The feasibility of adding wood quality traits as selection criteria in the Galician Pinus pinaster Aiton breeding program: case study

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Abstract

Pinus pinaster is a very important species for the Galician wood industry. A genetic breeding program was started in the 1980s to select plus trees based on growth and straightness. In this study, we estimated genetic parameters, juvenile-mature correlations and genetic gains in basic density (BD) and the dynamic modulus of elasticity (MOE_d) in Galician breeding families, as well as their relation to volume, straightness, and tree slenderness. All traits were measured at a tree age of 12 years in three half-sib progeny trials. Wood quality traits were also measured at 24 years in two other trials. All progeny trials followed a randomized complete block design and the data were analyzed using several mixed-model approaches. The individual heritability of MOE_d remained stable at both ages (~ 0.39) but decreased with age for BD (from 0.44 at age 12 to 0.24 at age 24). The high juvenile-mature correlations (0.51 for BD, 0.57 for MOE_d) observed support the viability of early selection for both traits at 12 years. Both wood quality traits correlated positively with each other and weakly with volume, straightness and tree slenderness. Selecting a minimum number of the best families, based on volume or any wood quality trait, would generate genetic gains for the selecting trait and prevent genetic losses of non-selecting traits. We also identified specific families showing positive genetic gains for all traits. The research indicates that either or both of these wood quality traits could be included as new selection criteria in the Galician breeding program.

1. Introduction

Maritime pine (*Pinus pinaster* Ait.) is an important forest species and native to Atlantic and Mediterranean regions of southern Europe and northern Africa. Currently, natural populations and productive reforestations of *P. pinaster* are distributed across 1.4 million of hectares in Spain (Bravo et al. 2017), approximately 700 000 hectares in Portugal, as reported in 2015 (ICNF 2019) and over 1 million hectares in France (IGN 2022). Although *P. pinaster* has diminished in recent years due to major wildfires (Picos and Rodríguez-Soalleiro 2019) and the preference for *Eucalyptus* spp. (Marey-Perez et al. 2017), it still covers more than 200 000 hectares in Galicia (NW Spain). This represents more than 50% of the region's coniferous forest area and nearly 40 million m^3 of wood stock (Picos and Rodríguez-Soalleiro 2019; Consellería do Medio Rural 2020), from which 1.9 million m^3 were harvested in 2021 (Instituto Galego de Estadística 2021).

In the 1980s, the Lourizán Forest Research Center started a genetic breeding program for *P. pinaster* by selecting ing plus trees– based on superior growth, straightness and branch habit – from stands located along the Galician Atlantic coast. A total of 116 plus trees were selected and replicated in a first-generation clonal seed orchard, to provide high-quality seed for reforestation in coastal areas of Galicia (Zas and Merlo 2008). Since 1995, several trials have been established across Galicia to evaluate progeny performance, as an indicator of seed suitability for planting in Galician coastal and inland areas (de la Mata et al. 2012). Four seed orchards and 14 progeny tests are currently active in this breeding program.

Until now, however, the breeding program has not considered wood quality traits as selection criteria, which is a common practice in many other improvement programs (Ericsson and Danell 1995; Wu et al. 2008). These traits need to be included in breeding programs because of their great influence on the physical and mechanical characteristics of final wood products (Zobel and van Buijtenen 1989). Current trends predict a large market niche for softwood production to meet construction needs in the coming years. In fact, the timber

industry is starting to demand these traits in the breeding material. The suitability of *P. pinaster* for structural wood in the construction industry (Louzada and Fonseca 2002; Reuling 2005; Bouffier et al. 2008b; Carballo et al. 2009) makes it advantageous to include wood quality traits as selection criteria.

