



Does selecting for improved growth affect wood quality of *Pinus pinaster* in Portugal?

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ABSTRACT

The selection criteria for the first generations in the Portuguese *Pinus pinaster* improvement program have been the growth rate and form traits. In this work we study the consequences of this selection on wood quality traits. This study assesses genetic and phenotypic correlation between growth, wood density components, lignin content and mechanical traits (radial modulus of elasticity and radial modulus of rupture) of 46 half sib families from a progeny trial located in Leiria, Portugal, originated from seed collected in a clonal seed orchard. A total of 552 seventeen-years-old trees (about half of full rotation age) were sampled at 2 m height. Height measured at 12 years old presented a higher genetic control ($h^2 = 0.34$) relatively to DBH, measured at 12 and 17 years old respectively ($h^2 = 0.17$ and $h^2 = 0.15$). The results of this study also showed that DBH growth is more dependent on latewood components than earlywood components and that higher growth in Mediterranean regions can be due to an increase of the period of latewood formation. Further, we can conclude genetic selection based on growth will not result in a decrease of wood density, will not affect the occurrence of spiral grain, and is possible to obtain an increase in the radial modulus of elasticity. The present study also showed that it is possible to select for increased growth with lower lignin proportion. Results also suggest that selection for growth at 12 years will probably not affect negatively the wood properties at 17 years.

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1. Introduction

Maritime pine (*Pinus pinaster* Ait.) is a highly valuable coniferous species (*Pinaceae*), broadly distributed in the western Mediterranean Basin, in Southern Europe and Africa, and the Atlantic coast of Portugal, Spain and France (Alía and Martín, 2003). It is one of the most important forest species in France, Portugal and Spain, used mainly for carpentry, construction, chipboard, pulp and paper production, floor boards and palettes. In Portugal, according to the National Forest Inventory (2005/2006), 23% of the national forest area is occupied by *P. pinaster* (DGRF, 2007), representing 11% of the total of forest product exports in 2000 (Correia et al., 2004). Due to the economic importance of *P. pinaster*, a national tree improvement plan for this species has been in operation since the early 1980s (Roulund et al., 1988). Presently, the maritime pine breeding programme is in its second generation of selection (the progeny

trials reported in this study are part of this programme), and the selection criteria for the first generations have been the growth rate and form traits. Such selection criteria might have an indirect effect on wood properties (Zobel and Jett, 1995), therefore, it's essential to know the nature and magnitude of the relationship between growth traits, wood density and other quality traits. The relationship between growth rate and wood density has been studied intensively, but the results obtained are contradictory. Zobel and van Buijtenen (1989) reviewed 55 hard pine studies up until 1986; 35 showed no relationship, 11 a significant reduction in density with increased growth and 4 reported that when trees grew faster, a higher density was observed. Wu et al. (2008) reviewed several studies on *Pinus radiata* and found that in a total of 64 genetic correlations between density and DBH (or ring width) the values ranged between -1.08 and 0.6 with a mean value of -0.51 .

More attention has been given to breeding for wood density and quality in recent years, because of shorter rotations and the recognition that increasing rotation markedly raises the effective growing cost (Wu et al., 2008). In a previous work by Gaspar et al. (2008a) on the heritability of wood density components in

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P. pinaster, it was concluded that ring density (RD) was the trait under strongest genetic control ($h^2 = 0.63$), and heritability values of earlywood components exceeded those of latewood components. Heritabilities increased with ring number from pith for almost all wood-density components, and there were high age–age genetic correlations for wood density traits ($r_g > 0.98$).

Sound knowledge of genetic correlations is important for both defining breeding goals and selecting right genotypes (Kumar et al., 2008). If improving one desired characteristic results in a reduced value for a second desirable property, a very careful consideration must be made as to the most effective breeding plan (Zobel and van Buijtenen, 1989). Consequently it is important to avoid problems derived from adverse correlations.

The aim of this study was to estimate genetic and phenotypic correlations between growth and wood quality traits and to evaluate the possible consequences of selection for growth at early ages on wood quality of maritime pine populations in Mediterranean conditions. These findings are of great importance for the continued development of maritime pine breeding programmes, providing a guideline to future generation's selection.

