What are the consequences of growth selection on wood density in the French maritime pine breeding programme?

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Title

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Abstract

Volume and stem straightness were the main selection criteria for the first two generations of the French maritime pine (*Pinus pinaster* Ait.) breeding programme. In this article, we investigate the consequences of this selection on wood quality. Wood density, as a predictor of wood quality, is studied both in the breeding populations and in commercial varieties.
Phenotypic and genetic correlations between wood density and growth traits are investigated in successive breeding populations with three genetic field experiments of respectively 30, 29 and 12 years old. Correlation estimates were either slightly negative or non-significantly different from zero depending on the test considered. Consequently, a low impact of growth selection on wood quality should be expected in improved seed sources. However, we observed a significant wood density decrease in two improved varieties as compared to unimproved seed sources at age 15.
In addition to this first effect on wood density, growth improvement is also expected to reduce the rotation age and thus increase the proportion of juvenile wood, which is known as having a lower density than mature wood. This change was studied and quantified using a growth model.
Finally, a wood density decrease reaching up to 6 % was predicted in the improved varieties compared to unimproved material, when both the observed decrease in wood density and the predicted increase in juvenile wood proportion were taken into account. Implications for the breeding programme were considered.

Keywords

Pinus pinaster Ait. . Correlation . Wood density . Growth . Juvenile wood

Introduction

The relationship between wood density and growth rate has been investigated in many tree species as these two traits are economically important in breeding programmes. The results appear very contradictory both between and within species. For hard pines, Zobel and Van Buijtenen (1989) reviewed 55 studies up to 1986: 35 showed no relationship, 11 a significant reduction in density with increased growth, and 4 a higher density when trees grew faster. Even within a species the results are not always consistent. For conifers other than hard pines (*Abies*, *Picea*, *Tsuga*…), the negative relationship between growth and wood density appears common (Zobel and Van Buijtenen 1989). Rozenberg et al. (1997) reviewed studies in the genus *Picea* and found a moderate to strong negative relationship between diameter growth and wood density. Similar results were found for Norway spruce between height growth and wood density (Hylen 1997). However, Yanchuck and Kiss (1993) estimated a non-significant genetic correlation and a negative phenotypic correlation between growth traits and density for interior spruce.

This paper examines the possible consequences of selection for growth on wood density in maritime pine (*Pinus pinaster* Ait.) populations in south-western France. The breeding objectives for this species were focused on growth rate and stem straightness for two generations of recurrent selection. Today genetic gains reach 30 % for volume in the most recent commercial varieties (GIS 2002). As wood density is a key parameter for wood quality (Zobel and Jett 1995), tree breeders are concerned by the following questions: Is wood density negatively correlated with growth traits? And, if so, how much wood density loss would occur in commercial varieties improved for growth?
Moreover, a second possible cause of lower density in varieties is the increase of juvenile wood proportion at final harvest due to the shortening of rotation age. Juvenile wood forms a central core around the pith from the base up to the top of the tree and is known to be limiting in factors such as low density. This consequence of growth improvement has thus to be evaluated in order to quantify the global wood density decrease in the wood collected from commercial varieties compared to unimproved material.

We first studied these two factors independently:

- wood density in commercial varieties and unimproved material were compared; then genetic correlations between wood density and growth traits in the breeding populations (where the parents of the seed orchards were selected) were estimated
- increase of juvenile wood proportion in varieties was quantified with computer simulations to take into account the entire rotation cycle.

We then discuss their impacts on wood density and quality by comparing theses traits in commercial varieties and unimproved material.

Materials and methods

The French maritime pine breeding programme

The maritime pine breeding programme is based on recurrent selection (Durel 1992; GIS 2002). The following breeding populations were considered (Figure 1):

- P0, the original unimproved population (i.e. the south-western French maritime pine forest in which "plus" trees were selected in the sixties)
- G0, the subset of "plus" trees phenotypically selected in P0
- P1, the progenies from G0 crossings
- G1, the trees genetically selected in P1
- P2, the progenies from G1 crossings

The best ranking trees of the breeding populations were selected to establish seed orchards producing commercial varieties.

Plant material

Genetic parameters of growth and wood density traits were estimated for the three following populations: P0, G0 and G1, each based on one half-sib progeny test, respectively: Rousset, Hermitage and Pissos.

- For P0, the Rousset experimental plantation was composed of non-selected open-pollinated families collected in south-western France.

- For G0, the Hermitage plantation comprised polycross progenies of G0 trees (obtained with a pollen mix of 28 G0 male parents).

- Finally, for G1, the Pissos plantation was composed of polycross progenies of G1 trees (obtained with a pollen mix of 20 G0 male parents).

These tests were arranged in randomized complete block designs. Their main characteristics are reported in Table 1.

The level of wood density in commercial varieties was estimated in the Morcenx plantation (Table 1). This test comprises an unimproved seed source (V0) and two improved varieties (V1 and V2) (Figure 1). Morcenx plantation differs from the tests established for breeding population evaluation by very large plots (75 trees per plot) and no family structure. Genetic units are evaluated under the same silviculture practices as those used in the maritime pine production area.

- V0 is an unimproved seed source (i.e. seeds from P0 trees), constituted by a bulk seed harvest of 11 stands from south-western France.

- V1 is a commercial harvest of a seedling seed orchard (Cabanac, 33, France: first generation seed orchard). The base material of Cabanac seed orchard is composed of seedlings from more than 500 full sib families (controlled crosses between G0 trees), it is then equivalent to P1 trees.

- V2 is the base material of a polycross seed orchard (Mimizan, 40, France: second generation seed orchard). The polycross seed orchard design (Baradat 1987) has been commonly used since the 80's to establish the French maritime pine seed orchards: elite trees (backward selected) are mated with a pollen mixture of a sub-group or all of the same trees. The polycross families are then used as the base material of the seed orchard. As neither genetic evaluation nor roguing occurs in this kind of orchard, it can be installed outside of the production zone where the genetic pollution is low (Baradat et al. 1992). Here, V2 is composed of 34 polycross families obtained by crossing 34 highly selected G0 trees with a pollen mix of the same trees. Thus, V2 is equivalent to G1 trees. As no selection is planned in the seed orchard, the base material V2 and the commercial variety should have the same genetic value, except from pollen contamination in the seed orchard.