In general, the two most important traits for indicating wood quality in any species are basic density of the wood (BD) and modulus of elasticity (MOE), especially the dynamic modulus of elasticity (MOE_d). Given their importance to the timber industry (Bacher and Krzosek 2014), a lot of literature has been published on these traits. In general, both traits are strongly and positively correlated with each other in conifers (Baltunis et al. 2007; Hong et al. 2014; Yasuda et al. 2021) but, usually, negatively correlated with yield traits such as growth and form. Determining how BD and MOE behave with respect to other traits is critical to improving multiple traits simultaneously in a breeding program. However, these relationships can vary depending on the species and even the populations. To advance in a breeding program, these relationships must be studied for each breeding population. When *P. pinaster* genotypes from the Landes genetic breeding program were improved for growth and stem form, BD decreased with respect to an unimproved seed lot (Bouffier et al. 2009). Similarly, negative correlations between growth traits and wood quality traits have been reported in several other pine species, such as *Pinus contorta* (Hayatgheibi et al. 2017, 2019), *Pinus radiata* (Wu et al. 2008) and *Pinus sylvestris* (Hong et al. 2014, 2015). In contrast, *Larix kaempferi* presented a positive correlation between diameter and BD (Fukatsu et al. 2015), and diameter in *Cryptomeria japonica* was positively correlated with both BD and MOE (Yasuda et al. 2021). Studies of *P. radiata* indicate that the higher the MOE_d, the higher the tree slenderness (TS) (Lasserre et al. 2008; Kimberley et al. 2015; Watt and Trincado 2019).

Shortening the breeding cycle is very important because it reduces time and costs for the forester. This makes early selection a valuable tool, but juvenile-mature correlations must be high. Findings from several authors for other species, such as *P. taeda* (Williams and Megraw 1994), *P. contorta* (Hayatgheibi et al. 2017) and *Picea abies* Chen et al. 2014) suggest that both BD and MOE_d are susceptible to be early selected. The *P. pinaster* juvenile-mature correlation (ages 12 and 30) has only been studied for BD in the Landes maritime pine breeding program, and high values were reported (Bouffier et al. 2008a). We have not found any bibliography on MOE_d juvenile-mature correlations for *P. pinaster*.

Selection for multiple traits in breeding programs is common, but the genetic gains for some interesting traits are frequently reduced and influenced by the breeder's selection criteria (Perek et al. 2022). Before including a wood quality trait as a selection criterion in the Galician breeding program for *P. pinaster*, its genetic parameters and interactions with yield traits such as volume, straightness and tree slenderness must be studied to avoid yield loss. Accordingly, in this study we aimed to identify: i) genetic variability and genotype-environment interactions for the wood quality traits of modulus of elasticity and basic density in tree families of the Galician breeding program; (ii) juvenile-mature correlations for both wood quality traits; (iii) correlations between wood quality and yield-related traits; (iv) study selection responses based on the selection criteria for wood quality traits. The results of this work will prove useful for advancing the next generation of seed orchards in the *P. pinaster* Galician breeding program.

2. Methods

2.1 Plant material

In this study, we used data collected from five test sites belonging to two series of multi-environment open-pollination progeny trials, one installed in 1995 and the other in 2005. The genetic material consisted of 116 half-sib families, obtained from plus trees replicated in a first-generation clonal seed orchard of the Galician *P. pinaster* breeding program. Plus trees were selected from stands located in the Galician Atlantic coast area, based on their superior growth, straightness and branch habits. Site characteristics, experimental design and climate information are shown in Table 1.

Table 1. Site description and climate information of each progeny trial

	Site				
	COR	**NOC**	**REB**	**LAL**	**GOM**
Plantation year	2005	2005	2005	1995	1995
Age at sampling time	12	12	12	24	24
Total num. of families per trial	116	116	116	94	101
Sampled families	116	116	116	60	60
Harmonic mean of trees measured per family	7.40	7.94	7.95	7.44	6.82
Spacing (m)	3 x 2	3 x 2	3 x 2	3 x 3	3 x 3
Longitude (W)*	8.71	7.43	8.46	7.98	8.06
Latitude (N)*	43.15	42.66	42.45	42.63	42.20
Elevation (m.a.s.l.)	239	569	476	630	500
Mean Annual Temperature (ºC)	13.2	11.9	12.4	11.4	12.4
Mean Annual Precipitation (mm)	1632.8	1471.7	2325.8	1380.0	1303.6

COR: Coristanco; NOC: Noceda; REB: Rebordelo; LAL: Lalín; GOM: Gomesende; *Coordinates are given in decimal degrees according to the ETRS89 UTM 29 North Zone projection; Climate information from climateDT software (https://www.ibbr.cnr.it/climate-dt/?id=2jljfpa1g6v9q5smujfn81hgqe); temporal range, 1992 to 2022.

