Incorporating Wood Density in Breeding Programs for Softwoods in Europe: a Strategy and Associated Methods

By Ph. Rozenberg[1]), A. Franc and C. Cahalan

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Abstract

In this paper, we introduce a strategy for incorporating wood density into breeding programs in Europe. We develop some related methods, and we present the preliminary results. We used covariance analysis to study the negative relationship between volume growth and wood density and its genetic variation in two important softwood species in Europe: Norway spruce and Douglas-fir. For both species, the same proportion of the observed variability for ring density can be explained by growth traits and genetic origin (respectively 54% and 57%). But the most explanatory factors are very different among the species: in Norway spruce, the ring width variable explains most part of the density variation, while in Douglas-fir the weight of genetic variability of ring density itself is much bigger. To explore such a relationship, we used a more refined description of the ring density profile than the usual earlywood-latewood model. This method was based on wavelets decomposition. Preliminary results suggest that a part of the within-ring density variation not accounted by the earlywood-latewood model is of genetic origin. Wavelets decomposition was also used to quantify a trait often quoted, wood homogeneity. High coefficients of variation at the between-clone level for both species let expect a possible high relative genetic gain for wood homogeneity.

Key words: Genetics, wood, ring density, ring width, co-variation, density profile, wood homogeneity, wavelets.

Introduction

In European forests, rotations are getting shorter for an unchanging (or slightly decreasing) merchantable size of trees. Hence the proportion of juvenile wood in the stem of harvested trees is increasing, and the quality of European softwood is decreasing (Kennedy, 1995). One way to reduce this loss of quality is to genetically improve the wood properties, especially those of the juvenile core (as reviewed in Zobel and Jett, 1995; Rozenberg and Cahalan, 1997; Zobel and Sprague, 1998).

In many European countries, wood collected from a given stand and even from a given tree may be used for a variety of end products (Kennedy, 1995). The wood properties which affect end product quality vary from one product to another (Larson, 1969), and relationships between wood properties and adaptation, growth and form traits are variable (Zobel and Jett, 1995). Tree breeding takes many years, while industrial processes evolve rapidly (Skog et al., 1995). It is therefore difficult to define selection objectives for wood properties that are general and constant over time.

In this context, the main reason for incorporating wood quality traits in tree breeding programs should be to avoid unfavourable correlated responses in wood properties when selecting for improved adaptation, growth and form (Rozenberg and Cahalan, 1997). Computing expectations of genetic gains for wood properties is generally not possible in terms of economic value. Instead, estimates should be made of the co-variation of wood properties with the adaptation, growth and form traits that are the main concern in breeding programs. A possible exception is wood heterogeneity, a defect which is often quoted but poorly defined, then barely studied (Zobel and Van Buijtenen, 1989; Zobel and Jett, 1995; Rozenberg and Cahalan, 1997; Zobel and Sprague, 1998).

Wood density is widely regarded as a key trait in determining the whole wood quality, and when measured on a fine scale it is strongly correlated with the properties of many end products (Elliot, 1970; Zobel and Van Buijtenen, 1989). Wood density is generally more heritable than growth traits, but the genetic variation of wood density is low (Cornelius, 1994) and it is sometimes unfavourably correlated with growth and adaptation traits (as reviewed for spruces in Rozenberg and Cahalan, 1997). Hence, there exist a consensus to choose, in the absence of a better proposal, wood density as a global indicator of wood quality.

The most comprehensive data on wood density are computed from microdensity profiles (Polge, 1978), as shown on *figure 1.* Progress in computer science has made possible the utilisation of statistical and modelling tools for more efficient use of these data (Barbour et al., 1996). In this context, we propose original methods, in order to: 1) study the volume growth – wood density relationship, 2) increase description efficiency of within-ring density models, and 3) measure within-tree density heterogeneity from density profiles.