Tree measurements

Total tree height (H), girth at breast height (D) and stem deviation to verticality (S) were measured on the studied plantations as mentioned in Table 1. To facilitate the correspondence with wood density data, the tree age is indicated by a number following the acronyms H, D and S. For example, at Rousset, height was measured at 11 years and will be referred to as H11.

Wood density measurements

A first assessment of traits was achieved in winter 2004 at Rousset, Hermitage and Pissos in order to estimate the correlation between density and growth. In each test, about 14 trees in each of 50 families, chosen at random, were cored at breast height from pith to bark with a 5 mm diameter increment borer (Table 1). A second sampling was done in winter 2005 at Morcenx where we randomly sampled about 90 trees from each of the three genetic units: V0 (unimproved material), V1 and V2 (two improved varieties).

The increment cores were cut to a constant thickness of 2 mm using a double blade saw and then resins were removed by soaking in pentane over 24 hours. Samples had an 11 % humidity rate when wood density was measured using an indirect-reading X-ray densitometer (Polge 1966). The radial density profile (one density measurement every 25.4 µm) was obtained by analysing the scanned images with WinDENDRO (Guay et al. 1992) and calibrated with a scale of known density. Ring limits were automatically determined and then manually checked and corrected using this software.

The first ring from the pith was systematically removed from the analysis because it was often incomplete. We chose to number the rings according to tree age, which means that, within a test, all the rings made during the same calendar year have identical indexes. Tree age reference was preferred to cambial age reference (Vargas-Hernandez and Adams 1992; Fujimoto et al. 2006) for two main reasons. First, tree age indexing avoids mixing quite different rings as wood density is highly dependent on annual environment. Second, a larger proportion of genetic effects can be captured when the analysis is based on tree age (Bouffier et al. 2008).

From the raw density profile, we calculated the following traits per ring:

- ring density (RD), ring width (RW)
- earlywood density, earlywood width
- latewood density, latewood width

The boundary between earlywood and latewood was calculated for each ring as the average between maximum and minimum ring density (Nicholls 1980; Vargas-Hernandez and Adams 1992; Kumar and Lee 2002). As density measures near the bark represent a higher volume than those closer to the pith, RD was obtained with a weighted mean: each density data was weighted by its respective cross-sectional area (Louzada 2003).

Two kinds of data sets were used for analyses on RD and RW: annual data and cumulative data. Annual data were extracted for each year. For example, RD12 (respectively RW12) is the density (respectively the width) of the ring produced when the tree was 12 years old.

Cumulative data are calculated over a period extending between a reference year and the tree age considered. The reference year is the first year cored at breast height in the majority of the trees in each test; the reference year varies according to the text because the studied tests were established at different years. The reference years are 1980, 1981, 1998 and 1996 for, respectively, Rousset, Hermitage, Pissos and Morcenx. For example, cRD12 (respectively cRW12) for Morcenx test is the weighted mean ring density (respectively total ring width) calculated on rings from 1996 to 2004. In each test, only trees with all rings present from the reference year to the sampling year were kept for further analyses.

Comparisons of means between genetic units were performed using a Student t-test with a p-value of 5 %.

Correlation parameters

Phenotypic and genetic sources of variation were estimated using the following linear mixed model:

$$Y_{ijk} = \mu + b_i + F_j + b_i \times F_j + E_{ijk}$$

where Y_{ijk} is the phenotypic individual observation, μ the general mean, b_i the block effect and F_j the family effect. b was considered as a fixed effect, while F and $b \times F$ were treated as random effects.

The phenotypic variance was estimated as $\hat{\sigma}^2{}_P = \hat{\sigma}^2{}_F + \hat{\sigma}^2_{b\times F} + \hat{\sigma}^2_{error}$ where $\hat{\sigma}^2{}_F$ is estimate of the family variance, $\hat{\sigma}^2_{b\times F}$ the interaction block × family variance and $\hat{\sigma}^2{}_{error}$ the residual variance. All families were assumed to be maternal half-sibs, therefore genetic variance was estimated as

$\hat{\sigma}^2_A = 4 \times \hat{\sigma}^2_F$.

The phenotypic correlation (r_P) and genetic correlation (r_G) between a wood density trait x and a growth trait y were estimated as follows:

$$\hat{r}_P = \frac{C\hat{o}v_P(x,y)}{\sqrt{\hat{\sigma}^2{}_{Px} \times \hat{\sigma}^2{}_{Py}}} \quad \text{and} \quad \hat{r}_G = \frac{C\hat{o}v_A(x,y)}{\sqrt{\hat{\sigma}^2{}_{Ax} \times \hat{\sigma}^2{}_{Ay}}}$$

where $Cov_P(x,y)$ and $Cov_A(x,y)$ are the phenotypic covariance and additive genetic covariance between traits x and y, respectively.

Analyses were conducted with the restricted maximum-likelihood method using the software ASReml (Gilmour et al. 2002). Correlations were estimated on cumulative data and the standard errors of the estimates were calculated by ASReml using a standard Taylor series approximation (Gilmour et al. 2002).

Simulations of juvenile wood proportion

Growth simulations were used to quantify the increase of juvenile wood proportion due to growth improvement and its impact on mean wood density. Juvenile wood proportion was estimated with the tree growth model Pp3 (derived from Lemoine 1991; Salas-González et al. 2001), implemented in the software platform CAPSIS (Computer-Aided Projection for Strategies In Silviculture) (De Coligny et al. 2003). Pp3 model, calibrated with unimproved tree growth data, simulates tree growth depending on site productive capacity (described as the stand dominant height at a reference age) and silviculture. The input data are the description of a real stand: stand age, stand surface, height and girth for each individual tree. The dominant height of the stand determines the mean growth dynamic by allocating the stand in a site quality class. Annual growth is simulated up to the final harvest with the chosen silvicultural scenario and thus a stem ring profile is obtained for each tree at any given age. In stem ring profiles, we considered juvenile wood as the wood produced until cambial age 16. The transition between juvenile and mature wood is often gradual on several rings (Zobel and Sprague 1998) and depends on the property studied. It can be estimated with mathematical models on density profiles of mature trees (Mutz et al. 2004). However many studies define juvenile wood by a fixed number of rings from the pith (Cown 1992; Gapare et al. 2006). So a fixed cambial age compatible with our field data was used here.

