Density appears to be weakly and negatively related to growth in *E. nitens* at age 7 years ($r_g = -0.2$), and diameter at 1.3 m is highly correlated with total tree volume at age 7 years ($r_g = 0.99$) – it is useful to confirm these relationships for *E. nitens*.

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Spruce and Wood Quality: Genetic Aspects (A Review)

By Ph. Rozenberg[1] and Ch. Cahalan[2]

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Summary

This paper is a review based on articles about the genetics of wood quality of Norway and Sitka spruce. Among the wood quality traits, wood density is the most widely used. The main topics of the paper are : genetic control (genetic control of wood density, change of genetic control with age, genotype-environment interaction), young-adult relationships, relationships between wood density and other wood properties, and relationships between wood density and growth and adaptation traits (especially about the widely studied unfavourable rela-

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[1] INRA Orléans, F-45160 Ardon, France

[2] The Biocomposite Centre, University of Wales, Bangor, Gwynedd, LL57 2UW, United Kingdom

tionship between diameter growth and wood density). Other wood properties are briefly mentioned, as they were far less studied than wood density. The conclusion summaries the main trends in the results, and proposes some frames and guidances for future studies.

Key words: Spruce, wood quality, wood density, genetics, review.

FDC: 165.3; 812.31; 812.214; 812.7; 811.4/5; 815.2; 851; 174.7 *Picea*; 174.7 *Picea abies*; 174.7 *Picea sitchensis*; (048.8).

1. Introduction

This review is mainly based on articles about the wood quality of Sitka and Norway spruce (*Picea sitchensis* and *Picea abies* (l.) KARST), the 2 spruce species planted in Europe. Facts from papers about North American species not grown in Europe (*Picea glauca*, *Picea mariana* and *Picea rubra*) are also used, as many trends in the results and the consequences for breeding strategies are similar for the 5 species.

2. Wood Quality

2.1 Decrease of Spruce Wood Quality

Forest resources in the northern hemisphere are turning from being dominated by rather slow-grown naturally regenerated stands to relatively fast-grown planted stands (KENNEDY, 1995; PERSTORPER *et al.*, 1995). This evolution will cause a significant decrease of Sitka and Norway spruce wood quality (PETTY *et al.*, 1990; THOMPSON, 1992; JOHANSSON *et al.*, 1992; THÖRNQVIST, 1993; KENNEDY, 1995; KLIGER *et al.*, 1995; PERSTORPER *et al.*, 1995). The quality decrease may be large enough to sometimes prevent Sitka and Norway spruce to be used for structural timber (PETTY *et al.*, 1990; SUTTER-BARROT and VAN POUCKE, 1992; FORD, 1993).

In France, 72% of the harvested volume of spruces and firs (figures are given for the group of species, but the principal species is Norway spruce) is mainly used for solid wood products. 28% is used for pulp and strands[3]) (BESSIÈRES *et al.* 1994).

When users of Sitka and Norway spruce lament about this decreasing quality, the main complaints are:

- low mechanical properties – the wood cannot be used for structural timber (MOTHE, 1983; PETTY *et al.*, 1990; SUTTER-BARROT and VAN POUCKE, 1992; CHANTRE and GOUMA, 1994);
- knots are too big and frequent (THOMPSON, 1992; JOHANSSON *et al.*, 1992);
- warp (THÖRNQVIST, 1993; JOHANSSON *et al.*, 1993). “ … more than one third of the measured studs were warped to such a degree that they would be rejected at the building site” (WOXBLOM, 1996). This seems to be the main complaint in Scandinavia.
- the wood is less decay resistant than was previously the case (THÖRNQVIST, 1993);
- too much variability (“the variability in properties of timber is one of its major disadvantages as an engineering material” (THOMPSON, 1992); “two wood properties almost always emphasized are uniformity and wood density …” (ZOBEL and JETT, 1995);

One may notice that these laments are related to uses which are not pulp and composite products, but solid wood products. Can we conclude that spruce wood properties are well adapted to pulp and composite production?

2.2 Wood Quality and Wood Properties

The wood quality decrease is very generally related to the increasing volumetric proportion of juvenile wood within the stems of fast grown, short rotation conifers (HARVALD and OLESEN, 1987; THOMPSON, 1992; FORD, 1993; THÖRNQVIST, 1993; JOHANSSON, 1993; KENNEDY, 1995; KLIGER *et al.*, 1995). Juvenile wood characteristics have been directly studied in Sitka spruce (HARVALD and OLESEN, 1987) and in Norway spruce (OLESEN, 1977; SARANPÄÄ, 1994) and were reviewed by THÖRNQVIST (1993). But in fact, all the authors working with young spruces, and/or studying radial variation of wood properties, deal with juvenile wood. CORRIVEAU *et al.* (1991) and BLOUIN *et al.* (1994) choose to describe the genetic variation in the radial pattern of wood density by computing a variable corresponding to the deviation between “the inner juvenile wood density and that of the outer juvenile wood”. BLOUIN *et al.* (1994) think that “a slight deviation represents a more homogeneous, better quality wood”.