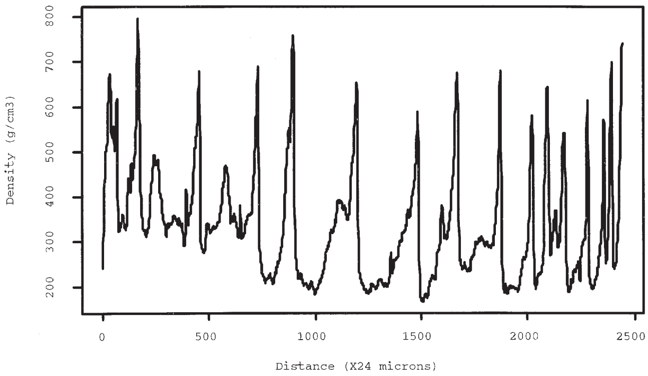

Figure 1. – Indirect radial X-ray density profile of a 20 year-old Norway spruce.

1) In the study, we explored the ring density-tree growth relationship in view to construct a model to predict wood density from traits easy to measure on standing trees. We investigated the influence of the genetic structure of the tree population on the model accuracy. For that purpose, we sampl-

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[1]) INRA, Station d'Amélioration, Génétique et Physiologie Forestières, BP 20619 Ardon, 45166 Olivet Cedex, France
Tel: +33 (0)2 38 41 78 73, Fax: +33 (0)2 38 41 78 79,
Email: rozenberg@orleans.inra.fr

ed two softwood species with different behaviour in respect to the growth-wood density relationship: Douglas-fir (with a moderate unfavourable relationship) and Norway spruce (with a strong unfavourable relationship).

2) Then, we investigated the same relationship as a general unfavourable relationship prohibiting the selection of genetic entries combining fast growth with high wood quality. We propose a method to explore the possibilities brought by a more refined description of the ring structure, different of the one proposed by Barbour et al. (1996).

3) Finally, we investigated an important, but rarely studied wood property: the within-tree homogeneity. We propose a method based on wavelets analysis of the ring density profile. We present some preliminary results on the genetic variation of traits describing wood homogeneity, in order to improve wood quality of juvenile wood.

Material and Methods, and Results

Norway spruce trees used in the study were sampled in a clonal test established at two sites (Hermanstorp and Knutstorp) in southern Sweden in 1978, in the frame of European Union Research Project Geniality (FAIR CT95 0909). At Hermanstorp 182 cuttings from 43 clones were selected, and 125 cuttings from 30 clones were selected at Knutstorp; 20 clones were common to both tests. Detailed information about the tests and the sampling is available in Cahalan (1999).

For Douglas-fir we sampled 166 Douglas-fir (24 year-old cuttings) from 50 clones located in one test site (Lower Saxony, Germany), within the frame of European Union Research Project Eudirec (FAIR CT98 3953). Clones were not randomly chosen within the test, hence it is not possible to compute unbiased estimates of genetic parameters. Detailed information about the tests and the sampling is available in Héois (1999).

One X-ray density profile was recorded for each tree. The density profiles were divided into rings, the rings were numbered from pith to bark (cambial age), then ring width and ring density were computed. The extreme average method (presented for example in Vargas-Hernandez et al., 1994) was used to set up the earlywood-latewood boundary. Then earlywood width and density, and latewood width and density were computed.

1. Genetic effect and growth-wood density co-variation

The negative correlation between radial growth and wood density is one of the most recognised and studied relationship. The strength of this relationship is very variable among softwood species: very significant for spruces and especially Norway spruce, and apparently very weak for some pine species. For Douglas fir, it was generally found to be moderate (Zobel and Jett, 1995).

Using these relationships to build models predicting wood density from growth characteristics could be useful to the wood user, providing inputs easy to measure on standing trees such as diameter at breast height and total height (Rozenberg et al., 1999). However, such a correlation was significant at the ring population level, and usually poor as far as an individual ring property prevision is concerned: at the population level, model Fisher's F is highly significant. At the individual level, there is a high variability, classically taken into account by a so called "Tree Effect", and model R^2 is low (Colin et al., 1992; Houllier et al., 1995; Guilley et al., 1999a and b).

This gap between statistical models and individual prevision is probably due to genetic effects on the relationships between wood properties and growth characteristics, which can occur at any level from the species to the tree (Rozenberg and Van de Sype, 1996; Rozenberg et al., 1999).

Which part of the residual effect can be explained by the genetic structure of the population?

Statistical method was covariance analysis. We used a comparison of nested models including and not including the genetic factor.

Results:

Results show that there was always a highly significant difference between models including and not including the clonal factor *(Table 1)*.

