

Age trends in genetic parameters of wood density components in 46 half-sibling families of *Pinus pinaster*

Maria João Gaspar, José Luís Louzada, Maria Emília Silva, Alexandre Aguiar, and Maria Helena Almeida

Abstract: This study contributes to the *Pinus pinaster* Ait. breeding programme, which is reaching the third generation by adding information on wood quality of 46 open-pollinated families from a progeny trial located in Leiria, Portugal, that originated from seed collected in a clonal seed orchard. A total of 552 seventeen-year-old trees were sampled at 2 m height. Trends were studied from the pith outward in variance components and narrow-sense heritability (h^2) of wood density components and ring-width characteristics as well as genetic correlations between cambial ages. Mean ring density (RD), minimum density (MND), maximum density (MXD), earlywood density (EWD), latewood density (LWD), earlywood width, latewood width, ring width, latewood percentage, and heterogeneity index were determined using X-ray densitometry procedures. RD had higher genetic control ($h^2 = 0.63$), and heritability values of earlywood components ($h^2_{\text{MND}} = 0.54$, $h^2_{\text{EWD}} = 0.60$) exceeded those of latewood components ($h^2_{\text{MXD}} = 0.34$, $h^2_{\text{LWD}} = 0.26$). 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 ($r_g > 0.98$).

Résumé : Cette étude s'inscrit dans le cadre d'un programme d'amélioration de *Pinus pinaster* Ait. qui débute son troisième cycle. Elle vise à documenter la qualité du bois chez 46 descendances issues de pollinisation libre découlant de semences récoltées dans un verger à graines clonal. Le test de descendances est situé à Leiria et un total de 552 arbres âgés de 17 ans ont été échantillonnés à une hauteur de 2 m. Les auteurs ont étudié les tendances des composantes de la variance et de l'héritabilité des composantes de la densité du bois et des caractéristiques des cerne annuels de la moelle à l'écorce de même que les corrélations génétiques entre les âges cambiaux. La densité moyenne des cerne (RD), la densité minimale (MND), la densité maximale (MXD), la densité du bois initial (EWD), la densité du bois final (LWD), la largeur du bois initial, la largeur du bois final, la largeur des cerne, le pourcentage de bois final et l'indice d'hétérogénéité ont été déterminés à l'aide de la densitométrie. Le contrôle génétique de RD ($h^2 = 0,63$) et les valeurs d'héritabilité des composantes du bois initial ($h^2_{\text{MND}} = 0,54$, $h^2_{\text{EWD}} = 0,60$) étaient plus élevés que ceux des composantes du bois final ($h^2_{\text{MXD}} = 0,34$, $h^2_{\text{LWD}} = 0,26$). Les héritabilités augmentaient de la moelle vers l'écorce pour la plupart des composantes de la densité du bois. Les corrélations génétiques entre différents cerne pour les caractères de densité du bois étaient élevées ($r_g > 0,98$).

[Traduit par la Rédaction]

Introduction

Pinus pinaster Ait. (maritime pine) is one of the most important native species in Portugal, occupying 30% of the national forestry area and representing 11% of the total value of forest product exports in 2000 (Correia et al. 2004). The economic importance of this species has led to the development of genetic improvement initiatives. A national tree improvement plan has been in operation since the early 1980s (Roulund et al. 1988) with the aim of increasing volume per hectare and improving stem straightness, which has traditionally been one of the species drawbacks. Currently, the maritime pine breeding programme has reached two generations of selection; the progeny trial reported in this study is

part of this programme. This trial contains plants produced from seed collected in the Escaroupim clonal seed orchard II (Aguiar 1993). This seed orchard includes 49 genotypes and was established by grafting in 1975–1980 to produce improved seed for afforestation of coastal regions in Portugal. The ortets were obtained from plus-trees selected in Mata Nacional de Leiria by the senior forester D.H. Perry in 1963–1964. The selection criteria used were based on volume, stem form, spiral grain, and branch habits. Details about the plus phenotypes selected and of scoring system employed are described in (Perry and Hopkins 1967).

It is widely recognised that wood quality and quantity cannot be treated in isolation from each other and that wood quality improvement should be integral to breeding

Received 7 July 2007. Accepted 23 January 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 6 May 2008.

