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Genetic correlations between wood density components in *Pinus pinaster* Ait.

José Luis P.C. Louzada*

ICETA/UTAD, Univ. Trás-os-Montes e Alto Douro, Dep. Florestal, 5000-911 Vila Real, Portugal

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Abstract – The main purpose of this work was the determination of the genetic correlations among the density components of *Pinus pinaster*. The material was collected from 180 trees by the extraction of an increment core from pith to the cambium, at breast height, in a open pollinated test with 15 families at 18 years growth. The wood density components were measured using the X-ray densitometry technique. Although initially the density components of all rings were defined, in this study it was only analysed rings with a 6, 10 and 13 cambial age. The Average Ring Density is more dependent on the Earlywood components, mainly on Earlywood Density, than Latewood ones. Among all the components analysed, Earlywood ones revealed the highest and most stable genetic control, without revealing any adverse genetic correlation with regard to other components. Therefore these are the most suitable ones to be included in future selection and improvement programmes. Even though the correlation coefficients are low, Ring Width is positively correlated at genetic and phenotypic level with Average Ring Density, Minimum Density, Earlywood Density and Latewood Percentage.

tree breeding / genetic correlations / wood quality / wood density components / *Pinus pinaster*

Résumé – **Corrélations génétiques entre les composantes de la densité du bois de *Pinus pinaster* Ait.** L'objectif principal de ce travail consistait à calculer les corrélations génétiques entre les composantes de la densité pour le bois de *Pinus pinaster*. Le matériel a été obtenu de 180 arbres à partir desquels il a été extrait une carotte de sondage de la moelle à l'écorce, à hauteur de poitrine. Les arbres appartenaient à un test de 15 descendance issues de pollinisation libre et âgés de 18 ans. Les composantes de la densité ont été obtenues par microdensitométrie aux rayons X. La densité moyenne du cerne apparaît fortement dépendante des composantes du bois initial, principalement la densité du bois initial ; elle est peu dépendante des composantes du bois final. Parmi toutes les composantes analysées, celles du bois initial démontrent le plus fort et le plus stable contrôle génétique sans présenter aucune corrélation génétique défavorable par rapport aux autres composantes. Il est suggéré de ce fait que, dans de futurs programmes de sélection et d'amélioration, les composantes du bois initial soient prises en considération. Bien que les coefficients de corrélation soient faibles, la largeur des cernes est positivement corrélée tant au niveau génétique qu'au niveau phénotypique avec la densité moyenne du cerne, la densité minimum et le pourcentage de bois final.

amélioration génétique / corrélations génétiques / qualité du bois / composantes de la densité du bois / *Pinus pinaster*

1. INTRODUCTION

Pinus pinaster is considered to be the principal forest species of Portugal. Not only because of the area it occupies (in a total of 3200000 ha of forest area, *Pinus pinaster* occupies about 1300000 ha, followed by *Quercus suber* with 660000 ha and *Eucalyptus globulus* with 500000 ha), but also, at economic level, for its multiple industrial application of wood (lumber and timber, plywood, particleboard, fiberboard, paper) and resin products. Thus, it can be considered as the only softwood source in the country.

This species is not only important for Portugal but also in almost all the Mediterranean basin, as it represents an important softwood supplier (mainly in France, Spain and Italy) and can become important for other countries where it has been introduced, such as South Africa, New Zealand and Australia. As an example, in South Africa its position is

special with more than 325000 ha [51] because it is particularly well adapted in the most humid parts under maritime influence in Cape Region. Inclusive, due to its great adaptability to their conditions, it has been considered as a invader plant and may be grown under controlled conditions only [33, 64, 65]. In Australia *Pinus pinaster* was introduced in the 1950's with the objective of planting 80000 ha. 30000 ha of the total were already planted by 1990 and the second step had already begun from a selection programme and a genetic breeding of this species installed in 200 ha of progeny tests [36].

With the trend in forest management to gradually shortening the rotation age, and with wood being the final product of many forestry activities, quality has become one of the major concerns of many forest product industries [11, 68, 79, 81].

* Correspondence and reprints
Tel.: (351) 259 350 212; fax: (351) 259 350 480; e-mail: jlousada@utad.pt

It has gradually been realised that wood quality and quantity cannot be treated as independent factors and that wood quality improvement should form an integral part of most breeding programmes [1, 2, 69, 76, 78, 80] and that wood density is an ideal subject for genetic manipulation [8, 9, 72, 78, 81].

However, understanding wood density variation can be more difficult due to the complex nature of this trait. In temperate softwood, the average ring density is fundamentally dependent on the earlywood and latewood proportion and the relative densities of each of them. Thus, a particular value of density can result from various combinations of components and be changed by the manipulation of one or more of them.

Therefore, studying the genetic control of those components will contribute greatly to a better understanding of the genetics of wood density, which will be essential for an efficient incorporation of this wood quality characteristic in tree breeding programmes.