The Lalín (LAL) and Gomesende (GOM) test sites were planted in 1995. The trials had a randomized complete block design of 10 replicates, with 94 and 101 half-sib families respectively, represented in each block by five contiguous trees spaced 3 × 3 m apart. For this study, we selected 60 families that were present at both sites.

The Noceda (NOC), Rebordelo (REB) and Coristanco (COR) test sites were planted in 2005. Each site comprised a randomized complete block design of 8 replicates, with 116 half-sib families represented in each block by three contiguous trees, spaced 3 × 2 m apart. We selected all 116 families for this study, to represent the entire genetic diversity of the Galician maritime pine breeding program.

2.2 Measurements

We sampled trees in the four blocks with the best survival at each site. Then, we chose the two trees with the largest diameter from each tree family in those blocks, for a total of eight trees per family and site. Due to mortality issues, however, all the blocks had to be included in the selection process for some families. In a few cases, we were unable to obtain eight live trees, so we measured all the living trees of that family. We measured 2 786 plants from 116 families in the three trials with trees from 2005, and 899 plants from 60 families in the two trials with trees from 1995.

Wood quality traits

The wood quality traits of basic density (BD) and dynamic modulus of elasticity (MOE_d) were evaluated at a tree age of 12 years for the trials installed in 2005 and at 24 years for those established in 1995.

We extracted one increment core per tree, from pith to bark, at breast-height using a 5 mm Pressler auger. Samples were transported to the laboratory stored in cold, anaerobic conditions to avoid moisture loss and later obtain the green density (p_v).

To estimate BD, we used the empirical method that considers each sample as a perfect cylinder. We measured the dimensions and the green weight of each core. Afterwards, all samples were heated at 60ºC until reaching 0% humidity, and weighed again to obtain the dry weight. Basic density (BD, $kg \cdot m^{-3}$) was calculated according to the following equation:

$$BD = \frac{W_d}{V_g} \quad (1)$$

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

To estimate MOE_d, two parameters were measured on the standing trees: stress-wave speed in the longitudinal direction of the tree trunk and the green wood density. We used Hitman ST300 (Fibre-Gen, NZ) ultrasonic equipment to record the impact wave speed. The final speed value for each tree was the mean of three records from the receiving probe, obtained as the average of eight impact waves from the transmitting probe. MOE_d (MPa) was then calculated according to the following function:

$$MOE_d = p_v \cdot V_e^2 \quad (2)$$

where p_v is the green density, in Kg/m^3, and V_e is the impact wave speed, in m/s.

Yield-related traits

We measured the yield-related traits for the 2005 progeny trial series (COR, NOR and REB) in the same trees where the wood quality traits were measured, since all 116 families from the breeding program were represented there. We defined several characteristics of interest to the wood construction industry as yield-related traits, including diameter at breast height (D, cm), total height (H, m) and straightness (S). The latter was recorded as a categorical variable using a six-level scale in which 1 indicated the most straightness and 6

the least straightness) (Galera et al. 1997). We also estimated volume (V, dm^3) according to Diéguez-Aranda et al. (2009) and tree slenderness (TS, $m \cdot m^{-1}$), as follows:

$$V = 3.974 \cdot 10^{-2} \cdot D^{1.876} \cdot H^{1.079} \quad (3)$$

$$TS = \frac{H}{D} \cdot 100 \quad (4)$$

where H is the total height, in m, and D is the diameter at breast height, in cm.

2.3 Data analysis

All statistical analyses were done with R software (R Core Team, 2020). We corrected the spatially dependent variables with the iterative spatial analysis (ISA) method (Zas, 2006) prior to genetic analysis. All mixed models were performed with the *lmer* function from the lme4 package (Bates et al. 2015). The best linear unbiased predictors (BLUPs) from each analysis were extracted using the *ranef* function from the arm package (Gelman et al. 2020). The significance of every random effect was determined using the likelihood ratio test (LRT) from the *ranova* function in the lmerTest package (Brockhoff and Christensen 2017). When the model assumptions were not fulfilled, we transformed the variables to obtain a normal and homoscedastic error.