Furthermore, there was always an increase of the adjusted R^2 from the general model to the models including the genetic factor. The increase was respectively very high for Douglas-fir clones (0.34), and very small for Norway spruce clones (0.02) *(Table 1)*.

The general conclusion is that a significant part of the residual effect in models relating ring density with ring width and cambial age (the so-called "tree effect") is due to the genetic structure of the populations. While significant, this part was very different for the two studied species. In our example it seems to be inversely related with the strength of the genetic relationship between growth traits and wood density traits. In general, for both species, the same proportion of the observed variability for ring density could be explained by growth traits and genetic origin (respectively 54% and 57%). But the repartition among the explanatory factors was very different: in Norway spruce, the ring width variable explained most part of the density variation, while in Douglas-fir the weight of the genetic factor for wood density was much bigger. Among the possibilities for exploring such a relationship, a more refined description of the ring density-ring width relationship, using more information from the ring density profile and its variation inside the ring, seems one possible direction to investigate.

2. The earlywood-latewood model, the step model and the growth-density relationship

In some species like spruces, and Norway spruce in particular, the growth-density relationship is especially strong: authors found correlations at the genetic entry level usually stronger than –0.6 (as reviewed in Zobel and Jett, 1995; and in Rozenberg and Cahalan, 1997).

This relationship is variable according to the type of genetic level studied:

Table 1. – Adjustement of wood quality data according to model 1 (without genetic entry), and model 2 (which includes clone as genetic entry).

	Genetic Level	Significance of difference between model 1 and 2	Adjusted R^2 for model 1	Adjusted R^2 for model 2
Douglas-fir	Clones	$<10^{-6}$	0.20	0.54
Norway spruce	Clones	$<10^{-6}$	0.55	0.57

It is stronger at the provenance level, intermediate at family level and lower at the clone level: *(Tab. 2)*.

Table 2. – Relationship between wood density (indirectly estimated by Pilodyn pin depth of penetration) and tree girth in Norway spruce at the genetic entry level.

Type of genetic entry	Coefficient of correlation	Probability
24 provenances	0.92	<.0001
126 families	0.83	<.0001
110 clones	0.79	<.0001

Plant material is composed of provenances, and of families, themselves composed of clones (see ROZENBERG and VAN DE SYPE, 1996, for plant material description).

The less unfavourable relationship is the clonal one. At this level, it is possible to select genetic entries with a reduced unfavourable combination of growth rate and wood density than at the family and provenance levels.

Such relationship is usually computed at the ring level, or at a bigger scale. In our study, we investigated the interest of studying this relationship using a ring density model not based on the earlywood-latewood model: the step model.

We restricted that part of the study to the Norway spruce sample.

Method: using the step model

The earlywood-latewood model is based on the definition of a boundary between the earlywood and the latewood. It is equivalent to trimming the ring in two parts and then computing the mean value and the length of each part *(Figure 2)*. According to that definition, the model coefficient of determination is very variable from one ring to the other: it usually ranges from 0.4 to 0.9.