The term “wood quality” is usually used to express a level of a single property, rather than fitness for a specific end-use. Timber quality should instead be defined as the ability of timber products to satisfy intended applications (PERSTORPER *et al.*, 1995). Hence selection criteria for wood quality should be defined as the key variables for product performance with respect to suitability for end uses. However, Norway spruce and Sitka spruce are used for very different purposes: pulp, fibre and chips for composite products, woodwork, furnitures, carpentry, structural timber and, sometimes, musical instruments (COLLARDET and BESSET, 1988). Key variables may be very different from one use to another: “If wood is to be grown for pulp or strands for composite products, then the best management practice may be to maximize volume of fiber produced per unit time. However, volume maximization may not produce the best physical properties for some engineered wood products, furniture, and paneling” (SKOG *et al.*, 1995). Most of the time, wood from one stand, and often from one single tree, is used for end products which cover the complete range: is it possible to fix one prevaling use for all the wood coming from one stand? Furthermore, a breeding program is a long term affair, lasting tens of years, and the key variables must have as many chances as possible of persisting as long as possible: they must not be affected by the evolution of the wood industry methods. “It is difficult to predict what wood properties will be needed in the future” (ZOBEL and JETT, 1995). For example in North America, in just 15 years, oriented strandboard has become a competitive substitute for softwood plywood in construction (SKOG *et al.*, 1995).

Hence, from the breeder’s point of view, key wood quality traits should be:

- as highly as possible correlated with as many as conceivable end-users-key-variables;
- unchanging with years;
- not (or not too) unfavorably genetically correlated with other selection traits, like growth and adaptation traits;
- as variable and as highly heritable as possible, to maximise potential genetic gain;
- as highly as possible correlated from age to age, and especially from young age to adult age, in order to accelerate the improvement progress.

Most breeders think (for example LACAZE and POLGE (1970); BIROT and NEPVEU (1979); AKACHUKU (1984) in ZOBEL and JETT (1995) that wood quality traits should be considered as secondary traits after growth and adaptation traits. In France, improved Norway spruce genotypes must combine adaptability,

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[3]) In contrast, *Pinus* species are nearly equally used for pulp (53%) and solid wood products (47%).

fast growth and straight stems with good or at least acceptable wood quality (FERRAND, 1986).

2.3 Wood Density

Among the wood quality traits, wood density is the most widely used, because it is very generally considered "of key importance in forest product manufacture" (ZOBEL and VAN BUIJTENEN, 1989). BUNN (1981) has said that "density is probably the single most important intrinsic wood property for most products, particularly if we are contemplating adopting short rotations". ZOBEL and VAN BUIJTENEN (1989) wrote that "it is so important that… it is usually the only wood characteristic that is genetically manipulated". In a review, ELLIOTT (1970) stated that "density is 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".

Few people are reluctant to think about wood density as the most general key trait, for the following reasons.

- Density is obviously correlated with weight. Dense boards are heavy and users may find it laborious to handle them. "From the end-user's point of view, density is generally an irrelevant parameter. In fact, it would be advantageous to have low density wood in construction products in order to facilitate handling. It is true that wood density is to some extent correlated to end-user key variables such as strength and stiffness" (PERSTORPER *et al.*, 1995). But as early as in 1970, ELLIOTT stated that "breeding program might well repudiate improvement in basic density in favour of improvement of… characteristics that have a more immediate impact on utilization practice; … equally cogent argument can be put in favour of improving basic-density values in species where they are considering limiting"
- Some pulp quality parameters such as sheet density, burst and tensile strength are lowered with increasing density (ELLIOTT, 1970), or at least not influenced by density (KENNEDY, 1995), nor by wider ring width (KENNEDY, 1995).
- Sitka and Norway spruce wood shrinkage is unfavourably correlated with density (GUILBAUD, 1985; MAZET and NEPVEU, 1991). Shrinkage is usually thought to be a component of warp (MAZET and NEPVEU, 1991).

3. Genetics of Wood Quality of Spruce

3.1 Genetic Control of Wood Density

a. Genetic control

Results from numerous authors establish that the genetic variation and the inheritance of wood density within spruces are respectively moderate and high, and that there exist large selection possibilities. These results are consistent with those compiled by CORNELIUS (1994) for a large number of tree species, which suggest that "heritability of specific gravity tends to be higher than for other traits, being almost greater than 0.3". Most values reported for Norway spruce are even higher than those reported by CORNELIUS (1994) for other species (mainly *Pinus* species). "Heritability values for spruces … vary considerably but are generally high, especially the broad sense values. Density of latewood has a higher inheritance value than that of earlywood." (ZOBEL and JETT, 1995).