In this simulator, a virtual logging tool allowed us to estimate the juvenile wood proportion calculated with different logs samplings:

- in the basal logs at final cutting (logs at tree base and with 6.3 m long),
- in all the logs at final cutting (i.e. all the logs between tree base and a fixed top tree girth 20 cm)
- in all the logs cut at each stage of the silvicultural scenario (i.e. at each thinning and at final cutting with the same definition of logging).

The first two values gave information on the final cutting; the last one gave information on the entire scenario.

In this paper, the first aim of the simulations was to estimate juvenile wood proportion in unimproved trees vs. improved trees. As the Pp3 model cannot simulate the growth dynamic of improved trees, we established the following assumption that a growth rate difference due to genetic improvement can be modelled as a difference in site productive capacity described as a difference in stand dominant height at the same age (site index). A stand in a high quality site would then represent improved trees. Thus we used unimproved tree dimensions from two stands established on a contrasting quality site: Morcenx and Mimizan. Morcenx, previously described, is known to be on a higher quality site than Mimizan (Table 1) and was chosen to represent improved tree growth. Initial data for simulation were defined by measured height and girth of each tree at age 16. Then each stand growth was simulated with the Pp3 model; thinnings were applied based on silvicultural strategies recommended by the French National Forest Office. Clear-cutting was simulated so that both stands reached similar wood volume per hectare.

Results

1/ Comparison of improved vs. unimproved material for wood density and growth

a) Based on cumulative data at 15 years

The mean values between unimproved material (V0) and the improved varieties (V1 and V2) were significantly different for all traits analysed (Table 2).

Wood density estimated on cumulative data at age 15 (cRD15) was lower and ring width (cRW15) greater in the improved varieties (V1 and V2) than in the unimproved seed source (V0). The difference was larger between V2 and V0 than between V1 and V0: wood density was 4.5 % (respectively 2.0 %) lower and ring width 14.8 % (respectively 8.3 %) greater for V2 (respectively V1) compared to V0.

Based on growth measurements done in 2006, the improved varieties had greater girth and height than unimproved seed source: D16 (respectively H16) was 7.8 % (respectively 6.7 %) higher for V1 and 6.4 % (respectively 6.5 %) higher for V2 compared to the unimproved seed source V0. Based on D16 and H16, there were no significant differences for growth between V1 and V2.

b) Based on annual data

Wood density and ring width were more precisely studied by analysing annual data. Whatever year was considered, V0 always exhibited higher wood density than V1, and similarly V1 showed higher wood density than V2 (Figure 2a). The annual density was highly variable between years. The ranking was the opposite (V2 > V1 > V0) for annual ring width (Figure 2b).

Wood density components were also studied based on annual data. For the sake of clarity, only results for V0 and V2 are presented (Figure 2) since V1 showed the same trend with intermediate values. Variations of annual earlywood (Figure 2c) and latewood density (Figure 2e) across years were similar for V0 and V2. Annual earlywood density was significantly higher in V0 than in V2 (except at tree age 10) with a mean difference of 4.4 % whereas annual latewood density showed a lower difference (mean difference of 2.1 % over all years) and those differences were not significant (except for tree ages 9, 11 and 12).

The increase of annual ring width in the improved genetic material was mainly due to larger earlywood. Indeed earlywood widths were significantly larger in V2 compared to the unimproved seed source (Figures 2d); the mean increase of earlywood width over all years was 26.5 %. There were no significant differences for latewood width up to tree age 11; from tree age 12, latewood width was higher in the improved varieties compared to unimproved material.

2/ Correlations wood density – growth traits in the breeding populations

a) Correlations wood density – ring width

Phenotypic correlations between wood density and ring width were negative but low (Figure 3a). Whatever the test considered, we observed that after a few years, the correlation rapidly tended towards an asymptotic value of -0.08, -0.14 and -0.06 for respectively Rousset, Hermitage and Pissos. These values were well estimated considering their low standard error (about 0.04).

Genetic correlations between wood density and ring width based on cumulative data appeared quite different depending on the test and reached 0.07 at Rousset, 0.61 at Hermitage and -0.47 at Pissos (Figure 3b). However, considering the standard errors (0.26, 0.79, 0.23 for respectively Rousset, Hermitage and Pissos), only the genetic correlation at Pissos was significantly different from 0.

b) Correlations wood density – height, and correlations wood density – deviation to verticality

Correlation between wood density and height was also considered in the three breeding populations (Table 3). Height was assessed at about 11 years (selection age). Here, wood density was estimated at breast height on a ring section from the pith to the ring corresponding to the year of the growth measurements. The phenotypic correlation was close to 0 whatever the test was. The genetic correlation was negative with a relatively high standard error. The same wood density data showed no significant correlation with stem deviation to verticality.

3/ Juvenile wood proportion

To reach a similar volume of wood at the final harvest on the two contrasting stands, clear-cutting was simulated at 36 years at Morcenx (mean breast height diameter was 42 cm and height was 25.0 m) and at 41 years at Mimizan (mean breast height diameter was 44.1 cm and height was 22.4 m). Fast growing trees (Morcenx) were constituted with 54.6 % juvenile wood compared to 44.9 % for slow growing trees (Mimizan). The difference was lower if we considered only the first 6.3 m logs (35.6 % vs. 31.3 %) which are the most valuable part of the stems (Table 4). Stem profiles (Figure 4) showing mature and juvenile wood are presented for an average tree from the high fertile test (Morcenx) and the moderate fertile test (Mimizan).

Discussion

As a consequence of selection for growth over two breeding generations, wood density is expected to be lower in the production population for two reasons:

- an indirect decrease of wood density due to the negative correlation between growth and wood density
- an increase in juvenile wood proportion (which is a less dense wood compared to mature wood) because of the shortening of rotation age.

These two effects, as well as their consequence on overall wood quality, are discussed below based on observed and simulated data.

