Torres-Sánchez *et al. Annals of Forest Science* (2024) 81:46
https://doi.org/10.1186/s13595-024-01266-3

Annals of Forest Science

RESEARCH PAPER **Open Access**

Volume-based selection in *Pinus pinaster* Aiton breeding: evaluating resistance to *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle and wood properties

Esteban Torres-Sánchez[1*], Juan José Acosta[2], Gary R. Hodge[2], Eva Prada[1], María Menéndez-Gutiérrez[1] and Raquel Díaz[1]

Abstract

Key message Genetic parameter estimates at age 12 years for trunk volume in *Pinus pinaster* displayed low to moderate heritability for growth and stem form, whereas wood properties showed high heritability. No correlation was detected between resistance to the nematode *Bursaphelenchus xylophilus* and growth, stem form, or wood properties. However, certain families stood out, showing favorable values across all traits, including resistance to the nematode.

Context The breeding program for *Pinus pinaster* should advance towards a second-generation breeding population based on volume, stem form, and resistance to *Bursaphelenchus xylophilus*, with the challenge of incorporating novel traits of importance.

Aims We focused on assessing the genetic parameters of growth, stem form, wood properties, and resistance to *B. xylophilus* as well as exploring the relationship between these traits.

Methods We evaluated 116 half-sib families at three ages (7, 12, and 17 years) in seven progeny trials established in 2005, analyzing growth, stem form, and wood traits. Resistance to *B. xylophilus* was assessed in 91 of the 116 half-sib families at age 2 by artificial inoculation tests under greenhouse conditions.

Results Advancing the selection age to 12 years proved to be feasible for volume selection in Galician *P. pinaster*. All traits, including resistance to *B. xylophilus*, showed potential for genetic improvement. Remarkably, resistance to *B. xylophilus* was not correlated to any other trait.

Conclusion Excluding the most susceptible families to *B. xylophilus* from the Galician *P. pinaster* breeding program would not result in a significant decrease in volume, stem form, or wood properties.

Keywords Maritime pine, Pinewood nematode, Basic density, Modulus of elasticity, Genetic correlations

---

Handling editor: Christelle Robinet

This article is part of the topical collection on "Advances in the understanding of the pine wilt disease and in its management strategy".

*Correspondence:
Esteban Torres-Sánchez
esteban.torres.sanchez@outlook.es
Full list of author information is available at the end of the article

1 Introduction

Maritime pine (*Pinus pinaster* Aiton) is, with radiata pine (*Pinus radiata* D. Don), one of the *Pinus* species with the greatest economic and ecological relevance in Galicia (northwest of Spain), making up half of the region's conifer stocks, with an annual harvest volume of 2.18 M m^3 (Picos and Rodríguez-Soalleiro 2019; Consellería do Medio Rural 2020). The Galician breeding program for *P. pinaster* was initiated in the 1980s to provide quality seed to the forestry sector (Zas and Merlo 2008). The first-generation breeding population was established by selecting 116 *P. pinaster* plus trees based on their superior growth and stem form along the Galician coastal area. Since then, several progeny trials and some seed orchards have been installed in different environments in Galicia. Currently, one of the main objectives of the Galician breeding program is to advance to a second-generation breeding population. The silvicultural models of *P. pinaster* in Galicia establish its rotation age between 25 and 40 years (Consellería do Medio Rural 2021), which implies long periods of time and significant financial efforts for family selection based on traits of interest. Selecting at younger ages has become a practical solution to solve this problem. Previous studies of *P. pinaster* at different ages have reported high age-age correlations for growth traits, suggesting the feasibility of advancing the age of selection (Kremer 1992; Magnussen and Kremer 1993; de la Mata et al. 2012).

Breeders generally need to simultaneously consider multiple traits to develop an efficient selection strategy. It is necessary not only to determine which are the interesting traits but also to estimate their genetic parameters and correlations to avoid undesirable results in multi-trait selection. While there is increasing attention on incorporating wood property traits (e.g., wood density and modulus of elasticity -MOE-) as selection criteria in conifer breeding programs (Louzada and Fonseca 2002; Verryn 2008; Hong et al. 2014; Takahashi et al. 2023), caution is needed due to the possibility of high negative correlations between growth and wood density (Fries and Ericsson 2006; Hannrup et al. 2000). Recent findings indicate substantial family variability and, consequently, heritability, in *P. pinaster* wood properties, suggesting its possible addition as selection criteria in the Galician breeding program (Torres-Sánchez et al. 2024).

Resistance to the pinewood nematode *Bursaphelenchus xylophilus* Steiner and Buhrer (PWN) is already being considered as a selection criterion in the Galician breeding program due to the threat of this pathogen to *Pinus* species. This nematode, considered an EU quarantine pest (EPPO 2022), has emerged in southern Galicia, with several outbreaks since 2010 (Xunta de Galicia 2019). Projections indicate that it will spread throughout Spain in the coming years (de la Fuente et al. 2018; de la Fuente and Saura 2021).

Previous artificial inoculation experiments performed in greenhouses have shown that *P. pinaster* exhibits moderate-high susceptibility to PWN (Menéndez-Gutiérrez et al. 2017, 2018; Carrasquinho et al. 2018; Torres-Sánchez et al. 2023). As a result of these assays, three families belonging to the breeding program have already been cataloged as resistant parents of families to PWN in the Spanish National Catalogue of Base Materials (Menéndez-Gutiérrez et al. 2022).

P. pinaster resistance to PWN and its relation to several morphological traits has been broadly studied (Zas et al. 2015; Carrasquinho et al. 2018; Menéndez-Gutiérrez et al. 2018; Torres-Sánchez et al. 2023). Nonetheless, the relationships between resistance to PWN and wood properties have never been explored in *P. pinaster*. To the best of our knowledge, only Ishiguri et al. (2021) have reported a null relationship between PWN resistance and wood properties in clones of *P. densiflora* Siebold et Zucc. Determining the relationship between PWN resistance and wood properties is essential to integrate both elements in a multi-trait selection along with growth traits, as for example, the research in *Picea abies* L. Karst considering growth, wood properties, and resistance to *Pissodes strobi* W. D. Peck (Lenz et al. 2020).

Therefore, after determining the appropriate age for family selection based on volume, the main aims of this study were (1) to estimate genetic parameters for growth, stem form, and wood property traits at the chosen age and for resistance to PWN at age 2 and (2) to determine how these traits are correlated with each other.

2 Material and methods

2.1 Field trials

Seven open-pollination progeny trials were installed in 2005 across Galicia (Table 1, Appendix Figure 1). These trials included 116 half-sib families from the Galician *P. pinaster* breeding program and three commercial seed lots, with the exception of one of them, which had 94 half-sib families. The seeds were collected from a first-generation clonal seed orchard (Sergude, Spain, 42.82° N, 8.45° W). All trials follow a randomized complete block design, with eight blocks, and three-tree row plots per experimental unit, spaced 3×2 m. On average, 24 trees were planted per family and per trial. The number of living trees per family decreased over time due to natural mortality. Site features are shown in Table 1.

2.1.1 Morphological traits

In each trial, we measured on each living tree diameter at breast-height (DBH), stem form (SF), number of whorls (nW), and the average insertion angle of the branch (BA)

Table 1 Site description for each progeny trial

Site	Coristanco	Chantada	Forgoselo	Friol	Mandín	Noceda	Rebordelo
Code	COR	CHA	FOR	FRI	MAN	NOC	REB
Longitude (W, decimal degrees)[a]	8.73	7.84	7.99	7.72	7.39	7.45	8.48
Latitude (N, decimal degrees)[a]	43.16	42.62	43.46	43.07	41.86	42.67	42.46
Elevation (m.a.s.l.)	300	680	550	520	600	550	350
Orientation	NE	E	W	NW	SW	S-SW	NW
Slope (%)	0	0	30	3	12	14	7
Families per trial	116	94[b]	116	116	116	116	116
P (mm)[c]	1,680	1,226	1,811	1,321	1,110	1,378	2,359
T (°C)[c]	13.7	12.2	13.0	12.6	13.7	12.9	13.8

NE North-east; *E*, east, *W* West, *NW* North-west, *SW* South-west, *S-SW* South south-west, *NW* North-west. *P*, annual mean precipitation, in mm; *T*, annual mean temperature, in °C

[a] Coordinates are represented in decimal degrees (WGS 84)

[b] Available families when the trial was stablished

[c] Climate data obtained from ClimateDT Tool for the period 1992–2022 (https://www.ibbr.cnr.it/climate-dt/, consulted in May 2023)

into the trunk. The height (H) was measured in those 100 trees per hectare with the largest DBH. After that, we estimated the height of each tree applying the function described by Diéguez-Aranda et al. (2009). Volume (V) was estimated according to the following formula (Diéguez-Aranda et al. 2009):

$$V = 3.974 \cdot 10^{-5} \cdot DBH^{1.876} \cdot H^{1.079}$$

where V is the volume, in dm^3; DBH is the diameter at breast-height, in cm; and H is the height, in m.