Tables 1 to *3* show some heritability estimates for spruces.

The ortet-ramet correlations presented in *table 4* are another way to estimate the genetic control of a given trait.

b. Change of genetic control with age

Heritability changes with the age of the cambium. According to ZOBEL and JETT (1995), few results are available, and they are mainly for *Pinus radiata* (NICHOLLS, 1966, in ZOBEL and JETT, 1995) and southern pines (ZOBEL, 1964; HODGE *et al.*, 1992, both in ZOBEL and JETT, 1995). These authors describe the trends in the variation of heritability from pith to bark for different wood characters.

In Norway spruce, LEWARK (1982) established that, within the 15 rings closest to the pith, heritability decreased with an increase in age.

Table 1. – Heritability estimates for Norway spruce (*Picea abies* (KARST.) L.). h^2 is narrow-sense heritability, and H^2 is broad-sense heritability.

Genetic level	Trait	h^2	H^2	References
29 progenies	density	0.80		Nilson 1963 in Mothe 1983
clones	specific gravity		0.84	Kennedy 1966
clones	specific gravity		0.84 or 0.65?	Kleinschmit and Knigge 1967 in Mothe 1983 and in Zobel and Jett 1995
clones	specific gravity		0.50 to 0.71	Worrall 1975
from 10 to 70 progenies, 4 year-old	specific gravity	0.12 to 0.47		Lacaze and Arbez 1971
provenances	specific gravity	0.48		Nanson *et al.* 1975
clones	specific gravity		0.29 to 0.49	Birot and Nepveu 1979
clones	minimum density		0.05 to 0.56	Lewark 1982
clones	maximum density		0.23 to 0.51	Lewark 1982
clones	mean density		0.32 to 0.47	Lewark 1982
clones	specific gravity		0.2 to 0.5	Mothe 1983
progenies / provenances	specific gravity	0.43 to 0.59		Mothe 1983

Table 2. – Heritability estimates for white spruce (*Picea glauca* (MOENCH) VOSS). h^2 is narrow-sense heritability, and H^2 is broad-sense heritability.

Genetic level	Trait	h^2	H^2	References
half-sib families	specific gravity	0.59		Corriveau *et al.* 1991
half-sib families	specific gravity	0.67		Yanchuk and Kiss 1993

Table 3. – Heritability estimates for black spruce (*Picea mariana* (MILL.)). h^2 is narrow-sense heritability, and H^2 is broad-sense heritability.

Genetic level	Trait	h^2	H^2	References
provenances	specific gravity	0.47		Khalil 1985
half-sib families	ring density earlywood density latewood density	0.56 0.68 0.59		Zhang and Morgenstern 1995

Table 4. – Ortet-ramet correlations for Norway spruce.

References	Trait	Adults	Juvenile	Data treatment	Results
Erichson 1956 in Zobel and Jett 1995	density	15 trees	cuttings	ortet-ramet correlation	0.76**
Gislerud 1973 in Zobel and Jett 1995	density	Plus trees	6 to 13 year old cuttings	ortet-ramet correlation	0.51** (47 df)
Wellendorf and Olesen in Zobel and Jett 1995	density	33 year old trees	18 year old cuttings	ortet-ramet correlation	0.56* (13 df)
Birot and Nepveu 1979	specific gravity	ortet 6-21 year old	ramets	ortet-ramet correlation	0.69***

CORRIVEAU *et al.* (1991), in white spruce which was 19 years old since planting, found a low genetic control for wood density in the rings near the pith, while they found a stronger genetic control in the six rings near the bark.

c. Genotype-environment interactions

According to BIROT and NEPVEU (1979), genotype-environment interactions have to be feared in Norway spruce. Effectively, MOTHE (1983) found quite a strong genotype-environment interaction for wood density. On the other hand, in a limited number of clones, CHANTRE and GOUMA (1994) did not find any clone-site interaction for wood density. Neither did they find clone site interactions for pilodyn pin penetration depth (an indirect method for measuring wood density) in a larger number of clones.

3.2 *Young-Adult Relationships for Wood Quality Traits*

Making a selection at a young age accelerates the improvement progress. From what age is it possible to accurately select for wood density? *Tables 5* and *6* show age-age correlations for spruces.

Juvenile-mature correlations are always positive and usually quite strong, except when juvenile wood is "too young". NEPVEU and BIROT (1979) wrote that early phenotypic selection for wood density is possible "a few years after planting". According to CHANTRE and GOUMA (1994), no accurate prediction can be made less than 6 years after planting. BLOUIN *et al.* (1994) found that relatively exact predictions about the density of a 70-year-old tree can be made on the basis of the density of the first 15 annual rings from the pith.

