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## Short Note: Genetic and Intra-Tree Variation in the Number of Sapwood Rings in *Quercus robur* and *Q. petraea*

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### Summary

This study investigates genetic control of the number of sapwood rings in *Quercus robur* and *Q. petraea*, and the variation of this trait with height up the stem and age of the tree. Ramets and open-pollinated progeny of the 2 species were sampled from a German clonal orchard and an unreplicated progeny trial; intra-tree variation was investigated from a sample of English woodland trees of both species. Estimates of the heritability of the number of sapwood rings were high ( $0.57 \pm 0.28$  on a narrow-sense basis;  $0.83 \pm 0.11$  on a broad-sense, clonal mean basis), consistent with comparable results for other species. The phenotypic correlation between family means, used here as the best available proxy to a genetic correlation, suggested a moderately negative relationship ( $r = -0.49$ ) in trees of the same age between the number of sapwood

rings and stem diameter at breast height. The number of sapwood rings and the proportion of rings that are sapwood varied with height, following a nonlinear relationship. The number of sapwood rings at breast height increases with the age of the tree, although the proportion of the total number of rings that are sapwood decreases with age. Whilst strong conclusions cannot be drawn from the limited experimental material on which this study is based, our results are generally consistent with those of other studies. They suggest that including the number of sapwood rings as a selection criterion could be beneficial in both breeding and clonal propagation programmes of *Q. robur* and *Q. petraea*.

*Key words:* Heritability, *Quercus robur*, *Quercus petraea*, sapwood, wood quality.

## Introduction

The anatomical, chemical and structural differences between sapwood and heartwood mean that both the absolute and relative amount of sapwood present in the stem of a tree can have major consequences for utilisation, particularly preservation and pulping (BAMBER, 1987; HILLIS, 1987; NICHOLLS and BROWN, 1974). This paper continues our investigations of genetic control over wood anatomical characteristics of *Quercus robur* L. and *Q. petraea* (MATTUSCHKA) LIEBL. (KANOWSKI et al., 1991; SAVILL and KANOWSKI, 1993), and draws on the limited data available to investigate genetic variation in the number of sapwood rings in these European oaks. Subsidiary studies investigated the relationship between the number of sapwood rings and stem diameter at breast height (DBH), and variation in the number of sapwood rings with height in the tree and with age class.

## Materials and Methods

### Genetic variation

The material from which genetic parameters were estimated is under the jurisdiction of the Niedersächsische Forstliche Versuchsanstalt, Germany. It originated from two separate sources, fully described by SAVILL and KANOWSKI (1993) and KANOWSKI et al. (1991), and is summarised in Table 1. In brief, the larger data set originated from an unreplicated open-pollinated progeny trial of 34 families in the Bramwald forest; the smaller data set originated from ramets of 10 clones in a seed orchard near Hanover. Data from the progeny trial were also used to investigate the relationship between the number of sapwood rings and DBH.

As in our earlier study (KANOWSKI et al, 1991), data from *Q. robur* and *Q. petraea* were pooled in these analyses. This was considered legitimate because of the extensive hybridisation and introgression between the two species; indeed, there is a continuing debate about their status as two separate species (COUSENS, 1962, 1965; GARDINER, 1970; VALEN, 1967; KREMER and PETIT, 1993). It was also desirable because of the small sample sizes involved.

### Variation of number of sapwood rings with height and age

Variation in the number of sapwood rings with height

up the tree was assessed by sampling at one metre intervals along the stem, to a height of 20 m, from 2 *Q. petraea* trees which had been growing in Bagley Wood, near Oxford, England. Variation with age was determined from breast height samples from 36 trees of both species, most of which had been felled in the Forest of Dean, in south west England.

## Field and Laboratory Procedures

For the progeny and clonal material, one bark-to-bark 5 mm core was taken at breast height from each tree with a Pressler increment borer. Only unsuppressed trees were sampled and leaning stems were avoided. Complete discs were taken from the English trees.

