

Genetic correlations between wood quality traits of *Pinus pinaster* Ait.

Maria João GASPAR^{1*}, José Luís LOUZADA¹, Alexandre AGUIAR², Maria Helena ALMEIDA³

¹ Centro de Investigação e de Tecnologias Agro-Ambientais e Biológicas, Departamento Florestal, Universidade Trás-os-Montes e Alto Douro, Portugal

² INIA - Instituto Nacional de Recursos Biológicos, Quinta do Marquês, Portugal

³ Universidade Técnica de Lisboa, Instituto Superior de Agronomia, Centro de Estudos Florestais, Portugal

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Abstract

- It is essential to understand how characteristics are related to each other in breeding programmes to select wood properties, in order to avoid that, in selecting for one trait, we are negatively affecting another. Moreover, measuring wood properties is time consuming and expensive.
- This study assesses genetic and phenotypic correlations between wood density components and spiral grain of 46 half-sib families of *Pinus pinaster* in seventeen-year-old trees.
- Results showed that genetic correlations for all wood density components were higher than corresponding phenotypic correlations. Furthermore, all wood density components were highly genetically correlated with ring density, and also closely associated among themselves. Results showed a higher genetic correlation of ring density with earlywood density ($r_g = 0.96$) than with latewood density ($r_g = 0.79$). A moderate to high positive genetic correlation was found between spiral grain and wood density characteristics (0.29–0.61).
- We conclude that ring density (overall wood density) can be improved by increasing either earlywood density, latewood percent, or both of these traits, and spiral grain can be modified in future plantations.

Résumé – Corrélations génétiques entre propriétés du bois chez *Pinus pinaster* Ait.

- En amélioration génétique, il est essentiel de connaître le degré de liaison entre caractères de manière à éviter lors de la sélection pour un caractère une contre-sélection pour un autre. De plus, la mesure des propriétés du bois est lourde et coûteuse.
- Dans cette étude, nous étudions les corrélations génétiques et phénotypiques entre les composantes de la densité du bois et l'angle du fil chez 46 familles de demi-frères de *Pinus pinaster* âgées de 17 ans.
- Les résultats montrent que les corrélations génétiques pour toutes les composantes de la densité du bois sont plus élevées que les corrélations phénotypiques. De plus, toutes les composantes de la densité sont fortement corrélées génétiquement avec la densité du cerne et étroitement liées entre elles. Les résultats indiquent une liaison génétique plus forte entre la densité du cerne et la densité du bois initial ($r_g = 0.96$) qu'avec le bois final ($r_g = 0.79$). Une corrélation génétique modérée à forte est mise en évidence entre l'angle du fil du bois et les caractéristiques de densité (0.29–0.61).
- Nous concluons que la densité du cerne peut être améliorée soit en augmentant la densité du bois initial, soit la proportion de bois final, soit les deux et que l'angle du fil peut être modifié pour les plantations futures.

1. INTRODUCTION

The 2005–2006 National Forest Inventory estimates the total forest area in Portugal at 3.4 million hectares. The volume of standing wood of the main species that supply industry is estimated at 67 million m³ for *Pinus* wood and 41 million m³

for *Eucalyptus* wood. Due to the economic importance of *Pinus pinaster* (Roulund et al., 1988), a national tree improvement plan for this species has been in operation since the early 1980's. The maritime pine breeding programme is presently in its second generation for selection (the progeny trials reported in this study are part of this programme). Selection of genotypes for seed orchards and breeding populations is usually

* Corresponding author: mjgaspar@utad.pt

based solely upon diameter, height and stem traits. Such selection criteria may have an indirect effect on different wood properties (Zobell and Jett, 1995), but there is little genetic information available on the relation between these selection traits and wood properties.