Stem form (SF) was assessed using a 6-point scale based on the straightness of the stem (1 = very crooked, 6 = straight, inverted scale from Galera et al. (1997)).

The average length between whorls (WL, cm) was calculated as:

$$WL = \frac{H}{(nW + 1) \cdot 100}$$

where H is the height, in m, and nW is the number of whorls.

Branch angle (BA) was assessed using a three-point scale regarding the stem (1 = angle 0–30°, 2 = angle 31–60°, 3 = angle between 61 and 90° from vertical axis, as suggested by Galera et al. (1997), but inverted in direction).

V and SF were assessed in all trials at ages 7 and 12. However, at age 17, V was measured in four trials (CHA, FOR, FRI, and MAN), while SF was measured in three (CHA, FOR and FRI). WL and BA were assessed in all trials at age 12.

2.1.2 *Wood properties*

Basic density (BD) and dynamic modulus of elasticity on standing tree (MOE) were evaluated as wood properties in three trials (COR, NOC, and REB) at age 12. To assess these traits, we selected 8 trees per family, those two with the largest diameter within the four blocks with the best survival.

We collected a complete sample from pith to bark of one increment core per tree at breast-height, using a 5-mm Pressler auger. Samples were stored in cold and anaerobic conditions and transported to the laboratory; subsequently, we determined the green wood density (p_v). After that, to obtain the dry weight, all samples were heated at 60 °C until reaching 0% humidity.

BD (kg¨m^{-3}) was calculated as:

$$BD = \frac{W_d}{V_g}$$

where W_d is the dry weight, in kg, and V_g is the green volume, in m^3.

The estimation of MOE was carried out by measuring the stress-wave speed in the longitudinal direction of the standing tree trunks and the green wood density. The impact wave speed was recorded using a Hitman ST300 (Fibre-Gen, NZ) ultrasonic equipment. Each record consisted of the average of eight impact waves. The mean of three records from the receiving probe was the final speed value. MOE (MPa) was calculated as:

$$MOE = p_v \cdot V_e^2$$

where p_v is the green wood density, in kg¨m^{-3}, and V_e is the impact wave speed, in m¨s^{-1}.

2.2 PWN inoculation experiments

The genetic variation in resistance to PWN was evaluated among 91 half-sib families from the Galician *P.*

pinaster breeding program. Two PWN inoculation experiments were carried out under greenhouse conditions at the Lourizán Forest Research Center (42° 24′ 33″ N, 8° 39′ 46″ W, Pontevedra, Spain). In both experiments, an isolate of *B. xylophilus* collected from naturally infected *P. pinaster* stand in Galicia in 2010 was used (Abelleira et al. 2011).

In experiment 1, 2-year-old seedlings from 50 half-sib families were evaluated in 2013. In experiment 2, 2-year-old seedlings from 47 half-sib families were tested in 2014. Six of these families were previously evaluated in experiment 1, and the other 41 were tested for the first time. Both experiments followed a randomized complete block design with 12 blocks. Twelve seedlings per family were inoculated with *B. xylophilus*, and three control seedlings per family were inoculated with distilled water. Mean temperature was 23.2 °C in experiment 1 and 23.5 °C in experiment 2.

For the inoculation, a cut was made in the stem, in the previous year's growth, exposing the xylem. Then, a suspension of 300 µl containing 600 *B. xylophilus* at mixed developmental stages was pipetted onto the wound. Control seedlings were inoculated with 300 µl of distilled water (Menéndez-Gutiérrez et al. 2017).

At the end of the experiments (66 days after the inoculation date), each seedling was evaluated for wilting symptoms (PWNW) and survival to PWN (PWNS). To evaluate PWNW, a 7-point scale was used based on the percentage of wilted needles, from 1 (no symptoms) to 7 (all needles wilted) (Menéndez-Gutiérrez et al. 2018). PWNS was assessed using a binary variable: 1—alive (less than 81% of needles wilted), 0—dead (81–100% of needles wilted).

2.3 Data analysis

Prior to main analyses, we removed the spatial heterogeneity from each trait by using models with spatially autocorrelated errors (Zas 2006; Muñoz and Sanchez 2023). As a result, we obtained variables free of the effect of spatial autocorrelation. Then, in each trial, we explored both *V* and SF at each age, as well as WL, BA, BD, and MOE at age 12, performing a single-site analysis by using mixed models with family as a random effect. After that, we standardized the volume (White et al. 2007; Hodge and Dvorak 2012, 2015) to interpret the mean volume as 100% and solve problems of heterogeneous variance. This new variable was named standardized volume (stV, %).

2.3.1 Multi-site analyses

We evaluated all traits at age 12 and stV at age 7 and 17 as well. We estimated the phenotypic mean, standard deviation, and phenotypic coefficient of variation (CVp) for each trait. To estimate the best linear unbiased predictors (BLUP) and variances for each trait, we employed the following mixed model:

$$Y_{ijm} = \mu + S_i + G_j + GS_{ij} + \varepsilon_{ijm}$$

where Y_{ijm} is the trait measured on tree "*m*" from family "*j*" located in trial site "*i*," μ is the overall mean, S_i is the fixed effect of the environment "*i*" (trial site), G_j is the random effect of the genotype "*j*" (family) and GS_{ij} is the random effect of genotype by environment interaction ($G\times E$) of family "*j*" in trial site "*i*," and ε_{ijm} is the random error term. We calculated the genetic coefficient of variation (CVg), family heritability ($h^2{}_f$), and the narrow-sense heritability ($h^2{}_i$) (Isik et al. 2017):

$$CVg = \frac{\sqrt{S^2_{fam}}}{X}$$

$$h^2_i = \frac{4 \cdot S^2_{fam}}{S^2_{fam} + S^2_{GxE} + S^2_{res}}$$

$$h^2_f = \frac{S^2_{fam}}{S^2_{fam} + \frac{S^2_{GxE}}{N} + \frac{S^2_{res}}{N\cdot E}}$$

where X is the phenotypic mean, $S^2{}_{\mathrm{fam}}$ is the estimated family variance, $S^2{}_{G\times E}$ is the estimated $G\times E$ variance, $S^2{}_{\mathrm{res}}$ is the estimated residual variance, N is the harmonic mean of individuals per family, and E is the number of trial sites.

The $G\times E$ for each trait was studied by estimating the genetic type-B correlation (*rBg*):

$$rBg = \frac{S^2_{fam}}{S^2_{fam} + S^2_{GxE}}$$

2.3.2 PWN inoculation experiments

To analyze the wilting symptoms (PWNW), we performed a single-experiment mixed model for each experiment:

$$PWNW_{ijm} = \mu + B_i + G_j + \varepsilon_{ijm}$$

where $\mathrm{PWNW}_{\mathrm{ijm}}$ is the wilting value of seedling "*m*" belonging to family "*j*" and located in the block "*i*," μ is the overall mean, B_i is the random effect of block "*i*," G_j is the random effect of family "*j*," and ε_{ijm} is the random error term.

Then, we performed a multi-experiment analysis, adding to the previous model the experiment as a fixed effect, and the family and the block nested into the experiment as random effects:

$$PWNW_{hijm} = \mu + E_h + B_i(E_h) + G_j(E_h) + \varepsilon_{hijm}$$

where W_{hijm} is the wilting value of seedling "*m*" belonging to family "*j*" and located in the block "*i*" of the experiment "*h*," μ is the overall mean, E_h is the fixed effect of experiment "*h*," $B_i(E_h)$ is the random effect of block "*i*" nested into experiment "*h*," $G_j(E_h)$ is the random effect of family "*j*" nested into experiment "*h*," and ε_{hijm} is the random error term.

