in vessel size; 2) estimate the heritability of vessel size; and 3) to find a means of recognizing shake-prone trees so that they could be removed during early thinning operations. Some of these aspects have been discussed further by Savill and Mather (1990).

MATERIALS AND METHODS

In each case, 5 mm increment cores were taken at 1.3 m.

The principal provenance trial, established by Krahl-Urban in 1950, was located in the Bramwald Forest. In 1951, the trial was replicated at Syke near Bremen, using seedling transplants from the Bramwald site. The sample objective for each site was 12 trees per provenance, 5 provenances per species (*Q robur* and *Q petraea).* The sample obtained fell short of the objective by 32 trees due to fewer surviving trees at Syke.

Heritability studies used material collected from a half-sib progeny trial, also located in Bramwald Forest near Kassel in Lower Saxony, Germany. The experiment, established in 1950, consisted of 32 half-sib families of *Q robur* planted in an unreplicated design.

Investigations into the association between the progress of flushing and vessel size were undertaken on 20 early and 20 late flushing trees to indigenous *Q petraea* stored coppice at Bagley Wood, Oxford.

Tree mean vessel areas, expressed in μm^2, were determined from radial measurements of vessels from 5 mm wood cores, using a travelling microscope equipped with an electronic digitizer that was accurate to $\pm$ 2 μm.

RESULTS AND DISCUSSION

Provenance study

The analysis of variance for the provenance trial data is presented in table I, from which it can be seen that the factors significantly influencing vessel size are the width of annual rings and provenances. There is also an interaction of provenance with sites which reinforces Kleinschmit's (1986) point that selection of desirable provenances should be specific to particular sites.

Heritability study

The model fitted to vessel area data may be expressed as:

$$VA_{ij} = \mu + g_i + e_{ij} \quad (1)$$

where VA_{ij} is the observation on individual j of genotype or family i, μ is the overall

Table I. Analysis of variance for vessel area with provenance effects.

Source of variation	*df*	*Sum of squares*	*Mean square*	F-*test*	P
Species	1	400	400	0.71	0.422
Provenances within each species	8	4424	553	6.61	< 0.001
Site	1	14	14	0.16	0.688
Species x site	1	148	148	1.77	0.185
Provenance within species x site	8	2338	292	3.49	0.001
Covariate ring width	1	12489	12 489	149.31	< 0.001
Residual	197	16478	84		
Total	217				

mean vessel area; g_i is the effect of genotype *i*, considered as random; e_{ij} is the normally and independently distributed random deviation of genotype *i*, with a mean of zero. Differences between families were highly significant ($P < 0.001$). Variance components were estimated by analysis of variance and narrow sense heritability estimated from variance components according to the expression:

$$h^2 = 4\sigma_g^2/(\sigma_g^2 + \sigma_e^2) \qquad (2)$$

where σ_e^2 and σ_g^2 are the components due to within-family and between family variation. Acknowledging the limitations of unreplicated trials, estimated values, respectively at 0.60 ± 0.25 on an individual tree basis and 0.79 ± 0.21 on a family mean basis (see table II), indicate that vessel area is under strong additive genetic control. This is consistent with results reported for wood characteristics in many species (Burley, 1982; Zobel and van Buijtenen, 1989), as well as from similar material in oaks (Nepveu, 1984). These results are discussed in more detail by Kanowski *et al* (1991).

Relationship between flushing dates and vessel sizes

The analysis of variance, summarized in table III, shows highly significant differences between early and late flushing trees ($P > 0.0001$) which accounted for almost 20% of all variation. Means and standard errors for vessel areas for early and late flushing trees were 67 134 ± 3 090 μm^2 and 83 754 ± 2 854 μm^2, respectively.

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

Basis of estimate	*Heritability ± standard error*	P *(differences between groups)*
Open-pollinated progeny; cores; individual basis	0.60 ± 0.25	< 0.001
Open-pollinated progeny; cores; family mean basis	0.79 ± 0.21	< 0.001

Table III. Nested analysis of variance for vessel area with time of flushing.

No of levels	*Source of variation*	*df*	*Mean square*	F*-ratio*	*Variation component*	*% of total variation*
2	Flushing category	1	1104.9	15.65	1.29	19.64
20	Trees in categories	38	70.6	5.39	1.44	21.81
2	Cores within trees	40	13.1	3.05	0.44	6.69
10	Rings within cores	720	4.3	1.72	0.91	13.78
2	Vessels within rings	800	2.5		2.51	38.08

Results showed clearly that early-flushing trees tend to have vessels of smaller cross-sectional areas than late flushing ones. In oak, new vessels are formed about 1 week after buds break. Indole-3-acetic acid (IAA) is believed to provide the stimulus for vessel growth (Longman and Coutts, 1974), and has been shown to produce earlywood vessels with larger lumen areas in ash (Doley and Leyton, 1968). The fact that IAA is also known to inhibit the emergence of buds in *Q alba* (Vogt and Cox, 1970) strongly suggests that leaf emergence and earlywood formation are inextricably linked through a common association with IAA.

CONCLUSIONS

Results from progeny and provenance trials suggest that selection and breeding at the level of provenances and individuals should both be effective in reducing the frequency of shake in oaks. Meanwhile, the tendency of trees with large earlywood vessels to flush latest provides a useful means for the early recognition and removal of shake-prone individuals. It should, however, be understood that selections made on vessel size may have other undetermined physiological consequences and also influence wood technical properties.

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