A consequence of future plantings is an increase in the proportion of juvenile wood due to the reduction of rotation age because of an increase in growth rate (Huyen, 1999; Zamudio et al., 2005). Despite some exceptions depending on the type of end product, juvenile wood is generally considered to be of lower quality than mature wood (Zamudio et al., 2005). An increase in the proportion of juvenile wood will represent a problem for most solid wood products due to its low strength and instability following drying (Zobel and Sprague, 1998). Juvenile wood in *Pinus* species is usually characterized by a shorter tracheid, and cell walls thinner than in mature wood, which often produces lower specific gravity, and also by a severe spiral grain (Zobel and Sprague, 1998).

Wood density is closely associated to the most important wood quality properties and technological traits, providing a vital index that confers important information in this area (Zobel and Jett, 1995; Zobel and van Buijtenen, 1989). Nevertheless, variations in wood density can be difficult to understand, since this complex trait is not a single property but a complex of several intra-ring components, including minimum and maximum wood densities, early and late wood densities, proportion of latewood etc (Pliura et al., 2006). Another important wood property is the spiral grain, a term applied to the helical orientation of the tracheids in a tree stem. This property confers a twisted appearance to the trunk after the bark has been removed, causing twisting in dried sawn timber through anisotropic shrinkage (Harris, 1989), and is recognised as one of the key properties determining the suitability of wood for use as sawn timber (Raymond, 2002), one of the main applications for *Pinus pinaster* wood in Portugal.

One way to reduce some of the negative effects of short rotations on wood quality is by breeding to improve juvenile wood characteristics (Nichols et al., 1980; Zamudio et al., 2005) as a result of improved knowledge of the genetic control of wood characteristics, wood growth, and their interrelationship. This process will result in increased selection efficiency for a selected trait through the modification of one or more characteristics (Louzada and Fonseca, 2002).

In a breeding programme that selects for wood properties, it is essential to understand how the characteristics are related to one another. Knowledge of additive genetic correlations is extremely important in any selection programme, since the measurement of wood properties is time consuming and expensive. Genetic correlations play an important role in the prediction of correlated responses and the development of effective selection indices.

The aim of this study was to estimate genetic and phenotypic correlations between intra-ring wood characteristics and spiral grain, and to evaluate the implications of these relationships in tree breeding for wood quality in *P. pinaster*. These findings are of great importance for the continued development of maritime pine breeding programmes to guide future generation's selection.

2. MATERIALS AND METHODS

2.1. Trial and measurements

2.1.1. Location

The field trial location was at Pinhal de Leiria situated in central coastal Portugal (lat. 39° 50', long. 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 four month period of summer drought. The Spodic Podzols (PZ sd) soils are derived from sand dunes of maritime origin. Seedlings were raised for nine months in the nursery in plastic bags (250 cm³ volume). Planting (2 × 2 m spacing) took place in March 1987 after harrowing and ploughing the site; no fertilizer was applied.

2.1.2. Genetic material

The trial included 46 open pollinated families, derived from seed collected in the Escaroupim clonal seed orchard II (Aguiar, 1993). 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 families were replicated in 8 blocks with 2×4 tree plots. In the year of 2003, wood samples were collected from a subset of 4 trees per family and block in the same 3 blocks, giving a total number of 552 trees. The sampled trees within each plot were randomly selected. 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. These radial samples were X-rayed perpendicular to the transverse section and their image scanned by microdensitometric analysis (Louzada, 2000). Growth ring boundaries were identified on the radial profiles by locating sharp density variations through cross-examination using visual observation of the macroscopic anatomical features. Annual rings were numbered from pith-to-bark, and the first and the last annual rings of each sample were excluded since they were usually incomplete.