To analyze the survival to PWN (PWNS), we performed both a single-experiment analysis and a multi-experiment analysis. Both analyses were performed by using generalized binomial mixed models (link function = logit) following the structure of the models previously described above for PWNW.

Both the CVg and the $h^2{}_i$ were also calculated for PWNW and PWNS.

2.4 Correlations

2.4.1 Age-age correlations

Age-age type A genetics correlations (*rAa*) for stV were calculated by using estimated variances and covariances from a multi-trait mixed model (Isik et al. 2017):

$$Y_{n\times d} = \mu + X_{n\times p}b_{p\times d} + Z_{n\times r}u_{r\times d} + \varepsilon_{n\times d}$$

where Y is the trait vector with a dimension of $n\times d$ (n—number of individuals; d—number of traits), μ is the overall mean vector, X is the design matrix with $n\times p$ dimensions (p—number of fixed predictors) and represents the fixed effect of trial site, b is the matrix of coefficients of fixed predictors effects with dimensions $p\times d$, Z is the design matrix with $n\times r$ dimensions (r—number of random effects) for random effects of family and genotype by environment interaction, u is the matrix of random effects with $r\times d$ dimensions, and ε is the random error vector with $n\times d$ dimensions.

This analysis included the stV at ages 7, 12, and 17 as dependent variables. Then, *rAa* was calculated according to:

$$rAa = \frac{S_{axay}}{\sqrt{S^2_{ax}\cdot S^2_{ay}}}$$

where S_{axay} is the family covariance between the stV measured at age x (ax) and age y (ay). In addition, $S^2{}_{\mathrm{ax}}$ and $S^2{}_{\mathrm{ay}}$ are the family variances for ages ax and ay, respectively.

We also estimated age-age correlations for stV applying Pearson's correlations to the BLUPS obtained from the multi-site mixed models.

2.4.2 Correlations between traits

Type A genetic correlations between traits (*rAt*) at age 12 were calculated using estimated variances and covariances from the multi-trait mixed model described above. Then, *rAt* was calculated according to:

$$rAt = \frac{S_{t1t2}}{\sqrt{S^2_{t1}\cdot S^2_{t2}}}$$

where S_{t1t2} is the family covariance between trait 1 (t1) and trait 2 (t2). $S^2{}_{\mathrm{t1}}$ and $S^2{}_{\mathrm{t2}}$ are the family variances for t1 and t2, respectively.

We also calculated Pearson's correlation between traits using the BLUPs from the multi-site analysis performed at age 12 and the multi-experiment analysis for PWNS and PWNW at age 2.

Phenotypic correlations between growth, stem form and wood properties at age 12 were calculated applying Pearson's correlation on phenotypic data.

All data analyses were performed using R (R Foundation for Statistical Computing 2020). The analyses using mixed models were implemented with the *breedR* package (Muñoz and Sanchez 2023) to estimate genetic parameters ($h^2{}_i$, $h^2{}_f$, *rBg*, *rAa*, and *rAt*) and their respective standard errors except for *rAa*. Standard errors of *rAa* were estimated according to Falconer and Mackay (1996). On the other hand, binomial generalized mixed models for survival analysis were carried out using the *lme4* package (Bates et al. 2015). Since the *lme4* package does not provide standard errors for heritability, we estimated them using the equations described in Wright (1976).

3 Results

3.1 Age-age correlations for standardized volume

At genetic level, stV at the three ages studied were highly correlated. The multi-trait analysis for ages 12 and 17 reported the highest type A genetic correlation (0.98). Accordingly, the correlations between estimated BLUPs from multi-site mixed models for age 12 and age 17 exhibited a higher correlation compared to that observed between age 7 and age 17. Furthermore, all the age-age BLUP correlations were significant and high (Table 2).

3.2 Multi-site analysis

The overall mean for each trait is shown in Table 3. When standardizing to the original volume (77.60 dm^3 at age 12), the average changed to 100%, with the standard deviation and CVp expressed as a percentage of the original volume.

In general, CVp presented moderate-low values (0.20–0.50) for all traits, except for BD (0.08), PWNS (0.63), and

Table 2 Age-Age correlation matrix for standardized volume. Upper diagonal: Age-age type A correlations (rAa, standard error in brackets). Lower diagonal: correlation for estimated BLUPs from multi-site mixed models of each age

Age	7	12	17
7		0.88 (0.01)	0.81 (0.03)
12	**0.81*****		0.98 (0.00)
17	**0.67*****	**0.85*****	

Significant age-age BLUP-correlations (*p*-values < 0.05) are highlighted in bold

*** *p* – value < 0.001

W (0.69, Table 3). CVg estimates were similar and relatively low for all field traits (0.02–0.07); in contrast, CVg was quite high for PWNS (0.51) and intermedium for PWNW (0.15).

We only found a considerable genotype by environment interaction for stV and WL (*rBg* ≈ 0.50), while it was weak for SF and BA (*rBg* > 0.70) and insignificant for MOE and BD (*rBg* ≈ 0.90) (Table 3). All *rBg* can be considered significant since all of them exceeded twice their standard errors.

Results from multi-site analyses showed low heritability (h^2_i) for all morphological traits and high values for wood properties. The lowest h^2_{i} was observed in stV (0.07), followed by BA, SF, and WL ($h^2_i < 0.20$). By contrast, both MOE and BD displayed values of h^2_i higher than 0.30. With respect to the PWNS and PWNW, we found a moderate h^2_i value (0.24 and 0.21, respectively). Regarding the family heritability, all the traits showed high values ($h^2_f \geq 0.49$).

Results of single-site analysis for field traits and single-experiment analysis for PWNS and PWNW are provided in the Appendix (Appendix Table 5, Table 6 and Table 7).

3.3 Correlations between traits

Two methods were used to examine genetic correlations among traits, i.e., type A genetic correlation from multi-trait analyses, and Pearson's correlation between estimated BLUPs multi-environment single-trait models. Similar results were obtained from both methods (Table 4). Negative relationships between SF and MOE with BA, as well as the positive correlations between both wood properties, were clearly obtained through both types of correlations. At BLUP level, just WL presented a positive significant correlation with stV. Only weak type A genetic correlations were found between stV and the other traits, with high standard errors.

With regard to PWNS and PWNW, both traits showed a high negative BLUP correlation with each other (− 0.88, *p*-value < 0.001). However, neither of these traits were strongly or significantly correlated with the other traits. Even so, we observed a weak negative correlation between PWNS and SF and a positive one with BD (− 0.12 and 0.12, respectively) as well as that of *W* with stV and BD (− 0.11 and − 0.14 respectively). However, none of them were significant (Table 4).

All phenotypic correlations, except that of BA with MOE and BD, showed similar trends to the genetic correlations (Appendix Table 8).

4 Discussion

Our findings still do that 12 years is a suitable age for selecting by volume, similar to what has been shown in other studies (Kremer 1981, 1992; Magnussen and Kremer 1993; Danjon 1994). We also showed the potential for improvement of other interesting traits for the breeding program at that age as well as how they relate to each other. The high potential to improve family resistance to PWN is of great importance, considering that PWN

Table 3 Mean (μ), standard deviation (sd), phenotypic variation coefficient (CVp), estimated family variance (S^2_{fam}), estimated genotype by environment interaction variance (S^2_{GxE}), estimated residual variance (S^2_{res}), genetic variation coefficient (CVg), type-B genetic correlation (rBg), standard error (se), individual heritability (h^2_i), and family heritability (h^2_f) for morphological, wood properties and pine wood nematode resistance traits