1/ Indirect selection on wood density

The comparative analysis of plantation established with improved varieties and unimproved material showed growth gains but also loss of wood density in the varieties. Thus, correlations between density and selected traits were investigated in the breeding populations to explain this possible consequence of selection.

a) Growth increase and wood density decrease in the varieties compared to unimproved seed source

This study shows that the greater the genetic gain is on growth, the greater is the loss on wood density in improved varieties.

At 16 years (when rotation age is about 40 years), improved varieties of first and second generations have a significantly better radial and height growth compared to unimproved material. The much greater gain for V2 on ring width at 15 years (cRW15) compared to gain on girth at 16 years (D16) is unexpected (Table 2). Girth is incontestably more precisely estimated when it is directly measured than when it is calculated using only one radius. Thus ring width is certainly overestimated in the V2 variety. The poor estimation of girth based on one measured radius is illustrated by the moderate correlation between girth and ring width (Pearson correlation coefficient = 0.6). This can be explained by variations in bark width and/or non-centred pith.

Volume gain at age 16 in Morcenx is 24.0 % for V1 and 20.6 % for V2 (compared to unimproved seed source). Raffin (personal communication) reported realised gains in volume (based on 15 large-plot trials evaluation), ranging from 10 to 20 % for V1 compared to V0 at age 15 , and an estimated volume gain (based on two progeny tests) for V2 compared to V0 of about 30 %. On Morcenx test, the growth performance of V2 is then lower than expected from previous results.

In the same test, a significant reduction of wood density is observed in the two improved varieties compared to the unimproved seed source: 2.0 % for V1 and 4.5 % for V2. Although weak, this decrease cannot be disregarded because of the low variability of wood density (Hylen 1999; DeBell et al. 2004; Bouffier et al. 2008). Whereas ring width improvement is particularly high for advanced cambial age, wood density decrease is nearly identical every year. This means that the loss in wood density is neither modified by environmental conditions nor by cambial age although wood density is highly variable over years.

Focusing on wood density components, we showed that the global wood density decrease could be attributed to two causes:

- a reduction of both earlywood and latewood density. Earlywood density decreased more than latewood density in the improved varieties. Earlywood density is much more heritable than latewood density (Louzada and Fronseca 2002; Bouffier et al. 2008) which could explain a higher shift due to indirect selection on earlywood than on latewood density.
- a higher increase on earlywood than on latewood width, leading to a reduction of latewood proportion in the improved varieties compared to V0. As latewood is the denser part of a ring, this change of proportion leads to a decrease of ring density..

b) Correlations between wood density and growth traits in the breeding populations

Correlation between growth and wood density has been scarcely studied in *Pinus pinaster* (Table 5). To our knowledge, the first study was conducted by Polge and Illy (1968) on 4-year-old trees. Based on one ring only, a highly positive genetic correlation was estimated between basic density and ring width. A non-significant phenotypic correlation between basic density and ring width on 38 provenances of 15-year-old maritime pines was reported (El Alami et al. 1996). Height and girth were very weakly positively correlated with density (correlation coefficients lower than 0.1). Wood density - ring width correlations on rings of cambial ages 6, 10 and 13 years were estimated in a progeny test established with seeds collected on trees from different Portuguese regions (Louzada 2003). Whatever the ring, the relationship between wood density and ring width was weakly positive: from 0.02 to 0.05 for phenotypic correlations and from 0.1 to 0.3 for genetic correlations. Pot et al. (2002) analysed X-ray microdensity profiles of 14-year-old progenies of plus trees from the French maritime pine breeding programme. They found a non-significant phenotypic correlation (-0.19) but a significant negative genetic correlation (-0.48) between tree height and density.

Previous studies on *Pinus pinaster* reveal that the wood density - growth phenotypic correlation is generally close to 0 whereas the genetic correlation varies from negative to positive values.

Our findings are consistent with these results. We found slightly negative phenotypic correlations between wood density and ring width in the three tests studied. Genetic correlations were more variable between tests. We found estimates ranging from positive to negative values; but if we consider standard errors of estimations, only the negative genetic correlation at Pissos is significant. The variability of the correlation estimates cannot be explained by the age of the measurement. Indeed, based on cumulative data, excluding the first cambial ages, the correlation for a given test seems stable over time (Figure 3).

Genetic correlations between wood density and height at 10-11 years are negative in the three tests. However standard errors also appear high compared to the absolute values of these correlations.

The highly variable relationship between wood density and growth is observed within several other conifer species (Table 5).

For example, in loblolly pine (*Pinus taeda*), a positive genetic correlation between density and height was reported (Matziris and Zobel 1973; Bridgewater et al. 1983) on respectively 5-year-old and 10-year-old trees whereas negative results were found on 20-25 year-old trees (Loo and Tauer 1984; Gwaze et al. 2001). Moreover, the relationship can depend on the growth trait considered: Bridgewater et al. (1983) showed a negative genetic correlation between density and diameter but a positive one between density and height. The wood density - growth phenotypic correlation also appears variable on loblolly pine: positive (Matziris and Zobel 1973), non significant (Loo and Tauer 1984) or weakly negative (Gwaze et al. 2001).

Phenotypic and genetic correlations from non-significant to weakly negative between wood density and growth traits were reported for *Pinus sylvestris* (Hannrup et al. 2000).

For *Pinus radiata*, several articles have been published about the wood density – growth genetic correlation showing a negative genetic correlation between wood density and diameter

(Wu et al. 2004; Kumar 2004). Some studies conducted at the ring level exhibited also negative relationship between ring density and ring width (Nicholls et al. 1980; Li and Wu 2005); whereas Zamudio et al. (2002) showed from negative to positive results depending on the ring.