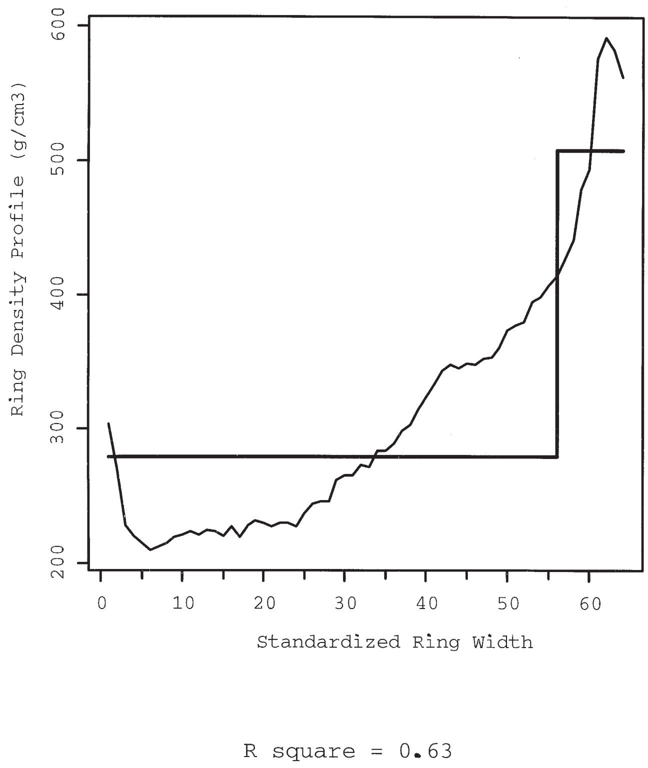

Figure 2. – Evolution of ring density as a function of the standardised ring width, according to the original ring or to the earlywood-latewood (ew-lw) model. The ew.-lw model explains, in that case, 63% of the ring density variation.

On the contrary, the method we developed is equivalent to trimming the ring into a variable number of steps. The location of the boundaries between the steps and the resulting number of steps are automatically chosen in order to 1) relate the step width with the profile slope (short steps for steep slopes, large steps for flat slopes) 2) always get a model coefficient of determination just over 0.9 (*Figure 3*). For this purpose we used the wavelet decomposition of the ring density profile (DAUBECHIES, 1992; ROZENBERG et al., 1997).

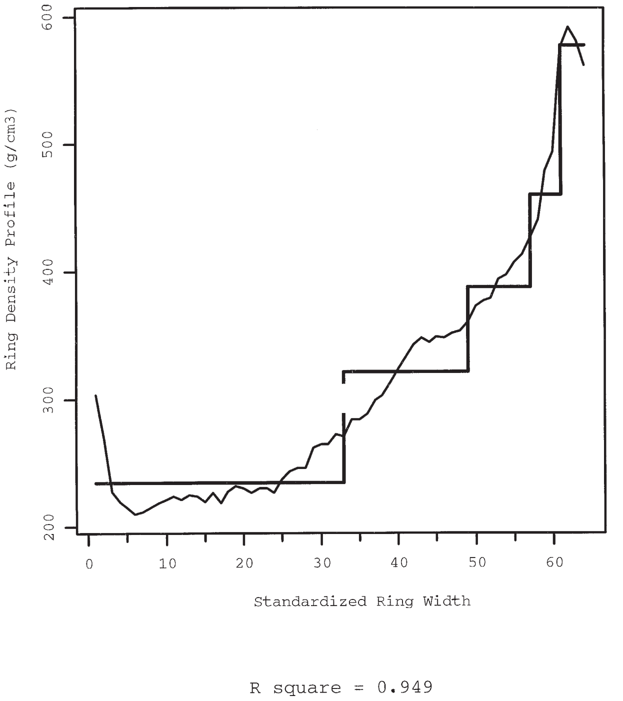

Figure 3. – Evolution of ring density as a function of the standardised ring width, according to the original ring or to the Wavelets adaptive step model. The step model explains, in that case, 95% of the ring density variation.

The model parameters are, for each step, its position within the ring (both from the beginning and the end of the ring), its mean density and its width.

Each ring step was arbitrarily affected to the classes earlywood, latewood, and for the steps in between, transition wood, according to the density values within the ring (low density steps are earlywood, high density steps are latewood).

As a first stage, in order to compare the earlywood-latewood and the step models, ANOVAs were successively conducted on the data sets. In order to simplify the ANOVA models, each method data set was split in two data subsets, one for each site. The chosen ANOVA model was the simple following model (in this preliminary approach, we chose to exclude all interaction effects):

$$D_{ijkl} = \mu + W_i + R_j + T_k + C_l + \varepsilon_{ijkl}$$

Where µ is the general mean

D_{ijkl} is the density of earlywood or latewood, or of each step

W_i is the width of earlywood or latewood, or of each step

R_j is the ring number from pith (cambial age)

T_k is the type of wood, either earlywood or latewood, or earlywood, transition wood and latewood.

C_l is the clone effect

ε_{ijkl} is the residual effect.

All effects are fixed, except residual one.

Results:

ANOVA tables for the ew-lw model: (*Tab. 3* and *4*)

Table 3. – Site Hermanstorp. ANOVA results for the earlywood-latewood model.