Trait	$\mu \pm$ sd	S^2_{fam}	S^2_{GxE}	S^2_{Res}	CVp/CVg	rBg (se)	h^2_i (se)	h^2_f (se)
stV	100.0 ± 48.9	39.79	41.71	2,308.24	0.49/0.06	0.49 (0.10)	0.07 (0.01)	0.59 (0.06)
SF	2.5 ± 1.0	0.03	0.01	0.87	0.40/0.07	0.75 (0.09)	0.13 (0.02)	0.75 (0.11)
WL	73.6 ± 21.0	11.07	10.88	249.87	0.28/0.05	0.50 (0.06)	0.16 (0.03)	0.74 (0.14)
BA	2.4 ± 0.3	0.006	0.002	0.26	0.23/0.05	0.75 (0.11)	0.09 (0.02)	0.68 (0.08)
MOE	10,906.6 ± 2,453.5	394,983.4	40,102	4,173,302	0.22/0.06	0.91 (0.13)	0.34 (0.06)	0.68 (0.10)
BD	411.7 ± 32.9	78.86	9.68	634.98	0.08/0.02	0.89 (0.10)	0.44 (0.07)	0.73 (0.12)
PWNS	71 ± 45	0.13		2.09	0.63/0.51		0.24 (0.05)	0.49 (0.07)
PWNW	3.23 ± 2.22	0.23		4.16	0.69/0.15		0.21 (0.07)	0.58 (0.06)

stV standardized volume (%), *SF* Stem form (scale 1–6), *WL* length between whorls (cm), *BA* Branch angle (scale 1–3), *MOE* Modulus of elasticity (MPa), *BD* Basic density (kg·m^{-3}), *PWNS* survival to pinewood nematode (%), *PWNW* Wilting symptoms

Table 4 Correlation matrix between traits. Upper diagonal: type A genetic correlation (standard error). Lower diagonal: Pearson's correlation for estimated BLUPs from mixed models

	stV	SF	WL	BA	MOE	BD
stV		−0.15 (0.15)	0.18 (0.14)	0.14 (0.16)	−0.11 (0.16)	0.06 (0.15)
SF	−0.05		−0.19 (0.13)	−0.37 (0.12)	0.09 (0.14)	0.14 (0.13)
WL	**0.23***	−0.14		0.09 (0.14)	0.10 (0.14)	−0.21 (0.13)
BA	0.05	**−0.24****	0.03		−0.31 (0.13)	−0.03 (0.14)
MOE	−0.10	0.08	0.07	**−0.21***		0.22 (0.13)
BD	0.05	0.11	−0.13	−0.02	**0.22***	
PWNS	0.02	−0.12	0.04	−0.06	0.08	0.12
PWNW	−0.11	0.07	−0.06	0.01	−0.06	−0.14

stV standardized volume, *SF* Stem form, *WL* length between whorls, *BA* Branch angle, *MOE* Modulus of elasticity, *BD* Basic density, *PWNS* survival to pinewood nematode, *PWNW* wilting symptoms. Significant BLUP-correlations (*p*-values < 0.05) are highlighted in bold

* *p*-value < 0.05

** *p*-value < 0.01

will disperse throughout Spain in the coming years (de la Fuente et al. 2018; de la Fuente and Saura 2021). Furthermore, the absence of significant correlations between resistance to PWN and the rest of the traits highlighted the possibility of improving resistance to PWN without detriment to the rest of the traits.

To determine a suitable age for volume-based selection, we set the reference age at 17 years, which is approximately half of the rotation age of *P. pinaster* in Galicia (Consellería do Medio Rural 2021). Studying the selection age in this way is comparable to considering the entire rotation age, assuming that genetic parameters are relatively constant from the half to the end of the rotation (e.g., Lambeth 1980; Jansson et al. 2003; Xiang et al. 2003; Isik et al. 2010; Kurt and Isik 2021).

Our results showed that age 12 revealed the highest age-age correlation with reference to age 17, consistent with findings from other authors (Magnussen and Kremer 1993). In addition, in our study, heritability for volume remained stable over time, supporting the efficiency of early selection (Burdon 1989). Furthermore, age 12 also proved to be appropriate for basic density selection in *P. pinaster* (Bouffier et al. 2008; Torres-Sánchez et al. 2024). Indeed, family selection at this age also appears to be a feasible alternative for growth and form traits, as we observed high family heritability values. On the other hand, the low to moderate individual heritability of stem form and branch angle may be underestimated because both are categorical traits (Williams and Lambeth 1988; Haapanen et al. 1997; Belaber et al. 2018). These results are consistent with other previous studies on growth and form traits (Atmaca et al. 2022; Belaber et al. 2018).

The G×E interaction was strong for volume and length between whorls while relatively weak for stem form and branch angle. Two primary approaches have been proposed to address the challenge of strong GxE interaction (Li et al. 2017): selecting genotypes that consistently perform well across sites or selecting genotypes specifically adapted to each environment to maximize genetic gain. Previous research within the Galician breeding program determined that the GxE interaction in volume and length between whorls was due to a few unstable families at age 8 (Zas et al. 2004b), which agrees with our results at age 12 (data not shown). Moreover, the possibility of establishing two distinct breeding areas within Galicia for these traits was rejected due to the inability to mitigate GxE interaction into these areas (de la Mata et al. 2012). Hence, we decided not to discard the few unstable families to maintain plasticity and possible high performances (Santini et al. 2010; Yang 2007).

Both wood traits, basic density and modulus of elasticity, displayed high heritability values and minimal GxE interaction, consistent with previous studies (Chen et al. 2014; Hong et al. 2014, 2015; Hayatgheibi et al. 2017). It seems that silvicultural practices play a more substantial role in controlling wood properties than environmental factors. Previous studies highlighted variations in both traits related to stand density and site quality (Louzada and Fonseca 2002; Lasserre et al. 2009; Dias et al. 2018; Moore et al. 2018), but families tend to be stable in different environments (Baltunis et al. 2010; Gapare et al. 2010; Hayatgheibi et al. 2019).

In accordance with previous findings (Menéndez-Gutiérrez et al. 2018), as well as with other studies (Carrasquinho et al. 2018), we confirmed the existence of family variability in both survival to PWN and wilting symptoms and their moderate heritability. These results indicate a high family potential for improving resistance to PWN. As we expected, wilting symptoms correlated strongly and negatively with survival to PWN (Carrasquinho et al. 2018; Menéndez-Gutiérrez et al. 2018; Torres-Sánchez et al. 2023). No correlation was detected between the two traits with volume, stem form, branch angle, length between whorls, or wood properties, highlighting the possibility of improving resistance to PWN without detriment to the rest of the traits. Similarly, Ishiguri et al. (2021) did not observe any significant relationship between the modulus of elasticity and resistance to PWN in *P. densiflora*. By contrast, previous artificial-inoculation experiments showed a significant negative correlation between PWN resistance and growth in seedlings (Menéndez-Gutiérrez et al. 2018; Torres-Sánchez et al. 2023). These results should be assessed under field conditions and adult trees. Nonetheless, it is not possible due to the restrictions imposed by the European authorities (EPPO 2022). Studies performed with other pine species suggest that PWN resistance increases with increasing age (Kuroda et al. 2007; Kishi 1999), and, for other diseases, literature indicates that resistance correlates positively between different ages (Lu and Derbowka 2012) or even tends to increase at older ages (Patton 1961). On the other hand, the experiments on PWN resistance performed here were run under controlled environmental conditions that favored the development of the disease. Hence, resistant genotypes are expected to remain resistant to PWN under field conditions. Furthermore, as far as we know, disease resistance is comparable between trials performed under controlled conditions and field trials (Isik et al. 2008; Hayden et al. 2013).

We found a significant and positive correlation between volume and length between whorls, similar to the results already reported by Zas et al. (2004a) in *P. pinaster* at a younger age. However, unlike us, they also reported a slight positive correlation between stem form and branch angle. Our results also showed a negative correlation between modulus of elasticity and branch angle. This requires caution, since what is desirable for the breeding program would be a positive correlation between both traits. Wider branch angles facilitate faster branch detachment and therefore fewer number of knots, improving the modulus of elasticity (Koman et al. 2013). Likewise, a higher modulus of elasticity is related to a better quality of wood for structural use (Matheson et al. 2008; Ivkovic et al. 2009; Eckard et al. 2010). On the other hand, developing smaller branch angles could be a strategy that optimizes the investment of resources in terms of mechanical support, but this could be related to lower wood qualities (Morgan and Cannell 1988; MacFarlane 2020). So far, we have not found other studies on the relationship between both traits. Regarding the positive correlation between the basic density and the modulus of elasticity, there is a large literature showing that both traits are positively correlated (Baltunis et al. 2007; Lenz et al. 2013; Hong et al. 2014; McLean et al. 2016; Hayatgheibi et al. 2017; Yasuda et al. 2021; Torres-Sánchez et al. 2024).