2. Materials and methods

2.1. Location

The field trial location was at Pinhal de Leiria, established in 1987 and situated in central coastal Portugal (latitude 39°50', longitude 8°55', alt 30 m). The site is characterized by a Mediterranean climate, with a mean air temperature between 12.5 °C and 15 °C, relative humidity between 80 and 85% and yearly rainfall values of 700 mm to 800 mm, with a 4-month period of summer drought. The Spodic Podzols (PZ sd) soils are derived from sands dunes of maritime origin. Seedlings were nursery raised for 9 months in plastic bags (250 cm³ volume). Planting (2 m × 2 m spacing) took place in March 1987 after harrowing and ploughing the site; no fertilizer was applied.

2.2. Genetic material

The progeny test used in this study was established in 1987. The trial includes 46 open-pollinated families, derived from seed collected in the Escaroupim clonal seed orchard II. The ortets were obtained from plus-trees selected in the Mata Nacional de Leiria by senior forester D.H. Perry in 1963–1964. The selection criteria used were based on volume, stem form, spiral grain and branch habits (Perry and Hopkins, 1967). This seed orchard includes 49 genotypes; it was established by grafting in 1975–1980 and belongs to the first generation of the breeding program. Only 46 families were considered in order to avoid poor seed production. The 46 families were replicated in 8 blocks with 2 × 4 trees plots. In 2004, wood samples were collected from a subset of 12 trees for every family in 3 blocks, giving a total number of 552 trees (the four trees per plot were selected by random). A single wood disc with a thickness of 10 cm was collected at a predetermined sampling height of 2 m. The disk was sawn into a 2 mm-thick radial strip segment from the pith to the bark, and then conditioned at 12% moisture content. Radial samples were X-rayed perpendicular to the transverse section and their images scanned by microdensitometric analysis (Hughes and Sardinha, 1975; Polge, 1978). The time of exposure to radiation was 300 s, at an intensity of 18 mA and an accelerating tension of 12 kV, with a 2.5 m distance between X-ray source and film. The data comprising the radial density profiles were recorded every 100 μm with a slit height (tangential direction) of 455 μm.

The first and last annual rings of each sample were excluded since they were usually incomplete. Growth-ring boundaries were identified on the radial profiles by locating the sharp density

variations through visual observation of the macroscopic anatomical features. For each ring, average ring density, minimum density (MND), maximum density (MXD), earlywood density (EWD), latewood density (LWD), earlywood width (EWW), latewood width (LWW), ring width (RW) and latewood percentage (LWP) were determined. The earlywood (EW) latewood (LW) boundary in each growth ring was assigned a fixed density of 500 kg m⁻³ as the limit between EW/LW. We used one fixed value of density as has been used for several conifer species (Barbour et al., 1994; Fujimoto et al., 2006), even though some researchers have been using the average of minimum and maximum ring density to define the transition point for EW/LW (Nicholls et al., 1980; Vargas-Hernandez and Adams, 1991; Zamudio et al., 2005). The advantages of this criterion for the EW/LW boundary based on a fixed density value were well explained by Rudman (1968) and Jozsa et al. (1987). This value of 500 kg m⁻³ was a result of an adjustment to the value proposed by Louzada (2000) for *P. pinaster*, where it compares different criteria and indicates that this one is the most correct for this species with 18 years old. Although this criterion does not allow identifying the beginning of the latewood, it allows indentifying the portions of the ring with a density higher than a threshold, which we call LW. Intra-ring density variation was quantified by the heterogeneity index (HI) proposed by Ferrand (1982), defined by the standard deviation of all density values across the annual ring. Because rings close to the pith have less volume than those near the bark, they contribute less to the whole disc volume. To compensate for this effect, wood density components were weighed for each ring density component by its respective cross-sectional area. These area-weighted cumulated traits are henceforth referred to simple as cumulated traits or values (Hysten, 1999).

The same strips were used to evaluate the radial modulus of elasticity (MOE_{Rad}) and the radial modulus of rupture (MOR_{Rad}), through three-point bending tests (Brancheriau et al., 2002). Before testing the specimen dimensions (thickness and width) were measured with a digital calliper (0.01 mm resolution). Bending tests were carried out in an electro-mechanical testing machine (Instron 5848 MicroTester[®]). The experiments were carried out at room temperature under displacement control (0.5 mm/min) and with a span of 40 mm.

