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Original article

Improving models of wood density by including genetic effects: A case study in Douglas-fir

Philippe Rozenberg*, Alain Franc, Catherine Bastien and Christine Cahalan

INRA Centre de Recherches d'Orléans, Avenue de la Pomme de Pin, BP 20169, Ardon, 45166 Olivet Cedex, France

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Abstract – Many models have been published for relating wood characteristics, such as wood density, to growth traits. At a tree population level, ring density is known to be significantly correlated with cambial age and ring width. However, at the individual tree level, the predictive value of models based on this relationship is usually poor, as there is an important, so-called "tree effect" in the residuals of such models. We hypothesise that this effect arises from within population genetic variability, and have tested this hypothesis by adjusting linear models for Douglas-fir populations with different levels of genetic variability, ranging from provenances to clones. The addition of a genetic effect significantly increased the predictive value of the model and decreased the residuals. At the clone level, for example, inclusion of the genetic effect increased the explained variance (adjusted R^2 value) from 20% to 54%. It is suggested that most of the observed variability in the wood density/growth relationship of Douglas-fir populations has a genetic origin.

genetics / model / wood density / ring width / cambial age / Douglas-fir

Résumé – Amélioration de modèles de densité du bois par l'introduction d'effets génétiques : une étude de cas chez le Douglas. De nombreux modèles ont été publiés, mettant en relation chez de nombreuses espèces des propriétés du bois avec des caractères de croissance. À l'échelle de la population d'arbres, on sait que la densité d'un cerne dépend significativement de sa largeur et de son âge cambial. Toutefois, la valeur prédictive de ce type de relation est généralement faible, à cause de l'existence d'un fort effet « arbre » sur les résidus du modèle. Nous proposons l'hypothèse que cet effet arbre est lié à l'existence d'une variabilité génétique intra-population. Nous avons testé cette hypothèse en ajustant un modèle linéaire à plusieurs populations de douglas structurées génétiquement, selon des niveaux génétiques différents variant de la provenance au clone. L'ajout d'un paramètre génétique au modèle permet d'augmenter significativement la qualité prédictive du modèle, et diminue les résidus. Au niveau clone, par exemple, la variance expliquée par le modèle passe de 20 à 54 %. Nous en déduisons que la plus grande partie de la variabilité observée pour la relation densité-croissance chez le Douglas est d'origine génétique.

génétique / modèle / densité du bois / largeur de cerne / age cambial / Douglas

* Correspondence and reprints
Tel. (33) 02 38 41 78 00; Fax. (33) 02 38 41 48 09; e-mail: rozenberg@orleans.inra.fr

1. INTRODUCTION

Foresters have been interested for several decades in quantifying the growth properties of trees, and this has resulted in the production of numerous growth models [37]. More recently, foresters have also become interested in the properties of wood, as similar volumes of wood can have very different values depending on their suitability for particular end products [21, 45]. This qualitative variation is difficult to define, as it depends mainly on the potential uses of the wood. Wood quality therefore cannot be measured routinely in the field in the way that wood quantity can be measured using established protocols [20].

Of the wood properties which affect utilisation, wood density is the most widely studied. It is generally considered to be "a good indicator of strength properties; it has often been strongly related to the general quality of wood and is frequently correlated with pulp yield" [8]. There are therefore good reasons for using wood density as an indicator of wood quality for various end uses [31, 45].

A negative relationship between radial growth and wood density has been widely reported. The strength of the relationship is very variable among softwood species; it is very strong for spruces (*Picea* spp.) and especially Norway spruce (*Picea abies*) (see [31, 46], and apparently very weak for some pine (*Pinus*) species [46]. Some evidence of intraspecific genetic variation in the relationship between growth and wood density has been presented by different authors. Lewark [22] proposed the selection of Norway spruce clones in which "the regression of the two traits [density and growth] is as low as possible". Mothe [24], also working on Norway spruce, found substantial differences (from –0.21 to –0.93) in the correlation coefficient for the growth rate – wood density relationship between genetic units. In the same species, Chantre and Gouma [4] found a strong clonal effect on the residuals of the model linking growth rate and wood density. In black spruce, " ... the relationship of wood density with growth rate, to some extent, may vary with genotype and environment, and silvicultural manipulations may modify the relationships" [44]. Finally, according to Rozenberg and van de Sype [30], the values of parameters of models describing the growth rate – wood density relationship can be used as secondary selection traits, after primary selection for wood density, to restrain the negative impact of growth rate on wood density.