The lack of a significant correlation between volume and stem form confirms earlier results (Belaber et al. 2018), who reported both positive and negative correlations with large standard errors between growth and stem form. Consistently to our results, Hill (2000) and Gaspar et al. (2009) found no correlation between volume and basic density, and Bouffier et al. (2009) also did not evidence any correlations between height and basic density. Louzada (2003) explained that the relationship between basic density and growth could vary depending on the environment of each trial. The rest of genetic correlations were also similar to results reported by other authors (Fries 2012; Gort et al. 2010; Hong et al. 2014; Lenz et al. 2020; Torres-Sánchez et al. 2024).

Regardless of the genetic correlations observed, we have families showing good performance for all traits studied, including resistance to PWN. Similarly, Gapare et al. (2009) reported families with good performance for all traits when studying the relationship among growth, stem form and wood properties in *P. radiata*.

5 Conclusion

Based on our results, we suggest a volume-based selection at age 12 instead of waiting until the rotation age. Moreover, our findings show that it is possible to carry out a multi-trait selection including resistance to PWN and also key wood properties, which have significant potential for improvement. The lack of correlations between field-measured traits and PWN resistance allows the Galician breeding program to explore several possible selection scenarios. Implementation of a multi-trait selection approach at age 12 appears to be a promising tool for the Galician *P. pinaster* breeding program.

Appendix

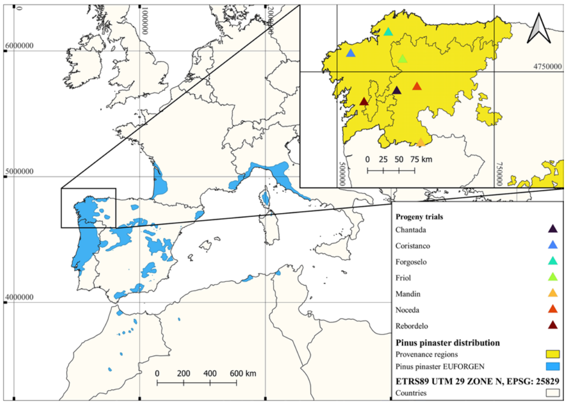

Fig. 1 Distribution of the seven half-sib progeny trials in Galicia

Table 5 Single-site analysis for volume (dm^3): mean (μ), standard deviation (sd), phenotypic variation coefficient (CVp), family variance (S^2_{fam}), residual variance (S^2_{Res}), genetic variation coefficient (CVg), individual heritability (h^2_i) and standard error (se). CHA, Chantada trial; COR, Coristanco trial; FOR, Forgoselo trial; FRI, Friol trial; MAN, Mandín trial; NOC, Noceda trial; REB, Rebordelo trial

Trial	Age	μ	± sd	CVp	S^2_{fam}	S^2_{Res}	CVg	h^2_i (se)
CHA	**7**	18.2	8.6	0.47	5.3	69.6	0.13	0.28 (0.08)
COR		7.0	4.9	0.70	0.9	23.0	0.13	0.15 (0.06)
FOR		7.4	5.2	0.69	0.6	26.0	0.10	0.09 (0.04)
FRI		8.7	5.9	0.68	0.7	34.1	0.10	0.09 (0.05)
MAN		6.5	4.7	0.72	0.67	21.6	0.13	0.12 (0.05)
NOC		2.5	2.2	0.89	0.11	4.67	0.13	0.09 (0.04)
REB		14.8	6.1	0.41	1.69	35.9	0.09	0.18 (0.06)
CHA	**12**	67.0	29.9	0.45	49.9	848	0.11	0.25 (0.07)
COR		90.1	49.3	0.55	152	$2.28\cdot10^3$	0.14	0.25 (0.07)
FOR		36.9	19.9	0.54	8.19	386	0.08	0.08 (0.04)
FRI		68.6	31.6	0.46	24.7	971	0.07	0.10 (0.05)
MAN		29.7	14.9	0.50	5.64	216	0.08	0.10 (0.04)
NOC		80.9	44.0	0.54	78.6	$1.86\cdot10^3$	0.11	0.16 (0.05)
REB		170	65.0	0.38	108	$4.12\cdot10^3$	0.06	0.10 (0.04)
CHA	**17**	265	124	0.47	831	$1.45\cdot10^4$	0.11	0.22 (0.07)
FOR		74.1	46.8	0.63	49.4	$2.14\cdot10^3$	0.09	0.09 (0.05)
FRI		188	86.8	0.46	297	$7.25\cdot10^3$	0.09	0.16 (0.06)
MAN		87.8	49.9	0.57	58.8	$2.43\cdot10^3$	0.09	0.09 (0.04)

Table 6 Single-site analysis for stem form (scale 1–6): mean (μ), standard deviation (sd), phenotypic variation coefficient (CVp), family variance (S^2_{fam}), residual variance (S^2_{Res}), genetic variation coefficient (CVg), individual heritability (h^2_i), and standard error (se). CHA, Chantada trial; COR, Coristanco trial; FOR, Forgoselo trial; FRI, Friol trial; MAN, Mandín trial; NOC, Noceda trial; REB, Rebordelo trial

Trial	Age	μ	± sd	CVp	S^2_{fam}	S^2_{Res}	CVg	h^2_i (se)
CHA	**7**	2.4	0.9	0.37	0.04	0.78	0.08	0.18 (0.06)
COR		5.5	0.9	0.15	0.01	0.71	0.02	0.07 (0.06)
FOR		5.2	1.0	0.19	0.01	0.98	0.02	0.04 (0.03)
FRI		3.4	1.7	0.49	0.12	2.62	0.10	0.18 (0.05)
MAN		5.8	0.6	0.11	< 0.01	0.37	0.01	0.04 (0.04)
NOC		5.3	1.0	0.18	< 0.01	0.96	0.01	0.01 (0.03)
REB		5.2	1.2	0.23	0.01	1.40	0.02	0.03 (0.04)
CHA	**12**	2.9	0.8	0.28	0.03	0.61	0.06	0.17 (0.06)
COR		2.3	1.0	0.42	0.03	0.91	0.08	0.14 (0.06)
FOR		2.8	0.9	0.30	0.02	0.70	0.05	0.11 (0.05)
FRI		2.5	1.1	0.45	0.07	1.18	0.10	0.21 (0.06)
MAN		3.0	0.9	0.31	0.03	0.81	0.06	0.13 (0.04)
NOC		1.8	0.9	0.50	0.03	0.79	0.10	0.16 (0.05)
REB		2.5	1.0	0.42	0.04	1.03	0.09	0.17 (0.05)
FOR	**17**	2.8	0.8	0.30	0.02	0.65	0.05	0.13 (0.05)
FRI		2.5	1.0	0.40	0.05	0.96	0.09	0.20 (0.06)
MAN		2.9	0.9	0.31	0.03	0.75	0.06	0.16 (0.05)

Table 7 Single-site analysis for length between whorls (WL, cm), branch angle (BA, scale) modulus of elasticity (MOE, MPa), basic density (BD, kg·m^{-3}), survival to PWN (PWN, %), and wilting symptoms (W, seven-point scale): mean (μ), standard deviation (sd), phenotypic variation coefficient (CVp), family variance (S^2_{fam}), residual variance (S^2_{res}), genetic variation coefficient (CVg), individual heritability (h^2_i), and standard error (se). CHA, Chantada trial; COR, Coristanco trial; FOR, Forgoselo trial; FRI, Friol trial; MAN, Mandín trial; NOC, Noceda trial; REB, Rebordelo trial