We tried to better understand the correlations by estimating wood density / ring width correlations on an annual basis. They appear highly variable depending on the year considered: for example, annual genetic correlations ranged from -0.55 to 0.40 at Rousset, from -0.98 to 0.84 at Hermitage and from -0.75 to 0.09 at Pissos depending on the years (data not shown). Nevertheless, no strong relationship arose from comparison between the wood density / growth correlation and the tree age or the climate data (analysis not shown).
Many studies report highly variable correlations (Dutilleul et al. 1998; Hannrup et al. 2000; Zamudio et al. 2002; Fujimoto et al. 2006). The genetic correlation between wood density and ring width, on *Pinus taeda*, was highly variable depending on the age (from -0.69 to 0.03) whereas the phenotypic correlation appeared less variable (Gwaze et al. 2001). Zamudio et al. (2002), on a 17-year-old radiata pine plantation, found also a high variability for the annual genetic correlation (from -0.33 to 1.15) with very large standard errors (from 0.35 to 3.65). Only Hannrup et al. (2000), working on *Pinus sylvestris*, obtained a general trend for the annual correlation: from a non-significant correlation in juvenile wood to a weakly negative correlation within more mature rings. Authors explained this change by the fact that, as ring width increases, wood density curvilinearly decreases towards an asymptotic value. Thus, no correlation is found for wider rings (juvenile wood) whereas a correlation appears on narrower i.e. older rings.

c) Effect of growth selection on wood density

Genetic correlations between wood density and growth traits appear to be non-significant or weakly negative in the breeding populations. Moreover no significant correlations were found between wood density and stem deviation to verticality. As trees were selected on growth and stem deviation to verticality, then wood density should only be slightly affected in the successive varieties. Several hypotheses can be proposed to explain for the significant decrease of wood density observed in the commercial varieties:

- large standard error for the estimation of the genetic correlation between wood density and growth traits, making it difficult to show a significant correlation

- genetic correlations are estimated within the whole breeding population whereas only the few best trees for growth and stem deviation to verticality are selected to create the varieties; these trees can display a relatively low wood density despite a general weak relationship between density and selection criteria
- trees selected to create the varieties display a lower deviation to verticality compared to unselected ones; then we can assume that they also have less compression wood. As compression wood is denser than normal wood, this can result in a decrease of wood density in selected trees. The absence of a significant correlation between wood density and stem deviation to verticality does not confirm this hypothesis, but global stem deviation to verticality is certainly a poor estimation of the presence of compression wood at 1.30 m.

Wood density changes can not be explained by changes in competition between trees because it has been shown that competition is similar whatever the genotypes considered (Von Euler et al. 1992). Thus competition is supposed to be equal in the tests with unimproved versus improved materials.

Few studies have been conducted on the change of wood density in trees that underwent selection for growth. As for the wood density - growth correlation, results appear contradictory. This study on wood density evolution in the successively improved varieties is the first one based on material from the French breeding maritime pine programme. Another study on *Pinus pinaster* in Western Australia was reported (Hill 2000); it revealed a 19 % greater volume for improved trees compared to unimproved trees with a similar wood density. Livingston et al. (2004) found that improved 24-year-old Sitka spruce (+71 % for volume) had a lower density than unimproved trees; but the difference was not significant (this study was conducted on a small sample of 65 trees). Zobel and Jett (1995) also reported several studies for various species (loblolly pine, radiata pine, western hemlock) where the selection on growth had no consequence on density. However, even within the same species, results can be contradictory. Based on a 20-year-old radiata pine trial gathering open pollinated progenies of plus trees and an unimproved control, Cown et al. (1992) concluded that intensive selection for growth and form had not affected average wood density. On the contrary, Li and Wu (2005) reported that “breeding for growth rate and tree form had reduced wood density slightly in radiata pine because of a negative genetic correlation between growth rate and wood density”.

Thus, it appears that wood density is usually not affected or weakly affected by selection on growth whatever the species considered. This can be explained both by low correlations between wood density and growth traits and by, generally, low wood density variability. However, the effect of selection on wood density seems to be highly dependant on the breeding programme considered (base population, selection criteria, breeding strategies…).

2/ Decrease of wood density due to increase of juvenile wood proportion

Improved varieties grow faster implying a reduction of rotation age and an increase of the final juvenile wood proportion. As juvenile wood is less dense than mature wood, the global wood density will thus be reduced (Zobel and Van Buijtenen 1989).

Many articles mention the increase of juvenile wood proportion due to growth improvement (Zamudio et al. 2005; Hylen 1999) but few give an estimation of this effect (Cameron et al. 2005). We tried to quantify the proportion of juvenile wood in improved trees compared to unimproved ones by growth simulations. Up to now, no model has been established to simulate growth of improved Maritime pine in France. Thus, we considered two stands of unimproved trees established on two contrasting sites in productive capacity as a case study to compare improved vs. unimproved trees. Two observations make this assumption realistic. First the two stands studied displayed, at juvenile stage, about the same wood volume difference as those observed between unimproved and improved trees growing on the same site. And second, clear-cutting age was modelled 5 years earlier in the fast growing stand, which is about the difference expected for improved varieties compared to unimproved material. Our simulations predict that the use of growth improved varieties may increase juvenile wood proportion by about 10 % (estimation based on the whole tree).

Personal data and studies cited by Zobel and Van Buijtenen (1989) allowed to estimate the following relationship between juvenile wood density (WD_j) and mature wood density (WD_m) for maritime pine: $WD_j = 0.85 \times WD_m$

As a consequence, and considering the simulation results of juvenile wood proportion, the shortening of rotation age due to the improvement of growth rate in the maritime pine varieties could reduce mean wood density by 1.5 %.

3/ Consequences of a wood density decrease on wood quality

We show that wood density decreases in maritime pine as a consequence of breeding for growth because of three main reasons:

- a reduction of earlywood and latewood density due to indirect selection on growth
- a decrease of latewood proportion because growth gain is higher on earlywood than on latewood width
- an increase of juvenile wood proportion when trees are harvested.

Our study demonstrates that reduction of wood density and decrease of latewood proportion reduce wood density from 2 % to 4.5 % depending on the variety considered. The effect of juvenile wood increase was estimated, in the previous paragraph, at 1.5 %. Thus, combining the three sources of wood density decrease, wood could be less dense by 3.5 to 6 % in an improved variety than in unimproved material.