In Douglas-fir (*Pseudotsuga menziesii*), the density – growth relationship is variable. Some authors have reported that there is no relationship [1], while others have found negative relationships ranging from moderate to quite strong [2, 19, 23, 33, 38, 40]. These results suggest that the relationship between wood density and growth may be specific to individual populations, and that there may be intra-specific genetic variation in this relationship.

For some species, statistical models have been designed to explain variation in wood density at the level of the individual growth ring by using ring width, cambial age and other variables (e.g. [10, 43]. In these studies, the population used to construct the statistical models corresponds biologically to a population of rings. Usually, the underlying structure of the sample has not been taken into account when validating and considering the explanatory power of the models. Hence, although most of these models give a very significant F value, demonstrating that the explanatory variables have an effect on density, they have little predictive value at the ring level. In other words, the model may give a very good fit at the ring population level, but a poor fit at the level of the individual ring.

Some authors have tried to improve the predictive power of models by including a variable called "tree level" [6, 10, 11, 15]. Many wood properties show considerable variability at the individual tree level, and there are two (not mutually exclusive) possible reasons for this: either wood properties are genetically inherited, or their expression depends on environmental factors. We do not pretend here to solve the classical problem of distinguishing between environmental response and heritability for a phenotypic trait displaying high variability at the individual tree level. We are aware this would require a better understanding of the loci involved in the control of a trait and the interactions between them, and that this understanding is not likely to be reached in the near future. However, it should be noted that one problem with using the variable "tree level" in models is that it does not allow the effects of genetic control and environmental response to be separated. A model fitted on a given tree, with parameters fitted for every tree, has a far higher predictive value.

The objective of the paper presented here is to take the genetic structure of samples explicitly into account in order to improve the predictive value of the model at the individual ring level. By genetic structure, we mean the relatedness between trees within a sampling unit. We used genetically structured material to investigate whether a given level of genetic characterisation (provenance, half-sib progeny, clone) can be used to increase the precision of models explaining variation in wood density.

2. MATERIAL

2.1. Plant material

Three types of genetic entries were used: provenances, half-sib progenies and clones.

The level of genetic characterisation for provenance is that all trees are grown from seed collected in the same geographic region, but are not explicitly related to each other. The material came from a provenance test on a site in Limousin (West Massif Central, France), in one of the best regions in France for growing Douglas-fir. The provenance test was planted in 1965. The 25 provenances in the test were commercial seedlots collected in the natural range of Douglas-fir, from Vancouver Island to northern Oregon and from the Pacific coast to the western side of the Cascades range. Four provenances (Skykomish, Santiam, Humptulips and Granite Falls) were chosen to represent the patterns of height growth seen in the test. Santiam was the slowest and Humptulips the fastest growing provenance. Skykomish was intermediate, with a very stable ranking over time. Granite Falls was fast growing until age 15–20, but was then overtaken by other provenances, including Humptulips [29]. In January 1995, when trees were 33 years old from seed, 100 trees (25 of each provenance) were felled, and a 10-cm-thick disk was taken at 2.5 m from each felled stem, between the first and the second log cut for commercial sale. Some trees or wood samples were excluded for methodological reasons, and the final sample was: Skykomish: 24 trees; Santiam: 23 trees; Humptulips: 24 trees; Granite Falls: 22 trees (a total of 93 trees).