2.3.1. Wood quality traits

We estimated the mean and standard deviation for 12-year-old trees from 116 families at the 2005 sites (COR, NOC and REB), and for 24-year-old trees from 60 families at the 1995 sites (GOM and LAL).

We analyzed BD and MOE_d for each age group using a mixed model that included the progeny test site as a fixed effect, while family and family × site interaction (genotype x environment interaction) were considered random effects. For the 2005 series, we analyzed all 116 families first and then assessed the set of 60 families it had in common with the 1995 series.

We then performed another analysis using a mixed model for the 60 families common to all sites. Age was considered a fixed effect while family and the family × age interaction were considered random effects. Site and the family × site interaction were excluded because they were not significant in the previous analyses.

2.3.2. Yield-related traits

We estimated the mean and standard deviation of yield traits (V, S and TS) for the 2005 sites (COR, NOC and REB) at age 12. All analyses used a mixed model that established the progeny test site as a fixed effect while family and family × site interaction were considered as random effects.

2.3.3. Correlations

We estimated the juvenile-mature correlations for wood quality traits by applying Pearson's correlation to the BLUPs obtained from the mixed models that analyzed the 60 common families.

Phenotypic correlations for yield and wood quality traits were obtained using Spearman's correlation for the 2005 series of progeny trials, due to the absence of normality. With the BLUPs obtained from mixed models, we also calculated the genetic correlation using Pearson's correlation. Then, we performed phenotypic and genetic correlations between BD and MOE for the 1995 series of progeny trials.

2.3.4. Genetic parameters

We estimated individual heritability (h^2_i), within-family heritability (h^2_w) and family heritability (h^2_f) as:

$$h_i^2 = \frac{4 \cdot \sigma_f^2}{\sigma_f^2 + \sigma_{fs}^2 + \sigma_r^2} \quad (5)$$

$$h_w^2 = \frac{3 \cdot \sigma_f^2}{\sigma_r^2} \quad (6)$$

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_{fs}^2}{N} + \frac{\sigma_r^2}{N \cdot S}} \quad (7)$$

where σ_f^2 is the family variance, σ_{fs}^2 is the variance for the family × site interaction, and σ_r^2 is the residual variance. N is the harmonic mean of families per experimental trial (Table 1), and is the number of experimental trials. Standard errors for both h^2_i and h^2_f were calculated from the equations described in Wright (1976).

The estimated genetic gain (ΔG, %) for each selected trait at age 12 was calculated as the average of the breeding values (BV) of the selected families divided by the phenotypic mean and multiplied by 100. The BV of each family was calculated from the family general combining ability (twice the family-trait BLUP obtained from the analysis of all families at age 12), h^2_w, and the within-family deviation of each tree (Isik et al. 2017; Perek et al. 2022). The correlated response for each non-selected trait was calculated in the same way using the corresponding BLUP based on selected families. Using BV for the calculations provides more accurate genetic gain estimates than traditional methodology (Dominik et al. 2017).

3. Results

3.1 Summary statistics for wood quality and yield-related traits

The means of both BD and MOE_d increased with age: the mean BD increased from 411.75 kg·m^{-3} at 12 years to 448.80 kg·m^{-3} at 24 years, whereas the mean MOE_d increased from 10 909.27 MPa at 12 years to 14 870.66

MPa at 24 years. The standard deviation of both traits also increased slightly from younger to older trees. Additionally, the minimum and maximum values observed in the 2005 trial set were lower than in the 1995 trial set (Table 2).

Table 2. Sampling age (Age), mean (μ), standard deviation (sd), minimum observed value (Min) and maximum observed value (Max) for wood quality and yield-related traits.

		Age (years)	μ	±	sd	Min.	Max.
Wood quality traits	**BD**	12	411.75	±	32.85	318.43	563.27
	MOE_d		10 909.27	±	2 417.97	4 955.48	21 204.17
	BD	24	448.80	±	39.50	352.99	672.82
	MOE_d		14 870.66	±	2 941.28	5 135.11	28 025.96
Yield-related traits	**S**	12	4.70	±	1.04	1	6
	V		126.16	±	67.23	8.06	423.60
	TS		57.05	±	9.45	33.59	118.18

BD: Basic density ($kg \cdot m^{-3}$); MOE_d: Dynamic modulus of elasticity (MPa); S: Straightness (scale: 1-6); V: Volume (dm^3); TS: Tree slenderness ($m \cdot m^{-1}$).