3.3 *Relationship Between Wood Density And Other Wood Properties*

a. Relationship between wood density and stiffness

NEPVEU (1982, in MOTHE (1983)), showed a good relationship between density and stiffness ($r = 0.742$). GENTNER (1985), working on *Picea sitchensis*, found $R^2 = 0.45$. CHANTRE (1989)

Table 5. – Age-age correlations in Norway spruce (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns not significant; "nothing" generally means "no information about on significance level").

Reference	Trait	Adults	Juvenile	Data treatment	Results
Nepveu and Birot 1979	specific gravity	rings 6-9 to 26-29 from center	rings 1-5 to 22-25 year old	Age-age canonical correlations	from ns to 0.81** (from 13 to 32 df)
Lewark 1982	mean and min. ring density	rings near the bark, on a total of 15 rings	rings near the pith	Spearman rank correlation	0.57** (mean ring dens.) 0.64*** (min. ring dens.)
Nepveu and Birot 1984 *in* Chantre and Gouma 1994	specific gravity	33 year old progenies	rings 1-10 from center	10 first rings / complete core correlations	0.80** (151 df)
Sarter 1986	volumic mass	15 prov., 22 year-old	15 prov., 4 year-old	mean of prov. correlations	0.27 ns
Chantre and Gouma 1994	specific gravity	rings 7-9 and 10-12 from center	rings 4-6 and 7-9 from center	Age-age correlations among clone means	>0.85** (6 df)
Blouin *and al.* 1994	specific gravity	35 trees, 70 year-old	rings 1-15	Age-age correlations	0.80***

Table 6. – Age-age correlations in white spruce (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns not significant; "nothing" generally means "no information about on significance level").

Reference	Trait	Adults	Juvenile	Data treatment	Results
Corriveau *et al.* 1987	specific gravity	mature wood from 80 populations	juvenile wood from same cores	Juvenile-mature wood correlations	0.679 (?)

found that density and stiffness of small within-ring samples of Norway spruce were very strongly related ($R^2 = 0.83$). De Reboul (1989) demonstrated that stiffness of standard Norway spruce samples could be accuratly predicted using a set of simple traits including wood density (R^2 from 0.70 to 0.75). In Douglas-fir, Rozenberg and Franc (1996) showed that accuracy of models relating stiffness and density could be increased when using new traits from density profiles rather than classical earlywood-latewood parameters. Hence they found a strong genetic effect on the shape and parameters of the models, thus concluding that different genetic units may have different ways to build their stiffness.

b. Relationship between wood density and shrinkage

Sitka and Norway spruce wood shrinkage is unfavourably correlated with density: shrinkage increases with wood density (Guilbaud, 1985; Mazet and Nepveu, 1991). Guilbaud (1985) found, in Sitka spruce, that different within-ring density parameters were significantly correlated with overall, radial shrinkage (for example, r between radial shrinkage and mean ring density ranges from 0.56 ($P < 0.001$) to 0.70 ($P < 0.001$) in mature wood).

Mazet and Nepveu (1991) found that Norway spruce wood density was quite strongly correlated with radial ($r = 0.70$, $P < 0.001$) and volumetric ($r = 0.65$, $P < 0.001$) shrinkage.

3.4 Relationship Between Wood Density and Growth and Adaptation Traits

a. Relationship between wood density and growth rate

This question is widely discussed today in tree breeding, especially for Sitka and Norway spruce, where a strong correlation between wood density and growth rate is often found. "There are a number of reports of a negative relationship between growth rate and wood density in several genera such as spruce" (Zobel and Jett, 1995).

The factors affecting growth rate are environment, age and heredity (Zobel and van Buijtenen, 1989; Nepveu, 1991; Johansson, 1993; Zobel and Jett, 1995; etc.). The evolution from juvenile to mature wood is the expression of the age effect. Foresters can influence growth rate with silvicultural practices, like initial spacing and thinning. Most studies on the influence of initial spacing or thinning intensity conclude that these factors have little effect on Sitka and Norway spruce wood density (Johansson, 1993). "Within the limits of normal silvicultural practice, initial spacing has little significance on basic-density values" (Elliott, 1970). According to Savill and Sandels (1983), "the possibilities of manipulating wood density through spacing and thinning are insignificant in comparison to the potential from breeding or vegetatively propagating trees from desirable characteristics".

Stand fertility seems to have more influence on wood density through growth rate than initial spacing (Savill and Sandels, 1983; Harvald and Olesen, 1987).

In *tables 7* to *12*, we present results about the relationship between diameter growth and wood density. The same trends are often found when researchers study the height growth-wood density dependence (Zobel and Jett, 1995).

The negative phenotypic and genetic relationships between diameter growth and wood density seem very general within the genus *Picea*. They are moderate for Sitka spruce and other North American spruces, and, most of the time, stronger for Norway spruce.