What are the consequences of this wood density decrease on wood mechanical properties? Two main parameters are commonly used to estimate wood mechanical properties: Modulus of Rupture (MOR) and Modulus of Elasticity (MOE) which characterize respectively wood strength and wood stiffness. Reuling (2005) studied more than 3000 boards coming from unimproved maritime pines of south-western France. From this data set, the coefficient of correlation between wood density and MOR (respectively MOE) was 0.56 (respectively 0.61). Moreover MOR and MOE were highly variable ($CV_{MOR} = 46$ % and $CV_{MOE} = 26$ %) compared to wood density ($CV_{density} = 8.7$ %). The mechanical properties can be expressed depending on wood density as follows:

$$y = r \times \frac{\sigma_y}{\sigma_x} \times \left(x - \bar{x}\right) + \bar{y}$$

With y the mechanical property (MOR or MOE), $\bar{y}$ its mean and σ_y^2 its variance

x the wood density, $\bar{x}$ its mean and σ_x^2 its variance

r the coefficient of correlation between x and y

Thus, a 6 % wood density decrease would be associated with an 18 % decrease for MOR and an 11 % decrease for MOE. Other studies reveal a lower variability for mechanical properties (Kumar et al. 2002; Johnson and Gartner 2006). Using the same reasoning, a 6 % density decrease would be associated with a reduction of 5.0 % for MOR and 7.6 % for MOE on radiata pine with data from Kumar et al. (2002); and with a reduction of 7.1 % for MOE on Douglas-fir with data from Johnson and Gartner (2006). However the higher variability of

MOR and MOE compared to density implies that a slight reduction of wood density will have a notable impact on physical properties. These calculations indicate the possible reduction mechanical properties due to the genetic selection for growth. Corrective actions should therefore be set to limit this reduction in the advanced generation breeding of maritime pine.

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References

Baradat P (1987) Méthode d'évaluation de la consanguinité chez les plants issus des vergers à graines de semis de première génération. Silvae Genet 36:134-144

Baradat P, Durel C-E, Pastuszka P (1992) The polycross seed orchard: an original concept. In: Proceedings of the IUFRO-AFOCEL Symposium, Mass Production Technology for Genetically Improved Fast Growing Forest Tree Species, Tome II, Editions AFOCEL, Bordeaux, France, pp 53-62

Bouffier L, Rozenberg P, Raffin A, Kremer A (2008) Wood density variability in successive breeding populations of maritime pine. Can J For Res (under press)

Bridgewater FE, Talbert JT, Jahromi S (1983) Index selection for increased dry weight in a young Loblolly pine population. Silvae Genet. 32:157-161

Cameron AD, Lee SJ, Livingston AK, Petty JA (2005) Influence of selective breeding on the development of juvenile wood in Sitka spruce. Can J For Res 35:2951-2960

Cown DJ (1992) Corewood (juvenile wood) in *Pinus radiata* – should we be concerned? N Z J For Sci 22:87-95

Cown DJ, Young GD, Burdon RD (1992) Variation in wood characteristics of 20-year-old half-sib families of *Pinus radiata*. N Z J For Sci 22(1):63-76

DeBell DS, Singleton R, Gartner BL, Marshall DD (2004) Wood density of young-growth western hemlock: relation to ring age, radial growth, stand density, and site quality. Can J For Res 34:2433-2442

De Coligny F, Ancelin P, Cornu G, Courbaud B, Dreyfus P, Goreaud F, Gourlet-Fleury S, Meredieu C, Saint-André L (2003) CAPSIS: computer-aided projection for strategies in silviculture, advantages of a shared forest-modelling platform. In: Amaro A, Reed D, Soares P, Modelling Forest Systems, CABI Publishing, Wallingford pp 319–323

Durel C-E (1992) Gains génétiques attendus après sélection sur index en seconde génération d'amélioration du pin maritime. Rev For Fr 44(4):341-355

Dutilleul P, Herman M, Avella-Shaw T (1998) Growth rate effects on correlations among ring width, wood density, and mean tracheid length in Norway spruce (*Picea abies*). Can J For Res 28:56-68

El Alami A, Sbay H, Sesbou A, Hachmi M (1996) Variabilité intraspécifique de quelques caractères de croissance et de qualité du bois chez le pin maritime. Ann Rech For Maroc 29:57-70

Fujimoto T, Kita K, Uchiyama K, Kuromaru M, Akutsu H, Oda K (2006) Age trends in the genetics parameters of wood density and the relationship with growth rates in hybrid larch (*Larix gmelinii* var. *japonica* × *L. kaempferi*) F1. J For Res 11:157-163

Gapare WJ, Wu HX, Abarquez A (2006) Genetic control of the time of transition from juvenile to mature wood in *Pinus radiata* D.Don. Ann For Sci 63:871-878

Gilmour AR, Gogel BJ, Cullis BR, Welham SJ, Thompson R (2002) ASReml User Guide Release 1.0 VSN International Ltd, Hemel Hempstead, HP1 1ES, UK

GIS, collective work, Alazard P, Canteloup D, Cremiere L, Daubet A, Lesgourgues Y, Merzeau D, Pastuszka P, Raffin A (2002) Genetic breeding of the maritime pine in Aquitaine, GIS Work Report

Guay R, Gagnon R, Morin H (1992) A new automatic and interactive tree-ring measurement system based on a line scan camera. Forest Chron 68(1):138-141

Gwaze DP, Bridgwater FE, Byram TD, Lowe WJ (2001) Genetic parameter estimates for growth and wood density in Loblolly pine (*Pinus taeda* L). Forest Genetics 8(1):47-55

Hannrup B, Ekberg I, Persson A (2000) Genetic correlations among wood, growth capacity and stem traits in *Pinus sylvestris*. Scand J For Res 15:161-170

Hill P (2000) Wood density of improved compared with unimproved maritime pine (*Pinus pinaster*). CALMScience 3(3):309-315

Hylen G (1997) Genetic variation of wood density and its relationship with growth traits in young Norway spruce. Silvae Genet 46:55-60

Hylen G (1999) Age trends in genetic parameters of wood density in young Norway spruce. Can J For Res 29:135-143

Johnson GR, Gartner BL (2006) Genetic variation in basic density and modulus of elasticity of coastal Douglas-fir. Tree Genetics and Genomes 3:25-33

Kumar S (2004) Genetic parameter estimates for wood stiffness, strength, internal checking, and resin bleeding for radiata pine. Can J For Res 34:2601-2610