Trait	Trial	Age	μ	± sd	CVp	S^2_{fam}	S^2_{Res}	CVg	h^2_i (se)
WL	**CHA**	**12**	67.8	14.7	0.22	10.9	206	0.05	0.20 (0.07)
	COR		86.1	23.2	0.27	47.2	491	0.08	0.35 (0.08)
	FOR		60.3	9.4	0.16	5.52	83.3	0.04	0.25 (0.06)
	FRI		89.0	21.8	0.25	44.0	433	0.07	0.37 (0.08)
	MAN		54.2	8.0	0.15	2.18	61.1	0.03	0.14 (0.05)
	NOC		80.0	20.6	0.26	25.7	399	0.06	0.24 (0.06)
	REB		83.5	14.2	0.17	20.0	180	0.05	0.40 (0.07)
BA	**CHA**	**12**	2.5	0.5	0.19	0.01	0.21	0.04	0.16 (0.06)
	COR		2.6	0.5	0.19	0.01	0.24	0.04	0.17 (0.06)
	FOR		2.6	0.5	0.19	0.01	0.22	0.04	0.17 (0.05)
	FRI		2.7	0.5	0.18	0.00	0.23	0.02	0.07 (0.04)
	MAN		2.5	0.5	0.20	0.00	0.24	0.02	0.05 (0.04)
	NOC		2.2	0.6	0.26	0.01	0.32	0.04	0.08 (0.04)
	REB		2.0	0.6	0.30	0.02	0.36	0.06	0.17 (0.05)
MOE	**COR**	**12**	$1.26\cdot10^{4}$	$2.35\cdot10^{3}$	0.19	$4.61\cdot10^{5}$	$5.10\cdot10^{6}$	0.05	0.33 (0.11)
	NOC		$9.74\cdot10^{3}$	$1.85\cdot10^{3}$	0.19	$4.19\cdot10^{5}$	$3.02\cdot10^{6}$	0.07	0.48 (0.11)
	REB		$1.05\cdot10^{4}$	$2.21\cdot10^{3}$	0.21	$4.45\cdot10^{5}$	$4.49\cdot10^{6}$	0.06	0.36 (0.10)
BD	**COR**	**12**	439	27.2	0.06	101	642	0.02	0.54 (0.12)
	NOC		403	27.9	0.07	65.5	712	0.02	0.34 (0.10)
	REB		395	25.5	0.06	101	551	0.03	0.62 (0.12)
PWNS	**2013 experiment**	**2**	78	41	0.53	0.11	2.09	0.43	0.21 (0.05)
	2014 experiment		63	48	0.76	0.09	2.09	0.47	0.16 (0.05)
PWNW	**2013 experiment**	**2**	2.75	2.20	0.80	0.04	4.37	0.07	0.04 (0.08)
	2014 experiment		3.74	2.13	0.57	0.39	3.99	0.17	0.36 (0.13)

Table 8 Phenotypic correlation matrix. stV, standardized volume; SF, stem form; WL, length between whorls; BA, branch angle; MOE, modulus of elasticity; BD, basic density. Significant phenotypic correlations (p-values < 0.05) are highlighted in bold

	BD	MOE	SF	stV	WL
MOE	**0.40**				
SF	0.01	**0.11**			
stV	0.00	**−0.22**	0.02		
WL	0.03	**0.05**	−0.02	**0.24**	
BA	**0.21**	**0.11**	0.00	−0.03	**−0.11**

Acknowledgements

We thank Ricardo Ferradás from CIF Lourizán and Esther Merlo from Madera+ for their technical assistance.

Code availability

The custom code and/or software application generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Authors' contributions

Conceptualization: RD; methodology: EP, MMG, RD; investigation: ETS, JJA, GRH, EP, MMG, RD; data curation: ETS, JJA, GRH, EP, MMG, RD; formal analysis: ETS, JJA, GRH, EP, MMG, RD; writing—original draft preparation: ETS; writing—review and editing: ETS, JJA, GRH, EP, MMG, RD; funding acquisition: RD; supervision: RD. The authors read and approved the final manuscript.

Funding

This work was funded with National Institute for Agricultural and Food Research and Technology (RTA2017-00012-C02-01, RTA2011-069-C03-01 projects), rural development program funds of Galicia 2017 co-financed 75% with FEADER fund, GENMac project, and INDITEX enterprise.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request. The custom code and/or software application generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare no competing interests.

Author details

[1]Centro de Investigación Forestal de Lourizán, Ctra. de Marín, Km. 4, 36153 Pontevedra, Spain. [2]Camcore, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695-8008, USA.

Received: 30 January 2024 Accepted: 8 October 2024

References

Abelleira A, Picoaga A, Mansilla JP, Aguin O (2011) Detection of *Bursaphelenchus xylophilus*, causal agent of Pine Wilt Disease on *Pinus pinaster* in northwestern Spain. Plant Dis 95:776–776. https://doi.org/10.1094/PDIS-12-10-0902

Atmaca C, Temel F, Taştan Y, Eken BU (2022) Genetic variation in height, diameter and second flushing in four-year old maritime pine progeny tests in Türkiye. Silvae Genet 71:99–106. https://doi.org/10.2478/sg-2022-0012

Baltunis BS, Wu HX, Powell MB (2007) Inheritance of density, microfibril angle, and modulus of elasticity in juvenile wood of *Pinus radiata* at two locations in Australia. Can J for Res 37(11):2164–2174. https://doi.org/10.1139/X07-061

Baltunis BS, Gapare WJ, Wu HX (2010) Genetic parameters and genotype by environment interaction in radiata pine for growth and wood quality traits in Australia. Silvae Genet 59:113–124. https://doi.org/10.1515/sg-2010-0014

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Belaber EC, Gauchat ME, Reis HD et al (2018) Genetic parameters for growth, stem straightness, and branch quality for *Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis* F1 Hybrid in Argentina. For Sci 64:595–608. https://doi.org/10.1093/forsci/fxy021

Bouffier L, Charlot C, Raffin A et al (2008) Can wood density be efficiently selected at early stage in maritime pine (*Pinus pinaster* Ait.)? Ann For Sci 65:106–106. https://doi.org/10.1051/forest:2007078

Bouffier L, Raffin A, Rozenberg P et al (2009) What are the consequences of growth selection on wood density in the French maritime pine breeding program? Tree Genet Genomes 5:11–25. https://doi.org/10.1007/s11295-008-0165-x

Burdon RD (1989) Early selection in tree breeding: principles for applying index selection and inferring input parameters. Can J for Res 19:499–504. https://doi.org/10.1139/x89-076

Carrasquinho I, Lisboa A, Inácio ML, Gonçalves E (2018) Genetic variation in susceptibility to pine wilt disease of maritime pine (*Pinus pinaster* Aiton) half-sib families. Ann For Sci 75:75–85. https://doi.org/10.1007/s13595-018-0759-x

Chen ZQ, Gil MRG, Karlsson B et al (2014) Inheritance of growth and solid wood quality traits in a large Norway spruce population tested at two locations in southern Sweden. Tree Genet Genomes 10:1291–1303. https://doi.org/10.1007/s11295-014-0761-x

Consellería do Medio Rural (2020) Anuario de Estatística Forestal 2019 (Xunta de Galicia., Ed.). Xunta de Galicia. Consellería do Medio Rural. Dirección Xeral de Planificación e Ordenación Forestal.

Consellería do Medio Rural (2021) ORDEN de 9 de febrero de 2021 por la que se modifica el anexo I de la Orden de 19 de mayo de 2014 por la que se establecen los modelos silvícolas o de gestión forestal orientativos y referentes de buenas prácticas forestales para los distritos forestales de Galicia. Xunta de Galicia. Consellería do Medio Rural. Dirección Xeral de Planificación e Ordenación Forestal.