Table 7. – Relationship between diameter growth and wood density in Norway spruce (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant).

Type of genetic relationship	Linear correlation coefficient	Plant material and tree number and reference
14 provenances mean	-0.60**	Nepveu 1984
30 progenies mean	-0.62**	Nepveu 1984
50 progeny means within 5 provenances	-0.75**	Nepveu 1984
19 provenance means	-0.66*	Nepveu 1984
26 clone means	-0.71**	Nepveu 1984
31 clone means	-0.44**	Nepveu 1984
?	-0.87	Stairs 1969 in Zobel and Jett 1995
16 provenances 4 year-old	-0.32	Lacaze and Polge 1970
19 provenances	-0.29 (gen.) and -0.43 NS (phen.)	Nanson et al.1975
20 provenances	-0.41	Velling 1980
clones, 15 rings	from -0.09 to -0.69*** according to the ring age	Lewark 1982
23 provenance means	-0.95***	Mothe 1983
15 provenance means 22 year-old	-0.21 and -0.41 ns	Sarter 1986
general	-0.75***	Chantre and Gouma 1994
19 provenance means	-0.66*	Blouin et al.1994

Table 8. – Relationship between girth and Pilodyn pin depth of penetration (*** P < 0.001).

Type of genetic relationship	Linear correlation coefficient	Plant material and tree number and reference
24 provenance means for Pilodyn pin depth of penetration and girth	+0.92***	Rozenberg and Van de Sype (not published)
126 family means for Pilodyn pin depth of penetration and girth	+0.83***	Rozenberg and Van de Sype (not published)
110 clone means for Pilodyn pin depth of penetration and girth	+0.79***	Rozenberg and Van de Sype (not published)

Table 9. – Relationship between diameter growth and wood density in Sitka spruce. (*** P < 0.001, ** P < 0.01, * P < 0.05, ns = not significant).

Type of genetic relationship	Linear correlation coefficient	Plant material and tree number and reference
provenance means	-0.62 (?)	Deleporte 1984
Family means	-0.46*	Yanchuk and Kiss 1993
clone means adjusted for ring width	-0.36NS	Costa e Silva *et al.* 1994

Table 10. – Relationship between diameter growth and wood density in black spruce. (*** P < 0.001, ** P < 0.01, * P < 0.05, ns = not significant).

Type of genetic relationship	Linear correlation coefficient	Plant material and tree number and reference
within population	from -0.35* to +0.46**	Hall 1984
between family means	-0.39 (phenotypic) and -0.41 (genotypic)	Zhang and Morgenstern 1995

Table 11. – Relationship between diameter growth and wood density in white spruce. (*** P < 0.001, ** P < 0,01, * P < 0.05, ns = not significant).

Type of genetic relationship	Linear correlation coefficient	Plant material and tree number and reference
27 provenance means	-0.45**	Corriveau *et al.* 1990
39 families, genetic correlations	-0.63	Corriveau *et al.* 1991

Table 12. – Relationship between diameter growth and wood density in other spruce species. (*** P < 0.001, ** P < 0.01, * p < 0.05, ns = not significant).

Species	Linear correlation coefficient	Plant material and tree number and reference
Picea asperata	-.20 NS	Zhang 1995
Picea koraiensis	-.74**	Zhang 1995

For Norway spruce, LACAZE and POLGE (1970) apprehend that selecting for growth "may lead to a reduction of wood density if adequate precautions are not taken". Different ways of handling this unfavourable relationship have been proposed by researchers.

- BIROT and NEPVEU (1979) believe that clonal selection could be a way to break this relationship in Norway spruce.
- Also for Norway spruce, LEWARK (1982) proposes 2 possible strategies: fixing a lower threshold for wood density, or selecting clones where "the regression of the two traits is as low as possible".
- MOTHE (1983), identified some Norway spruce trees with favourable combination of growth and wood density traits.
- In black spruce, HALL (1984) found that growth rate and wood density were not closely related, and thus proposed a method of selection which combines a rapid growth rate and a high wood density in the selected trees.
- For Norway spruce, NEPVEU (1984) and BLOUIN *et al.* (1994), and for white spruce, BEAULIEU and CORRIVEAU (1985), CORRIVEAU *et al.* (1987, 1990) proposed to conduct mass selection for wood density within fast growing populations. NEPVEU (1984) thinks that controlled crossings between well-chosen genitors may produce fast growing offsprings with high wood density.
- CORRIVEAU *et al.* (1991) found, in white spruce, that selecting on height would produce a density increase, while "each volume productivity gain could result in a slight reduction in wood density".
- YANCHUK and KISS (1993) suggest that in white spruce it seems possible, but not certain, to achieve gains in both growth traits and wood density by selecting "correlation breakers" as parents. They wrote that "the decision whether or not to include density as a trait for selection before 15 must be carefully considered".
- According to COSTA E SILVA *et al.* (1994), in Sitka spruce "It seems possible to choose clones with very favourable combinations of characters. ... it is possible to select clones for both high volume production and high basic density".
- CHANTRE and GOUMA (1994) wrote that it is possible to select fast growing Norway spruce clones with high wood density at ages after 6 years from planting.