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programmes (Zobel and Talbert 1984; Zobel and Jett 1995). Further, reducing rotation age or increasing growth rate typically incurs the risk of increasing the proportion of juvenile wood (Kennedy 1995; Hylén 1999). In *Pinus* species, juvenile wood is usually characterized by shorter tracheids and thinner cell walls than mature wood, which often produces wood of lower specific gravity. Because of its low strength and instability upon drying, juvenile wood still presents a problem for most solid wood products (Zobel and Sprague 1998). One way of reducing some of the negative effects of short-rotation trees on wood quality is to breed to increase juvenile-wood density (Zamudio et al. 2005; Gapare et al. 2006). Further, a trait in mature wood that is highly correlated with its value in juvenile material also presents advantages in the breeding programme, because the overall length of the programme will be reduced; hence, forest tree breeding will be more effective. Early selection would speed up the breeding process and increase the genetic gain achieved per unit time (Lambeth 1980; McKeand 1988). A prerequisite of early tests is a high correlation between the expression of the juvenile and mature traits (Nanson 1970).

Among the desirable wood-quality properties to breed for, wood density is considered the most significant for improvement (Zobel and van Buijtenen 1989) because of its close relationship with important properties related to technological traits and because it is relatively easy to measure. However, given the complex nature of this trait, variations in wood density can be difficult to interpret, because a particular wood density value can be derived from various combinations of components. Overall ring density depends on earlywood (EW) and latewood (LW) densities, and the relative proportions of each (Vargas-Hernandez and Adams 1991). Wood uniformity is another characteristic benefit to be expected from the application of genetics to wood properties (Zobel and van Buijtenen 1989). Wood heterogeneity is an important defect, and uniformity of juvenile wood is usually lower than that of mature wood (Zobel and van Buijtenen 1989; Zobel and Jett 1995). Thus, reducing variability is usually a main objective of a breeding program involving wood properties. The knowledge of genetic control of these characteristics would contribute to a better understanding of the genetics of overall wood density, permitting manipulation through the alteration of one or more components and, ultimately, leading to a possible increase in the efficiency of selection for this trait (Louzada and Fonseca 2002). Studies on different species have found that wood density is usually a trait with strong genetic control (for review see (Zobel and van Buijtenen 1989). However, there are contradictory results concerning density components.

The aim of this study is to evaluate the inheritance of mean ring density (RD) and its components at different cambial ages. The work contributes to the *Pinus pinaster* breeding programme by adding information on wood quality of 46 open-pollinated families that belong to the first generation of the maritime pine breeding programme.

Materials and methods

The study trial site was Pinhal de Leiria (established in 1987), located in central coastal Portugal (39°50'N, 8°55'W,

altitude 30 m). The site has a Mediterranean climate, with a mean air temperature of 14.2 °C, a mean annual rainfall of 880 mm, and Spodic Podzols soils derived from coastal sand dunes. Seedlings were raised for 9 months in the nursery in plastic bags (250 cm³ volume). Seedlings were planted at 2 m × 2 m spacing in March 1987 after harrowing and ploughing the site; no fertilizer was applied. The trial included 46 open-pollinated families that were 17 years old originated from seed collected in the Escaroupim clonal seed orchard II (Aguar 1993).

The 46 families were replicated in 3 blocks with 4 trees per plot, giving a total of 552 trees for analysis. Trees were sampled at 2 m height. One internodal wood disc, 10 cm thick, was collected and sawn into a 2 mm thick radial strip segment from the pith to bark. The strips were 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 the 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, because 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, RD, 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 EW–LW boundary in each growth ring was assigned a fixed density of 500 kg·m⁻³. This density has been used for several conifer species (Barbour et al. 1994; Fujimoto et al. 2006), even though some researchers used the mean of the 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 using a fixed density to determine the EW–LW boundary have been 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), who compared different criteria and indicated that this is the best density for 18 year old *Pinus pinaster*. Although this criterion does not allow identification of the beginning of the LW, it can be used to designate the portions of the ring with a density higher than the threshold as LW. Intraring density variation was quantified using the heterogeneity index (HI) proposed by Ferrand (1982), defined as 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 weighted for each ring density component by its respective cross-sectional area.

Data analysis

All traits, for every ring, were analysed using the following model:

Table 1. Descriptive statistics table for different wood density components weighted for the last ring and respective heritability estimates (with SEs given in parentheses).

