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Original article

The heritability of wood density components in *Pinus pinaster* Ait. and the implications for tree breeding

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Abstract – The main objective of this work was to evaluate the genetic control of *Pinus pinaster* wood quality by estimating the heritability of wood density components and its age evolution. The material was collected from 180 trees by the extraction of an increment core, in a progeny test at 18 years old. The wood density components were measured using the X-ray densitometry technique. The highest and most stable age heritability values were obtained by the earlywood components (minimum density and earlywood density), followed by the average ring density. The latewood percentage, ring width and heterogeneity revealed middle values, while the latewood components (maximum density and latewood density) always presented the lowest and most unstable heritability values. Thus, it was concluded that, amongst all components, the earlywood density mostly depends on genetic effects, and could be used in future selection and tree breeding programs to improve wood quality. The inclusion of the latewood components in the selection criterion will not give any significant genetic advantage.

tree breeding / heritability / wood quality / wood density components / *Pinus pinaster*

Résumé – Héritabilité des composantes de la densité du bois chez *Pinus pinaster* Ait. et implications pour l'amélioration génétique. L'objectif principal de ce travail était l'étude du contrôle génétique de la qualité du bois du *Pinus pinaster* Ait., grâce à l'estimation de l'héritabilité des composantes de la densité et de son évolution avec l'âge. Des carottes de sondage ont été extraites de 180 arbres appartenant à un test de comparaison de descendances maternelles âgés de 18 ans depuis la plantation. Les composantes de la densité ont été définies à l'aide de la microdensitométrie sur radiographie aux rayons X. Les valeurs d'héritabilité les plus élevées et les plus stables avec l'âge cambial sont des composantes du bois initial (densité minimale et densité du bois initial), suivies de la densité moyenne. Le pourcentage de bois final, la largeur des cernes et l'hétérogénéité ont présenté des valeurs moyennes, alors que les composantes du bois final (densité maximale et densité du bois final) ont toujours présenté les valeurs les plus basses et les plus instables d'héritabilité. Ainsi, on a pu conclure que, parmi toutes les composantes, la densité du bois initial apparaît la plus dépendante des effets génétiques. Donc, elle pourra être utilisée dans de futurs programmes de sélection et d'amélioration génétique. Quant aux composantes du bois final, leur introduction parmi les critères de sélection, n'apporte aucun bénéfice en terme de gain génétique.

amélioration génétique / héritabilité / qualité du bois / composantes de densité du bois / *Pinus pinaster*

1. INTRODUCTION

Pinus pinaster (Maritime Pine) is the main forest species in Portugal. This is not only because of the area it covers, but is also, at the economic level, due to its multiple industrial wood applications (lumber and timber, plywood, particleboard, fiberboard, paper, as well as resin products); it can also be considered as the only softwood source in the country.

This species is also an important softwood supplier in almost all the Mediterranean Basin (France, Spain, Italy), as well as in South Africa, New Zealand and Australia, where it was introduced between 1940–1950. According to Hopkins and Butcher [23], in Western Australia alone, 30 000 ha of this species had already been planted by 1990.

With the trend in forest management to gradually short the rotation age (using younger and younger trees) and as wood is

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the final product of many forestry activities, quality has become one of the major concerns of many forest product industries [6, 39, 51, 53].

It has gradually been realized that wood quality and quantity cannot be treated as independent factors and that wood quality improvement should form an integral part of most breeding programs [1, 2, 40, 48, 50, 52]. Therefore there is no doubt that wood density is an ideal subject for genetic manipulation. Wood density constitutes a key characteristic of wood quality [11, 33, 53]; it presents great variations between trees as well as high heritability [4, 5, 43, 50] with a reduced Genotype × Environment interaction [45, 46].

However, the understanding of 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 density components and then can be manipulated through the alteration of one or more of them.

Therefore, the knowledge of 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 programs.

So, several studies have been made in different species, and all of them agree that wood density is under a strong genetic control, but they have revealed some contradictory results in terms of density components.

For instance, while Nicholls et al. [32] verified that, in *Pinus radiata* wood, maximum density was the component which allowed the highest genetic control, in *Cryptomeria japonica*, Fujizawa et al. [16] concluded that genetic control is carried out by average ring density, followed by earlywood components, though latewood components and latewood percentage always produced the lowest heritability values.