	Df	Mean Square	F Value	Pr(F>)
Width	1	96229231	21659	0
Ring	14	563736	127	0
Type	1	55492694	12490	0
Clone	42	113963	24	0
Residual	10069	4436		

Adjusted model R^2 : 0.79. Residual coefficient of variation: 0.15.

Table 4. – Site Knutstorp. ANOVA results results for the earlywood-latewood model.

	Df	Mean Square	F Value	Pr(F>)
Width	1	62541700	14356	0
Ring	14	624183	143	0
Type	1	30836988	7079	0
Clone	29	60459	14	0
Residual	6684	4356		

Adjusted model R^2 : 0.78. Residual coefficient of variation: 0.15.

ANOVA tables for the step model: (*Tab. 5* and *6*)

Table 5. – Site Hermanstorp. ANOVA results for the step model.

	Df	Mean Square	F Value	Pr(F>)
Width	1	160119646	24069	0
Ring	14	587844	88	0
Type	1	204880279	30797	0
Clone	42	242600	36	0
Residual	19675	6653		

Adjusted model R^2 : 0.75. Residual coefficient of variation: 0.19.

Table 6. – Site Knutstorp. ANOVA results for the step model.

	Df	Mean Square	F Value	Pr(F)
Width	1	108339354	16427	0
Ring	14	975174	148	0
Type	1	114422316	17349	0
Clone	29	125120	19	0
Residual	13497	6595		

Adjusted model R^2 : 0.73. Residual coefficient of variation: 0.19.

All effects were highly significant ($p<10^{-7}$). Because experimental designs were not the same in the earlywood-latewood data set and in the step data set, a direct comparison of F-values is not meaningful.

ANOVA model R^2 was greater when the ring model was the earlywood-latewood model: a larger part of the observed variation for wood density was not accounted by the same ANOVA model when the ring model was the step model. But the proportion of the density variation explained by the clonal effect was bigger when the ring model was the step model.

These results can be interpreted as follows: a part of the within-ring variation is of genetic origin. Among this genetic variation, a fraction cannot be accounted by the earlywood-latewood model, but can be revealed by the step model. Such a genetic effect is a hint for the existence of a significant genetic variation for the cambium reaction to an external stimulus, like for example within-growing season climatic events. In other words, breeders can use the fine within-ring density variation as accounted by the step model to monitor some aspects of tree adaptation and of its evolution with time. Hence, we have recently started to explore the relevance of this hypothesis, as an ongoing work.

3. An approach for the genetic improvement of juvenile wood: wood homogeneity

The juvenile wood is the central core in the tree stem, where wood properties are changing rapidly from pith to bark, while mature wood is the outest wood, where wood properties are more stable along the radius (ZOBEL and SPRAGUE, 1998). While some properties of juvenile wood are lower than in mature wood (especially mechanical properties), others are better (especially some properties related with paper quality, like tensile strength) (as reviewed in THORNQVIST, 1996 and ZOBEL and SPRAGUE, 1998). Hence, the superiority of mature wood properties over those of juvenile wood was sometimes discussed (ZOBEL and SPRAGUE, 1998). But mature wood is always more homogeneous than juvenile wood. This is always considered as a strong advantage of mature wood over juvenile wood (ZOBEL and VAN BUIJTENEN, 1991; ZOBEL and JETT, 1995; ROZENBERG and CAHALAN, 1997; ZOBEL and SPRAGUE, 1998).

Hence, following LOO and al. (1985), CORRIVAULT et al. (1991), ABDEL-GADIR and KRAHMER (1993) and BLOUIN et al. (1994), we think that very general selection objectives related with juvenile wood properties could be defined as follow:

- more homogeneous juvenile wood,
- lower difference between juvenile and mature wood (more within-tree homogeneity).

How to define the within-tree homogeneity?

This trait is obviously related with the chosen measurement scale: for solid wood products, the relevant scale is the tree dimension. For smaller or thinner samples, like chips or peeled veneer, the relevant scale can be very small, just over one millimetre.

Hence, homogeneity should be defined at the relevant scales.

Wavelets analysis allows a multiresolutional decomposition of any signal, including the density profile (DAUBECHIES, 1992). The original signal is decomposed into a fixed number of signals, each describing the variations within a given frequency class, from high to low frequency.