Trait ^a	Mean	SD	CV	Minimum	Maximum	h^2 (SE)
RD (kg·m ⁻³)	474	510.051	10.68	336	655	0.63 (0.190)
MND (kg·m ⁻³)	308	370.037	12.11	207	445	0.54 (0.184)
MXD (kg·m ⁻³)	707	600.060	8.51	558	917	0.34 (0.164)
EWD (kg·m ⁻³)	386	260.026	6.69	304	463	0.60 (0.191)
LWD (kg·m ⁻³)	618	340.034	5.43	535	732	0.26 (0.141)
LWP (%)	38.196	16.927	44.31	6.420	82.240	0.46 (0.168)
EWL (mm)	2.674	0.876	32.74	0.900	6.100	0.32 (0.137)
LWW (mm)	1.556	0.907	58.29	0.300	6.400	0.31 (0.156)
RW (mm)	4.224	0.901	21.33	2.500	8.600	0.10 (0.111) ^b
HI (kg·m ⁻³)	120	0.019	16.05	7	196	— ^{bc}

^aRD, mean ring density; MND, minimum density; MXD, maximum density; EWD, earlywood density; LWD, latewood density; LWP, latewood percentage; EWL, earlywood width; LWW, latewood width; RW, ring width; HI, heterogeneity index.

^bIn the analysis of variance, the differences among families were not significant ($P > 0.05$)

^cThe heritability was quantified with the null value.

$$[1] \quad Y_{ijk} = \mu + B_j + F_i + B \times F_{ij} + \epsilon_{ijk}$$

where Y is the phenotypic individual observation, μ is the overall mean, B_j is the effect of the j th block (fixed), F_i is the effect of the i th family (random), $B \times F_{ij}$ is the effect of the statistical interaction between the i th family and the j th block (random), and ϵ is the residual error. Variance components for family (σ_f^2), family \times block interaction ($\sigma_{f \times b}^2$) and residual errors (σ_e^2), with their standard errors, were estimated by restricted maximum likelihood, using the mean information REML algorithm implemented in the AS-REML program (Gilmour et al. 1998).

Narrow sense heritability (h^2) was estimated for each trait measured at each cambial age (ring number) as

$$[2] \quad h^2 = \frac{\sigma_a^2}{\sigma_p^2}$$

where σ_a^2 represents the additive genetic variance and σ_p^2 represents the total phenotypic variance. Families were assumed to be maternal half-siblings; therefore, the $\sigma_a^2 = 4\sigma_f^2$ relationship was assumed to estimate the genetic parameters. It should be noted that the half-sib relation is an assumption that can be violated to some degree and an inherent upward bias in estimates of additive genetic variance can be expected.

Phenotypic variance was estimated as $\sigma_p^2 = \sigma_f^2 + \sigma_{f \times b}^2 + \sigma_e^2$. Standard errors for heritability were estimated by AS-REML using a Taylor series approximation (Gilmour et al. 1998).

Genetic correlations within the same trait measured at two different cambial ages (X and Y) were evaluated as follows using a multivariate extension of eq. 1:

$$[3] \quad r_a = \frac{\text{cov}_a(x, y)}{\sqrt{\sigma_{ax}^2 \times \sigma_{ay}^2}}$$

where $\text{cov}_a(x, y)$ is the additive genetic covariance between two different cambial ages, and σ_{ax}^2 and σ_{ay}^2 are the additive variance components for cambial ages X and Y , respectively.