The level of genetic characterisation for half-sib progeny is that all trees have the same female parent, but unknown male parents from the same provenance (in the case of open-pollinated progeny the number of possible male parents may be high). The material came from progeny tests growing at three test sites: Epinal (North-Eastern France, foothill of Vosges mountains), Faux-la-Montagne (West-Central France, Limousin) and St Girons (south of France, foothill of Pyrénées mountains). The tests were planted in 1978. The 125 progenies in tests came from 24 French provenances, but the origin in the Douglas-fir natural range of the different provenances is unfortunately not known. Thirty progenies were selected for height and DBH growth, time of budburst, branching angle and depth of pilodyn pin penetration (pilodyn is a non-destructive tool for indirect assessment of wood density, see for example [30]. The objective of the selection was to sample the complete range of variation for all these traits. The 30 selected families came from 13 different provenances. Ten living trees were randomly sampled within each family and test site (10 trees × 30 families × 3 sites). One increment core was collected at breast height (1.3 m) from each tree during 1994, when trees were 16 years old. Some trees or samples were excluded at different stages of the sampling, and the final number of samples was 777.

The level of genetic characterisation for clones is that all tree are genetically identical. The material came from a clonal test growing at a site in the forest district of Kattenbuehl, Lower Saxony, Germany. The clones were selected from seedlings grown at Escherode (Germany) from a large seed collection made in Canada (British Columbia) and the USA (Washington and Oregon, west of the Cascade range). The test was planted in 1978, using rooted cuttings from the best seedlings of the best provenances (selection based on survival and growth). After selection of the best 20% clones in 1992, a thinning was conducted of the 80% clones not selected as superior. During the winter of 1997–1998, 50 clones were selected in the clonal test with the objective of maximising the variation in DBH and depth of pilodyn pin penetration within the selection. Such a sampling procedure is likely to over-estimate the genetic variation in wood properties related to density. In March 1998, when trees were 24 years old, one radial increment core was collected at breast height (1.3 m) from 179 trees (see *table I*).

2.2 Data collection

One radial X-ray density profile was obtained from each sample (disks for the provenances, increment cores for the half-sib progenies and clones), following the indirect method described by Polge [26]. Each disk or increment core was sawn to 2.40 mm (±0.02 mm)-thick. The indirect method measures the attenuation of a very thin (250 × 24 microns in this case) light ray crossing the X-ray picture of a wood sample.

Table I. Number of tree per clone.

Number of clones	Number of tree per clone
28	3
15	4
7	5

3. METHOD OF DATA ANALYSIS

Density profiles were separated into rings, using functions developed under Splus statistical software [36]. Then, for each ring, three parameters were computed:

– ring width (width);

– ring density (density);

– ring cambial age (age).

Each ring can be identified chronologically by two parameters: the ring number from pith to bark (cambial age at time of ring formation); or the calendar year in which the ring was formed (determined by counting from bark to pith). There is not a perfect correspondence over all trees between the two traits due to variation in the rate of height growth. Models usually predict ring characteristics using cambial age rather than calendar year [15].

In total, data were collected from 11 028 rings of 1 036 trees sampled from 84 genetic entries growing at five test sites.

Data available

For all genetic structures (provenance, half-sib progeny and clone), the following variables were available and used for explaining ring density (*D*): ring width (*W*), ring cambial age (*CA*) and genetic identity (provenance *P*, family *F*, clone *C*). In one case (half-sib progeny), an additional geographical variable was added, as samples came from three test sites in three different regions of France.

Data analysis

The general relationship used in all models of this kind is $D = f(W, CA)$.

In this study, we decided to restrain ourselves to linear models, using covariance analysis. We compared nested models of type (1) and (2), as shown in the appendix, with one set of models for provenances, one set of models for half-sib progenies and one set of models for clones. We compared models using the *F* ratio, defined as

$$F = \frac{\dfrac{RSS_1 - RSS_2}{df_1 - df_2}}{\dfrac{RSS_2}{df_2}}$$

where RSS_1 and RSS_2 are respectively the residual sums of squares of models 1 and 2, and df_1 and df_2 are respectively the degrees of freedom of models 1 and 2. If the probability value associated with *F* is less than or equal to 0.05, then the models 1 and 2 are significantly different. When models were significantly different, adjusted R^2 values were computed and compared.