Several studies have been made in different species, and all of them agree that wood density is subject to strong genetic control, but they have revealed some contradictory results in terms of their components.

Concerning *Pinus pinaster* wood, already in the 1970's Nicholls [56] could begin his article by complaining that "Although there are extensive stands of *Pinus pinaster* throughout the world, there is surprisingly little published information dealing with its wood characteristics."

At the moment, even though there is already some awareness about the genetic variation of the growth traits and tree form [5, 15, 30, 31, 32, 35, 36, 45], and alongside studies developed in France by Polge and Illy [63], Keller [41], Nepveu, [55], Chaperon et al. [18], deep gaps still exist in the extent of the knowledge about the genetic control of the *Pinus pinaster* wood properties.

In a previous work by Louzada and Fonseca [48] about the heritability of wood density components in *Pinus pinaster*, it was concluded that the highest and most stable with age heritability values were obtained by the Earlywood Components (Minimum Density: $0.59 < h_1^2 < 0.85$ and Earlywood Density: $0.52 < h_1^2 < 1.01$), followed by the Average Ring Density: $0.53 < h_1^2 < 0.74$, while the Latewood Components (Maximum Density: $0.03 < h_1^2 < 0.55$ and Latewood Density: $0.03 < h_1^2 < 0.52$) always presented the lowest and most unstable heritability values.

Nevertheless, in order to estimate the implications of genetic control of one characteristic, we need to know not only the heritability values but also how this characteristic acts between juvenile and mature wood and between this analysed characteristic and the others.

This aspect is highly important because if, two traits are related to each other, a change in one trait may cause an inadvertent change in the second. For example if one selects for high wood specific gravity, and if it is negatively correlated with growth rate, one would unintentionally select for slow growth as well. About this, is to mention that although a lot of research has been done on the relationship between wood specific gravity and growth rate over decades, a general relationship is still very ambiguous.

As Zobel and van Buijtenen [81] described: "Despite the very widespread interest and study over the years there still is much controversy, and a search of the literature will yield publications which can be used to support nearly any chosen point of view" (p. 157).

A recurring question about the effect of growth rate on conifer wood is related to the relative control of specific gravity by the environment, compared to control by genetics. This question can only be answered satisfactorily with well-designed experiments.

Moreover, the published information relative to wood properties and growth is so voluminous that it will not be possible to cite more than a small part of it.

However, at a phenotypic level this subject was very well summarised by Zobel and van Buijtenen [81] and they found that both positive and negative phenotypic correlations have been reported in these studies. Specially for the hard pines, there are 59 references (table 5.2; p. 166–168) among which 35 showed no relationship between growth rate and specific gravity, 9 exhibited a small correlation, while 11 showed a significant reduction in specific gravity with faster growth rate, and only 4 showed a higher specific gravity for the fastest growing trees. Nevertheless, sometimes different authors have been reported conflicting results for the same species.

At a genetic level Zobel and Jett [78] reviewed 38 references and found that there is a number of reports of a negative genetic correlation between growth rate and wood density in several genera such as *Picea* spp. and *Abies* spp., but especially for the hard pines it shows a little or no meaningful genetic correlation between these traits. As well as Megraw [50] summarised for *Pinus taeda*: "An inherent relationship between growth rate and specific gravity does not exist. Fast growth rate does not imply lower specific gravity" (p. 36).

Specially for *Pinus pinaster* wood, Polge and Illy [62] mentioned that wide rings with high density are really rare, even this conclusion was very circumscribed due was obtained based on a material with only four years old. Also Chaperon et al. [18] obtained a high and negative genetic correlation between density and circumference, but Chaperon et al. [19] indicated a positive relationship between density and ring width. Nevertheless, there is a common acceptance among many foresters (namely in Portugal) that if hard pine trees grow rapidly, low wood density will be the result.

So, in this context, this work intends to complete the work of Louzada and Fonseca [48] carried out with the purpose of estimating, ring by ring, the genetic correlations between overall wood density components, and to evaluate the implications of these relationships in tree breeding for wood quality.

2. MATERIALS AND METHODS

Wood samples were collected from 15 open-pollinated Portuguese families in one progeny test, which were planted in 1979 (plants with one year old) in the North of Portugal near Bragado (41° 30' N, 7° 39' W, elevation 750 m), and established in 3 complete randomised blocks represented by 10 trees per plot. In each plot 4 trees were sampled, giving a total of 180 trees.

Table I. Form of variance analysis for overall density components weighted at each age.

Sources of Variation	Degrees of Freedom	Expected Mean Squares
Block (B)	$b-1$	$\sigma_{\epsilon}^2 + t\sigma_{FB}^2 + tf\sigma_B^2$
Family (F)	$f-1$	$\sigma_{\epsilon}^2 + t\sigma_{FB}^2 + tb\sigma_F^2$
B \times F	$(b-1)(f-1)$	$\sigma_{\epsilon}^2 + t\sigma_{FB}^2$
Residual (Trees/F/B)	$(t-1)fb$	σ_{ϵ}^2

b = number of blocks (3); f = number of families (15); t = number of trees/family/block (4).