Kumar S, Jayawickrama KJS, Lee J, Lausberg M (2002) Direct and indirect measures of stiffness and strength show high heritability in a wind-pollinated radiata pine progeny test in New Zealand. Silvae Genet 51(5-6):256-261

Kumar S, Lee J (2002) Age-age correlations and early selection for end-of-rotation wood density in radiata pine. Forest Genetics 9(4):323-330

Lemoine B (1991) Growth and yield of maritime pine (*Pinus pinaster* Ait): the average dominant tree of the stand. Ann For Sci 48:593–611

Li L, Wu HX (2005) Efficiency of early selection for rotation-aged growth and wood density traits in *Pinus radiata*. Can J For Res 35:2019-2029

Livingston AK, Cameron AD, Petty JA, Lee SL (2004) Effect of growth rate on wood properties of genetically improved Sitka spruce. Forestry 77(4):325-334

Loo JA, Tauer CG (1984) Juvenile – mature relationships and heritability estimates of several traits in loblolly pine (*Pinus taeda*). Can J For Res 14:822-825

Louzada JLPC (2003) Genetic correlations between wood density components in *Pinus pinaster* Ait. Ann For Sci 60:285-294

Louzada JLPC, Fonseca FMA (2002) The heritability of wood density components in *Pinus pinaster* Ait and the implications for tree breeding. Ann For Sci 59:867-873

Matziris DI, Zobel BJ (1973) Inheritance and correlations of juvenile characteristics in Loblolly pine (*Pinus taeda* L). Silvae Genet 22(1/2):38-45

Mutz R, Guilley E, Sauter UH, Nepveu G (2004) Modelling juvenile-mature wood transition in Scots pines (*Pinus sylvestris* L.) using nonlinear mixed-effects models. Ann For Sci 61:831-841

Nicholls JWP, Morris JD, Pederick LA (1980) Heritability estimates of density characteristics in juvenile *Pinus radiata* wood. Silvae Genet 29 (2):54-61

Polge H (1966) Etablissement des courbes de variation de la densité du bois par exploration densitométrique de radiographies d'échantillons prélevés à la tarière sur des arbres vivants. Ann For Sci 23(1):1-206

Polge H, Illy G (1968) Héritabilité de la densité du bois et corrélations avec la croissance étudiées à l'aide de tests non destructifs sur plants de Pins maritimes de quatre ans. Silvae Genet 17:173-181

Pot D, Chantre G, Rozenberg P, Rodrigues JC, Jones GL, Pereira H, Hannrup B, Cahalan C, Plomion C (2002) Genetic control of pulp and timber properties in maritime pine (*Pinus pinaster* Ait). Ann For Sci 59:563-575

Reuling D (2005) Potentiel d'utilisation du Pin maritime dans la construction en fonction des conditions de croissance définies dans le modèle Pp3. Master of Science, Université Bordeaux1 France, p 70

Rozenberg P, Cahalan C (1997) Spruce and wood quality: genetics aspects (a review). Silvae Genet 46:270-279

Salas-González R, Houllier F, Lemoine B, Pignard G (2001) Forecasting wood resources on the basis of national forest inventory data. Application to *Pinus pinaster* Ait in southwestern France. Ann For Sci 58:785-802

Vargas-Hernandez J, Adams WT (1992) Age-age correlations and early selection for wood density in young coastal Douglas-fir. Forest Science 38(2):467-478

Von Euler F, Baradat P, Lemoine B (1992) Effects of plantation density and spacing on competitive interactions among half-sib families of maritime pine. Can J For Res 22:482-489

Wu HX, Yang J, McRae TA, Li L, Powell MB (2004) Genetic relationship between breeding objective and early selection criterion traits in Australia radiata pine population CSIRO

Forestry and Forest Technical Report 1402 and Southern Tree Breeding Association Technical Report TR04-01, CSIRO, Canberra

Yanchuk AD, Kiss GK (1993) Genetic variation in growth and wood specific gravity and its utility in the improvement of interior spruce in British Columbia. Silvae Genet 42:141-148

Zamudio F, Baettig R, Vergara A, Guerra F, Rozenberg P (2002) Genetic trends in wood density and radial growth with cambial age in a radiata pine progeny test. Ann For Sci 59:541-549

Zamudio F, Rozenberg P, Baettig R, Vergara A, Yañez M, Gantz C (2005) Genetic variation of wood density components in a radiata pine progeny test located in the south of Chile. Ann For Sci 62:105-114.

Zobel BJ, Jett J (1995) Genetics of wood production. Springer-Verlag, Berlin

Zobel BJ, Sprague JR (1998) Juvenile wood in forest trees. Springer-Verlag, Berlin

Zobel BJ, Van Buijtenen JP (1989) Wood variation: its causes and control. Springer-Verlag, Berlin

Tables

Acronyms used:

H*x* is height at age *x* (m)
D*x* is girth at breast height at age *x* (mm)
S*x* is stem deviation to verticality at age *x* (cm)
cRD*x* is the cumulative wood density up to the tree age *x* ($g.cm^{-3}$)
cRW*x* is the cumulative ring width up to the tree age *x* (mm)
Vol 16 is the tree volume at age 16 (m^3) estimated as $\frac{(G16)^2 \times H16}{12 \times \pi}$
CV is the coefficient of variation
gain is the relative gain compared to the unimproved seed source V0
V0 is an unimproved seed source
V1 and **V2** are two improved varieties

Table 1

Tests characteristics and sampling procedure.