Figure 4 shows an example of a Douglas-fir density profile fractionated into 7 *crystals* (BRUCE and GAO, 1994, individual signals), each signal describing the density variations for a given frequency class.

A simple way to measure the signal homogeneity within a given frequency class is to compute the signal variance.

Hence, for each density profiles, we computed the variance of each atom (VD1, VD2, VD3, VD4, VD5, VD6, VS6), where D1 is the highest frequency elementary signal, and S6 the decomposition of lowest frequency within the original density profile. We also computed the total variance of the density profile (VT). The method is similar to that promoted by VONNET et al. (1985), except that it does not depend on ring limits location. Therefore it is extended to a full range of scale, directly computed at the tree level. We added to this set of new variables two classical variables, tree diameter (length of the density profiles, L), and mean of density profile (D). Then we studied the between-clone variation of each of these new variables, and compared the results.

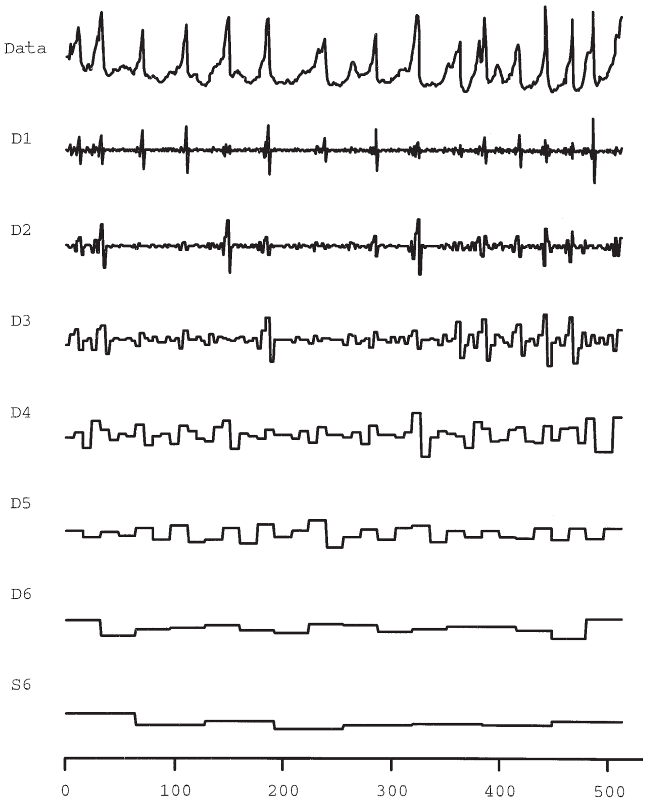

Figure 4. – Multiresolution decomposition of a Norway spruce density profile using Wavelets modelling. D1 to S6 decompose the signal from fine to coarse scales. D1 and D2 are finer scale details components of the original signal. D6 and S6 correspond to lower frequency oscillations. X axis is the length of the standardised density profile.

ANOVA models were the following:

Norway spruce clones: $X_{ijk} = \mu + S_i + C_j + (CS)_{ij} + \varepsilon_{ijk}$

Douglas-fir clones: $X_{ij} = \mu + C_i + \varepsilon_{ij}$

Where X_{ijk} is the trait of interest, S_i is the site effect, C_j is the clone effect and $(CS)_{ij}$ is the corresponding interaction. All effects were considered fixed.

Results (Tab. 7):

There was a strongly significant clonal effect for all the study variables, including the new homogeneity variables. The clonal effect was maximum for D, L and VT. There were strong differences among the variables according to the Site effect, and to the Clone x Site interaction (*Tab. 8*).

Both at the individual or clonal level, the coefficient of variation for L and D were as expected (CORNELIUS, 1994): quite high for L, and low for D. But the coefficient of variation of some homogeneity traits were higher than the coefficient of variation of L: it was 21% for VD3, 21% for VD4, and reached 37% and 39% respectively for VD6 and VS6 (*Tab. 9*).

There was a strongly significant clonal effect for some study variables, including some of the new homogeneity variables. The strongest clonal effect was for D, then for VT (*Tab. 10*).

Like for Norway spruce, we found results in accordance with CORNELIUS (1994): there is a high coefficient of variation for L, and a low one for D. But we find higher coefficient of variation for some homogeneity traits, and especially for VD5, VS6 and VD6.