Identical results were obtained by Vargas-Hernandez and Adams [40, 41] with *Pseudotsuga menziesii*, but Zhang and Morgenstern [48] and Zhang and Jiang [49] demonstrated that in *Picea mariana* the density component which best expresses the higher genetic differences among trees is not average ring density, but earlywood density.

Concerning *Pinus pinaster* wood, as early as 1970 Nicholls [31] began 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 growth traits and tree form [3, 7, 18–20, 22, 23, 27], and notwithstanding studies developed in France by Polge and Illy [36], Keller [26] Nepveu [30], and Chaperon et al. [8], big gaps still exist in the extent of knowledge about the genetic control of the wood properties of this species.

This research continues the studies started by Gomes [18] about the evaluation of some genetic parameters, for the seeding, growth and tree form of the most important forest species of Portugal, now complemented for wood quality through density.

In this context, the present investigation does not intend to be more than an initial study of the species, carried out with the aim of estimating, ring by ring, the relative contribution of genetic and environmental factors in the variation of average ring density, and its components, and evaluating some implications for tree breeding.

2. MATERIALS AND METHODS

The material, used in this study, was obtained from a progeny test with 15 open-pollinated families, collected by Gomes [18] in different regions of Portugal (5 in Viana do Castelo, 5 in Mondim de Basto, and 5 in Leiria), planted in 1979 in the North of Portugal near Bragado (41º 30' N, 7º 39' W, elevation 750 m), and established in 3 completely randomized blocks represented by 10 trees per plot [18]. In each plot 4 trees were sampled, giving a total of 180 trees.

The material submitted to analysis was collected 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-rayed and their image scanned by microdensitometric analysis in order to determine the density components according to the process described by Louzada [29]. A comprehensive description of X-ray densitometry analysis can be found in Polge [34, 35], Hughes and Sardinha [24].

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 the fixed value of 0.550 g cm^{-3} density as the limit between Earlywood/Latewood. The advantages of this criterion for the EW/LW boundary based on a fixed density value are explained by Jozsa et al. [25]. In the present study, we chose this fixed value of 0.550 g cm^{-3} because it is the most accurate for *Pinus pinaster* wood of more or less 20 years old [29]. The intra-ring density variation was quantified by the Heterogeneity Index (HI), proposed by Ferrand [13], expressed by the standard deviation of density values (all X-ray data points) across the annual ring.

The genetic control of these wood density components, weighted in each ring by their respective sectional area, was evaluated by estimating individual-tree heritability (h^2_i) according to Falconer [12]. However, because open-pollinated families in the progeny test came from parent trees in wild stands, the additive genetic variance (σ^2_A) was estimated as 3× the family component variance (σ^2_F). The coefficient of relationship did not assume a 0.25 value (as it is usual), but 0.33 because some degree of inbreeding (about 10%) was thought to have occurred in the relatively small populations, making heritability values more conservative [37]. Therefore, the individual

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	$\sigma^2_\varepsilon + t\,\sigma^2_{FB} + tf\,\sigma^2_B$
Family (F)	f-1	$\sigma^2_\varepsilon + t\,\sigma^2_{FB} + tb\,\sigma^2_F$
B × F	(b-1) (f-1)	$\sigma^2_\varepsilon + t\,\sigma^2_{FB}$
Residual (Trees/F/B)	(t-1) $f\,b$	σ^2_ε

b = number of blocks (3); f = number of families (15); t = number of trees/family/block (4). σ^2_B, σ^2_F, σ^2_{FB}, and σ^2_ε are variance components due to block, family, block × family interaction and residual (or error), respectively.

heritability (h^2_i), additive genetic variance (V_A), and total phenotypic variance (V_P) estimators were calculated as follows:

$V_P = \sigma^2_F + \sigma^2_{FB} + \sigma^2_\varepsilon$

$V_A = 3.\ \sigma^2_F$

$h^2_i = V_A/V_P$,

where σ^2_F (Family variance), σ^2_{FB} (Family × Block variance), and σ^2_ε (Residual variance) were estimated by the analysis of the variance, presented in *table I*.

The standard errors of heritability σ^2_{hi} were computed as follows [44]:

$$\sigma^2_{hi} = \frac{\left(1-\frac{h^2}{4}\right)\times\left[1+(b\times t-1)\frac{h^2}{4}\right]}{\sqrt{\frac{b\times t}{2}(b\times t-1)\times(f-1)}}$$

where h^2_i is the individual heritability and b, f, and t, are the number of blocks, families, and trees/family/block, respectively.