- KENNEDY (1995) states that "There still will be individual trees that … proceed to form mature, relatively dense wood early in spite of accelerate growth".

- ZHANG and MORGENSTERN (1995), for black spruce, proposed to select on bole volume and dry mass weight using "a selection index imposing the restriction of no change in wood density". Lately, some researchers have found some genetic variation for this relationship.

- MOTHE (1983), on Norway spruce, found substantial differences between genetic-units for the coefficient of correlation of the within-genetic-unit growth rate-wood density relationship (from –0.21 to –0.93).

- Also in Norway spruce, CHANTRE and GOUMA (1994) 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" (ZHANG *et al.*, 1996).

- According to ROZENBERG and VAN DE SYPE (1996), the values of the parameters of the models describing the growth rate-wood density relationships can be used as secondary selection traits, after wood density, to restrain the negative impact of growth rate on wood density.

Another way to simulteanously take into account growth rate and density is to study, as a trait, weight increment along the radius and along the stem. Recently, some researchers have used this trait: in Sitka spruce, FORD (1993a and b) said that density itself and anatomical measures may not be the best indicators for developing selection indicators for high juvenile wood density under fast growth rates, and that the relative changes in wood volume to wood weight increments along the main stem should be studied. In black spruce ZHANG and MORGENSTERN (1995) wrote that "It is necessary to compromise the gain or loss in wood density and bole volume … Selection for dry mass weight production would be more profitable than selection for volume production if black spruce stands are managed for pulpwood… Selection for dry mass weight … would result in less reduction in wood density [than selection for individual growth]."

ZHANG *et al.* (1996) believe that the controversial results found in some species like black spruce concerning the growth rate-wood density relationship may be related with differences among experiments in environment and silviculture.

b. Wood density and adaptation traits

Results are contradictory:

- THIERCELIN (1970) found that the ring density of early flushing populations is slightly less than that of late flushing populations;

- LACAZE and POLGE (1970) found, at age 4 in Norway spruce, a significant negative relationship between lateness of budburst and wood density – early flushing populations would produce denser wood;

- NANSON (1975) found a slightly negative relationship between "earliness of budburst and wood density";

- BIROT and NEPVEU (1979) found "no unfavourable relationship between wood density and lateness of budburst".

3.5 Other Wood Properties

Genetic control of other wood properties has been far less studied on spruces. However, some of the properties studies maybe interesting for breeders: NANSON *et al.* (1975) estimate narrow-sense heritability estimate for fiber length as 0.89 (provenances, 4 years from planting). They also found very large differences among provenances for this trait.

Fibre length is very generally and strongly correlated with microfibrillar angle (MEGRAW, 1985, in ZOBEL and JETT, 1995). According to CAVE and WALKER (1993), microfibrillar angle is strongly and positively correlated with stiffness (radiata pine). In black spruce, not only fibre length, but also fibre diameter, lumen diameter, solubility in alcohol-benzene and solubility in sodium hydroxide are under strong genetic control, while fibre wall thichness is under weak genotypic control (KHALIL, 1985).

3.6 Dealing with Juvenile Wood

A few attempts have been made to separately study the genetic variation of the juvenile and the mature wood, the deviation between some wood properties of the juvenile and mature wood (CORRIVEAU *et al.*, 1991 on white spruce; BLOUIN *et al.*, 1994 on Norway spruce), and the genetic variation in the amount of juvenile wood within the stems (LOO *et al.*, 1985, in *Pinus taeda*; ABDEL-GADIR and KRAHMER, 1992; and VARGAS-HERNANDEZ *et al.*, 1994 in Douglas-fir). The last 3 papers demonstrate directly or indirectly that there is genetic control of the juvenile wood quantity within the stem.

CORRIVEAU *et al.* (1991) found that the density of white spruce wood was under strong genetic control in the "outer wood", but much more influenced by environmental factors in the "inner wood". BLOUIN *et al.* (1994) state that "the deviation between the inner juvenile wood density and that of the outer juvenile wood is an indication of the density radial variation pattern, with a slight deviation representing a more homogeneous, better quality wood". They found that selection on height growth would reduce this deviation.