σ_B^2 , σ_F^2 , σ_{FB}^2 and σ_{ϵ}^2 are variance components due to block, family, block \times family interaction and residual (or error), respectively.

The material submitted to analysis was collected in 1996 at breast height (1.3 m) and obtained by extraction of one increment core per tree, from pith to bark. From these increment cores, radial samples were taken out with a constant thickness of 2 mm which, after being chemically extracted with a toluene-alcohol (2:1) solution for 48 hours, were dried to 12% moisture content. These radial samples were X-ray exposed and their image scanned by microdensitometric analysis in order to determine the density components according to the process described by Louzada [47]. A comprehensive description of X-ray densitometry analysis can be found in Polge [60, 61], Hughes and Sardinha [37].

The first and the last annual rings of each sample were rejected because they were usually incomplete. For each ring scanned, Average Ring Density (RD), Minimum Density (MND), Maximum Density (MXD), Earlywood Density (EWD), Latewood Density (LWD), Ring Width (RW) and Latewood Percentage (LWP) were determined, taking as the limit between Earlywood/Latewood, the fixed value of 0.550 g cm⁻³ density.

Even though some researchers have been using the average of minimum and maximum ring density to define the transition point for EW/LW [20, 57, 69], we used one fixed value of density as several authors have been using for different kind of conifer species [3, 7, 22, 24, 25, 29, 34, 42, 59]. The advantages of this criterion for the EW/LW boundary based on a fixed density value are well explained by [39, 58, 66]. In the present study, we choose this fixed value of 0.550 g cm⁻³ which has been proposed by Polge [60] for *Pinus pinaster* wood and in one previous study [47] it compares different criteria, this one is the most correct for this species with more or less 20 years old. The intra-ring density variation was quantified by the Heterogeneity Index (HI), proposed by Ferrand [28], expressed by the standard deviation of density values (all X-ray data points) across the annual ring.

In this study only three years aged 6, 10 and 13 from the pith (cambial age) were considered, due to the huge number of data.

Because rings close to the pith represent less volume than those near to the bark, they contribute less to the whole disc. To alleviate this problem, wood density components weighted were performed weighting each ring density component value by its respective cross-sectional area as described by [7, 38, 46, 69, 76].

The genetic relationship of these wood density components, weighted at ages 6, 10, and 13, was evaluated by estimating the genetic correlation based on family variance and covariance following Falconer [26]:

$$r_G = \frac{\text{Cov}_{F(xy)}}{\sqrt{\sigma_{F(x)}^2 \cdot \sigma_{F(y)}^2}}$$

where $\sigma_{F(x)}^2$, $\sigma_{F(y)}^2$ are the family variance component of the traits x and y , respectively, obtained from analysis of variance using the model presented in *table I*, and $\text{Cov}_{F(xy)}$ the family covariance component between traits x and y , obtained from one analysis of covariance using the model present in *table I* also, but where the mean squares were replaced by corresponding mean cross products.

The standard errors of genetic correlation (σ_{r_G}) were computed following Falconer [26]:

$$\sigma_{r_G} = \frac{(1-r_G^2)}{\sqrt{2}} \cdot \sqrt{\frac{\sigma_{h_x^2} \cdot \sigma_{h_y^2}}{h_x^2 \cdot h_y^2}}$$

where $\sigma_{h_x^2}$, $\sigma_{h_y^2}$ are the standard errors of individual heritability for x and y traits, and h_x^2 , h_y^2 the individual heritability for x and y traits, respectively.

3. RESULTS

The summary statistics for each wood density component and respective heritability value for three different cambial ages are presented in *table II*.

Among various characteristics studied, intraring wood density characteristics (RD, MND, MXD, EWD, and LWD) exhibit remarkably less phenotypic variation (CV ranges from 5.0 to 11.5%) than LWP (23.7 to 31.3%). RW and HI exhibit an intermediate variation (14.1 to 15.3%). A similar case was noted in *Pseudotsuga menziesii* [4] and *Picea mariana* [74]. Nevertheless, even RD, MND and EWD show small phenotypic variation, a large part of this phenotypic variation is due to families so, they are under strong genetic control. *Table II* shows that RD, MND and EWD have a higher heritability (from 0.541 to 1.001) than MXD and LWD (from 0.000 to 0.097). LWP, RW and HI present intermediate values (from 0.172 to 0.435). This agrees with previous studies reported for *Cryptomeria japonica* [29], *Pseudotsuga menziesii* [69, 70] and *Picea mariana* [75, 76].

3.1. Age-age genetic correlations

Age-age genetic correlations between three different ring ages, and the age-age genetic correlation between each ring number from the pith and the corresponding value at ring 13, for each wood density components, are presented in *table III* and *figure 1*, respectively.