3. RESULTS

The summary statistics, at tree level, and the individual heritability values, ring by ring up to 13 years old, of each density component are given in *tables II* and *III*.

Table II. Descriptive statistics table for different wood density components at tree level (for 180 trees).

Trait	mean	std. dev.	coeff. var.	min.	max.
RD (g cm^{-3})	0.483	0.041	8.4	0.359	0.585
MND (g cm^{-3})	0.354	0.038	10.8	0.240	0.454
MXD (g cm^{-3})	0.779	0.061	7.8	0.618	0.921
EWD (g cm^{-3})	0.411	0.031	7.6	0.324	0.489
LWD (g cm^{-3})	0.687	0.035	5.0	0.590	0.765
LWP (%)	25.9	6.1	23.7	7.4	45.0
RW (mm)	5.13	0.73	14.2	3.10	7.80
HI (g cm^{-3})	0.134	0.019	14.4	0.077	0.179

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.

3.1. Average ring density (RD)

These results emphasize, first of all, the fact that the average ring density (RD) is under a strong genetic control, with heritability values always higher than 0.528.

Comparatively, Chaperon et al. [8] estimated, also for a 14 years old *Pinus pinaster* wood, an h^2_i = 0.44 value for specific density. Identical h^2_i values ranging between 0.43 and 0.47 were obtained by Nicholls et al. [32] for *P. radiata*, Talbert et al. [38] for *P. taeda* and Yanchuk and Kiss [45] for *Picea engelmannii*. Only Vargas-Hernandez and Adams [41] and Zhang and Morgenstern [48] estimated an h^2_i = 0.60 value for RD for *Pseudotsuga menziesii* and *Picea mariana*, respectively.

3.2. Earlywood components vs. latewood components

Another important aspect is the fact that the heritabilities of earlywood components (MND, EWD) are always greater than RD and even greater than the latewood components (MXD, LWD). Inclusively, for all the density components analyzed, the highest heritability values were always obtained in earlywood and the lowest in latewood components.

Although these results were expected, in a certain sense because of the results from previous works [14, 15, 28], they take on an extraordinary relevance as they should and will be able to condition the future operational strategies of tree breeding and genetic improvement programmes in this species.

On the one hand, they confirm, unequivocally, that in Maritime Pine the genetic control of wood density is much more intense in earlywood components, so that they should respond well to breeding in future improvement programmes, while the variation of latewood components is almost entirely dependent on environmental factors.

On the other hand, they clarify the issue about the possible advantage or disadvantage of including density components in the selection criteria. In the study done by Vargas-Hernandez and Adams [40] of 60 families of the *Pseudotsuga menziesi*i at 15 years old, the conclusion was that although the density components varied significantly among families and displayed a moderate genetic control, none of them presented a higher heritability than RD (these results correspond with those obtained by Nicholls et al. [32] for the *P. radiata* and Fujizawa et al. [16] for the *Cryptomeria japonica*). So, these components should have, in theory, a limited value in the improvement of the selection efficiency for wood density.

One year later, these results were confirmed by complementary work also carried out by Vargas-Hernandez and Adams [41] in the same experiment. They verified that the inclusion of the three density components (EWD, LWD,

Table III. Heritability values (with standard errors given in brackets) estimated ring by ring at age 13, for different wood density components.