Discussion and Conclusion

1. Genetic effect and growth-wood density co-variation

There was a significant clonal effect on the ring density and ring width relationship. Although significant for both the studied species, this clonal effect was very variable. It was very strong for Douglas-fir and much smaller for Norway spruce. This result suggests that there are selection possibilities at the ring level for Douglas-fir for genetic entries (clones) combining quite fast growth and high wood density. But for Norway spruce, there is a need for more refined studies at the within-ring level. Such studies could help to understand why the ring density-ring width relationship is so strong for that species, and maybe could give the breeder some hints for selection objectives in Norway spruce.

Table 7. – ANOVA results for Norway spruce clones.

		VD1	VD2	VD3	VD4	VD5	VD6	VS6	VT	L	D
Site	F	1.189	13.096	17.794	2.334	3.471	0.002	47.753	2.530	0.066	28.522
	Pr(F>)	0.276	0.000	0.000	0.127	0.063	0.962	0.000	0.112	0.798	0.000
Clone	F	3.497	3.168	4.710	5.515	4.850	3.898	2.707	9.096	10.109	9.358
	Pr(F>)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CloneXSite	F	1.452	1.247	2.088	1.432	2.366	1.208	1.102	1.205	2.797	1.993
	Pr(F>)	0.098	0.214	0.005	0.106	0.001	0.246	0.345	0.248	0.000	0.008

VD1 to VS6 are the variance of density profile components. D1 is the high frequency component, and S6 the decomposition of lowest frequency within the original profile. VT is the total variance of the density profile. L is the profile length (tree radius) and D is the profile mean density.

Table 8. – Coefficient of variation for the Norway spruce clones.

	VD1	VD2	VD3	VD4	VD5	VD6	VS6	VT	L	D
Individual	0.20	0.17	0.17	0.21	0.27	0.37	0.39	0.15	0.20	0.08
Clonal	0.18	0.11	0.16	0.18	0.22	0.26	0.34	0.12	0.16	0.06

VD1 to VS6 are the variance of density profile components. D1 is the high frequency component, and S6 the decomposition of lowest frequency within the original profile. VT is the total variance of the density profile. L is the profile length (tree radius) and D is the profile mean density.

Table 9. – ANOVA results for the Douglas-fir clones.

		VD1	VD2	VD3	VD4	VD5	VD6	VS6	VT	L	D
Clone	F	1.279	1.054	1.738	2.484	2.082	1.546	1.024	5.024	4.845	6.116
	Pr(F>)	0.147	0.402	0.009	0.000	0.001	0.032	0.450	0.000	0.000	0.000

VD1 to VS6 are the variance of density profile components. D1 is the high frequency component, and S6 the decomposition of lowest frequency within the original profile. VT is the total variance of the density profile. L is the profile length (tree radius) and D is the profile mean density.

Table 10. – Coefficient of variation for the Douglas-fir clones.

	VD1	VD2	VD3	VD4	VD5	VD6	VS6	VT	L	D
Individual	0.37	0.34	0.32	0.34	0.35	0.89	0.77	0.22	0.28	0.12
Clonal	0.23	0.20	0.20	0.24	0.26	0.55	0.44	0.19	0.25	0.10

VD1 to VS6 are the variance of density profile components. D1 is the high frequency component, and S6 the decomposition of lowest frequency within the original profile. VT is the total variance of the density profile. L is the profile length (tree radius) and D is the profile mean density.

2. The earlywood-latewood model and the step model: comparison of the two models for the growth-density relationship

Obviously, the step model allowed a better description of the within-ring variation than the earlywood-latewood model. Furthermore, this additional variation could be partly accounted for by the clone factor. There could be a strong interest for a study of the effect of the successive introduction of the factors of the experimental design in the ANOVA models. Such a data analysis could help for better understanding the respective weights of the different variables on the density variations. First results raise the question of the cambium reaction to within-growing season climatic events: is there a genetic variation for the tree reaction to, for example, climatic stresses? What is the consequence of such a genetic variation on basic wood properties? These questions are especially important in the frame of the study of the co-variation of adaptative traits (which are among the main traits for all breeders) and basic wood properties.