Danjon F (1994) Heritabilities and genetic correlations for estimated growth curve parameters in maritime pine. Theor Appl Genet 89:911–921

de la Fuente B, Saura S, Beck PSA (2018) Predicting the spread of an invasive tree pest: the pine wood nematode in Southern Europe. J Appl Ecol 55:2374–2385. https://doi.org/10.1111/1365-2664.13177

de la Fuente B, Saura S (2021) Long-term projections of the natural expansion of the pine wood nematode in the Iberian Peninsula. Forests 12. https://doi.org/10.3390/f12070849

de la Mata R, Voltas J, Zas R (2012) Phenotypic plasticity and climatic adaptation in an Atlantic maritime pine breeding population. Ann For Sci 69:477–487. https://doi.org/10.1007/s13595-011-0173-0

Dias A, Gaspar MJ, Carvalho A, et al (2018) Within- and between-tree variation of wood density components in *Pinus nigra* at six sites in Portugal. Ann For Sci 75: https://doi.org/10.1007/s13595-018-0734-6

Diéguez-Aranda U, Rojo Alboreca A, Castedo-Dorado F, et al (2009) Herramientas gestión forestal sostenible en Galicia. Lugo. ISBN: 978–84–692–7395–1

Eckard JT, Isik F, Bullock B et al (2010) Selection efficiency for solid wood traits in *Pinus taeda* using time-of-flight acoustic and micro-drill resistance methods. For Sci 56:233–241. https://doi.org/10.1093/forestscience/56.3.233

EPPO (2022) EPPO Standard PM 1/2 EPPO A1 AND A2 lists of pests recommended for regulation as quarantine pests

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Harlow, England: Prentice Hall. ISBN: 978-05-822-4302-6

Fries A (2012) Genetic parameters, genetic gain and correlated responses in growth, fiber dimensions and wood density in a Scots pine breeding population. Ann For Sci 69:783–794. https://doi.org/10.1007/s13595-012-0202-7

Fries A, Ericsson T (2006) Estimating genetic parameters for wood density of Scots pine (*Pinussylvestris* L.). Silvae Genet 55(2):84–92. https://doi.org/10.1515/sg-2006-0013

Galera RM, Martín S, Alía R, Aguado A, Notivol E (1997). Manual de selección de masas productoras de semillas. Evaluación de caracteres. Monografias INIA 97, 1^{a} edn. Madrid

Gapare WJ, Baltunis BS, Ivković M, Wu HX (2009) Genetic correlations among juvenile wood quality and growth traits and implications for selection strategy in *Pinus radiata* D. Don Ann For Sci 66:606–606. https://doi.org/10.1051/forest/2009044

Gapare WJ, Ivković M, Baltunis BS et al (2010) Genetic stability of wood density and diameter in *Pinus radiata* D. Don plantation estate across Australia. Tree Genet Genomes 6:113–125. https://doi.org/10.1007/s11295-009-0233-x

Gaspar MJ, Lousada JL, Rodrigues JC et al (2009) Does selecting for improved growth affect wood quality of *Pinus pinaster* in Portugal? For Ecol Manage 258:115–121. https://doi.org/10.1016/j.foreco.2009.03.046

Gort J, Zubizarreta-Gerendiain A, Peltola H, Kilpeläinen A, Pulkkinen P, Jaatinen R, Kellomäki S (2010) Differences in branch characteristics of Scots pine (*Pinussylvestris* L.) genetic entries grown at different spacing. Ann For Sci 67(7):1–8. https://doi.org/10.1051/forest/2010030

Haapanen M, Velling P, Annala ML (1997) Progeny trial estimates of genetic parameters for growth and quality traits in Scots Pine. Silva Fennica 31:3–12. https://doi.org/10.14214/sf.a8506

Hannrup B, Ekberg I, Persson A (2000) Genetic correlations among wood, growth capacity and stem traits in *Pinus sylvestris*. Scand J For Res 15. https://doi.org/10.1080/028275800750014966

Hayatgheibi H, Fries A, Kroon J, Wu HX (2017) Genetic analysis of lodgepole pine (*Pinus contorta*) solid-wood quality traits. Can J for Res 47:1303–1313. https://doi.org/10.1139/cjfr-2017-0152

Hayatgheibi H, Fries A, Kroon J, Wu HX (2019) Estimation of genetic parameters, provenance performances, and genotype by environment interactions for growth and stiffness in lodgepole pine (*Pinus contorta*). Scand J for Res 34:1–11. https://doi.org/10.1080/02827581.2018.1542025

Hayden KJ, Garbelotto M, Dodd R, Wright JW (2013) Scaling up from greenhouse resistance to fitness in the field for a host of an emerging forest disease. Evol Appl 6(6):970–982. https://doi.org/10.1111/eva.12080

Hill P (2000) Wood density of improved compared with unimproved maritime pine (*Pinus pinaster*). Calmscience 3:309–315

Hodge GR, Dvorak WS (2015) Provenance variation and within-provenance genetic parameters in *Eucalyptus urophylla* across 125 test sites in Brazil, Colombia, Mexico, South Africa and Venezuela. Tree Genet Genomes 11: https://doi.org/10.1007/s11295-015-0889-3

Hodge GR, Dvorak WS (2012) Growth potential and genetic parameters of four Mesoamerican pines planted in the Southern Hemisphere. South for 74:27–49. https://doi.org/10.2989/20702620.2012.686192

Hong Z, Fries A, Wu HX (2014) High negative genetic correlations between growth traits and wood properties suggest incorporating multiple traits selection including economic weights for the future Scots pine breeding programs. Ann For Sci 71:463–472. https://doi.org/10.1007/s13595-014-0359-3

Hong Z, Fries A, Wu HX (2015) Age trend of heritability, genetic correlation, and efficiency of early selection for wood quality traits in Scots pine. Can J for Res 45:817–825. https://doi.org/10.1139/cjfr-2014-0465

Ishiguri F, Nezu I, Endo R et al (2021) Inheritance of the wood properties of the Japanese red pine (*Pinus densiflora* Siebold et Zucc.) from the open-pollinated families selected as resistance to the pine wood nematode. Silvae Genet 70:186–194. https://doi.org/10.2478/sg-2021-0016

Isik F, Amerson HV, Whetten RW, Garcia SA, Li B, McKeand SE (2008) Resistance of *Pinus taeda* families under artificial inoculations with diverse fusiform rust pathogen populations and comparison with field trials. Can J for Res 38(10):2687–2696. https://doi.org/10.1139/X08-111

Isik K, Kleinschmit J, Steiner W (2010) Age-age correlations and early selection for height in a clonal genetic test of Norway spruce. For Sci 56(212–22):1. https://doi.org/10.1093/forestscience/56.2.212

Isik F, Holland J, Maltecca C (2017) Genetic data analysis for plant and animal breeding (1st ed.). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-55177-7

Ivkovic M, Gapare WJ, Abarquez A et al (2009) Prediction of wood stiffness, strength, and shrinkage in juvenile wood of radiata pine. Wood Sci Technol 43:237–257

Jansson G, Li B, Hannrup B et al (2003) Time trends in genetic parameters for height and optimal age for parental selection in Scots pine. For Sci 49:696–705. https://doi.org/10.1093/forestscience/49.5.696

Kishi Y (1999) Influence of tree age on wilt and mortality of pines after inoculation with *Bursaphelenchus xylophilus*. Nihon Ringakkai Shi/J Jpn For Soc 81(4):330–333. https://doi.org/10.11519/jjfs1953.81.4_330

Koman S, Feher S, Abraham J, Taschner R (2013) Effect of knots on the bending strength and the modulus of elasticity of wood. Wood Res 58(4):617–626

Kremer A (1981) Déterminisme génétique de la croissance en hauteur du Pin maritime (*Pinuspinaster* Ait.). III. - Evolution descomposants de la variance phénotypique et génotypique. Ann For Sci 38(3):355–375. https://doi.org/10.1051/forest:19810304

Kremer A (1992) Predictions of age-age correlations of total height based on serial correlations between height increments in Maritime pine (*Pinus pinaster* Ait.). Theor Appl Genet 85:152–158. https://doi.org/10.1007/BF00222853

Kuroda K, Ohira M, Okamura M, Fujisawa Y (2007) Migration and population growth of the pine wood nematode (*Bursaphelenchus xylophilus*) related to the symptom development in the seedlings of Japanese black pine (*Pinus thunbergii*). J Jpn for Soc 89(4):241–248. https://doi.org/10.4005/jjfs.89.241

Kurt Y, Isik K (2021) Age-age correlations and prediction of early selection age for diameter growth in a 35-years old *Pinus brutia* Ten. genetic experiment. For Syst 30. https://doi.org/10.5424/fs/2021303-17745

Lambeth CC (1980) Juvenile-mature correlations in Pinaceae and implications for early selection. For Sci 26:571–580. https://doi.org/10.1093/forestscience/26.4.571

Lasserre JP, Mason EG, Watt MS, Moore JR (2009) Influence of initial planting spacing and genotype on microfibril angle, wood density, fibre properties and modulus of elasticity in *Pinus radiata* D. Don Corewood for Ecol Manage 258:1924–1931. https://doi.org/10.1016/j.foreco.2009.07.028