The other traits assessed were spiral grain (SPG) determined for all trees as explained in Gaspar et al. (2008b) In each disc, the grain angle was measured at the most recent formed latewood of the last ring, using a grain slope detector (Harris, 1989) and the pith as a reference (Hannrup et al., 2002).

The proportion of lignin content (LG) was estimated by near infrared spectroscopy (NIR) on extractive-free wood meal samples according to Rodrigues et al. (2006) and Perez et al. (2007). Being an indirect method, NIR needs calibration. The accuracy of NIR spectroscopy is influenced by the spectral noise and the reference data noise (Geladi, 2002). However statements such as “NIR predictions can never be better than the primary reference method” were refuted (DiFoggio, 1995; Rodrigues et al., 2006).

Height (HT) was assessed with a telescopic rod at age 12, and breast height diameter (DBH) was measured over bark using standard procedures, at age 12 and 17, in all trees of the trial.

2.3. Data analysis

The mixed linear model associated with the data for a given trait was:

$$Y_{ijk} = \mu + B_j + F_i + B \times F_{ij} + \varepsilon_{ijk} \quad (1)$$

where Y represents the phenotypic individual observation; μ is the overall mean; B_j : the effect of the j th block (fixed); F_i : the effect of

the *i*th family (random); $B \times F_{ij}$: the effect of the interaction between the *i*th family and the *j*th block (random) and ε : the residual error. All terms in the model 1, except B, is assumed to be normally and independently distributed with mean zero and corresponding variances (σ^2). Variance components for family (σ_f^2), family-block interaction ($\sigma_{f \times b}^2$) and residual errors (σ_ε^2), with the respective associated standard errors, were estimated by restricted maximum likelihood, using the average information REML algorithm implemented in the ASREML programme (Gilmour et al., 1998).

Narrow sense heritability (h^2) was calculated for each trait as:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2} \quad (2)$$

where σ_a^2 represents the additive genetic variance and σ_p^2 the total phenotypic variance. Total phenotypic variance was estimated as:

$$\sigma^2 P = \sigma_f^2 + \sigma_{f \times b}^2 + \sigma_\varepsilon^2 \quad (3)$$

and estimated additive variances as:

$$\sigma_a^2 = \frac{1}{2\theta} \times \sigma_f^2 \quad (4)$$

where the coancestry coefficient ($\theta = 0.13$) was obtained (in the absence of selfing) from correlated paternity r_p' estimated by molecular markers see (Gaspar et al., 2008c) as:

$$\theta = 0.250 \times r_p' + 0.125 \times (1 - r_p') \quad (5)$$

Standard errors for heritability were estimated by ASREML using a Taylor series approximation (Gilmour et al., 1998).

Genetic and phenotypic correlations between all wood traits were calculated using a multivariate extension of model (1). When the family effect was found to be null for any of the traits analysed in the univariate analysis, this effect was not included in the multivariate analysis. Genetic correlations between traits (X and Y) were evaluated as follows:

$$r_g = \frac{cov_a(x,y)}{\sqrt{\sigma_{ax}^2 \cdot \sigma_{ay}^2}} \quad (6)$$

where $cov_a(x,y)$ is the additive genetic covariance, and σ_{ax}^2 and σ_{ay}^2 are the additive variance components for traits X and Y , respectively.

The phenotypic correlation between traits (X and Y), was estimated as:

$$r_p = \frac{cov_p(x,y)}{\sqrt{\sigma_{px}^2 \cdot \sigma_{py}^2}} \quad (7)$$

where $cov_p(x,y)$ is the phenotypic covariance between traits X and Y , estimated as $cov_p(x,y) = cov_f(x,y) + cov_{fb}(x,y) + cov_\varepsilon(x,y)$, which is the sum of the family, interaction, and residual covariance components. σ_{px}^2 and σ_{py}^2 are the phenotypic variances for traits X and Y , respectively. Standard errors for genetic and phenotypic correlations were estimated by ASREML a Taylor series approximation (Gilmour et al., 1998).

Selecting for one trait x will result in a correlated response of other traits, and the correlated response of a trait y can be estimated by using the equation of indirect response (Falconer and Mackay, 1996):

$$Cr_{y/x} = i \cdot h_x \cdot h_y \cdot r_{g(xy)} \cdot \sigma_{py} \quad (8)$$

where h_x and h_y are the square root of appropriate narrow sense heritabilities for traits X and Y respectively; $r_{g(xy)}$ is the additive genetic correlation between traits X and Y and σ_{py} is the phenotypic standard deviations of trait y .