This method does not always provide a straightforward comparison between two models. A genetic effect may affect the significance level of a model in at least two ways: either as a main factor, as in analysis of variance (ANOVA), or within an interaction term when associated with another cofactor, such as ring width or cambial age. We tested the effect of each of these possibilities with the same tool of *F* ratio.

Analyses of variance were conducted using the aov (analysis of variance) procedure of Splus (Type I sum of squares in the notation of SAS GLM). The ring width (*W*) co-variable was transformed in order to linearise the ring density – ring width relationship. The chosen transformation was $W^{0.5}$. In all three cases, model 1 is the most complete model not including the genetic factor, and model 2 the most complete model including the genetic factor. Factors were introduced step by step from model 1 to model 2 in the following order:

1) ring width;
2) cambial age;
3) site when relevant (progeny test);
4) provenance, half-sib family or clone, that is, the relevant genetic factor;
5) then the respective interactions, following the same order.

Residuals plots and other plots were drawn to check the validity of the linear model assumptions. Coefficients of covariables and of interactions with genetic entries were estimated using Splus functions [36].

4. RESULTS

Figure 1 shows the range of the variation (mean values and confidence intervals) in density and ring width of genetic entries at the three genetic levels (provenance, half-sib progeny and clone). The between-genetic entry variation is minimum at the provenance level, maximum at the clone level and intermediate at the family level.

Tables II and *III* show that introduction of the genetic entry always significantly improves the fit of the model. This effect is greatest with the clonal material, where the adjusted R^2 increases from 0.202 in model 1 to 0.539 in model 2; in both cases the *p* value of the *F* ratio is less than 10^{-7}.