Lenz P, Auty D, Achim A, Beaulieu J, Mackay J (2013) Genetic improvement of white spruce mechanical wood traits-early screening by means of acoustic velocity. Forests 4(3):575–594. https://doi.org/10.3390/f4030575

Lenz PRN, Nadeau S, Mottet MJ et al (2020) Multi-trait genomic selection for weevil resistance, growth, and wood quality in Norway spruce. Evol Appl 13:76–94. https://doi.org/10.1111/eva.12823

Li Y, Suontama M, Burdon RD, Dungey HS (2017) Genotype by environment interactions in forest tree breeding: review of methodology and perspectives on research and application. Tree Genet Genomes 13: https://doi.org/10.1007/s11295-017-1144-x

Louzada JLPC (2003) Genetic correlations between wood density components in *Pinus pinaster* Ait. Ann For Sci 60:285–294. https://doi.org/10.1051/forest:2003020

Louzada JLPC, Fonseca FMA (2002) The heritability of wood density components in *Pinus pinaster* Ait. and the implications for tree breeding. Ann For Sci 59:867–873. https://doi.org/10.1051/forest

Lu P, Derbowka D (2012) Effects of seedling age on blister rust resistance assessments in eastern white pine and its hybrid backcrosses. Can J for Res 42:67–74. https://doi.org/10.1139/X11-164

MacFarlane, D. W. (2020). Functional relationships between branch and stem wood density for temperate tree species in North America. Front For Glob Change 3. https://doi.org/10.3389/ffgc.2020.00063

Magnussen S, Kremer A (1993) Selection for an optimum tree growth curve. Silvae Genet 42(6):322–335

Matheson AC, Gapare WJ, Ilic J, Wu HX (2008) Inheritance and genetic gain in wood stiffness in radiata pine measured acoustically in young standing trees. Silvae Genet 57:56–64. https://doi.org/10.1515/sg-2008-0009

McLean JP, Moore JR, Gardiner BA, Lee SJ, Mochan SJ, Jarvis MC (2016) Variation of radial wood properties from genetically improved Sitka spruce growing in the UK. Forestry 89(2):109–116. https://doi.org/10.1093/forestry/cpv035

Menéndez-Gutiérrez M, Alonso M, Toval G, Díaz R (2018) Testing of selected *Pinus pinaster* half-sib families for tolerance to pinewood nematode (*Bursaphelenchus xylophilus*). Forestry 91:38–48. https://doi.org/10.1093/forestry/cpx030

Menéndez-Gutiérrez M, Alonso M, Toval G, Díaz R (2017) Variation in pinewood nematode susceptibility among *Pinus pinaster* Ait. provenances from the Iberian Peninsula and France. Ann For Sci 74 https://doi.org/10.1007/s13595-017-0677-3

Menéndez-Gutiérrez M, Prada Ojea E, Díaz Vázquez R (2022) Catalogación de progenitores de familia de *Pinus pinaster* tolerantes a la enfermedad del marchitamiento del pino causada por *Bursaphelenchus xylophilus*. 8° Congreso Forestal Español 1–7

Moore JR, Dash JP, Lee JR et al (2018) Quantifying the influence of seedlot and stand density on growth, wood properties and the economics of growing radiata pine. Forestry 91:327–340. https://doi.org/10.1093/forestry/cpx016

Morgan J, Cannell MGR (1988) Support costs of different branch designs: effects of position, number, angle and deflection of laterals. Tree Physiol 4:303–313. https://doi.org/10.1093/treephys/4.4.303

Muñoz F, Sanchez L (2023) breedR: statistical methods for forest genetic resources analysts. R package version 0.12–5, 1–36. Available at: https://github.com/famuvie/breedR

Patton R (1961) The effect of age upon susceptibility of eastern white pine to infection by *Cronartium ribicola*. Phtyopathology 51:429–434

Picos J, Rodríguez-Soalleiro R (2019) Retos para la selvicultura del pino pinaster en Galicia. In: Fundación HAZI Fundazioa (ed) NUEVAS PERSPECTIVAS DEL PINO PINÁSTER EN ESPAÑA, 1ª edn. Vitoria-Gasteiz, pp 37–51

R Foundation for Statistical Computing (2020) A language and environment for statistical computing. R Core Team

Santini A, Pecori F, Pepori AL et al (2010) Genotype × environment interaction and growth stability of several elm clones resistant to Dutch elm disease. For Ecol Manage 260:1017–1025. https://doi.org/10.1016/j.foreco.2010.06.025

Takahashi Y, Ishiguri F, Takashima Y et al (2023) Inheritance of wood properties and their radial variations in full-sib families of 36-year-old Japanese larch (*Larix kaempferi* (Lamb.) Carr.). Ann For Sci 80:1–15. https://doi.org/10.1186/s13595-022-01168-2

Torres-Sánchez E, Menéndez-Gutiérrez M, Villar L, Díaz R (2023) The effects of provenance, climate, and chemical defense on the resistance of *Pinus pinaster* Aiton to *Bursaphelenchus xylophilus* (Steiner and Buhrer). Ann For Sci 80: https://doi.org/10.1186/s13595-023-01202-x

Torres-Sánchez E, Prada E, Díaz R (2024) The feasibility of adding wood quality traits as selection criteria in the Galician *Pinus pinaster* Aiton breeding program: case study. Eur J For Res. https://doi.org/10.21203/rs.3.rs-2669379/v1

Verryn SD (2008) Breeding for wood quality - a perspective for the future. N Z J for Sci 38:5–13

White TL, Adams WT, Neale DB (2007) Forest genetics. Cambridge. ISBN 978–0–85199–348–5

Williams CG, Lambeth CC (1988) Bole straightness measurement for advanced-generation Lobolly pine genetic test. Silvae Genet 38:212–217

Wright JW (1976) Introduction to Forest Genetics. Academic Press

Xiang B, Li B, McKeand S, Weir R (2003) Genetic gain and selection efficiency of loblolly pine in three geographic regions. For Sci 49:196–208. https://doi.org/10.1093/forestscience/49.2.196

Xunta de Galicia (2019) RESOLUCIÓN de 28 de diciembre de 2018, de la Dirección General de Ganadería, Agricultura e Industrias Agroalimentarias, por la que se declara en el territorio de la Comunidad Autónoma de Galicia la presencia de cinco nuevos positivos del organismo de cuarentena *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle et al. (nemátodo del pino) y se ordena comenzar las medidas para su erradicación. Diario Oficial De Galicia 8:1559–1573

Yang RC (2007) Mixed-model analysis of crossover genotype-environment interactions. Crop Sci 47:1051–1062. https://doi.org/10.2135/cropsci2006.09.0611

Yasuda Y, Iki T, Takashima Y, Takahashi M, Hiraoka Y, Mishima K (2021) Genetic gains in wood property can be achieved by indirect selection and nondestructive measurements in full-sib families of Japanese cedar (*Cryptomeria japonica* D. Don) plus tree clones. Ann For Sci 78:50(2):1–10. https://doi.org/10.1007/s13595-021-01064-1

Zas R (2006) Iterative kriging for removing spatial autocorrelation in analysis of forest genetic trials. Tree Genet Genomes 2:177–185. https://doi.org/10.1007/s11295-006-0042-4

Zas R, Merlo E, Fernández-López J (2004a) Genetic parameter estimates for maritime pine in the Atlantic coast of north-west Spain. For Genet 11(1):45–53

Zas R, Merlo E, Fernández-López J (2004b) Genotype x environment interaction in maritime pine families in Galicia, Northwest Spain. Silvae Genet 53(4):175–182. https://doi.org/10.1515/sg-2004-0032

Zas R, Moreira X, Ramos M et al (2015) Intraspecific variation of anatomical and chemical defensive traits in Maritime pine (*Pinus pinaster*) as factors in susceptibility to the pinewood nematode (*Bursaphelenchus xylophilus*). Trees - Struct Funct 29:663–673. https://doi.org/10.1007/s00468-014-1143-6

Zas R, Merlo E (2008) El programa de mejora genética de *Pinus pinaster* en Galicia. Boletín Del CIDEU, 5–24. Available at: http://digital.csic.es/handle/10261/45946

Publisher's Note