For each ring, average ring density (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 for each ring. The earlywood-latewood boundary or Earlywood/Latewood limit in each growth ring was assigned a fixed density of 0.5g cm⁻³. Similar to several authors in the study of other conifer species (Fujimoto et al., 2006; Hodge and Purnell, 1993), we used a single fixed value of density; even though some researchers have used the average of minimum and maximum ring density to define the EW/LW transition point (Vargas-Hernandez and Adams, 1991; Zamudio et al., 2005). The advantage of the former criterion for determining the EW/LW boundary is explained in detail by Jozsa et al. (1987) and Rudman (1968). This criterion does not allow identification of the beginning of latewood, but does allow identification of ring portions with a higher density over a certain threshold, which we define here as LW. The applied value of 0.5 g cm⁻³ was derived from an adjustment to the value proposed by Louzada (2000) for *Pinus pinaster* in the comparison of different criteria, and was considered

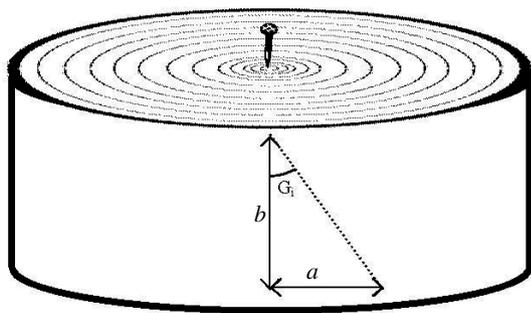


Figure 1. Procedure for measuring spiral grain angle (G_i) on wood discs. $G_i = \arctan(a/b)$, a : distance from the reference line to the line traced with the needle, b : thickness of the disc.

the most correct value for 18 years old specimens of this species. Intra-ring density variation was quantified using the heterogeneity index (HI), defined by the standard deviation of all density values across the annual ring. Rings close to the pith have less volume than those closer to the bark, thereby contributing less to overall disc volume. In order to compensate for this effect, wood density components were weighted for each ring density component by its respective cross-sectional area (Ferrand, 1982).

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). To define this reference, nails were hammered into the pith from both sides of the disc and a string was tied between them so that the cord ran through a vertical line. The spiral grain angle (SPG) was calculated as the arctangent of the ratio of the distance from the reference line (a) to the line traced with the needle of the slope of the grain detector and the thickness of the disc (b) (Fig. 1).

Following the protocol given by Harris (1989), spirality direction was indicated by assigning a positive sign to the left handed angles. Measurements in each disc were taken in two opposite radii, and the mean grain angle was calculated as the mean of the absolute value of the angles, ignoring differences in sign.

2.1.3. 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. 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 AS-REML programme (Gilmour et al., 1998).

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

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

Table I. Descriptive statistics table for different wood traits and respective heritability estimates (standard errors given in brackets).

Trait	Mean	Std. Dev.	Coeff. Var.	Min	Max	h_i^2 (se)
RD (gcm ⁻³)	0.474	0.051	10.68	0.336	0.655	0.63 (0.190)
MND (gcm ⁻³)	0.308	0.037	12.11	0.207	0.445	0.54 (0.184)
MXD (gcm ⁻³)	0.707	0.060	8.51	0.558	0.917	0.34 (0.164)
EWD (gcm ⁻³)	0.386	0.026	6.69	0.304	0.463	0.60 (0.191)
LWD (gcm ⁻³)	0.618	0.034	5.43	0.535	0.732	0.26 (0.141)
LWP (%)	38.196	16.927	44.31	6.420	82.240	0.46 (0.168)
EW (mm)	2.674	0.876	32.74	0.900	6.100	0.32 (0.137)
LW (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)a
HI (gcm ⁻³)	0.120	0.019	16.05	0.07	0.196	----- a
SPG	4.2	2.259	53.40	-1.30	13.11	0.47 (0.150)

RD = Average Ring Density, MND = Minimum Density, MXD = Maximum Density, EWD = Earlywood Density, LWD = Latewood Density, LWP = Latewood Percentage, EW = Earlywood Width, LW = Latewood Width, RW = Ring Width; SPG = Spiral grain.

^a In the analysis of variance the differences among Families were not significant ($P > 0.05$).

----- The heritability value was quantified with the null value.

where σ_a^2 represents the additive genetic variance and σ_p^2 represents the total phenotypic variance. Families were considered to be maternal half-siblings, therefore the $\sigma_a^2 = 4 \times \sigma_f^2$ relationship was assumed to estimate the genetic parameters. Phenotypic variance was estimated as $\sigma_p^2 = \sigma_f^2 + \sigma_{f \times b}^2 + \sigma_\varepsilon^2$. Standard errors for heritability were estimated by ASREML using a Taylor series approximation (Gilmour et al., 1998).