First of all, these results emphasise that Average Ring Density (RD) and Earlywood Components (Minimum Density (MND) and Earlywood Density (EWD)) always show higher genetic correlations (close to 1 in almost ring ages) than Latewood Components (Maximum Density (MXD) and Latewood Density (LWD)) (0 or close to 0 in almost ring ages). The genetic correlations for the Latewood Percentage (LWP), the Ring Width (RW) and the Heterogeneity Index (HI) increased during the first rings and only were close to 1 after ring 6.

While determining optimum selection age is not the focus of this paper, some initial considerations are possible. Namkoong et al. [53] have suggested that, even correlations are as low as 0.6, it could be useful in early selection. Therefore, we consider that for RD, MND and EWD the high

Table II. Descriptive statistics table for each wood density component and respective heritability value for three different cambial ages (540 rings sampled).

Trait	mean	std. dev.	coeff. var.	min.	max.	h_i^2 (*)
			Ring 6 from pith	(180 rings)		
<i>RD</i> (g cm ⁻³)	0.452	0.039	8.5	0.326	0.573	0.738
<i>MND</i> (g cm ⁻³)	0.330	0.038	11.5	0.215	0.426	0.837
<i>MXD</i> (g cm ⁻³)	0.731	0.057	7.8	0.513	0.889	0.097
<i>EWD</i> (g cm ⁻³)	0.397	0.029	7.3	0.312	0.470	1.001
<i>LWD</i> (g cm ⁻³)	0.651	0.033	5.0	0.513	0.734	0.000
<i>LWP</i> (%)	21.4	6.7	31.3	0.6	46.4	0.435
<i>RW</i> (mm)	7.34	1.12	15.2	4.50	10.80	0.199
<i>HI</i> (g cm ⁻³)	0.119	0.017	14.1	0.071	0.160	0.275
			Ring 10 from pith	(180 rings)		
<i>RD</i> (g cm ⁻³)	0.473	0.040	8.5	0.352	0.579	0.577
<i>MND</i> (g cm ⁻³)	0.346	0.038	11.0	0.228	0.440	0.697
<i>MXD</i> (g cm ⁻³)	0.774	0.062	8.0	0.593	0.933	0.000
<i>EWD</i> (g cm ⁻³)	0.404	0.031	7.6	0.319	0.480	0.838
<i>LWD</i> (g cm ⁻³)	0.684	0.036	5.3	0.576	0.782	0.000
<i>LWP</i> (%)	24.1	6.0	24.9	4.3	40.6	0.360
<i>RW</i> (mm)	5.86	0.83	14.2	3.50	8.80	0.316
<i>HI</i> (g cm ⁻³)	0.133	0.020	15.3	0.076	0.183	0.172
			Ring 13 from pith	(180 rings)		
<i>RD</i> (g cm ⁻³)	0.483	0.041	8.4	0.359	0.585	0.541
<i>MND</i> (g cm ⁻³)	0.354	0.038	10.8	0.240	0.454	0.631
<i>MXD</i> (g cm ⁻³)	0.779	0.061	7.8	0.618	0.921	0.028
<i>EWD</i> (g cm ⁻³)	0.411	0.031	7.6	0.324	0.489	0.749
<i>LWD</i> (g cm ⁻³)	0.687	0.035	5.0	0.590	0.765	0.033
<i>LWP</i> (%)	25.9	6.1	23.7	7.4	45.0	0.356
<i>RW</i> (mm)	5.13	0.73	14.2	3.10	7.80	0.286
<i>HI</i> (g cm ⁻³)	0.134	0.019	14.4	0.077	0.179	0.312

RD = Average Ring Density; *MND* = Minimum Density; *MXD* = Maximum Density; *EWD* = Earlywood Density; *LWD* = Latewood Density; *LWP* = Latewood Percentage; *RW* = Ring Width; *HI* = Heterogeneity Index; (*) - source: Louzada and Fonseca [48].

genetic correlation between young age and the same trait at older ages makes it possible to perform a selection at a very juvenile cambial age (< 6 years old).

On the other hand, as these traits show consistent high heritability values in some rings (cambial age) [48], it would be forecasted that these wood density components are controlled by the some genes over the time, and the genetic variation appears to be large enough to permit reliable selections for these traits.

For the *LWP*, *RW* and *HI*, as age-age genetic correlations only were close to 1 after ring 6, and exhibit lower heritability values, the estimate of these adult wood density components will not be made before the 6th ring age.

Regarding Latewood Components (*MXD* and *LWD*), both age-age genetic correlations and heritability values are very low or even null. So, the inclusion of these components should have in theory a very limited value in future breeding programmes.

Although it is extremely rare to find bibliographic references about age-age genetic correlations for wood density components, these results are the same in a certain way of these obtained for *Picea abies* [38] and *Pseudotsuga menziesii* [70]. The Earlywood Density components at cambial age 12 or 15, respectively, showed strong genetic correlations with their respective trait at all younger ages and Latewood components showed a somewhat slower appearance and it generally remained below other traits.