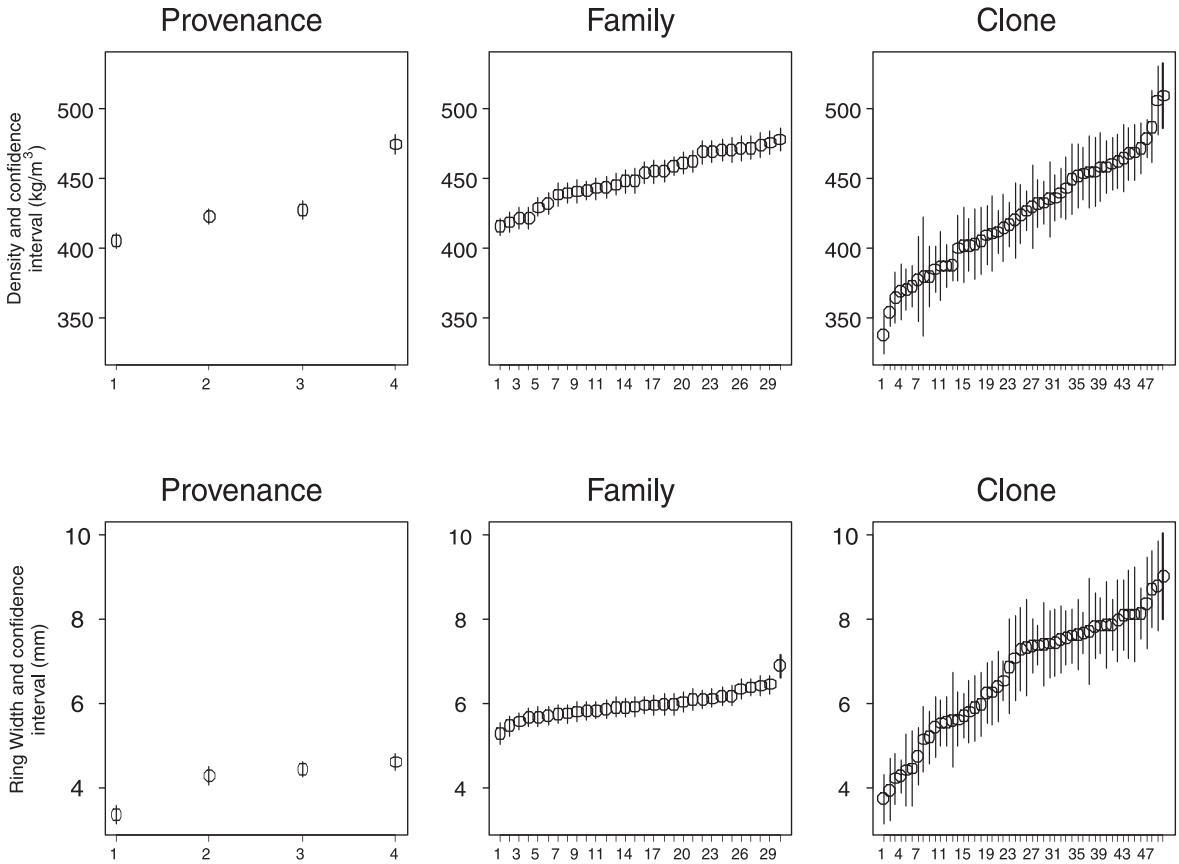

Figure 1. Mean values and corresponding confidence intervals at 95% for density (top) and ring width (bottom) of genetic entries at three genetic levels. Genetic entries are arranged in order of mean value for the character of interest.

Table II. Model statistics (*F* ratio = *F*; degrees of freedom = *df*; probability value = *p* value; model adjusted R^2) for each model and genetic level. The increase of adjusted–R^2 from model 1 to model 2 is moderate for provenances and progenies, and pronounced for clones.

	Model 1			Model 1b			Model 2		
Variation explained by linear model	Provenance	Family	Clone	Provenance	Family	Clone	Provenance	Family	Clone
F	763	1314	423.4	–	1748.8	–	999.3	3004.9	2088.6
p value	$<10^{-7}$	$<10^{-7}$	$<10^{-7}$	–	$<10^{-7}$	–	$<10^{-7}$	$<10^{-7}$	$<10^{-7}$
Adjusted R^2	0.268	0.152	0.202	–	0.193	–	0.323	0.281	0.539

Table III. *F*-test for significance of differences between models. Improvement from model 1 to model 2 is always highly significant.

	Significance between models 1 and 2 (*p* value)
Provenance	$<10^{-6}$
Family	$<10^{-6}$
Clone	$<10^{-6}$

Table IV. Results of analysis of variance for the most complete model (model 2) for provenances. *DF* is "degrees of freedom", *F*, is Fishers's statistics and *p*-value is the probability associated to *F*.

Source of variation	*Df*	*F*-test	*p* value
Ring width $W^{0.5}$	1	792	$<10^{-7}$
Cambial age *CA*	1	27	2×10^{-7}
Provenance *P*	3	52	$<10^{-7}$
$W^{0.5}$**CA*	1	0.14	0.71
$W^{0.5}$**P*	3	1.9	0.12
*CA*P*	3	6.3	3×10^{-4}
Res	2 060		

Table V. Results of analysis of variance for the most complete model (model 2) for half-sib progenies. *DF* is "degrees of freedom", *F*, is Fishers's statistics and *p*-value is the probability associated to *F*.

Source of variation	*Df*	*F*-test	*p* value
Ring width $W^{0.5}$	1	1461	$<10^{-7}$
Cambial age *CA*	1	51	$<10^{-7}$
Site *S*	2	118	$<10^{-7}$
Family *F*	29	20	$<10^{-7}$
$W^{0.5}$**CA*	1	45	$<10^{-7}$
$W^{0.5}$**S*	2	15	$<10^{-7}$
$W^{0.5}$**F*	29	3.3	$<10^{-7}$
*CA*S*	2	76	$<10^{-7}$
*CA*F*	29	2.1	7×10^{-4}
*S*F*	58	5.1	$<10^{-7}$
Res	7 143		

Table VI. Results of analysis of variance for the most complete model (model 2) for clones. *DF* is "degrees of freedom", *F*, is Fishers's statistics and *p*-value is the probability associated to *F*.