Table 1

Descriptive statistics table for diameter measured at 17 and 12 years old and total height measured at 12 years old, respective narrow heritability (h^2) estimates and phenotypic and additive variances (V_a and V_p , respectively).

	DBH ₁₂ (cm)	HT ₁₂ (m)	DBH ₁₇ (cm)
Mean	10.28	6.9	13.26
SD	2.66	1.16	3.20
CV (%)	29	18	27
Max	18.0	10.0	22.0
Min	5.0	9.0	5.1
V_a	1.15	0.41	1.50
V_p	6.68	1.19	9.80
h^2	0.17 (0.06)	0.34 (0.10)	0.15 (0.05)

Standard errors given in brackets.

DBH₁₂ = diameter measured at 12 years old; HT = total height measured at 12 years old; DBH₁₇ = diameter measured at 17 years old.

3. Results and discussion

Summary statistics for growth traits and respective heritability estimates are given in Table 1.

Results showed a lower heritability for DBH ($h^2_{(12)} = 0.17$ and $h^2_{(17)} = 0.15$) compared to HT ($h^2 = 0.34$) because the phenotypic variance is relatively higher than the additive variance.

Results for DBH are in agreement with those observed for the same species by Kusnadar et al. (1998) and Zas et al. (2004), but lower than those found by Costa and Durel (1996). Our estimated heritabilities for HT correspond well with those found in previous studies of maritime pine [0.27–0.45] (Kremer and Lascoux, 1988; Danjon, 1995; Pot et al., 2002), but lower values [0.11–0.17] for this trait were observed by (Kusnadar et al., 1998; Zas et al., 2004). Although a higher genetic control of HT relatively to DBH was reported by Zas et al. (2004), other authors have suggested the opposite (Costa and Durel, 1996; Kusnadar et al., 1998); i.e. higher heritability values for DBH. According to Costa and Durel (1996) diameter is more affected by competition between trees and microenvironment effects than height. In fact, larger additive and phenotypic variances observed for DBH were observed in this work. Contributing to this higher competition between trees may be the fact that this trial was installed with a narrower spacing (2 × 2) than usual for this species.

Relatively small changes in DBH heritability with age (0.17 versus 0.15), were also observed by Danjon (1994), Costa and Durel

Table 2

Phenotypic (r_p) and additive genetic (r_g) correlations between diameter measured at 17 years old and the other wood traits.

	r_p	r_g
RD	0.24 (0.04)	0.04 (0.32)
MND	0.00 (0.04)	−0.05 (0.22)
MXD	0.24 (0.04)	0.04 (0.25)
EWD	0.07 (0.05)	−0.04 (0.22)
LWD	0.20 (0.05)	−0.09 (0.28)
LWP	0.33 (0.04)	0.24 (0.22)
EWV	0.00 (0.05)	−0.17 (0.26)
LWV	0.42 (0.04)	0.13 (0.25)
SPG	0.24 (0.04)	0.15 (0.23)
MOR _{rad}	0.07 (0.05)	−0.02 (0.25)
MOE _{rad}	0.49 (0.03)	0.30 (0.24)
LG	−0.19 (0.05)	−0.41 (0.23)

Values in brackets are the standard error for the genetic correlations.

DBH₁₇ = diameter measured at 17 years old; RD = average ring density, MND = minimum density, MXD = maximum density, EWD = earlywood density, LWD = latewood density, LWP = latewood percentage, EWV = earlywood width, LWV = latewood width, SPG = spiral grain; R_{rad} = radial modulus of rupture; MOE_{rad} = radial modulus of elasticity; LG = proportion of lignin content.

(1996) and Kusnadar et al. (1998) although most of these authors mentioned that heritability increases with age.

Phenotypic (r_p) and additive genetic (r_g) correlations between DBH measured at 17 years old and the other wood traits are presented in Table 2.