The genetic and phenotypic correlations between all wood density components 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) measured at 17 years-old were evaluated as follows:

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

where $\text{cov}_a(x, y)$ 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:

$$r_p = \frac{\text{cov}_p(x, y)}{\sqrt{\sigma_{px}^2 \cdot \sigma_{py}^2}} \quad (4)$$

where $\text{cov}_p(x, y)$ is the phenotypic covariance between traits X and Y , estimated as $\text{cov}_p(x, y) = \text{cov}_f(x, y) + \text{cov}_{fb}(x, y) + \text{cov}_\varepsilon(x, y)$, 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).

3. RESULTS AND DISCUSSION

Summary statistics for each characteristic and the respective heritability estimation are shown in Table I. The

Table II. Phenotypic (upper triangle) and genetic (lower triangle) correlations coefficients (with standard errors given in brackets) between all traits.

	RD	MND	MXD	EWD	LWD	LWP	EWV	LWW	SPG
RD	–	0.66 (0.0273)	0.80 (0.0173)	0.67 (0.0264)	0.72 (0.0260)	0.90 (0.0084)	–0.72 (0.0215)	0.80 (0.0164)	0.18 (0.046)
MND	1.02 (0.0782)		0.42 (0.0389)	0.79 (0.0180)	0.33 (0.0414)	0.54 (0.0339)	–0.52 (0.0337)	0.42 (0.0390)	0.16 (0.046)
MXD	0.90 (0.0838)	0.95 (0.1940)		0.34 (0.1637)	0.93 (0.0630)	0.69 (0.0239)	–0.57 (0.0301)	0.60 (0.0292)	0.10 (0.046)
EWD	0.96 (0.0647)	1.06 (0.0440)	0.88 (0.1934)		0.19 (0.0451)	0.49 (0.0361)	–0.37 (0.0396)	0.46 (0.0371)	0.18 (0.046)
LWD	0.79 (0.1340)	0.72 (0.2481)	0.97 (0.0235)	0.72 (0.2556)		0.59 (0.0293)	–0.54 (0.0316)	0.46 (0.0356)	0.05 (0.045)
LWP	0.96 (0.0269)	0.95 (0.1244)	0.91 (0.1022)	0.86 (0.1280)	0.80 (0.1582)		–0.76 (0.0191)	0.87 (0.0110)	0.15 (0.197)
EWV	–0.85 (0.0946)	–0.91 (0.1349)	–0.59 (0.2083)	–0.85 (0.1634)	–0.39 (0.2756)	–0.89 (0.0858)		–0.49 (0.0338)	–0.04 (0.046)
LWW	0.99 (0.0553)	1.00 (0.1963)	0.89 (0.1479)	0.88 (0.1614)	0.83 (0.2076)	1.00 (0.0386)	–0.83 (0.1788)		0.19 (0.044)
SPG	0.55 (0.181)	0.61 (0.177)	0.31 (0.233)	0.57 (0.179)	0.29 (0.258)	0.55 (0.197)	–0.59 (0.239)	0.51 (0.210)	

RD = Average ring density, MND = minimum density, MXD = maximum density, EWD = earlywood density, LWD = latewood density, LWP = latewood percentage, EWV = earlywood width, LWW = latewood width; SPG = spiral grain.

intraring wood characteristics values were previously reported by Gaspar et al. (2008).