Cores and discs were dried and polished so that vessels and tyloses were clearly exposed in cross section. As other workers (eg CHATTAWAY, 1952; HOLLSTEIN, 1978) have noted, precise determination of the location of the sapwood-heartwood boundary is not easy. In this study, the 2 criteria used to determine the sapwood-heartwood boundary were colour of the wood and presence of tyloses; samples were examined subjectively for colour change and, using a light microscope at between x 20 and x 100 magnification, for the presence of tyloses in the earlywood vessels. Within the region of colour change, the first line of earlywood vessels at which tyloses were present in 75% or more of the vessels was nominated as the sapwood-heartwood boundary. The number of rings between that line of vessels and the bark was recorded as the number of sapwood rings; the total number of rings was also recorded. This process was repeated for both radii of the core samples, and on 2 radii of the disc samples.

## Analyses and Results

### Genetic control of the number of sapwood rings

The mean number of sapwood rings for each tree was calculated from the estimates for each radius, and used in subsequent analyses. The average total number of rings for each tree was similarly derived, and used as a covariate in these analyses.

Variance components were estimated from analyses of covariance using the GENSTAT and MINITAB packages; parameter estimates were computed by the GENSTAT REML directive (progeny data) or by hand (clonal data).

Table 1. — Details of experimental material.

| Source   | Species           | Replication          | Data for estimation of heritability       |
|--|-------------------|----------------------|---|
| Progeny trial,<br>Bramwald   | <i>Q. robur</i>   | 1 family x 33 trees  | Two 5 mm Pressler<br>cores from each tree |
|  |                   | 3 families x 9 trees |   |
|  |                   | 6 families x 8 trees |   |
|  |                   | 3 families x 7 trees |   |
|  |                   | 4 families x 6 trees |   |
|  |                   | 6 families x 5 trees |   |
|  |                   | 3 families x 3 trees |   |
| Clonal orchard,<br>Hanover   | <i>Q. robur</i>   | 4 clones x 5 ramets  | Two 5 mm Pressler<br>cores from each tree |
|  | <i>Q. robur</i>   | 1 clone x 4 ramets   |   |
|  | <i>Q. petraea</i> | 3 clones x 5 ramets  |   |
|  | <i>Q. petraea</i> | 1 clone x 4 ramets   |   |
|  | hybrid            | 1 clone x 5 ramets   |   |
| <b>Totals: 192 trees of 26 families and 48 ramets of 10 clones</b> |                   |                      |   |

Table 2. — Expected mean squares for analyses of covariance of progeny material.

| Source of variation | Degrees of freedom | Mean square | Expected mean squares        |
|---------------------|--------------------|-------------|------------------------------|
| Covariate           | 1                  | 7.03        |                              |
| Family              | 25                 | 7.76        | $\sigma_e^2 + k_1\sigma_g^2$ |
| Within-family       | 165                | 3.58        | $\sigma_e^2$                 |

Table 3. — Expected mean squares for analyses of covariance of clonal material.

| Source of variation | Degrees of freedom | Mean square | Expected mean squares        |
|---------------------|--------------------|-------------|------------------------------|
| Covariate           | 1                  | 5.08        |                              |
| Clone               | 9                  | 8.18        | $\sigma_e^2 + k_2\sigma_g^2$ |
| Within-clone        | 37                 | 1.41        | $\sigma_e^2$                 |

The model fitted to data from each trial is described by Equation (1):

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

where:  $Y_{ij}$  = the mean number of sapwood rings of individual  $j$  of genotype  $i$ ;

$\mu$  = the overall experimental mean;

$g_i$  = the effect of genotype (family or clone)  $i$ ;

$e_{ij}$  = the normally and independently distributed random deviation, with mean zero, of individual  $j$  of genotype  $i$ .

Genotypes were either families of half-sib progeny (Bramwald) or ramets of a clone (Hanover).

Results of the analyses of covariance for the progeny and clonal data sets are shown in tables 2 and 3, respectively. Differences between families or clones were significant at  $p < 0.001$ . In neither case was the covariate significant at  $p < 0.05$ .

Variance components were estimated from the analyses of variance by equating the appropriate mean squares to the expectations shown in tables 2 and 3. In these tables,  $\sigma_e^2$  is the variance component due to within-family or within-clone variation,  $\sigma_g^2$  is the variance component due to family or clone, and  $k_1$  is a coefficient dependent on the harmonic mean number of observations per family or clone. In these analyses,  $k_1 = 7.23$  and  $k_2 = 4.80$ .

The progeny data were used to estimate narrow-sense heritability on an individual tree basis, according to equation (2):

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

The standard error of this heritability was estimated by the GENSTAT REML directive.