3. An approach for the genetic improvement of juvenile wood: wood homogeneity

The most promising results of this study may be summarised as follows: it is possible to simply and objectively describe homogeneity of wood density, whatever is the desired scale. The trends observed on Douglas-fir and Norway spruce where also observed on Maritime pine (non published results). The method can be extended to any wood property measured along an axis. There is a highly significant between-clone variation for most of the homogeneity traits within both species. Furthermore, very high individual and clonal coefficients of variation let expect a high genetic gain when selection uses these traits. These results encourage us to continue such studies. We plan to compute heritabilities, genetic coefficients of variation, expectations of genetic gains from different data sets of different species for these homogeneity traits. The next step could be to study the relationship between the observed genetic variation for wood homogeneity, and its consequence on important end-users properties.

4. General conclusion

The direct or indirect wood microdensitometers were developed simultaneously in different countries during the years 1960 to 1970 (Polge, 1978). At this time, computer science was juste beginning, and use of the complete information in a density profile was not possible. New tools like the Silviscan 1 and 2 in Australia, were recently developed (Evans et al., 1995). Such tools aim to gain rapidly a very comprehensive set of traits allowing to thoroughly describe within tree variation for a number of traits. In genetic studies, the number of trees to be measured in order to precisely study genetic variation is always high. Size of the data sets collected for studying the genetic determinism of wood properties is then strongly increasing. At the same time, recent progress in computer science has made possible the utilisation of statistical and modelling tools for more efficient use of these heavy data sets. This paper is an illustration of recent progress that were made possible by the use of these tools, in the frame of important topics related with the recent evolution of European forests: the announced and sometimes observed quality decrease related with the growth rate increase (Rozenberg and Cahalan, 1997).

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Genetic Variation Among Paper Birch (*Betula Papyrifera* Marsh.) Populations in Germination, Frost Hardiness, Gas Exchange and Growth

By A. Benowicz1), R. Guy1), M. R. Carlson2) and Y. A. El-Kassaby1)3)

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Abstract

Patterns of genetic variation in paper birch (*Betula papyrifera* Marsh.) were evaluated at the population level. A sample of 18 populations from the south interior, central interior and north coast of British Columbia were examined in a number of traits related to germination (germination capacity, germination speed, peak value and germination value), fall and winter frost hardiness, gas exchange (transpiration rate, stomatal conductance, net photosynthesis, instantaneous water use efficiency and mesophyll conductance) and biomass accumulation after the first and the second growing season. Analysis of variance or covariance revealed significant differences among the populations in all studied attributes except for stomatal conductance and height after the second growing season. Proportion of total variance attributed to population effect was up to 92% for germination parameters, 63% for fall frost hardiness, 22% for winter frost hardiness, 63% for biomass after the first growing season, 20% for biomass after the second growing season, and 5% for gas exchange variables. Germination speed and capacity were positively correlated and were higher in populations from colder climates. Central interior populations had the highest level of fall frost hardiness and were the most uniform with respect to that trait. There were large variations in fall frost hardiness within north coastal and south interior populations. Revealed patterns of variations have implications for paper birch genetic resources management and conservation.

Key words: inter- and intra-population variation, quantitative and adaptive attributes, geographic trend.

Introduction

Paper birch (*Betula papyrifera* Marsh.) is a pioneer tree occurring throughout British Columbia except for the outer coastal mainland and northwestern part of Vancouver Island. It can be found over a wide range of environmental conditions but grows best at low and middle elevations in moist and warm locations (Simard and Vyse, 1992). It tolerates low winter temperatures as well as high summer temperatures if water supply is sufficient. Paper birch seedlings have high growth potential that is often not fully realized on sites where nutrient and water supply is somewhat limited.

Paper birch is one of the three commercially most important hardwood species in the interior of British Columbia (Massie et al., 1994). Its economic importance may increase in the future

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1) Department of Forest Sciences, Faculty of Forestry, The University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

2) British Columbia Ministry of Forests, Kalamalka Research Station, 3401 Reservoir Road, Vernon, British Columbia, Canada V1B 2C7

3) Correspondence should be addressed to Yousry A. El-Kassaby
phone: (250) 381-1404
fax: (250) 381-0252
e-mail: yelkassaby@cellfor.com