In contrast to *Picea* species, where negative genetic correlation between wood density and growth traits is usually reported (Yanchuk and Kiss, 1993; Zhang et al., 1996; Hannrup et al., 2004), studies on several *Pinus* species have revealed often contrasting results (Zobel and Jett, 1995; Fries and Ericsson, 2006; Wu et al., 2008). Even in *P. pinaster*, correlation values between wood density and growth rate are contradictory. While Keller (1973) and Louzada (2003) obtained positive correlations between density and growth (0.43 and 0.11 respectively), Pot et al. (2002) and Chaperon et al. (1989) found negative genetic correlations in the same species (−0.48 and −0.89). For *P. pinaster* in France Bouffier et al. (2008), reported that these two traits were weakly negatively correlated both phenotypically and genetically. In the present study, phenotypic correlations between DBH₁₇ and RD were weakly positive (0.24) but genetic correlation was close to zero (0.04), indicating that selection based on growth will not result in a decrease of wood density.

In a comprehensive review on the reasons for these contradictory results, Louzada (2003) suggested that the relationship between wood density and growth rate is site specific. From our data (Table 2) it can be observed that DBH was more dependent on Latewood components (MXD, LWD) than Earlywood components (MND, EWD). Increase in DBH₁₇ was due to an increase in LWP (0.42) and not an enhancement in EWW (0.0). Further, it is clear that larger trees tended to present higher values of RD, LWD, LWW and LWP, explaining why faster growing trees do not have necessarily lower densities. Results suggest that one possible reason for higher or lower wood density in fast growing trees depends upon growth being due to an increase of LWW or EWW, respectively. In a study on *Abies balsamea* Koga and Zhang (2004) reported a negative phenotypic correlation between RD and RW (−0.48), a strong positive correlation between RW and EW (0.96), but no correlation between RW and LW (0.05), i.e. larger radial growth was caused by an increase in EW. In *Picea abies* Steffenrem (2008) refers that RW variation can be explained by earlywood zone width, while the width of the latewood barely varies. The existence of more LW or EW can be associated with the growing conditions of trees. Higher growth rates observed in higher latitudes can be a consequence of the early onset of cambial initiation, resulting in a higher proportion of EW. On the other hand, higher growth in Mediterranean regions can be due to an increase of the period of latewood formation, since the main tree growth constraining factors in this region are the high temperatures and water stress during the summer. When growth conditions are favourable in summer (water availability), trees present higher RW due to an enlargement of LWW and, consequently, higher RD. Conversely, during drought summers trees will present less LWW, RW and RD. A significant association of *P. pinaster* growth with water supply was observed in a study performed in central Spain (Bogino and Bravo, 2008). Also for three pine species (*P. sylvestris*, *P. nigra* and *P. uncinata*) a positive effect of summer rainfall on growth has also been observed in Spain and Portugal (Andreu et al., 2007).

Also Campelo et al. (2007) in a study performed in *P. pinea* in Portugal, verified that climate explained between 59 and 76% of the tree ring variance, that latewood width was more sensitive to climate variations than earlywood and that earlywood development was mostly pre-determined at the beginning of the growing season. Moreover, results from a previous work (Gaspar et al., 2008a), performed on the same samples used in this study, showed that heritability estimates for earlywood components

($h^2_{(MND)} = 0.54$, $h^2_{(EWD)} = 0.60$) were superior to those obtained for latewood components ($h^2_{(MXD)} = 0.34$, $h^2_{(LWD)} = 0.26$, confirming that for *P. pinaster* earlywood characteristics are subject to stronger genetic control and that latewood components are more subject to environmental factors. Earlywood formation is made partially at the expense of stored carbohydrates rather than products of current photosynthesis (Hill et al., 1995), while latewood formation depends mainly on current photosynthesis and, hence latewood traits are more closely related to current climate conditions than earlywood (Zhang, 1997; Lebourgeois, 2000).

The relationship between wood density and growth also differs with location to some extent (Zhang et al., 1996). To this author it seems that in a species where exists a negative relationship between wood density and growth this relation tends to be weaker in trees growing in a more favourable environment. For Downes et al. (2002) and Wimmer and Downes (2003) it is evident that the relationship between annual growth rate and density will depend largely on the relative size of the increments produced at different times of the year. These authors stated that when large rings are accompanied with the increased proportion of latewood, a positive relationship between density and growth is also possible.