The trait under strongest genetic control was average ring density (RD, $h_i^2 = 0.63$) among the heritability values, whilst RW showed the lowest heritability estimation ($h_i^2 = 0.10$). No significant differences ($P > 0.05$) were observed between families for this trait, indicating that the variation in growth characteristics most likely derives from environmental factors rather than genetic ones (Gaspar et al., 2008). Growth characteristics (diameter) frequently exhibit relatively low values of heritability (Bouffier et al., 2008; Cotterill et al., 1987; Harfouche et al., 1995; Hopkins and Butcher, 1994; Zas et al., 2004) In a study carried out after 12 years in this progeny trial, Aguiar et al. (2003) estimated a heritability value for diameter of 0.18. The grain angle presented a coefficient of variation (CV) of 53 with an average value of 4.2°. Spirality was predominantly left-handed (98%), with a few trees displaying a weak level of right-handed spirality. This conforms to the general pattern of spirality in conifers, where the grain angle is usually left handed in early years, followed by a gradual change towards right-handed spirality with increasing age (Harris, 1989). Heritability estimates for SPG were 0.47, indicating moderate to strong genetic control of this characteristic. Our estimated heritability for this trait is higher than that derived by Arbez et al. (1978) from a previous study on maritime pine ($h_i^2 = 0.16$) but similar to values reported for other coniferous species (Hansen and Roulund, 1997) observed that individual narrow-sense heritability of the spiral grain in Sitka spruce was 0.63 and 0.78. In *Picea abies*, (Hannrup et al., 2002) reported a broad-sense heritability of 0.42, whilst (Hallingback et al., 2008) and (Silva et al., 2000) reported narrow-sense heritability for this species from [0.32–0.44] and [0.29–0.47] respectively. Heritability for spi-

ral grain in *Pinus sylvestris* has been found to be 0.4 (Hannrup et al., 2003). In *Pinus radiata*, Gapare et al. (2007) estimated a narrow-sense heritability of 0.44 and 0.46. Zobel and Jett (1995) pointed out that much of the variation in spiral grain within a species derives from the different methods used to assess this characteristic. Nevertheless, our findings indicated that potentially, tree breeders can modify spiral grain in future plantations.

Genetic correlations between traits

Phenotypic and additive genetic correlations between all traits are presented in the Table II.

Data shows that genetic correlations for all traits (except for SPG) were higher than the corresponding phenotypic correlations, indicating that the use of phenotypic correlations, rather than genetic ones, to evaluate traits will result in the underestimation of potential gains from indirect selection. All wood characteristics studied showed a strong genetic correlation with RD, and between themselves, indicating that these traits are probably controlled, to a large extent, by the same set of genes (Vargas-Hernandez and Adams, 1991), and that selection for one characteristic should result in a simultaneous response of associated traits. The strong genetic relationship between density and each one of its components highlights the fact that overall density is a complex trait resulting from different combinations of the fraction, and relative density of each component (Hysten, 1997). All correlations with RD were positive, with the exception of EWV where strong negative genetic correlations were detected, due to the fact that, contrary to latewood, earlywood is characterized by lower density, larger lumens, and thinner cell walls (Hysten, 1999;

Kumar, 2002; Loo et al., 1984; Talbert et al., 1983; Vargas-Hernandez and Adams, 1992; Williams and Megraw, 1994; Zobel and van Buijtenen, 1989). These results are consistent with those obtained in studies on *Pseudotsuga menziesii* (Hodge and Purnell, 1993) and *Picea mariana* (Abdel-Gadir et al., 1993). Zhang (1998) suggested that such trends were most likely due to a direct reaction of differentiating cells in the cambial zone due to the relative availability of photosynthates and growth regulators at different times during the growing season.