Source of variation	*Df*	*F*-test	*p* value
Ring Width $W^{0.5}$	1	507	$<10^{-7}$
Cambial Age *CA*	1	226	$<10^{-7}$
Clone *C*	49	21	$<10^{-7}$
$W^{0.5}$**CA*	1	1.4	0.23
$W^{0.5}$**C*	49	2.8	$<10^{-7}$
*CA*C*	49	3.7	$<10^{-7}$
Res	1 506		

Tables IV to *VI* show the results of analysis of variance for model 2 at each genetic level. Most covariables, factors and interactions were highly significant at all genetic levels. The exceptions were the interaction between ring width and provenance (*table IV*), and the interaction between ring width and ring cambial age for provenances (*table IV*) and clones (*table VI*).

5. DISCUSSION AND CONCLUSION

We have shown that in Douglas-fir the introduction of information on the genetic relatedness between individual trees within samples significantly increases the accuracy of the prediction, at the ring level, of wood density from cambial age and ring width. As relatedness increases from provenance to clone, there is a parallel improvement in the fit of the models. This improvement is especially marked from the half-sib progeny to the clone level.

This is consistent with the evidence of genetic variability in wood density and ring width in Douglas-fir, as reported by several authors [2, 7, 9, 14, 17, 38, 39, 41]. If individual heritability is relatively high (0.5–0.7), the amount of genetic variation is weak at the provenance level (i.e. between provenances) [7], moderate within provenances (between progenies) and even higher between individual trees (clones).

The increase in the fitting quality associated with the most complete model is due not only to the main genetic effect, but also to the interactions between the genetic factor and both ring width and cambial age. The main genetic effect is always stronger than all the interactions. As reported elsewhere for Douglas-fir [2, 19, 23, 38], the relationship between wood density and ring width is moderately unfavourable. The significant interaction between the genetic factor and respectively ring width (progenies and clones, *tables V* and *VI*) and cambial age (provenances, progenies and clones, *tables IV*, *V* and *VI*) suggests that there is genetic control of the general $D = f(W, CA)$ relationship.

The distributions in *figure 2* demonstrate that it is possible to find clones in which there is a positive relationship between growth (ring width) and density; in these clones, wood density increases as ring width increases. For half-sib progenies, the narrower distribution does not extend beyond zero. This is an illustration of the magnitude of improvement that can be reached at the half-sib progeny and clone levels.