Results and discussion

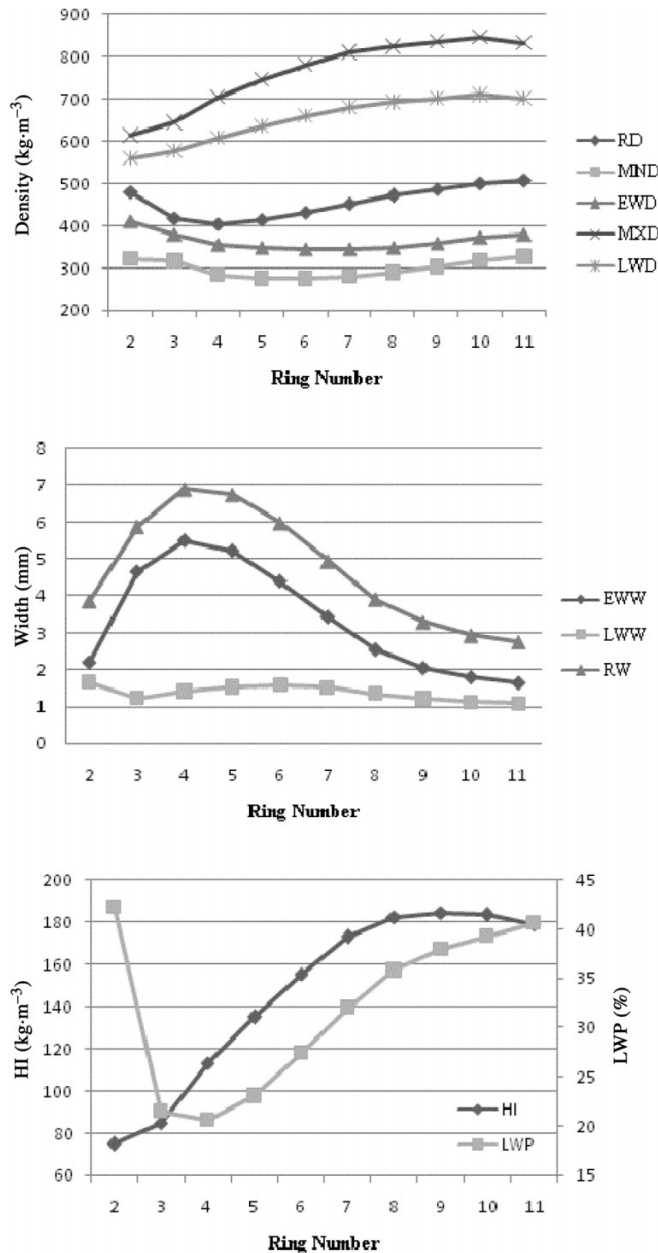
Table 1 lists summary descriptive statistics for different wood density components and respective heritability estimates.

The RD (474 kg·m⁻³), LWD (618 kg·m⁻³), and EWD (386 kg·m⁻³) are similar to values reported elsewhere (Louzada and Fonseca 2002; Markussen et al. 2003) for young *Pinus pinaster* trees. Considering these values (LWD 1.6 times higher than the EWD), we can conclude that this wood can be considered homogeneous when compared with *Pseudotsuga menziesii* (Mirb.) Franco, where the LW is 3.5 to 4 times as dense as EW (Polge 1964). For the ring width characteristics, EWL is larger (2.67 mm) than LWW (1.56 mm) and has the larger coefficient of variation (CV). All the growth variables (RW, EWL, LWW, and LWP) have CVs of >21%, whereas wood density variables tend to have coefficients of <12%.

Mean values of individual rings for the traits LWD and MXD increased throughout the core (Fig. 1). For the other density traits (RD, MND, and EWD) the density values decreased over the first successive rings, then increased. Both RW and EWL increased remarkably in the first tree rings, followed by a gradual decline, whereas LWW was much more constant (Fig. 1). Latewood proportion started with a significant decrease but, at age 4, began to increase gradually to a mean of 40% at ring number 11 (Fig. 1). The pronounced decline in LWP was due to an enlargement in EWL.

RD was the trait under strongest genetic control ($h^2 = 0.63$; Table 1), which is consistent with results from previous studies on this species. Chaperon et al. (1989) estimated an h^2 value of 0.44 for specific density, whereas Louzada and Fonseca (2002) obtained higher heritability values, varying from 0.53 to 0.74, for mean ring density. However, in on 15-year-old trees of the same species in France Pot et al. (2002) obtained considerably lower values ($h^2 = 0.29$) for the same trait. Differences may result from distinct environmental conditions, because the heritability of a certain trait can vary with the population, age, and test location or from random estimation errors.

Fig. 1. Mean values of density components for rings 2–11. See Table 1 for trait abbreviations.



Studies on other *Pinus* species reveal a multiplicity of results with heritability estimates ranging from 0.43 to 0.85 for *Pinus radiata* D. Don (Nicholls et al. 1980; Kumar 2002; Zamudio et al. 2002; Kumar 2004) and for *Pinus taeda* L (Talbert et al. 1983). Heritability estimates for EW components ($h^2_{\text{MND}} = 0.54$, $h^2_{\text{EWD}} = 0.60$) are superior to those obtained for LW components ($h^2_{\text{MXD}} = 0.34$, $h^2_{\text{LWD}} = 0.26$), confirming that, for *Pinus pinaster*, EW characteristics are subject to stronger genetic control and that LW components are almost entirely subject to environmental factors. In fact, LWD appears to be more sensitive to climatic fluctuations (Lebourgeois 2000). Xylogenesis (wood formation) is controlled by both exogenous (e.g., photoperiod, water availability, and temperature) and endogenous (phytohormones) factors (Paiva 2006). According to Plomion et al.