It is important to point out that in order to assess the real influence of growth rate on wood density, analyses must be carried out among homogeneous age classes. According to Zobel and van Buijtenen (1989) it is not acceptable to relate wood properties to ring width with rings of different ages. Nevertheless, this has been and still is frequently done, resulting in false and controversial ideas on the effect of growth rate, and may be another factor contributing for multiplicity of results obtained. It is of great importance to define difference between juvenile and mature wood when studying the effect of growth rate on basic density (Saranpää, 2003). Wide growth rings and low density are associated with juvenile wood, and narrow growth rings with high density are characteristic for mature wood. Therefore, a negative correlation between ring width and density will be evident if juvenile and mature wood are both included in the analysis (Saranpää, 2003).

Formation of spiral grain is under considerable genetic control, while its expression may be at least partly dependent on factors affecting the growth conditions of trees (Harris, 1989). Other works have revealed high level of spiral grain to be correlated with a fast growth rate (Eklund et al., 2003). These authors demonstrated a positive relationship between growth, ethylene evolution and a high left-handed spiral grain. Results from this work indicate the existence of a positive but low phenotypic and genetic correlation between growth and spiral grain (0.24 and 0.15 respectively), indicating that grain inclination tend to be maintained in fast growing trees. Similar findings were reported for *P. abies* by Costa e Silva et al. (2000) and Hallingback et al. (2008). Lower but inconsistent correlations were obtained for *Pinus caribaea* (Harding et al., 1991), *Pinus sylvestris* (Hannrup et al., 2003) and *P. abies* (Hansen and Roulund, 1997; Hannrup et al., 2003).

As observed in the present work, phenotypic correlations between these traits were higher than genetic ones, meaning that the relation between spiral grain and growth traits is more influenced by environmental conditions than genetic conditions. Thus, selecting for fast growing trees will not affect the occurrence of spiral grain since environmental conditions can exert a more pronounced effect.

Correlations between growth and mechanical traits highlighted a moderate positive phenotypic correlation between diameter growth and MOE_{Rad} (0.49) while genetic correlation, although also positive, presented a more moderate value (0.30). For MOR_{Rad} a very weak positive phenotypic correlation was obtained (0.07)

Table 3

Phenotypic (r_p) and additive genetic (r_g) correlations between different wood traits and DBH (diameter) and HT (total height) measured at 12 years old.

	DBH ₁₂		HT ₁₂	
	r_p	r_g	r_p	r_g
RD	0.25 (0.04)	0.11 (0.21)	0.31 (0.04)	0.06 (0.19)
MND	-0.14 (0.05)	0.09 (0.21)	0.11 (0.05)	-0.05 (0.19)
MXD	0.25 (0.04)	0.03 (0.24)	0.29 (0.04)	-0.01 (0.22)
EWD	0.08 (0.05)	0.05 (0.21)	0.13 (0.05)	-0.03 (0.19)
LWD	0.21 (0.04)	-0.08 (0.27)	0.25 (0.04)	-0.08 (0.24)
LWP	0.32 (0.04)	0.29 (0.21)	0.36 (0.04)	0.25 (0.20)
EWV	-0.05 (0.05)	-0.32 (0.24)	-0.13 (0.04)	-0.13 (0.32)
LWW	0.40 (0.04)	0.14 (0.24)	0.37 (0.04)	0.23 (0.21)
SPG	0.20 (0.04)	0.22 (0.21)	0.12 (0.05)	0.17 (0.20)
MOR _{rad}	0.03 (0.05)	-0.14 (0.24)	0.04 (0.05)	-0.11 (0.22)
MOE _{rad}	0.44 (0.04)	0.16 (0.25)	0.41 (0.04)	0.29 (0.22)
LG	-0.23 (0.04)	-0.31 (0.24)	-0.28 (0.04)	-0.42 (0.23)

Note: see Table 2 for abbreviations.

while the genetic correlation presented a weak but negative value. Several works on *P. radiata* (Kumar et al., 2002; Kumar, 2004; Baltunis et al., 2007), *Pseudotsuga menziesii* (Johnson and Gartner, 2006) and *P. abies* (Steffenrem, 2008) gave negative correlations between growth and modulus of elasticity, but it should be highlighted that the mechanical traits were evaluated in the longitudinal direction in these studies. Results from a previous work (Gaspar et al., submitted for publication-b) performed on the same samples used in the present study, indicated that MOE_{Rad} was more dependent on latewood components, either the density (MXD and LWD) or growth components (LWP and LWW). The higher positive genetic correlation observed in this work was between MOE_{Rad} and LWW, indicating that selecting for and enlargement of the latewood percentage would increase wood stiffness. So, it is possible that LWW, which also has a high association with growth rate, is responsible for the positive correlation between growth and radial MOE.