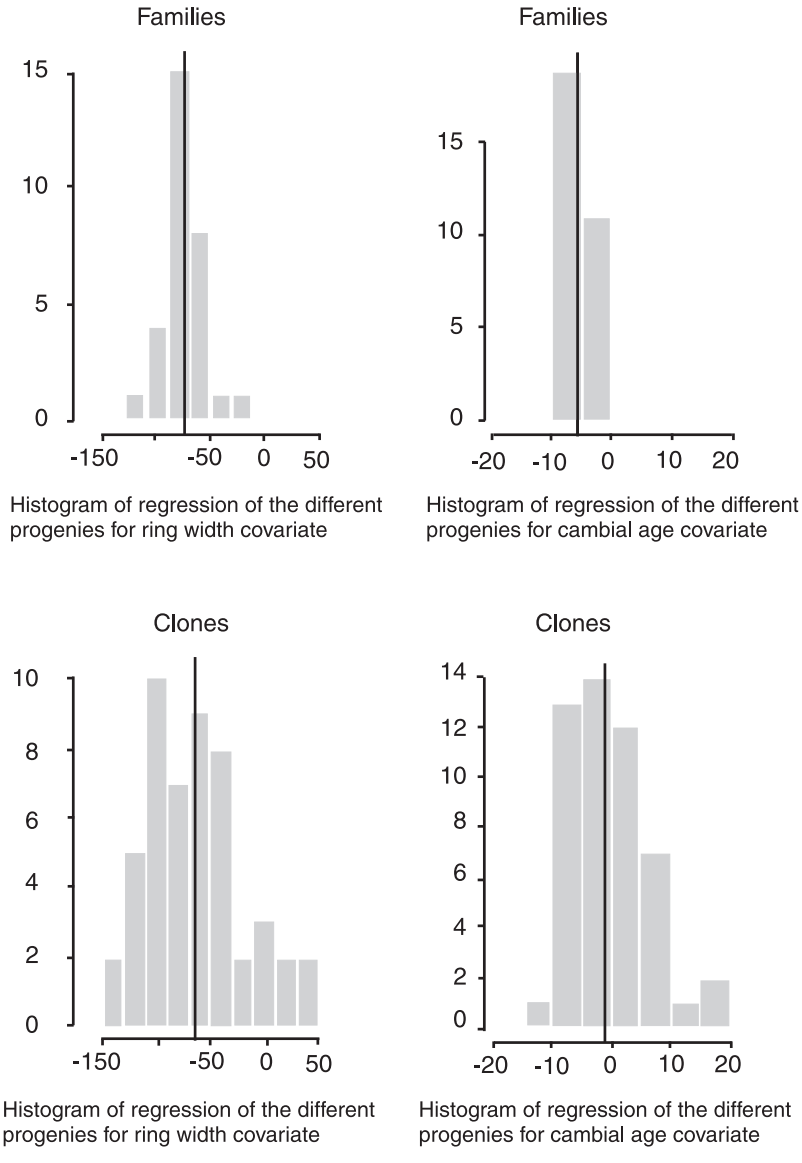

Figure 2. Distributions of the density – ring width and density – cambial age regression coefficients for half-sib progenies and clones. The vertical line is the location of the mean. At the progeny level, all interaction coefficients are negative, while there are some positive values at clone level.

Possible explanations for the genetic variability in the $D = f(W)$ relationship may be proposed. Strengthening and testing this hypothesis will require further and more detailed anatomical studies. Increased growth (ring width) might result from an increase in the size (diameter) of a constant number of cells of constant wall thickness. In this case a negative correlation between ring width and density is expected. It is well known that anatomical characteristics such as tracheid diameter and lumen diameter are under strong genetic control [16, 25, 34, 46]. However, if cell wall thickness increases in parallel with cell diameter, there may be no relationship between growth and density. In Douglas-fir, there may be variation in the genetic control of important anatomical properties such as cell wall thickness. It should be possible to detect such variation by examining the relationship between ring width and each anatomical property in different genetic entries.

Similar studies should also be done for the relationship $D = f(CA)$, since the interaction between ring width and cambial age is significant. It has been suggested [18] that there may be differential expression in the juvenile and mature phases of genes responsible for the production of wood. Another possibility arises from the fact that the micro-environments of a young and a mature Douglas-fir are very different. If the expression of some genes is under environmental control, then a change in the environment may lead to the expression of different genes and a shift in phenotype. It seems probable that the genetic control of the relationship $D = f(CA)$ is a consequence of both processes.

Such changes over time in the control of wood formation may explain why many authors have found only low or moderate age-age phenotypic correlations for wood properties when the older trees are close to rotation age [3, 13, 14, 39]. There are fewer reports of age-age genetic correlations, but they seem to be higher than phenotypic correlations [13, 42]. This observation supports the theory that major differences between the environments of young and adult trees are responsible for the low phenotypic correlations.

A direct consequence of our results is that models predicting wood properties can be significantly improved if the genetic structure of the population is known and can be included in the model. Indeed, most of existing models are well fitted at the population level, and are suitable for purposes such as regional resource assessment [6, 10, 11, 15, 21], whereas their predictive value for a given tree is low. This problem is generally circumvented by adding a so-called tree effect [6, 10, 11, 15], but without specifying its biological meaning. We demonstrate that this tree effect is a mixture of environmental response and heredity. The increase in explanatory power of models resulting form the inclusion of genetic effects has been quantified in our results. The magnitude of the improvement depends on level of genetic chacterisation (minimum for provenances, maximum for clones) and, almost certainly, on the species. Improvement should be considerable for species, such as pines, with a poor phenotypic relationship at the individual tree level between growth rate and wood density [5, 28, 35, 46]. It should be less marked for species, such as Norway spruce, in which the phenotypic relationship between growth rate and wood density is strong at the individual tree level [31, 46]. Improvement should be intermediate for species, such as Douglas-fir, with a variable relationship between growth and density.