3.2. Genetic correlations between traits

Table IV lists the estimated genetic correlations and its associated standard deviation, as well as the phenotypic correlations for all density components at different ages.

The high and positive phenotypic relationships for some traits had apparently strong genetic basis. In these traits, the genotypic correlations was consistently higher than phenotypic

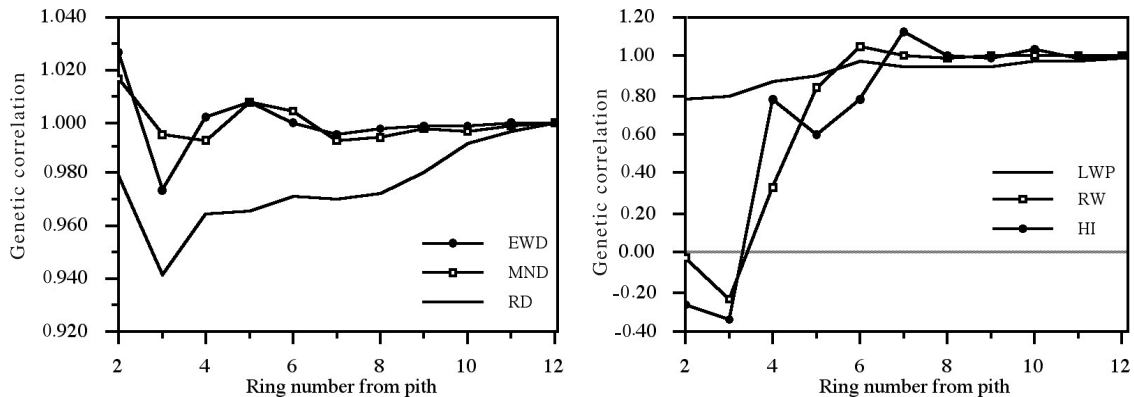


Figure 1. Age-age genetic correlation between each ring number from the pith and the corresponding value at ring 13, for different traits. (*MXD* and *LWD* are not represented because their estimate were quantified with 0 value, or not calculated, in almost rings).

Table III. Age-age genetic correlation (standard error in brackets) between three different ring ages (6, 10 and 13) for each wood density components.

Wood density component	Age		10	13
	Age			
<i>RD</i>	6		0.986 (0.0020)	0.972 (0.0040)
	10			0.992 (0.0012)
<i>MND</i>	6		1.003 (—)	1.004 (—)
	10			0.996 (0.0006)
<i>MXD</i>	6		NC	0.000 (0.3996)
	10			NC
<i>EWD</i>	6		1.001 (—)	1.000 (—)
	10			0.999 (0.0001)
<i>LWD</i>	6		NC	NC
	10			NC
<i>LWP</i>	6		0.991 (0.0016)	0.972 (0.0052)
	10			0.977 (0.0046)
<i>RW</i>	6		1.024 (—)	1.045 (—)
	10			1.001 (—)
<i>HI</i>	6		0.822 (0.0436)	0.774 (0.0448)
	10			1.041 (—)

RD = Aver. Ring Dens.; *MND* = Min. Dens.; *MXD* = Max. Dens.; *EWD* = Earlywood Dens.; *LWD* = Latewood Dens.; *LWP* = Latewood Perc.; *RW* = Ring Width; *HI* = Heterogeneity Index. NC = Not Calculated (the estimate of the family mean squares was null in at least one ring). (—) = It was quantified with null value (correlation coefficient is ≥ 1).

ones. Nepveu [54] noted that if environmental effects are assumed to be independent, the phenotypic covariance becomes a genetic covariance. He further suggest that the phenotypic correlation becomes a lower limit for the corresponding genetic correlation.

In this study at least for *RD*, *MND*, *EWD* and *LWP* phenotypic correlation coefficients can help to explain the corresponding genetic correlations and, as these coefficients are high, it suggests that selection for one trait should result into a simultaneous response in other traits.

3.2.1. Average Ring Density (*RD*), Earlywood Components (*EW*) and Latewood Components (*LW*)

The Average Ring Density (*RD*) represents an important dependency with Earlywood components (*MND* and *EWD*),

to which the genetic component should be associated in a large measure.

Given that in *RD* and *EW* components the difference between progenies are always significant statistically ($P < 0.05$), their genetic correlation coefficients themselves are always high and present a reduced standard deviation, at any age. Therefore, in principle, they should be controlled simultaneously by the same set of genes. So, the selection of one of these components will result in a substantial correlated response in the others. This surprisingly high importance of the earlywood in affecting other traits was enhanced by Zobel and van Buijtenen [81] and also confirmed for *Picea mariana* [74, 76] and *Pseudotsuga menziesii* [69].

On the other hand Latewood components (*MXD* and *LWD*) not only reveal a genetic correlations globally inferior between

Table IV. Genetic (upper triangle) and phenotypic (lower triangle) correlation coefficients between all wood density components weighted at ages 6, 10 and 13.