Ring	RD	MND	MXD	EWD	LWD	LWP	RW	HI
2	0.6092	0.5863	0.5450	0.5154	0.5155	0.4001	0.0569 a	0.2659
	(0.0746)	(0.0733)	(0.0710)	(0.0693)	(0.0693)	(0.0622)	(0.0375)	(0.0532)
3	0.7362	0.8441	0.2888 a	0.8650	0.0522 a	0.2748	0.1571 a	0.0629 a
	(0.0812)	(0.0862)	(0.0548)	(0.0871)	(0.0371)	(0.0538)	(0.0453)	(0.0380)
4	0.7340	0.8519	0.3350 a	1.0103	0.1153 a	0.2678 a	0.1372 a	0.2705 a
	(0.081)	(0.0865)	(0.0579)	(0.0929)	(0.0421)	(0.0533)	(0.0438)	(0.0535)
5	0.6804	0.7625	0.2129 a	0.9149	0.0874 a	0.2795 a	0.2042	0.2834 a
	(0.0784)	(0.0825)	(0.0494)	(0.0892)	(0.0399)	(0.0541)	(0.0488)	(0.0544)
6	0.7382	0.8374	0.0971 a	1.0014	---- a	0.4355	0.1994	0.2751 a
	(0.0813)	(0.0859)	(0.0407)	(0.0926)		(0.0644)	(0.0484)	(0.0538)
7	0.6939	0.7650	---- a	0.9833	---- a	0.4197 a	0.2374	0.1121 a
	(0.0791)	(0.0826)		(0.0919)		(0.0634)	(0.0511)	(0.0418)
8	0.6644	0.7511	---- a	0.9341	---- a	0.4368 a	0.3020	0.1835 a
	(0.0776)	(0.0819)		(0.0900)		(0.0645)	(0.0557)	(0.0472)
9	0.6369	0.7265	---- a	0.9022	---- a	0.4135 a	0.3206	0.1639 a
	(0.0761)	(0.0807)		(0.0887)		(0.0630)	(0.0569)	(0.0458)
10	0.5774	0.6971	---- a	0.8381	---- a	0.3596 a	0.3160	0.1718 a
	(0.0728)	(0.0792)		(0.0859)		(0.0595)	(0.0566)	(0.0464)
11	0.5288	0.6497	---- a	0.7797	---- a	0.3419 a	0.3142	0.2363 a
	(0.0701)	(0.0768)		(0.0833)		(0.0583)	(0.0565)	(0.0511)
12	0.5280	0.6430	---- a	0.7752	---- a	0.3459 a	0.3020	0.2918 a
	(0.0700)	(0.0764)		(0.0831)		(0.0586)	(0.0557)	(0.0550)
13	0.5411	0.6309	0.0282 a	0.7486	0.0329 a	0.3560 a	0.2858	0.3120 a
	(0.0708)	(0.0758)	(0.0352)	(0.0818)	(0.0356)	(0.0593)	(0.0546)	(0.0564)

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, because the estimate of the expected mean square among Families was also null.

LWP) in the selection criteria would only give an advantage in the case of the selection made between 7 and 10 years old, although with a reduced increase of the relative efficiency (between 1 and 6%). Above or below those ages, the inclusion of those components did not produce any advantage in genetic terms, so that its practical use was extremely limited.

Zhang and Morgenstern [48], Zhang and Jiang [49] and Zhang [47] also obtained for the *Picea mariana* values of individual heritability (restricted sense) for some density components (EWD and LWD) which were slightly higher than those of the RD, but without a significant increase in the use of these components in the selection criterion only proportioned by RD (+ 3.42% and 3.30% respectively). For the current *Pinus pinaster* study, due to the important superiority in hereditary transmission terms shown by EW components related to LW and even RD ones, we think that their inclusion in selection criteria should be very advantageous in future genetic programmes.

In this way, it is possible to increase EWD; this one will provide not only an increase of wood density, but also a decrease of wood heterogeneity. It allows one to improve the wood quality of this species significantly.

3.3. Latewood percentage (LWP), ring width (RW) and heterogeneity index (HI)

For the other density components (LWP, RW and HI), it was shown that even though they did not produce significant statistical differences ($P > 0.05$) between progenies in many cases, an important part of this variation is not due to genetic factors but, on the contrary, to environmental ones. That is why heritability values are in general moderate or low, lower than RD values and EW components, but substantially higher than LW components.

As for the RW, and considering the fact that for *Pinus pinaster* the characteristics related to the increase (in diameter) almost always present rather low heritability values [8, 10, 19, 23], the study produces surprisingly significant RW differences ($P < 0.05$) between families where heritability values reach 0.3 or even slightly higher. This proves that diameter growth can also be under an appreciable genetic control, and, if it does not express negative genetic correlations with the other density components, it will allow the genetic manipulation of the wood quantity and quality of this species.