(2001), EW in temperate zones is formed early in the growing season when temperature, water availability, and photoperiod are optimal for active growth. Earlywood has thin-walled tracheids or fibers with a large radial diameter. The LW, which is formed in summer or autumn when cambial cell division and expansion rates decline, has narrower lumens and thicker cell walls. Spring provides optimal conditions for tree growth, and it is during this period that genetic effects stand out. In summer, growth conditions are less stable because of high temperatures and water stress, which may increase the phenotypic variance and lead to reduced heritability.

In this study, density components varied significantly among families and displayed high genetic control; however, none of them presented a higher heritability than RD, even though there were slightly higher levels for the EW components (MND and EWD). These results are consistent with those obtained for *Pinus radiata* (Nicholls et al. 1980), *Pseudotsuga menziesii* (Vargas-Hernandez and Adams 1991, 1992), and *Cryptomeria japonica* (L.f.) D. Don (Fujisawa et al. 1993). In contrast, other studies on *Pinus pinaster* (Louzada and Fonseca 2002), *Pinus radiata* (Kumar 2002), and *Picea mariana* (Mill.) BSP (Zhang and Morgenstern 1995; Zhang 1998; Zhang and Jiang 1998) indicate that EWD is the component most dependent on genetic effects.

In theory, these components are of limited value in improving selection efficiency for wood density (Vargas-Hernandez and Adams 1991). Several authors (Vargas-Hernandez and Adams 1992; Zhang and Morgenstern 1995; Zhang 1998; Zhang and Jiang 1998) observed no significant gain in the target trait when using the EW components, compared with those obtained using RD, meaning that inclusion of these components would not augment wood density. In contrast, the results of Louzada and Fonseca (2002), indicate that selection on the basis of EW components could result in increased wood density and a decrease in ring heterogeneity. Indeed, wood uniformity (see Zobel and Jett 1995) could be cited as one of the wood properties most closely associated with profitability (being much sought after by product managers). Nevertheless, the inconsistency of results between studies highlights the importance in identifying the genetic control of these traits.

For other ring characteristics, variation among families did not produce statistically significant differences ($P > 0.05$) for RW and HI. Variation of these two components is most likely due to environmental factors, not genetic ones. The low estimates for heritability are easily understandable, because growth characteristics (diameter) often exhibit relatively modest heritabilities (Cotterill et al. 1987; Hopkins and Butcher 1994; Harfouche et al. 1995). In a study by Aguiar et al. (2003) carried out after 12 years in this progeny trial, heritability of diameter was estimated at 0.18. Remaining ring characteristics (LWP, LWW, and EWW) displayed intermediate heritability. Our estimated heritabilities for these traits are similar to those from previous studies of *Pinus pinaster* (Louzada and Fonseca 2002) and other conifer species (Nicholls et al. 1980; Vargas-Hernandez and Adams 1991, 1992; Fujisawa et al. 1993; Zhang and Morgenstern 1995; Zhang and Jiang 1998; Kumar 2002). Although we observed low heritabilities for RW, the moder-

Table 2. Estimated heritability values (with SEs given in parentheses) of wood density components for rings 2–11.