Phenotypic and genetic correlations between the DBH and lignin were negative (-0.19 and -0.41, respectively). The moderate to high value obtained for genetic correlation indicates that it is possible to select for increased growth with a lower lignin proportion, which is beneficial to pulp production. This relation can also be explained by the fact that lignin proportion was more dependent on latewood portion presented at the ring (LWP and LWW), suggesting that these traits may be controlled, at least partially by the same set of genes, and that increasing the existence of more latewood would decrease the lignin proportion (Gaspar et al., submitted for publication-a). Thus, trees with higher DBH and higher proportion of Latewood are expected to have lower LG. Results observed in this work are opposite those observed for other conifers including *P. pinaster* where positive genetic correlations were observed between growth traits and lignin proportion (Costa e Silva et al., 1998; Pot et al., 2002; Sykes et al., 2006). These results are understandable since the relation between growth and wood density in these works was negative, and wood density is usually negatively correlated with lignin proportion.

Table 3 presents phenotypic (r_p) and additive genetic (r_g) correlations between wood quality traits evaluated at 17 years old, and DBH and HT measured at 12 years old, while in Table 4 are presented the expected correlated response for each trait considering a selection for growth traits with an intensity of 10%.

Early evaluation of genotypes for adaptative and volume traits are an important component of tree improvement strategy when long rotations are used in forestry. However, attention should be given to the effect of this selection process on wood quality. Our results indicate that since genetic and phenotypic correlations between wood quality traits and growth traits (DBH and HT) at age 17 were of the same order and direction as correlations with the

Table 4

Expected correlated response for each trait considering selection for growth traits with an intensity of 10%, genetic gain give in trait units (GG) and in percent (CG%).

	HT ₁₂		DBH ₁₂		DBH ₁₇	
	GG	CG%	GG	CG%	GG	CG%
RD (kg m ⁻³)	0.53	11	0.64	35	0.58	22
MND (kg m ⁻³)	0.27	-13	0.43	41	0.23	-26
MXD (kg m ⁻³)	0.70	-1	0.74	5	0.69	-2
EWD (kg m ⁻³)	0.36	-7	0.46	19	0.34	-13
LWD (kg m ⁻³)	0.57	-7	0.54	-12	0.53	-14
LWP (%)	38.20	1	38.39	1	38.38	-1
EWV (mm)	2.59	-3	2.34	-13	2.52	-6
LWW (mm)	1.69	9	1.69	10	1.82	18
SPG	4.27	1	4.34	3	4.33	3
MOR _{rad} (MPa)	13.61	-1	13.53	-1	13.54	-1
MOE _{rad} (GPa)	1.32	16	1.30	14	1.48	30
LG (%)	27.86	-1	27.79	-1	27.60	-2

Note: see Table 2 for abbreviations.

same traits at 12 years old, we can conclude that selection for growth at 12 years will not negatively affect the wood properties at 17 years. In some situations like for RD and EWV, the correlations were higher with DBH₁₂ (0.11 and -0.32) than with DBH₁₇ (0.04 and -0.17), indicating that early selection can be suitable for these traits. The correlated responses presented in Table 4 between these traits corroborate this point; however we have to stress out the high errors associated with the correlation estimates. Concerning the genetic correlations with HT₁₂, all were lower than the ones observed with DBH₁₂, excepting for the correlations with LWW and MOE_{Rad}, but the expected correlated responses are not very different.

4. Conclusions

Based on the results of this study we can conclude that for the *P. pinaster* Portuguese breeding programme a genetic selection based on growth can be performed without a consequent decrease of wood density, it will not affect the occurrence of spiral grain, and is possible to obtain an increase in the radial modulus of elasticity. The present study also showed that it is possible to select for increased growth with lower lignin proportion. Further, our results suggests that for Maritime pine in Mediterranean conditions, DBH growth is more dependent on latewood components that early-wood components, and that an increase in this trait is due to an increase in LWP and not due to an enhancement in EWV. Results also suggest that selection for growth at 12 years will not negatively affect the wood properties at 17 years.

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