When the genetic structure of the sample is not known, the variable "tree" does not allow the genetic control and environmental response to be distinguished. In the case of provenances and progenies, there is some genetic variability between and within genetic entries. In this case, the variable "tree" will include a fraction of the within-entry genetic variability. In the case of clones, all trees within a given clone are genetically identical, and all the within-clone differences accounted for by the "tree" variable are the result of micro-environmental variation. The methods described in this article can be used to estimate the amplitude of the tree effect, and to compare it with other effects, especially that due to clone. Such a study is in progress and the results will be presented in another article.

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APPENDIX

The chosen models are presented below for the three levels of genetic control. In each model W is ring width (covariable), CA is cambial age (covariable), P is provenance (factor), S is site (factor), F is family (factor) and C is clone (factor). a, b, c, are covariation coefficients (slopes) at the general level (a_0, b_0, c_0), and at the levels of the genetic entries (a_i, b_i, c_i). Indices are consistent among expressions:

– k is tree index;

– i is genetic index (in P_i for provenance, F_i for families and C_i for clones);

– j is site index (for the families only).

Covariation coefficients have the same index as the main corresponding effect. Index 0 is used for general relationships at the population level. Index i is corresponding to the relationships at the level of the genetic entry.

Because, in all experiments, genetic entries were selected and not randomly chosen, they were treated as fixed effects.

Provenance level

Model 1

$$D_k = \mathrm{m} + a_0 \cdot W_k^{0.5} + b_0 \cdot CA_k + c_0 \cdot W_k^{0.5} \cdot CA_k + \mathrm{e}_k .$$

Model 2

$$D_{ik} = \mathrm{m} + a_0 \cdot W_{ik}^{0.5} + b_0 \cdot CA_{ik} + P_i + a_i \cdot W_{ik}^{0.5} + b_i \cdot CA_j + c_0 \cdot W_{ik}^{0.5} \cdot CA_{ik} + \mathrm{e}_{ik} .$$

Half-sib family level

Model 1

$$D_{ijk} = \mathrm{m} + a_0 \cdot W_{ijk}^{0.5} + b_0 \cdot CA_{ijk} + c_0 \cdot W_{ijk}^{0.5} \cdot CA_{kij} + \mathrm{e}_{ijk} .$$

Model 1b

This model is specific to this level as it includes a site factor S_j and the corresponding interactions:

$$D_{ijk} = \mathrm{m} + S_j + a_0 \cdot W_{ijk}^{0.5} + b_0 \cdot CA_{ijk} + c_0 \cdot W_{ijk}^{0.5} \cdot CA_{ijk} + a_j \cdot W_{ijk}^{0.5} + b_j \cdot CA_{ijk} + \mathrm{e}_{ijk} .$$

Model 2

$$D_{ijk} = \mathrm{m} + S_j + a_0 \cdot W_{ijk}^{0.5} + b_0 \cdot CA_{ijk} + c_0 \cdot W_{ijk}^{0.5} \cdot CA_{ijk} + F_i + a_j \cdot W_{ijk}^{0.5} + b_j \cdot CA_{ijk} + F \cdot S_{ij} + a_i \cdot W_{ijk}^{0.5} + b_i \cdot CA_{ijk} + \mathrm{e}_{ijk} .$$

Clonal level

Model 1

$$D_{ik} = \mathrm{m} + a_0 \cdot W_k^{0.05} + b_0 \cdot CA_k + c_0 \cdot W^{0.05} \cdot CA_{ik} + \mathrm{e}_{ik} .$$

Model 2

$$D_{ik} = \mathrm{m} + a_0 \cdot W_k^{0.05} + b_0 \cdot CA_k + C_k + a_k \cdot W_k^{0.05} + b_k \cdot CA_k + c_0 . W^{0.05} \cdot CA_{ik} + \mathrm{e}_{ik} .$$