3.7 New Tools: Biotechnologies

The latest developments of molecular biology methods open new perspectives to the tree breeder. Using marker assisted selection for improving wood quality could help shorten the generation length, and improve the selection response (WILLIAMS and NEALE, 1992). Plant transformation techniques are another way to deal with elite genotypes in the last steps of a clonal selection (PILATE, pers. comm.). Work has started recently on spruces in North America (PILATE, PRAT and ZHANG, pers. comm.) and in Europe, in particular within the EU project PL 95 424 "Timber" (BOUDET, 1995). The main objectives of the proposal concern the improvement of several tree species, including Norway spruce, through an optimization of their lignin profile. The techniques for transformation of Norway spruce are being developed. To our knowledge, no result is available today.

4. Discussion, Conclusions and Propositions

A lot of work has been done on the genetics of wood properties in spruces, and especially in Norway spruce. The main trends in the results are presented and discussed as follows.

4.1 Tree Breeding and Spruce Wood End-Uses

It is clear that the main laments about Norway spruce wood quality are related to its transformation into solid wood products. When pulp is the main product, the first selection criteria should be gross weight yield. Other selection traits could be defined according to the pulp industry requirements; in that case, the first step of such studies could be to estimate the inter-relationships among, on the one hand, these pulp-production related traits, and on the other hand, the growth, adaptation and "classical wood quality" traits.

4.2 Tree Breeding and Spruce Wood Basic Properties

There is no convincing argument that wood density should be repudiated as the main wood quality selection trait. However, it is clear that it is advantageous to study complete density profiles, rather than only the mean density of wood samples, whose size cannot be easily smaller than a ring width. It is also certain that other wood quality traits should be studied, and in particular, traits related to warp (like grain angle, PERSTORPER *et al.*, 1995b). A study of the relationships among density and anatomical traits, and traits describing the fitness of wood for a specific end-use (like warp and stiffness), should be conducted. Genetic variation in these relationships should also be studied, as it is probable that different genetic-units do not build their wood properties in the same way. Such work could help finding genetic-units combining favourable wood properties. Description of these relationships should be conducted using not only classical within-ring density parameters based on the earlywood-latewood boundary, but also parameters established using new techniques to describe the shape of density profiles.

4.3 Wood Uniformity

Special attention should be paid to characters describing wood uniformity. Its key position is very clear (BLAIR and OLSON, 1984, in ZOBEL and JETT, 1995). How to define it? This can be done at different levels: stand level, genetic-unit level, tree or stem level, and ring level.

a. Within-stand and within-genetic-unit homogeneity

Uniformity can be assessed using the within-genetic-unit variance. It is obvious that the kind of genetic-unit with least heterogeneity is the clone (ZOBEL and JETT, 1995). The only remaining differences between trees of a clone are the environmental differences. To some extent, the forester can deal with them through site choice and silviculture.

b. Within-stem homogeneity

Two main within-tree trends are commonly identified:

- the maturation-aging trend, from pith to bark, also called juvenile-mature wood (ZOBEL and VAN BUIJTENEN, 1989; WIMMER, 1994);
- from base to top (ZOBEL and VAN BUIJTENEN, 1989; WIMMER, 1994). This trend can be considered, to some extent, as another expression of the maturation trend: wood from the same ring near the bark at the base of the tree is mature wood, while it is juvenile wood in the same ring inside the crown of the tree (WIMMER, 1994).

A selection criterion can be defined as the contrast between juvenile and adult wood, associated with the juvenile wood volume. Hence defining precisely what is juvenile wood and what is mature wood in spruce species is of major importance.

c. Within-ring homogeneity

The wood density variation inside the ring, known as “from earlywood to latewood”, is the largest source of variation, especially for wood density (MEGRAW, 1985, in ZOBEL and VAN BUIJTENEN, 1989). Wood density usually varies, inside a Norway spruce ring, from 200 g/dm^3 to 800 g/dm^3 (THIERCELIN, 1970; LEWARK, 1982). The density pattern within a ring is perfectly described using density profiles, recorded using, for example, the indirect X-ray method set up by POLGE (1966). The main tendency of the shape of the density profiles varies from the rings near the pith to the rings near the bark (WIMMER, 1994). This is an expression of the aging trend along the radius.

The classical way to describe within-ring homogeneity is to compute the density contrast, that is the difference between the ring maximum and minimum density (POLGE, 1966). FERRAND (1982) proposed to estimate it using the within-ring density variance.

No results are available for spruces to tell whether increasing the within-ring homogeneity is or not favourable In Douglas-fir, MOTHE (1988) showed that increasing the minimum ring density was a way to increase the strength and quality of peelings, and that this minimum ring density was positively related with ring density contrast.

To reduce the large amount of data produced by densitometers, most researchers traditionally choose to separate the ring into 2 distinct and homogeneous parts, earlywood and latewood. Then they calculate simple within ring parameters for each part, such as width and mean density (BARBOUR, 1996; FRANC and ROZENBERG, 1996). Nowadays, modern computation techniques allow researchers to develop procedures to characterize more precisely the shape of wood density profiles. Some first attempts have been made on Douglas fir (BARBOUR, 1996; FRANC and ROZENBERG, 1996) but, to our knowledge, nothing has been tried on spruce species. ROZENBERG and FRANC (1996) demonstrated in Douglas-fir that using such new parameters may lead to significant progress in the use of density profiles.