	Age	RD	MND	MXD	EWD	LWD	LWP	RW	HI
RD	6		0.990 (0.0015)	0.975ab (0.0075)	0.978 (0.0031)	NC	0.992 (0.0014)	0.323 (0.1035)	-0.505ab (0.0773)
	10	1.011 (-)		NC	0.998 (0.0003)	NC	1.045a (-)	0.096b (0.1053)	-1.011ab (-)
	13	1.003 (-)	1.003 (-)	0.327ab (0.2552)	0.990 (0.0017)	0.050ab (0.2654)	1.060a (-)	0.108 (0.1105)	-0.692ab (0.0567)
MND	6	0.966		0.831ab (0.0454)	1.008 (-)	NC	0.953 (0.0080)	0.364 (0.0968)	-0.661ab (0.0564)
	10	0.965	1.005 (-)	NC	1.005 (-)	NC	1.098a (-)	0.165 (0.0981)	-1.018ab (-)
	13	0.967	0.060ab (0.2729)	0.060ab (0.2729)	1.004 (-)	-0.259ab (0.2379)	1.106a (-)	0.253 (0.1003)	-0.780ab (0.0408)
MXD	6	0.788	0.639		0.814ab (0.0470)	NC	1.227ab (-)	0.049ab (0.2250)	-0.096ab (0.2006)
	10	0.637	0.443	0.609	NC	NC	NC	NC	NC
	13	0.619	0.435	0.419	0.041ab (0.2607)	1.217ab (-)	0.820ab (0.1056)	-1.588a (-)	0.701ab (0.1708)
EWD	6	0.959	0.996	0.971		NC	0.923 (0.0122)	0.377 (0.0909)	-0.691ab (0.0497)
	10	0.959	0.998	0.985	0.609	NC	1.059a (-)	0.191 (0.0923)	-1.034ab (-)
	13	0.960	0.997	0.983	0.401	-0.271ab (0.2253)	1.063a (-)	0.263 (0.0951)	-0.804ab (0.0351)
LWD	6	0.708	0.534	0.971	0.507		NC	NC	NC
	10	0.573	0.375	0.985	0.350	0.794	NC	NC	NC
	13	0.521	0.327	0.983	0.291	0.203ab (0.2878)	0.203ab (0.2878)	-0.593a (0.2084)	0.324ab (0.2799)
LWP	6	0.955	0.865	0.854	0.845	0.640	0.794	0.232 (0.1268)	-0.245ab (0.1130)
	10	0.967	0.888	0.709	0.874	0.640	0.640	0.126ab (0.1198)	-1.016ab (-)
	13	0.972	0.908	0.677	0.891	0.575	0.575	0.171ab (0.1225)	-0.660ab (0.0693)
RW	6	0.180	0.208	-0.008	0.254	-0.074	0.091		-0.598a (0.0990)
	10	0.028	0.082	-0.203	0.120	-0.242	0.009		-0.879a (0.0354)
	13	0.048	0.123	-0.236	0.156	-0.310	0.045		-0.959a (0.0105)
HI	6	0.024	-0.215	0.580	-0.255	0.670	0.256	-0.334	
	10	0.009	-0.236	0.742	-0.266	0.782	0.165	-0.396	
	13	-0.026	-0.257	0.739	-0.295	0.808	0.093	-0.456	

-RD = Aver. Ring Dens.; MND = Min. Dens.; MXD = Max. Dens.; EWD = Earlywood Dens.; LWD = Latewood Dens.; LWP = Latewood Percent.; RW = Ring Width.; HI = Heterogeneity Index.

-“NC” genetic correlation was not calculated, because the estimate of the family expected mean squares was null in at least one of the traits.

- Standard errors of genetic correlation are given in parentheses and (-) indicates that this one was quantified with null value because the correlation coefficient is ≥ 1 .

- “a” - in the analysis of variance the differences among families were not significant ($P > 0.05$) in at least one of the traits.

- “b” - in the analysis of covariance the differences among families were not significant ($P > 0.05$).

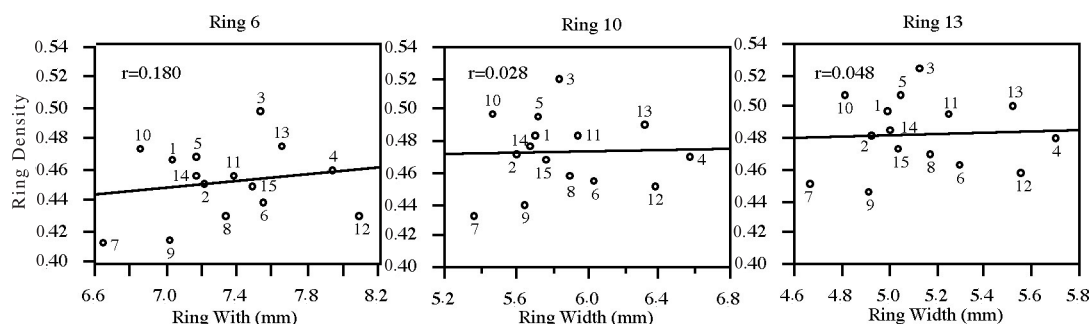


Figure 2. Regression plot between Ring Width (*RW*) and Average Ring Density (*RD*) at ring ages 6, 10 and 13. The symbol (○) represents one family, with respective number.

them as do the other components (which means that these ones should be controlled by different set of genes). Also they do not inspire confidence due to the fact that they are associated with high standard deviations and according to the results of variance and covariance analysis, the differences between families are not statistically significant.