Ring	RD	MND	MXD	EWD	LWD	EW	LW	RW	LWP	HI
2	0.49 (0.169)	0.20 (0.138)	0.37 (0.148)	0.28 (0.138)	0.40 (0.147)	0.29 (0.133)	0.32 (0.154)	0.08 (0.107) ^a	0.40 (0.157)	0.078 (0.131) ^a
3	0.45 (0.170)	0.21 (0.139)	0.37 (0.148)	0.31 (0.143)	0.40 (0.147)	0.29 (0.135)	0.33 (0.155)	0.08 (0.108) ^a	0.40 (0.157)	0.077 (0.132) ^a
4	0.45 (0.1712)	0.23 (0.142)	0.39 (0.150)	0.33 (0.148)	0.41 (0.148)	0.28 (0.133)	0.32 (0.154)	0.08 (0.109) ^a	0.40 (0.158)	0.092 (0.133) ^a
5	0.51 (0.173)	0.26 (0.146)	0.38 (0.150)	0.35 (0.153)	0.40 (0.148)	0.29 (0.132)	0.31 (0.154)	0.067(0.109) ^a	0.40 (0.158)	0.094 (0.134) ^a
6	0.52 (0.176)	0.29 (0.151)	0.40 (0.154)	0.37 (0.158)	0.41 (0.149)	0.29 (0.132)	0.32 (0.157)	0.067(0.112) ^a	0.41 (0.160)	0.098 (0.135) ^a
7	0.54 (0.179)	0.33 (0.158)	0.41 (0.155)	0.40 (0.166)	0.40 (0.149)	0.31 (0.136)	0.33 (0.158)	0.06 (0.113) ^a	0.42 (0.161)	0.092 (0.135) ^a
8	0.57 (0.181)	0.38 (0.166)	0.42 (0.157)	0.44 (0.172)	0.38 (0.145)	0.33 (0.139)	0.32 (0.157)	0.10 (0.117) ^a	0.43 (0.163)	0.065 (0.130) ^a
9	0.60 (0.184)	0.42 (0.171)	0.38 (0.156)	0.50 (0.179)	0.33 (0.141)	0.33 (0.140)	0.34 (0.158)	0.10 (0.115) ^a	0.45 (0.164)	— ^{ab}
10	0.60 (0.186)	0.46 (0.176)	0.31 (0.156)	0.55 (0.185)	— ^{ab}	0.32 (0.138)	0.32 (0.158)	0.11 (0.116) ^a	0.45 (0.166)	— ^{ab}
11	0.60 (0.187)	0.50 (0.179)	0.30 (0.156)	0.56 (0.187)	0.13	0.31 (0.137)	0.32 (0.157)	0.11 (0.113) ^a	0.45 (0.167)	— ^{ab}

Note: See Table 1 for trait abbreviations.

^aThe differences among families were not significant ($P > 0.05$).

^bThe heritability value quantified with the null value.

ate values obtained for EWW and LWW provide a basis for the genetic manipulation of the wood quantity and quality of this species in the absence of adverse genetic correlations with other density components.

Trends in heritability with ring number

This study allows the assessment of temporal change in the genetic control of these characteristics, because the heritabilities of the different wood properties were estimated ring by ring. This is important, because genetic control of wood frequently changes with ring number from the pith (Zobel and Jett 1995). Only density components showed statistically significant family variation (RW and HI were excluded) in all rings (Table 2; Fig. 2).

Heritability estimates increased with ring number for most density components except for LWD and MXD, which showed decreases from ring 7. Phenotypic variance decreased with age across all measured density components. This initial period of high phenotypic variance could be due to juvenile trees sensitivity to climate fluctuations, land preparation, and establishment history (Louzada and Fonseca 2002), meaning that genetic potential can only be expressed from the 7th to 9th years of cambial age. The observed increase of the estimated heritabilities in the components analysed was never attributable to enhanced additive variance. Additive variance is higher for RD, MXD and LWP. However, only RD presents high heritability, whereas MXD and LWP exhibit both high additive variance and phenotypic variance, resulting in low heritabilities. This indicates that LW formed during the summer months is subject to strong environmental influences that largely override the genetic factors.

Results from other species concur that wood density is subject to strong genetic control. However, conflicting results have been reported concerning changes in genetic control for wood density and its components with ring number. Previous studies have found similar increases in the heritability of RD and its components. For example, in *Pseudotsuga menziesii*, Vargas-Hernandez and Adams (1992) reported that heritability estimates increased with age for all density traits. Hylén (1999) observed a similar pattern in young *Picea abies* (L.) Karst.. More recently, Li and Wu (2005) observed an increase of heritability values to 0.4 in *Pinus radiata* for area-weighted density over 14 rings from the pith, a value that remained stable in older trees. In contrast, in *Pinus pinaster*, Louzada and Fonseca (2002) found an initial increase in the heritability values of the density features followed by a slight decrease. They also found a tendency for increased heritability up until sixth to eighth ring followed by stabilization in the genetic control of the evolution of LWP and RW characteristics. In *Pinus elliotii* Engelm., Hodge and Purnell (1993) observed that heritabilities for density components in the rings near the pith were slightly higher than those nearer the bark. Nicholls et al. (1980) reported that the heritability of basic density in *Pinus radiata* decreased from the pith outward, reaching a minimum at approximately the ninth growth ring from the pith, followed by an increase in heritability with further increase in age. It is possible that the considerable variability of results in the estimates of genetic parameters in previous studies could have been affected by several factors such as site

Fig. 2. Age trends in phenotypic (σ_p^2) and additive (σ_a^2) variance components and individual heritability (h^2) for mean ring density and its components.