4.4 Juvenile Wood

Among the traits of interest for spruces, special emphasis should be given to characters related to juvenile wood description, as it is obvious that the question of the juvenile wood properties and volume will be a crucial one for spruce wood quality during the coming years. Here again, new parameters from density profiles may help to describe efficiently the juvenile wood-mature wood trend. The breeder may want to reduce the juvenile wood volume inside the stem, or to improve its properties.

4.5 Genetic Variation of Wood Properties

Wood quality traits are less variable, but much more heritable than growth and adaptation traits. Genetic variability for wood quality traits cannot be estimated accurately at a very early age: it seems reasonable to wait for the trees to reach at least an age of between 5 and 7 years. Heritability may vary with age, but the few results available are contradictory. More studies seem necessary to better understand the evolution of heritability with age. Genetic variation and inheritance of new parameters from density profiles should be studied. More variable parameters could be defined as reference traits for some first attempts in using marker aided selection in breeding spruces for wood quality. Special attention should be paid to the sampling of the genetic units used to estimate genetic parameters, as the precision of estimation may be very variable from one study to another.

4.6 Between-Traits Relationships

The wood quality traits are inter-correlated, correlated with growth and maybe, to a lesser extent, to adaptation traits. Some correlations are often strong and unfavourable, like the widely studied growth rate – wood density relationship. Hence no selection on growth, nor on adaptation can be conducted without carefully monitoring the evolution of wood properties. One way to take both traits into account at once is to study weight increment along the radius and, maybe, along the stem. Study of the genetic variation of these relationships conducted on a large scale in different environments may help understand the somewhat contradictory results found in the literature, and thus help decide what could be the best selection strategies.

4.7 Juvenile-Mature Relationships

The juvenile-mature correlation for wood quality traits exists and is quite strong, and it seems reasonable to believe that prediction of adult wood quality can be performed from the properties of trees of an age not under 6 years.

4.8 Estimation of Genetic Parameters

In a number of studies of the genetic control of the wood quality of spruces, the authors raise some doubts about the accuracy of the estimation of the study parameters (Lacaze and Arbez, 1971; Birot and Nepveu, 1979; Lewark, 1982; Mothe, 1983; Yanchuk and Kiss, 1993). This is quite common in wood quality studies, where measurements are tedious and expensive and cannot be conducted on as many trees and genetic-units as requested by quantitative genetics, and where the choice of the genetic units is sometimes limited. New studies on the genetic control of the wood properties of Sitka and Norway spruce would be interesting only if they had a very good chance of bringing to light relevant answers to the questions and problems addressed above. One condition for that is to pay very special attention to the plant material that would be sampled, and in particular:

- choice of the experimental sites;
- quality of the genetic tests (block definition in particular);
- choice of the genetic units within the tests. It is clear that use of clonal material would give a much better chance of answering the questions than other kinds of genetic units (separation of genetic and environmental effects). It is clear also that the choice of the genetic units themselves within the study population is of primary importance.
- number of trees per genetic units, of genetic units per block and per test, of trees per block. There must be enough trees to estimate properly all parameters, especially the genetic ones.

4.9 Measuring Wood Properties

Very special attention should also be paid to the quality of the assessment of wood properties, in order to increase the precision of estimation. Some methodological studies seem of direct interest for the future developments of softwood, and especially Sitka and Norway spruce, breeding programs.

- It is clear that no breeding of Norway spruce can be conducted without carefully monitoring the evolution of wood quality when selection is conducted on growth and adaptation traits. As breeding implies a lot of measurements, development of wood quality assessment techniques is essential.
- Any improvement of the density profile recording chain is of interest for the breeder, from the workshop tools to the data treatment methods, especially improvements related with the huge and recent progress in computer techniques.
- Non-destructive methods to assess wood quality on standing stems are of primary interest for the breeder, as trees in the genetic tests are often valuable plant material that can't be felled. Among them, it seems possible to rapidly gain interesting results from a field machine able to assess the standing trunk stiffness (Koizumi, 1987; Mamdy, 1995), and from a portable tool to record density profiles on the field (Rinn *et al.*, 1996).
- There is a a great need to improve the laboratory methods used to assess a number of anatomical traits, especially with regard with increasing the measurement speed.

5. General Conclusion and Recommendation

Increasing the accuracy of estimation of genetic parameters could be the most important goal for the future Norway spruce studies on the genetics of wood quality.

This can be achieved by:

– paying more attention to the plant material and the sample sizes;

– increasing the precision of estimation of the wood properties,

– improving the measurement techniques.

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