So, there is no doubt that LW is much more affected by environmental variations than the EW. This (EW) not only reflects a better tree genetic potential but also is controlled over years, in a large way, by the same genes. The EW manipulation allows a significant correlated response in other components (*RD* and *LWP*) and all estimations may be done earlier than those obtained from *LW* components. These results are in some way confirmed for *Picea mariana* [74, 77] and *Pseudotsuga menziesii* [69].

3.2.2. Latewood Percentage (*LWP*)

For the *LWP*, we can verify that it is positively genetically correlated with the other components (except the *HI*) but coefficients are globally higher and standard deviation is less in *EW* components (*MND* and *EWD*), relative to *LW* (*MXD* and *LWD*). In this way, it is easy to expect that the *LWP* increase selection has a correlated response by an improvement of *RD* and *EW* components; this response is much more expressive than those obtained by *LW* components. These results confirm [74] but disagree with [4, 10, 76].

3.2.3. Ring Width (*RW*)

We can easily understand that the relationship of wood density with growth rate is highly important, not only of a scientific interest, but of crucial importance to tree breeders and forest managers [78, 81]. “This relationship directly influences genetic gain, economic return of breeding program, and the quality of wood from intensively managed plantations” [77] (p. 98). Although many researchers have been undertaken on this relationship over decades, many controversial results have been reported.

Many foresters believe that faster growing trees have lower density. Though this appears to be the cause for some tree species such as *Picea abies* [17, 52] and *Picea sitchensis* [67], Abdel-Gadir et al. [4] said “...most hard pines show a lack of correlation between growth rate and wood density”. The same conclusion was expressed by Zobel and Buijtenen [81]: “In

summary, it appears that for the hard pines there is generally little or no relationship between wood specific gravity and growth rate” (p. 170) and by Zobel and Jett [78]: “... weak or moderately positive genetic correlations have been found in loblolly pine, slash pine, maritime pine, and poplar hybrids.” (p. 279) and “Most of the conifers with dense wood, especially the hard pines, show little or no meaningful relationship between growth rate and specific gravity. These are, however, numerous exceptions” (p. 217).

Effectively, even though some works have shown a negative genetic and/or phenotypic correlation for *Pseudotsuga menziesii* [44, 49, 69] and *Tsuga heterophylla* [24], others have shown a very low or an inexistent genetic and/or phenotypic correlation for *Pseudotsuga menziesii* [4], *Picea mariana* [74, 76, 77], *Picea abies* [23], *Abies grandis* [14], *Pinus radiata* [21, 57], *Pinus taeda* [10, 50] and for several conifers [73], while [71] mentions a moderately positive genetic correlation for *Pinus taeda*, [40] for several conifers, and [13] a high and positive phenotypic correlation for *Pinus peuce*.

In this context, the small but consistently positive genetic correlations between the *RW* and *RD* are highly important (figure 2).

Although these positive correlations between wood density and ring width agree with other works done in Portugal [30, 47], Spain [27] and a work done in France [41] where he obtained genetic correlation between 0.38 and 0.49, they disagree with other studies done in France. One [18] obtained genetic correlations between -0.64 and -0.89 . Another one [16] mentioned a phenotypic correlation of -0.44 . Nevertheless, it is important to point out that, in that study, the age effect is confounded (juvenile wood/mature wood). So, according to Zobel and Buijtenen [81]: “... it is not acceptable to relate wood properties to ring width with rings of different ages. Yet, this has frequently been done in the past and is still being done, leading to false and controversial ideas about the effect of growth rate” (p. 159).

However, if we admitted that *Pinus pinaster* in France exhibits a negative relationship between density and ring width, this does not mean that this relationship can not be different in another site or in other conditions. As an example [4] concluded for *Pseudotsuga menziesii* wood that “Being negatively correlated with Earlywood Width and positively with Latewood Width, tree average Ring Density appears to

have a weak, nonsignificant phenotypic correlation with Ring Width, but a very strong correlation with Latewood Percentage in both juvenile and mature wood. When data are sorted by plantation, tree Ring Density relates negatively to Ring Width at the less favourable site, but the relationship is weak in the fast-growing trees at the more favourable site. Based on provenance or family averages over plantations, the relationship between Wood Density and Ring Width is either positive or non-existent" (p. 190).