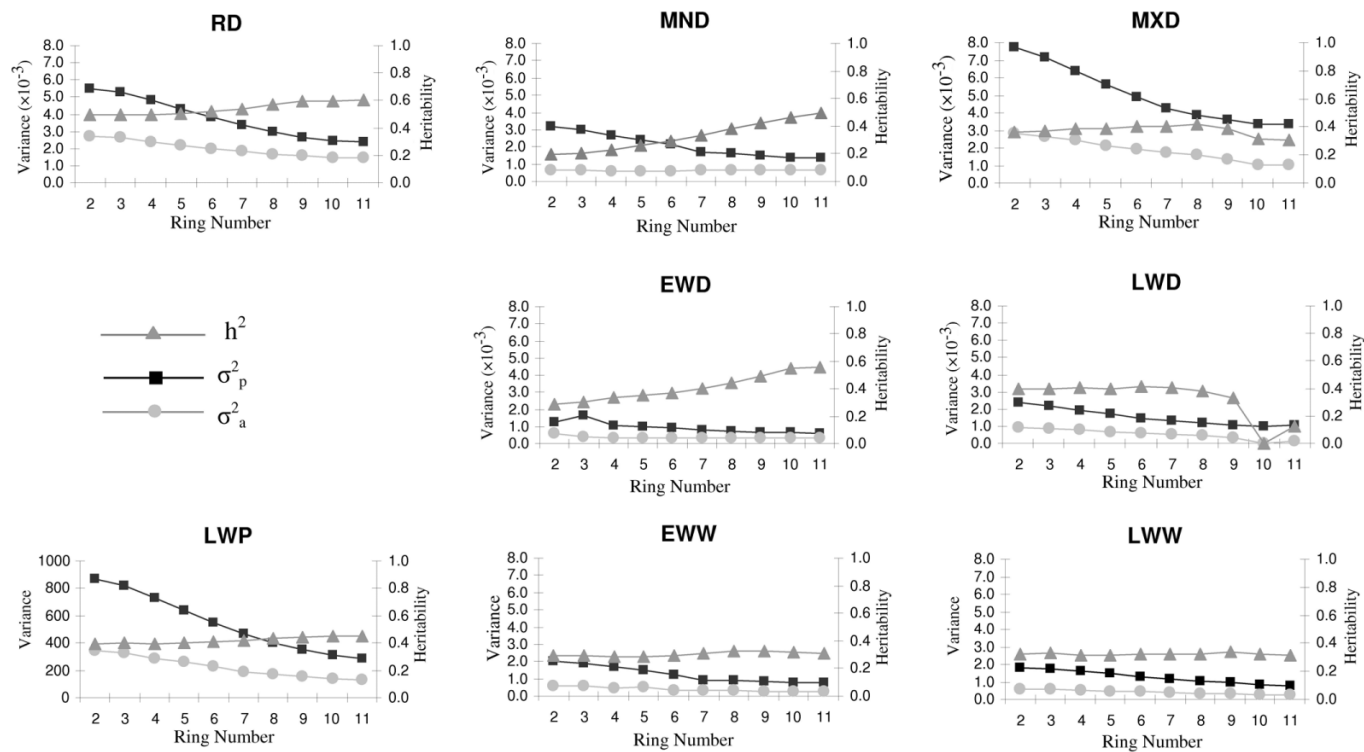


Table 3. Age–age genetic correlation (SEs in parentheses) among three different ring numbers (3, 6, and 11) for each wood density components.