Regarding the HI, moreover the differences between families are not statistically significant ($P > 0.05$), heritability

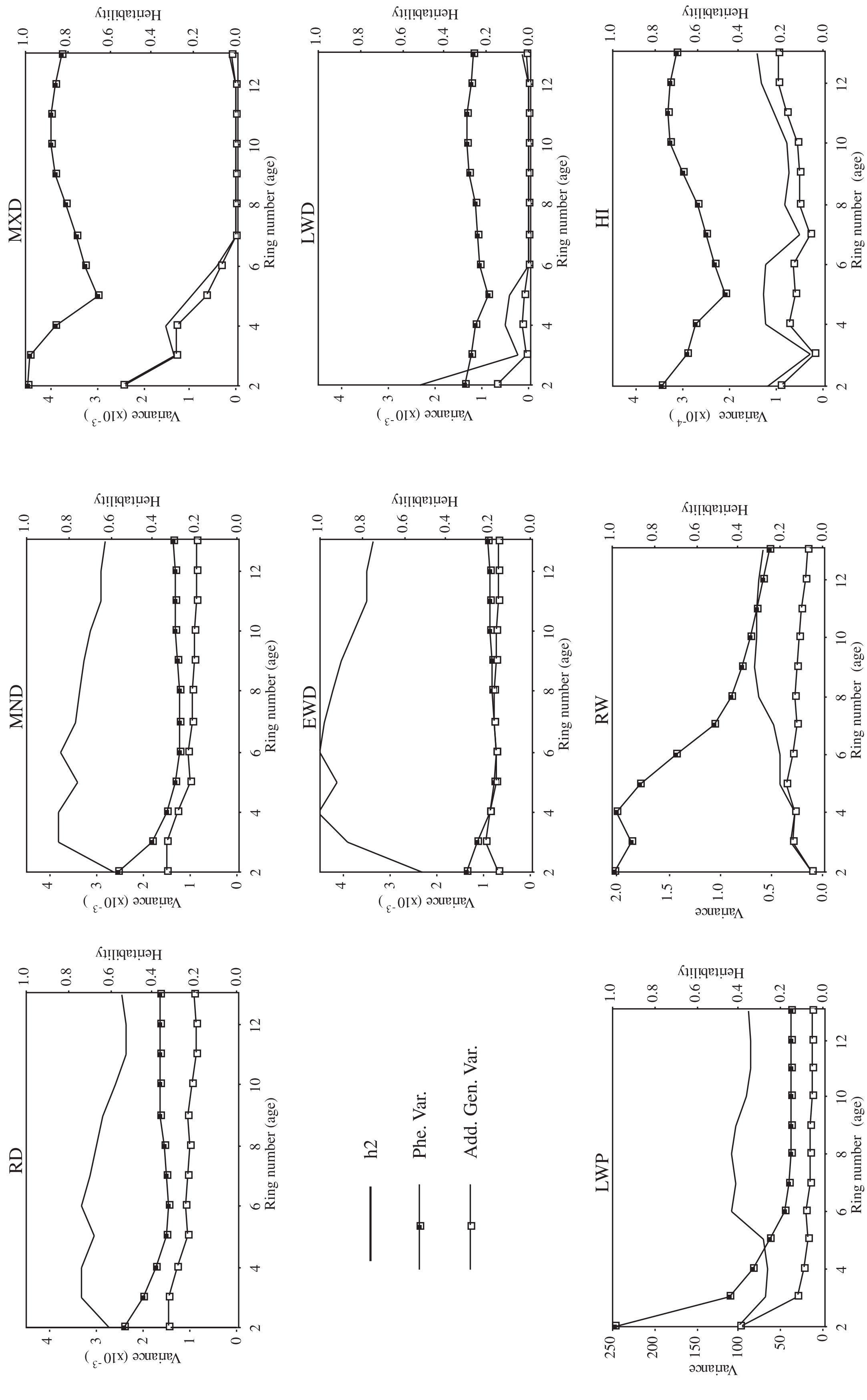

Figure 1. Age trends in phenotipic (—■—) and additive (—□—) variance components, and individual heritability (———), for average ring density and its components.

values are almost all nearly median, so the expected profits from the tree breeding of the ring heterogeneity will not be promising.

3.4. Heritability value variation with age

Given that in this study the heritability values of the different wood characteristics were estimated ring by ring, it is also possible to evaluate the temporal changes of the genetic control of these characteristics. This information is important because it is not possible to delay the tests till rotation age, so the efficiency of the tree breeding programmes really depends on the capacity to be able to predict mature wood characteristics at a young age; characteristics which are conditioned, in their turn, by the maintenance of high heritability values in juvenile and adult stages and by strong genetic correlations between these two types of wood [9, 17, 21, 41, 42].

In order to interpret the evolution of heritability values with age more easily, the values already presented in *table III* are presented graphically in *figure 1*, along with the age evolution of additive genetic and phenotypic variances.