Also [77] refers "The relationship between wood density and growth, to some extent, also varies with location. It appears that in a species where a negative relationship between wood density and growth exists, the negative relationship tends to be weaker in the trees growing in a more favourable environment. In other words, growth rate of the trees growing in a favourable environment probably has less negative impact on wood density than that of the trees growing in a less favourable environment" (p. 97).

Thus we can conclude that the relationship between wood density and growth rate found in one location can not necessarily be applied to the others.

This aspect is important. In the genetic point of view it is important because it may define some future strategies in breeding programmes (if this relationship is positive, a designed change in one characteristic results in a designed change in the other). But it is also true in the economic point of view. Unfortunately, in Portugal remains still the idea that fast-growing timber will not be strong and it has been the main impediment for the *P. pinaster* wood with large growth to be ranked as good quality wood. Inclusive, Fernandez-Golfín and Diez [27] mentioned that based on unadjusted rules for the species and the environmental conditions of the South of Europe, this point has contributed to creating technical barriers in using fast growth species woods, and has favoured slow growth species from northern regions.

For the other traits, we did not detect any adverse correlation. The correlations between the RW and EW or LWP components are consistently positive and are negative with the HI. On the other hand, these correlations present a mixed behaviour with Latewood components (some of them present a positive relation, some of them negative and some of them independent), but with no great practical importance. Big mistakes in the estimate go beyond the coefficient correlation value itself in some cases.

So, we may expect that the RW selection has a genetically correlated response expressed as a small increase of RD, EWD and LWP without a Latewood significant change, which allows a decrease of the intraring variability (HI).

3.2.4. Heterogeneity Index (HI)

Heterogeneity Index (or intraring variability) is one of the most important wood features [50, 55, 68, 80, 81]. The wish of most wood industries is to have more uniformity in the wood raw material, not only at inter-ring level (Juvenile/Mature wood), but also at intraring one (Earlywood/Latewood). Zobel and Jett [78] said: "Uniformity in wood is a major demand by the manufacturers of all wood products" [16]. It will be less expensive to manufacture, and the wood uniformity will make a more uniform product [81]. For example, high heterogeneity

causes a variation increase of veneer thickness and more veneer fissures [6, 12, 43]. The knowledge of the genetic relationships among wood density components and the heterogeneity (HI) might help to minimise hypothetical undesirable correlated responses when it is selected for increasing wood density [57, 69].

In this study we usually find that HI is negatively correlated with RD, MND, EWD, LWP and RW, and positively with MXD and LWD. This favourable association has also been observed for *Picea mariana* [74, 77], but not for *Pseudotsuga menziesii* [69].

Another favourable association is the negative correlation between HI and RW. In this way, we can anticipate that the selection for wood density and/or ring width might be rewarded by a significant reduction in intraring variability (HI).

Nevertheless, we have to mention that this work cannot extrapolate these results in other circumstances and cannot obtain credible conclusions about genetic relationship between HI and other density components, because the differences between families are not significant ($P > 0.05$) and the standard deviation presents high values.

4. CONCLUSION

The age-age genetic correlations for Average Ring Density (RD) and Earlywood components (MND and EWD) are sufficiently strong to suggest that the retention of progeny tests to 13 years gives a little future advantage over selection at 6 years, or even younger. The innermost 6 rings could provide an information equivalent to those obtained at 13 years old.

The Average Density (RD) depends much more on Earlywood components (MND, EWD) with which it maintains a high genetic correlation than on Latewood components (MXD, LWD). In this case it is possible to make a good estimate of the genetic gain to be obtained by the RD through the genetic gain related to the EW density selection, and also to make an early selection, because these correlations exist at the early ages of the trees (juvenile wood).

On the other hand, Latewood components reveal fewer and unstable genetic correlation values. This means that, despite exhibiting a weaker dependence, they are controlled by different gene sets. So, will not afford any significant genetic gain.

Even the LWP is positively and genetically correlated to the other components (except with HI), where is evident that the result is higher with EW components than with LW ones. So, we may expect that a selection for LWP increase has a correlated response, improving RD and EW components, which are more expressive than LW ones. Then it will lead to a ring heterogeneity decrease.

Regarding ring width (RW), no unfavourable genetic correlations with the other components have been detected. Correlation coefficients are globally low and positively correlated genetically with RD, MND, EWD and LWP, negatively with HI, and irregular with MXD and LWD. The antagonism between growth rate and wood density mentioned for other species has not yet been confirmed for *Pinus pinaster* in this environment. Thus it permits to refute, once again, the wrong idea, which is, unfortunately, deeply established in many researchers and wood users' minds, that trees with a

higher radial growth produce bad wood quality, mainly a lower density and LWP.

About Heterogeneity Index (HI), although the differences between families have always been not significant ($P > 0.05$) and standard deviation values of the correlation coefficients have been usually high, this study revealed an favourable negative correlation between this trait and wood density components and ring width. This is one of the most appreciated characteristic of wood industries, considering the production of an uniform product.

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