The present study showed a higher genetic correlation of RD with EWD than with LWD, and a higher phenotypic correlation of RD with LWD than with EWD. Louzada (2003) reported that *P. pinaster* earlywood density has a higher genetic and phenotypic correlation with overall wood density than latewood density. Similar results were obtained in *Pseudotsuga menziesii* by Vargas-Hernandez and Adams (1991). Also Abdel-Gadir et al. (1993) studied *Abies balsamea* and observed higher phenotypic correlation between wood density and earlywood than with latewood density. Conversely, although similar results for the genetic correlation among overall wood density and earlywood density were obtained, Zhang and Morgstern (1995) also encountered strong negative genetic correlation (-0.73) between overall wood density and latewood density. Louzada (2003) reported the same conclusions concerning *P. pinaster* namely “EWD not only reflects a better tree genetic potential but also is controlled over years, in a large way, by the same genes”. This study verified that EWD manipulation resulted in a significant genetically correlated response in other components (RD and LWP), whilst latewood density appeared to be more sensitive to climate variation. Latewood is formed later in the growing season, when cambial cell division and expansion declines. In this period, conditions in Mediterranean regions are suboptimal due to constraining factors such as high temperatures and water stress which mask genetic effects, leading to reduced heritability ($h^2_{i(MND)} = 0.54$, $h^2_{i(EWD)} = 0.60$, $h^2_{i(MXD)} = 0.34$; $h^2_{i(LWD)} = 0.26$), confirming that, for *P. pinaster*, earlywood characteristics are subject to stronger genetic control, and that latewood components are more susceptible to environmental factors (Gaspar et al., 2008). Our findings indicate that earlywood density is most likely a result of genetic factors, but that latewood density depends mostly on environmental factors.

Most authors emphasize the importance of percentage of latewood as the source of variation in pine wood density (Zobell and Jett, 1995). Occasionally, the relationship between specific gravity and latewood percentage in conifers is not as high as could be expected (Zobell and Jett, 1995). This study revealed a very high genetic and phenotypic correlation between RD and LWP (0.96 and 0.90, respectively). Significant genetic correlations between these two traits have been reported elsewhere (Fujisawa et al., 1993; Hodge and Purnell, 1993) although (Vargas-Hernandez and Adams, 1991; Zhang and Morgenstern, 1995) obtained only moderate genetic correlation values between these traits. We conclude that the reported differences related with LWP possibly result from different methodologies used to define the threshold value be-

tween EW and LW. Some researchers used the average of minimum and maximum ring density (Cown and Parker, 1978; Fujimoto et al., 2006), whilst others use a fixed density value (Nichols et al., 1980; Vargas-Hernandez and Adams, 1991). This study adopted the latter approach to define the EW/LW threshold and the results suggest that ring density can be improved by increasing earlywood density, latewood percent, or both of these traits.

A moderate to high positive genetic correlation was observed between spiral grain and wood density characteristics (0.29–0.61). However, other studies have obtained lower genetic correlations between spiral grain and wood density (Eisemann et al., 1990; Hannrup et al., 2004). SPG presented a higher dependency on earlywood components (MND and EWD), and had high genetic correlation with RD (0.547), being more dependent on earlywood ($rg_{(SG,EWD)} = 0.57$) than on latewood ($rg_{(SG,LWD)} = 0.29$). Also, genetic correlations between SPG and intra-ring width characteristics (EWW and LWW) were high but presented contradictory signs (-0.59 and 0.51 respectively). The opposite signs were expectable as EWW and LWW are highly negatively correlated ($rg = -0.83$), consequently if SPG is positively correlated with LWW, it will be negatively correlated with EWW. Generally correlations between grain angle and growth have been weak (Eisemann et al., 1990; Hannrup et al., 2004; Hannrup et al., 2003; Hallingback et al., 2008), indicating that there won't be genetic loss in growth when breeding for low SPG, or the other way around. Unfortunately in this study we weren't able to evaluate the magnitude of this correlation, but it should be investigated further.

4. CONCLUSIONS

The results of this study showed that genetic correlations for all wood density components were higher and more stable than the corresponding phenotypic correlations. Furthermore, all wood density components were strongly genetically correlated with RD, and were also strongly associated among themselves.

The present study also showed that EWD has a higher genetic correlation with RD than LWD, while RD presented higher phenotypic correlation with LWD than with EWD. These results indicate that, in *Pinus pinaster*, earlywood characteristics are more subject to genetic control whereas latewood components are more strongly influenced by environmental factors. Results also suggest that ring density (overall wood density) can be improved by increasing either earlywood density, latewood percent, or both of these traits. In addition, our results indicate that, potentially, tree breeders can modify spiral grain in future plantations.

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