So, it is possible to verify that, compared to LW, EW components are under a strong genetic control and also present a higher genetic age stability.

Effectively, in EW components, an important part of the phenotypic variance is due to the additive genetic component (which results in a higher heritability value), for which variance stays practically unchanged with age, particularly after the 5th year. In LW components, only the first years present a small, but unstable, genetic control which is due to a sudden decreased tendency related to age, that culminates in very low or even null additive genetic variance values, from the 6th or 7th year.

On the other hand, with regard to the genetic control evolution in the characteristics related to the radial growth of trees (LWP and RW), a tendency for an increase of the heritability till the 6th to 8th year is noticed, followed by a stabilization. This tendency was not related to the possible increase of the additive genetic variance, but only to an accentuated decrease of the phenotypic variance until this age. This high phenotypic variance during the first years (due mainly to environmental components) could be related to the fact that the juvenile trees are very sensitive to the interaction between climate condition and the effects of land preparation, installation and individual adaptation. So only from 6 to 8 years old can they express clearly all genetic potential.

Regarding the HI, the study has verified that even though the extreme analogy between the age evolution of the heritability and the additive genetic variance values, present really low values, with a certain instability and do not reveal any great confidence (the F value for the Families is always not-significant). Nevertheless, the results obtained from ring heterogeneity should be very low in comparison with the other characteristics, mainly the EW ones.

4. CONCLUSION

Even though the average ring density (RD) is a wood characteristic under a strong genetic control, their components behave very differently. While the EW ones show a high dependency on genetic effects (with high and stable heritability values in relation to age) the LW ones present the lowest and least stable heritability values. Thus, LW does not appear to be controlled to a great extent by the genetic effects, but much more by environmental effects.

The LWP, RW and HI always present heritability values situated between moderate and low; they were slightly higher than LW components but nevertheless inferior to the EW ones.

Thus, if, in a future programme of selection and forest tree breeding, it is thought positive to combine the quantity and quality of wood traits, this study concludes that even though it is possible to use the RD, the EWD will clearly be the characteristic with better results.

Finally, it is important to mention that, in order to estimate the implications of the genetic control of one characteristic, we need to know heritability values on one hand. On the other hand, we also need to study how this is genetically correlated in juvenile/mature wood and between different characteristics.

So, this work will be followed by another paper, which is going to be published in the near future and is about the genetic correlation between juvenile/mature wood and between different wood density components.

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REFERENCES

[1] Abdel-Gadir A.Y., Krahmer R.L., Estimating the age of demarcation of juvenile and mature wood in Douglas-fir, Wood Fiber Sci. 25 (1993) 242–249.

[2] Abdel-Gadir A.Y., Krahmer R.L., Genetic variation in the age of demarcation between juvenile and mature wood in Douglas-fir, Wood Fiber Sci. 25 (1993) 384–394.

[3] Alia R., Gil L., Pardos J.A., Catalan G., Interaccion procedencia-edad en 52 procedencias de *Pinus pinaster* en España, Investigacion Agraria-Sistemas y Recursos Forestales 0 (1991) 11–24.

[4] Barnes R.D., Mullin L.J., Battle G., Genetic control of eight year traits in *Pinus patula* Schiede and Deppe, Silvae Genet. 41 (1992) 318–326.

[5] Barnes R.D., Birks J.S., Battle G., Mullin L.J., The genetic control of ring width, wood density and tracheid length in the juvenile core of *Pinus patula*, Suid-Afrikaanse Bosboutydskrif; S. Afr. For. J. 169 (1994) 15–20.

[6] Bendtsen B.A., Properties of wood from improved and intensively managed trees, Forest Prod. J. 28 (1978) 61–72.

[7] Butcher T.B., Hopkins E.R., Realised gains from breeding *Pinus pinaster*, For. Ecol. Manage. 58 (1993) 211–231.

[8] Chaperon H., Raoux H., Siohan A., Alazard P., Variabilité génétique des proprietés technologiques du bois de pin maritime, Annales Afocel, Annales de Recherches Sylvicoles 1988/1989-AFOCEL, Class. Oxford 174.7: 86: 232.13 (1989) 327–345.

[9] Costa P., Durel C.E., Time trends in genetic control over height and diameter in maritime pine, Can. J. Forest Res. 26 (1996) 1209–1217.