The clonal data were used to estimate broad-sense heritabilities on a clonal mean basis, following RUSSELL and LIBBY (1986), according to equation (3):

$$h^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_e^2/n) \quad (3)$$

where  $n$  is the average number of ramets per clone. The standard error of this heritability was estimated by adapting WRIGHT's (1976, p. 248) procedure. WRIGHT noted that the estimates thus produced were likely to underestimate the true standard errors.

Heritabilities and associated standard errors are presented in table 4.

#### Relationship between number of sapwood rings and DBH

Given the problems inherent in the estimation of genetic correlations (BURDON, 1989), it was not surprising that the data set from the progeny trial proved to be too small and unbalanced to allow the use of any program designed to estimate genetic correlations. The phenotypic correlation between family means could be estimated with a standard statistical package (in this case, MINITAB), and was used here as the best proxy of the genetic correlation; its value was  $-0.49$ .

#### Variation in the number of sapwood rings with height up the tree

There was an approximately constant difference between the number of sapwood rings in the 2 trees examined, and both followed approximately the same pattern of variation with height up the stem. Correlation coefficients for the polynomial regression lines fitted to each data set are given in table 5. The number of sapwood rings was quite stable for the first 10 to 11 metres of the stem, but then decreased rapidly. The ratio of the number of sap-

Table 4. — Heritability estimates for number of sapwood rings.

| Source   | Heritability<br>± standard error | Basis                         |
|----------|----------------------------------|-------------------------------|
| Bramwald | 0.57 ± 0.28                      | Narrow sense; individual tree |
| Hanover  | 0.83 ± 0.11                      | Broad sense; clonal mean      |

Table 5. — Correlation coefficients for polynomial regressions of number and proportion of sapwood rings vs height up the stem.

| Regression                            | $r^2$  |        |
|---------------------------------------|--------|--------|
|                                       | Tree 1 | Tree 2 |
| Number of sapwood rings vs height     | 0.76   | 0.68   |
| Proportion of sapwood rings vs height | 0.87   | 0.90   |

Table 6. — Mean number of sapwood rings in four age classes.

| Age Class | Sample Size | Mean number of sapwood rings (std deviation) | Number of sapwood/total rings (variance) |
|-----------|-------------|--|--|
| <50       | 2           | 12.0 (1.41)                                  | 0.27 (0.032)                             |
| 51 - 100  | 13          | 21.2 (3.32)                                  | 0.26 (0.035)                             |
| 101 - 150 | 13          | 24.0 (4.65)                                  | 0.20 (0.029)                             |
| >150      | 8           | 28.9 (10.57)                                 | 0.15 (0.038)                             |

wood rings to the total number of rings shows a curvilinear relationship with height up the tree, rising at an increasing rate with increasing height.

From these trends it is possible to visualize the stem of the tree as 2 nested modified cones with slightly convex rather than straight sides. There is an approximately constant thickness of sapwood outside the central core of heartwood. The taper of the core increases with increasing height.

#### Variation in the number of sapwood rings with age

The 36 trees were divided into 4 age classes; means and standard deviations were calculated for each class, and are presented in table 6. The mean number of sapwood rings, and variation around that mean, increase with age but, as might be expected, the number of sapwood rings comprises a decreasing proportion of the total number of rings as the tree ages.

It is of interest that the number of sapwood rings observed in the Bramwald material, averaging 9.5 ( $\pm$  2.2) at age 40, is consistent with the results for English trees shown in table 6.

### Discussion

#### Genetic control of the number of sapwood rings

As noted in our earlier work based on the progeny and clonal material (KANOWSKI *et al.*, 1991), discussion of results originating from them must acknowledge the severe limitations of the experimental material. In the absence of any better data, or any prospect of it in the next decade or more, these results offer the best available estimates of the true genetic parameters.