		BREEDING POPULATIONS			VARIETIES	
Test		**Rousset**	**Hermitage**	**Pissos**	**Morcenx**	**Mimizan**
Plantation year		1974	1975	1992	1991	1989
Blocks		5	4	5	6	10
Trees per plot		3 to 19	3, 6 or 9	10	75	45
Seedlings		bare-roots	bare-roots	containers	containers	containers
Plantation spacing		4m * 1.1m	4m * 1.1m	4m * 2m	4m * 2m	4m * 2m
Estimation		P0	G0	G1	V0 V1 V2	V0 V1
Wood density measures	tree age	30 years	29 years	12 years	15 years	no sampling
	families sampled	44	51	51	- - -	- -
	number of trees sampled	534	470	751	79 92 83	- -
Growth and form measures		H10, D10, S10	H12, D12, S12	H11, D11, S13	H16, D16	H13, D13

Table 2

Comparison of growth and wood density in the three genetic units of Morcenx test.

		cRD15			cRW15			D16			H16			Vol16		
	number of trees	**mean**	**CV**	**gain**	**mean**	**CV**	**gain**	**mean**	**CV**	**gain**	**mean**	**CV**	**gain**	**mean**	**CV**	**gain**
V0	79	0.428	6.5%	-	47.7	18.8%	-	577	15.4%	-	12.30	7.8%	-	0.109	35.3%	-
V1	92	0.420	6.6%	**-2.0%**	51.6	15.2%	**8.3%**	622	12.9%	**7.8%**	13.12	7.3%	**6.7%**	0.135	31.3%	**24.0%**
V2	83	0.409	7.0%	**-4.5%**	54.7	17.6%	**14.8%**	614	16.0%	**6.4%**	13.10	7.9%	**6.5%**	0.131	35.0%	**20.6%**

Table 3

Wood density – height, and wood density – deviation to verticality correlations in the breeding populations (Rousset, Hermitage and Pissos).

	Correlation cRD - H			Correlation cRD - S		
	Rousset	**Hermitage**	**Pissos**	**Rousset**	**Hermitage**	**Pissos**
	cRD10-H10	cRD12-H12	cRD11-H11	cRD10-S10	cRD12-S12	cRD12-S13
phenotypic correlation (se)	**0.04** (0.05)	**0.02** (0.05)	**0.13** (0.04)	**-0.02** (0.04)	**0.00** (0.05)	**0.00** (0.04)
genetic correlation (se)	**- 0.32** (0.27)	**- 0.13** (0.31)	**- 0.24** (0.26)	**-0.24** (0.61)	**- 0.05** (0.71)	**0.07** (0.21)

Table 4

Clear-cutting characteristics and proportion of juvenile wood estimated with growth simulations from Pp3 based on data from Morcenx and Mimizan tests.

		Mimizan slow growing trees	**Morcenx** fast growing trees
clear-cutting characteristics	tree age	**41 years**	**36 years**
	mean height (m)	22.4	25.0
	mean diameter (cm)	44.1	42.0
proportion of juvenile wood	in first 6.3m logs of final harvest trees	31.3%	35.6%
	in all logs of final harvest trees	**44.9%**	**54.6%**
	in all logs of thinnings and final harvest trees	50.4%	62.3%

Table 5

Phenotypic and genetic correlations between wood density and growth in several conifer species.

Species	Authors	Site	Tree age	Density trait	Growth trait	Phenotypic correlation	Genetic correlation	
							value	se
Pinus taeda	Matziris and Zobel 1973	1	5	basic density on whole core	height	0.27	0.23	-
					diameter	0.23	0.02	-
	Bridgwater et al. 1983	1	10	basic density on whole core	height	-	0.29	-
					diameter	-	-0.08	-
	Loo and Tauer 1984	1	25	basic density on whole core	height	0.07	-0.46	-
					diameter	0.03	-0.39	-
	Gwaze et al. 2001	4	20	basic density on whole core	height	-0.21 to 0.04	-0.50 to -0.07	0.23 to 0.49
					diameter	-0.22 to -0.09	-0.54 to -0.23	0.21 to 0.38
Pinus sylvestris	Hannrup et al. 2000	1	33	basic density on core sections	ring width	-0.06 to -0.37	-0.11 to -0.81	0.08 to 0.24
			13	basic density on 3 rings	height	-0.04	0.02	0.23
Pinus radiata	Nicholls et al. 1980	2	-	basic density on rings 3 and 4	ring width	-0.28 to -0.50	-0.94 to 0.50	ns
	Zamudio et al. 2002	1	17	X-ray density analysed ring by ring	ring width	-0.23 to 0.19	-0.30 to 1.15	0.35 to 3.65
	Kumar 2004	4	13-15	basic density on whole core	diameter	-0.25 to -0.12	-0.46 to -0.16	0.14 to 0.39
	Wu et al. 2004 (review)	17	<10	-	-	-	-0.66 to -0.08	-
	Li and Wu 2005	2	27 and 31	X-ray density analysed ring by ring	ring width	-0.60 to -0.20	-0.70 to -1.00	0.08 to 0.25
Picea abies	Hylen 1997	1	28	X-ray density on whole core	height	-0.19	-0.68	0.25
					diameter	-0.45	-	-
	Rozenberg and Cahalan 1997 (review)	15	-	basic density	diameter	generally moderate to strongly negative		-
Picea glauca	Yanchuk and Kiss 1993	2	18	basic density on whole core	height	-0.4	0,00	0.28
					diameter	-0.46	0.08	0.41
Pinus pinaster	Polge and Illy 1968	1	4	basic density on one ring	ring width	-	0.85	-
					height	-	0.42	-
	El Alami et al. 1996	1	15	basic density on whole core	ring width	0.13 ns	-	-
					girth	0.06	-	-
					height	0.09	-	-
	Pot at al. 2002	1	14	X-ray density on whole core	height	-0.19 ns	-0.48	-
	Louzada 2003	1	14	X-ray density analysed for rings 6, 10 and 13	ring width	0.02 to 0.05	0.10 to 0.32	0.10 to 0.11
	Present study	**3**	**30, 29 and 12**	**X-ray density on whole core**	**ring width**	**-0.14 to -0.06**	**-0.47 to 0.61**	**0.23 to 0.79**
			11, 12 and 13	**X-ray density on whole core**	**height**	**0.02 to 0.13**	**-0.32 to -0.13**	**0.26 to 0.31**

Figure captions

Figure 1

Title:

Breeding populations and varieties of the French maritime pine breeding programme.

Figure 2

Title:

Annual wood density and ring width for the genetic units of Morcenx test.

Legend:

"*" indicates a significant annual difference between V0 and V2

"+" indicates a significant annual difference between V0 and V1

Figure 3

Title:

Phenotypic (a) and genetic (b) correlations between cumulative wood density and cumulative ring width in the breeding populations.

Figure 4

Title:

Juvenile and mature wood for (a) a slow growing tree (Mimizan) and (b) a fast growing tree (Morcenx).