[10] Cotterill P.P., Dean C.A., van Wyk G., Additive and dominance genetic effects in *Pinus pinaster*, *P. radiata* and *P. elliottii* and some implications for breeding strategy, Silvae Genet. 36 (1987) 221–232.

[11] Elliott G.K., Wood density in conifers, Commonwealth Agricultural Bureaux, Technical Communication 8 (1970) 44 p.

[12] Falconer D.S., Introduction to quantitative genetics, Third Edition, Longman Scientific & Technical, England, 1989.

[13] Ferrand J.C., Réflexions sur la densité du bois. 2e Partie : Calcul de la densité et de son hétérogénéité, Holzforschung 36 (1982) 153–157.

[14] Fonseca F.M.A., Variação na Madeira de *Pinus pinaster* Ait., Univ. Trás-os-Montes e Alto Douro, Vila Real, Portugal, 1989, 245 p.

[15] Fonseca F.M.A., Louzada J.L.P.C., Silva M.E.C.M., Correlation between density components of juvenile and adult wood on *Pinus pinaster* Ait., All Division 5 Conference – IUFRO, Nancy, France, 1992, 11 p.

[16] Fujisawa Y., Ohta S., Tajima M., Wood characteristics and genetic variations in sugi (*Cryptomeria japonica*) II. Variation in growth ring components among plus trees clones and test stands, Mokuzai Gakkaishi (J. Japan Wood Res. Soc.) 39 (1993) 875–882.

[17] Gill J.G.S., Juvenile-mature correlations and trends in genetic variances in sitka spruce in Britain, Silvae Genet. 36 (1987) 189–194.

[18] Gomes A.L., Preliminares de Melhoramento Florestal na Zona Norte do País-Ensaios Juvenis de Algumas Essências, Univ. Trás-os-Montes e Alto Douro, Vila Real, Portugal, 1982, 262 p.

[19] Harfouche A., Baradat P., Durel C.E., Variabilité intraspécifique chez le pin maritime (*Pinus pinaster* Ait.) dans le sud-est de la France. I. Variabilité des populations autochtones et des populations de l'ensemble de l'aire de l'espèce, Ann. Sci. For. 52 (1995) 307–328.

[20] Harfouche A., Baradat P., Kremer A., Variabilité intraspécifique chez le pin maritime (*Pinus pinaster* Ait.) dans le sud-est de la France. II. Hétérosis et combinaison de caractères chez des hybrides interraciaux, Ann. Sci. For. 52 (1995) 329–346.

[21] Hodge G.R., White T.L., Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding, Silvae Genet. 41 (1992) 252–262.

[22] Hopkins E.R., Butcher T.B., Provenance comparisons of *Pinus pinaster* Ait. in Western Australia, CALMScience 1 (1993) 55–105.

[23] Hopkins E.R., Butcher T.B., Improvement of *Pinus pinaster* Ait. in Western Australia, CALMScience 1 (1994) 159–242.

[24] Hughes J.F., Sardinha R.M.A., The Application of optical densitometry in the study of wood structure and properties, J. Microsc. 104 (1975) 91–103.

[25] Jozsa L.A., Richards J.E., Johnson S.G., Calibration of Forintek's direct reading X-ray densitometer, Report No. 36a, Forintek Canada Corp., Vancover, B.C., 1987, 16 p.

[26] Keller R., Caractéristiques du bois de pin maritime – Variabilité et transmission héréditaire, Ann. Sci. For. 30 (1973) 31–62.

[27] Kremer A., Lascoux D.M., Genetic architecture of height growth in maritime pine (*Pinus pinaster* Ait.), Silvae Genet. 37 (1988) 1–8.

[28] Louzada J.L.P.C., Variação nas Componentes da Densidade na Madeira de *Pinus pinaster* Ait.-Série Técnica-Científica, Ciências Aplicadas (12), Univ. Trás-os-Montes e Alto Douro, Vila Real, Portugal, 1991, 113 p.

[29] Louzada J.L.P.C., Variação fenotípica e genética em características estruturais na madeira de *Pinus pinaster* Ait.-Série Didáctica, Ciências Aplicadas (143), Univ. Trás-os-Montes e Alto Douro, Vila Real, Portugal, 2000, 293 p.

[30] Nepveu G., L'Amélioration de la qualité de la production forestière : le cas du pin maritime, Intervention à la 3e Rencontre Recherche - Formation - Professionnels du Bois et de la Forêt, E.N.I.T.A. Bordeaux, France, 1984, 31 p.