Both narrow- and broad-sense heritability estimates suggest that the number of sapwood rings is under strong genetic control, much of it additive. Given their limitations, these estimates are not inconsistent with the only vaguely comparable results reported in the literature, for the proportion of heartwood in *Pinus radiata* growing in southern Australia. In 2 sets of studies based on samples taken at a height of 1.2 m, NICHOLLS (1965) and NICHOLLS and BROWN (1974) reported broad sense heritabilities for

this parameter averaging around 0.37, with standard errors of around 0.19, and a narrow-sense heritability estimate of  $0.20 \pm 0.14$ . Their broad-sense estimates derived from 2 sets of clones, and was computed on an "unreplicated genotype" basis (sensu RUSSELL and LIBBY, 1985); the corresponding estimate for our material is  $0.50 \pm 0.16$ . The narrow-sense estimates are directly comparable. It is difficult to judge how much of the difference between the 2 sets of estimates should be attributed to differences between species and the different form in which traits were assessed; our study is based on the absolute number of sapwood rings, and those for *P. radiata* on the proportion of stem cross-sectional area which was heartwood. However, both parameters are assessing, from different perspectives, the extent of heartwood formation, so one might expect some comparability.

The relatively strong genetic control over the number of sapwood rings in *Q. robur* and *Q. petraea* evident from these estimates is consistent with estimates for other wood characteristics of the species (SAVILL and KANOWSKI, 1993), and with the relatively high level of genetic control evident for many wood properties in many species (ZOBEL and VAN BUIJTENEN, 1989).

#### The relationship between the number of sapwood rings and DBH

It would not be wise to place any great confidence in the correlation reported here between the number of sapwood rings and DBH. At face value, this correlation between family means, at around  $-0.5$ , suggests that faster growing trees (those with larger diameters) tend to have fewer sapwood rings. This negative correlation does not necessarily imply that the sapwood in faster growing trees is narrower, because rings in such trees tend to be wider than those in slower growing individuals, so the total width of sapwood in fast- and slow-growing trees may be similar, or even greater in the former, as noted by BAMBER (1987) and HILLIS (1987). The value of the correlation implies that faster growing oaks will have a higher number of their rings as heartwood, and that genes for faster growth in *Q. robur* and *Q. petraea* are associated with a faster transition to heartwood. If this is so, selec-

tion for fast growth would have the additional advantage of reducing the number of sapwood rings, with favourable consequences for the market value of the timber produced. However, the limitations of the experimental material place a major caveat on the strength with which such conclusions can be drawn, and there is little relevant evidence on which to draw from the literature, although the result reported here is consistent with that found in a comparison of dominant and suppressed trees from various *Quercus* species (TRENDELENBURG and MAYER-WEGELIN, 1955; In: HILLIS, 1987). As HILLIS' (1987) review demonstrates, there is little consistency in the results of other studies which have attempted to relate the amount of sapwood to growth rate, or to other factors. For *Q. robur* and *Q. petraea*, the relationship will only be resolved by further study of more comprehensive data sets.

#### *Variation in the number of sapwood rings with height up the tree*

Earlier studies of variation in the number of sapwood rings, rings, or sapwood width, with height in the tree have been reviewed by HILLIS (1987). The few studies of *Quercus* (TRENDELENBURG and MAYER-WEGELIN, 1955; MCGINNIS and SHIGO, 1975; both in HILLIS, 1987) report little change with height in the number of sapwood rings, consistent with our results for the first 10 m of stem. More generally, the results reported by ESPINOSA-BANCALARI *et al.* (1987) for *Pseudotsuga menziesii*, in which sapwood width remained approximately constant but the number of sapwood rings declined gradually up the stem, appear typical (see HILLIS, 1987).

#### *Variation in the number of sapwood rings with age*

Limited though they are, the results reported here are consistent with more comprehensive surveys of European oaks (BAILLIE *et al.*, 1985; ECKSTEIN *et al.*, 1986; HOLLSTEIN, 1978; summarised in HILLIS, 1987), although the oldest trees we examined appear to have more sapwood rings than were identified in earlier studies, where a maximum of 26 have been recorded. The mean number of sapwood rings increases with age, but decreases if expressed as a proportion of the total number of rings. Together with the results of preceding section, these findings suggest that, in terms of sapwood and heartwood, the upper part of an older tree can be thought of as corresponding to the lower part of a younger tree.

### Conclusion

The limited material available for this study restricts the generality of conclusions which can be drawn from it. However, it is encouraging to note that our results are generally consistent with those from anatomical studies of many species. The apparently strong genetic control over the number of sapwood rings (or, by implication, the

number of heartwood rings) emphasizes the importance of evaluating wood quality traits and incorporating them in the breeding objectives of tree improvement programmes.

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