Trait	Ring No.	Ring No.	
		6	11
RD	3	0.990 (0.0046)	0.933 (0.0309)
	6	—	0.973 (0.0142)
MND	3	0.989 (0.0078)	0.932 (0.0462)
	6	—	0.978 (0.0189)
MXD	3	0.979 (0.0116)	0.900 (0.0612)
	6	—	0.937 (0.0373)
EWD	3	0.981 (0.0119)	0.855 (0.0733)
	6	—	0.940 (0.0326)
LWD	3	0.980 (0.0112)	0.874 (0.1398)
	6	—	0.922 (0.1236)
EWW	3	0.972 (0.0164)	0.880 (0.0645)
	6	—	0.968 (0.0222)
LWW	3	0.995 (0.0027)	0.986 (0.0083)
	6	—	0.996 (0.003)
LWP	3	0.997 (0.0018)	0.980 (0.0108)
	6	—	0.992 (0.0049)
RW	3	0.900 (0.0896)	0.652 (0.2689)
	6	—	0.915 (0.0771)

Note: See Table 1 for trait abbreviations.

conditions, genetic material, experimental and measurement procedures for wood density, and other factors (Wright 1976; Zobel and Jett 1995). Moreover, limiting environmental factors can occur in the spring (EW) in some regions and summer (LW) in other regions. RD, MND, and EWD are

shown to be highly heritable traits, suggesting that large gains can be obtained for these characters.

Age–age genetic correlations

In this context, it is essential to know not only the heritability value of a specific character, but also how that characteristic is correlated age by age and with others factors to fully assess the implications of its selection.

Results in Table 3 express the age–age genetic correlations between three different ring ages.

Age–age genotypic correlations between the third and sixth rings were close to 1 for most wood density components. Correlations between wood density traits of the 6th and 11th rings were always higher than those between the 3rd and the 11th in all traits. For most characteristics, the high correlation values (>0.9) clearly indicate that it does not compensate to wait 6 or 11 years for evaluation, because the third ring produces identical information. This is a very important result regarding the advantages of early selection. According to Wu et al. (1998), there are three main advantages to early selection in tree breeding: (i) increased selection intensity or reduced field testing size; (ii) a shortened generation interval; and (iii) genetic information from early testing can be used to enhance selection efficiency at mature age. However, in the traits EWD, LWD, and EWW, it may be preferable to wait until the 6th year to carry out a more accurate evaluation of individuals. According to Hylen (1999), this can indicate that accumulation over rings smoothes out environmental effects and that genetic control of traits is more strongly manifested. RW correlations between the 3rd and 11th ring ($r_g = 0.65$) are considerably inferior to those of the remaining characteristics. However,

between the 6th and 11th ring, the value is 0.92; thus, it can be assumed that families with larger growth rates at the 6th ring retain this tendency in subsequent ages. This indicates that growth characteristics are not genetically controlled to the same extent as the remaining traits, suggesting that early tests for *Pinus pinaster* should increase the efficiency of the tree-breeding programme, for at least some characteristics. Zobel and Jett (1995) state that, even when this age-age correlation is fairly weak, such early evaluations are valuable in eliminating families with undesirable wood density properties.

Our results are consistent with previous studies on *Pinus pinaster* (Louzada 2003) namely that, for RD, MND and EWD traits, the high genetic correlation between young and older ages makes it possible to select at a very young cambial age. Studies on other species also indicate that age-age genetic correlations for wood density traits tend to be high (Talbert et al. 1983; Loo et al. 1984; Zobel and van Buijtenen 1989; Vargas-Hernandez and Adams 1992; Williams and Megraw 1994; Hylen 1999; Kumar 2002). An extreme example is the finding of Nepveu and Birot (1979, cited in Zobel and van Buijtenen 1989) in *Picea abies*, where they found that adult specific gravity could be predicted even from a single ring at the juvenile stage.

Conclusions

This study indicates that in *Pinus pinaster* RD is the most heritable of the variables studied, suggesting that large gains can be obtained from selecting on the basis of this variable. Estimated heritabilities for the EW components (MND and EWD) were superior to those obtained from LW components (MXD and LWD), indicating that, in this species, EW characteristics are subject to stronger genetic control than LW components, which depend more on environmental factors. Pith to bark trends show that heritability values increase with age for almost all wood density components and that age-age genetic correlations for wood density components are generally high. The genetic correlations between rings 2 and 10 were always greater than 0.97, except for EWW, EWD, and LWD, allowing early selection for all but these traits.

Acknowledgements

The first author was funded by the Portuguese Foundation for Science and Technology (doctoral grant SFRH/BD/27412/2006).

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