[31] Nicholls J.W.P., Selecting Portuguese *Pinus pinaster* for tree improvement in Australia. Part II - Wood Quality Assessment, J. Inst. Wood Sci. 26 (1970) 37–41.

[32] Nicholls J.W.P., Morris J.D., Pederick L.A., Heritability estimates of density characteristics in juvenile *Pinus radiata* wood, Silvae Genet. 29 (1980) 54–61.

[33] Panshin A.J., de Zeeuw C., Textbook of Wood Technology. Vol. I – Structure, Identification, Uses, and Properties of Commercial Woods of the United States and Canada, 3rd ed., The American Forestry Series, Vaux H.J. (Ed.), McGraw-Hill Book Company, 1970, 705 p.

[34] Polge H., Établissement des courbes de variation de la densité du bois par exploration densitométrique de radiographies d'échantillons prélevés à la tarière sur des arbres vivants – Applications dans les domaines technologique et physiologique, Ann. Sci. For. XXIII (1966), 206 p.

[35] Polge H., Fifteen years of wood radiation densitometry, Wood Sci. Technol. 12 (1978) 187–196.

[36] Polge H., Illy G., Observations sur l'anisotropie du pin maritime des Landes, Ann. Sci. For. 24 (1967) 205–231.

[37] Squillace A.E., Average genetic correlations among offspring from open-pollinated forest trees, Silvae Genet. 23 (1974) 149–156.

[38] Talbert J.T., Jett J.B., Bryant R.L., Inheritance of wood specific gravity in a unimproved loblolly pine population: 20 years of results, Silvae Genet. 32 (1983) 33–37.

[39] Tsoumis G., Wood as Raw Material – Source, Structure, Chemical, Composition, Growth, Degradation and Identification, Pergamon Press, 1968, 276 p.

[40] Vargas-Hernandez J., Adams W.T., Genetic variation of wood density components in young coastal Douglas-fir: Implications for tree breeding, Can. J. Forest Res. 21 (1991) 1801–1807.

[41] Vargas-Hernandez J., Adams W.T., Age-age correlations and early selection for wood density in young coastal Douglas-fir, Forest Sci. 38 (1992) 467–478.

[42] Vásquez J., Dvorak W.S., Trends in variances and heritabilities with stand development of tropical pines, Can. J. Forest Res. 26 (1996) 1473–1480.

[43] Woods J.H., Kolotelo D., Yanchuk A.D., Early selection of coastal Douglas-fir in a farm-field test environment, Silvae Genet. 44 (1995) 178–186.

[44] Wright J.W., Introduction to Forest Genetics, Academic Press, New York, 1976, 463 p.

[45] Yanchuk A.D., Kiss G.K., Genetic variation in growth and wood specific gravity and its utility in the improvement of interior spruce in British Columbia, Silvae Genet. 42 (1993) 141–148.

[46] Yanchuk A.D., Carlson M.R., Murphy J.C., Ortet-ramet relationships of wood specific gravity in lodgepole pine, West. J. Appl. For. 5 (1990) 40–42.

[47] Zhang S.Y., Effect of age on the variation, correlations and inheritance of selected wood characteristics in black spruce (*Picea mariana*), Wood Sci. Technol. 32 (1998) 197–204.

[48] Zhang S.Y., Morgenstern E.K., Genetic variation and inheritance of wood density in black spruce (*Picea mariana*) and its relationship with growth: Implications for tree breeding, Wood Sci. Technol. 30 (1995) 63–75.

[49] Zhang S.Y., Jiang Z.H., Variability of selected wood characteristics in 40 half-sib families of black spruce (*Picea mariana*), Wood Sci. Technol. 32 (1998) 71–82.

[50] Zobel B.J., Jett J.B., Genetics of Wood Production, Springer Series in Wood Science, Timell T.E. (Ed.), Springer Verlag, 1995, 337 p.

[51] Zobel B.J., Sprague J.R., Juvenile Wood in Forest Trees, Springer Series in Wood Science, Timell T.E. (Ed.), Springer Verlag, 1998, 300 p.

[52] Zobel B.J., Talbert J., Applied Forest Tree Improvement, John Wiley & Sons, New York, 1984, 511 p.

[53] Zobel B.J., van Buijtenen J.P., Wood Variation – Its Causes and Control, Springer Series in Wood Science, Timell T.E. (Ed.), Springer Verlag, 1989, 363 p.