The means for yield-related traits at 12 years were 4.70 for straightness (S), 126.16 dm^3 for volume (V) and 57.05 $m \cdot m^{-1}$ for tree slenderness (TS). The standard deviation of V was relatively high and the range of V values was wide due to the extreme minimum and maximum values observed (8.06 and 423.60 dm^3). The minimum and maximum values observed in the 2005 progeny trials for the other traits are also shown in Table 2.

3.2 Family performance

Our results showed differences among families and sites for both wood quality traits at both ages, though family by site interactions were not significant (Table 3). We obtained similar results when we considered only the 60 common families at age 12.

Table 3. Mixed-model results for wood quality traits and yield-related traits for each set of trial sites at the same sampling age: degrees of freedom (DF), likelihood ratio significance test (LRT); individual heritability (h_i^2) ± standard deviation (s.d.); family heritability (h_f^2) ± standard error (s.e.).

		Fixed effect			Random effect				Heritability			
		Site			Family		Family x Site					
Age	Trait	DF	*F-value*	P>*F*	*LRT*	P>χ^2	*LRT*	P>χ^2	h_i^2		h_f^2	
12[1]	BD	2, 236.03	695.82	***	70.6	***	1.25	n.s.	0.44	0.01	0.87	0.12
	MOE_d	2, 226.97	451.77	***	56.2	***	0.38	n.s.	0.36	0.01	0.85	0.10
12[2]	BD	2, 117.18	368.5	***	50.8	***	0.02	n.s.	0.55	0.02	0.91	0.2
	MOE_d	2, 114.45	225.63	***	40.0	***	0.09	n.s.	0.46	0.02	0.89	0.18
24	BD	1, 854.65	224.21	***	10.0	**	_[3]	_[3]	0.24	0.02	0.65	0.09
	MOE_d	1, 850.01	512.88	***	13.4	***	_[3]	_[3]	0.39	0.02	0.76	0.12
12	V	2, 236.87	760.24	***	11.5	***	4.28	*	0.13	0.01	0.53	0.03
	S	2, 235.88	97.30	***	10.4	**	0.09	n.s.	0.11	0.01	0.65	0.04
	TS	2, 237.52	46.85	***	4.9	*	0.29	n.s.	0.07	0.0004	0.61	0.05

[1] Analysis with 116 families;

[2] Analysis with the 60 families common to all progeny trials;

[3] Mixed models resulted in a singular fit due to the low sample size and raw data variance. Therefore, this effect was removed from the analyses (Bates et al. 2015);

BD: Basic density, MOE_d: Dynamic modulus of elasticity; V: Volume; S: Straightness; TS: Tree slenderness;

*: p-value < 0.05; **: p-value <0.01; ***: p-value < 0.001; n.s.: not significant

Both individual (h_i^2) and family heritability (h_f^2) showed moderate to high values at 12 years, and BD values were higher than those of MOE_d. At 24 years, however, the individual heritability of BD decreased to 0.24, while MOE_d values decreased only slightly. The h_f^2 values also decreased for both traits from age 12 to 24. (Table 3).

Site had a very significant effect on the three yield-related traits in the study. Family also showed significant differences for these traits, especially volume, but the family × site interaction was only significant for volume (Table 3). The family variance (0.18) and family × site interaction variance (0.14) reported for volume in the

mixed model was low compared to the residual variance (4.97, data not shown). However, this significant interaction was not considered important because the ratio of family × site interaction variance to additive variance (four times the family variance) was 0.19 (Shelbourne 1972; Zhelev et al. 2003).

All the yield traits showed low values for individual heritability (<0.13) but high family heritability values (>0.53). Even so, both heritability types had lower values than those obtained for wood quality traits (Table 3).

When the age was considered in the model, family and age showed significant differences, but their interaction did not (Table 4).

Table 4. Mixed-model results for wood quality traits from all trial sites at both ages: degrees of freedom (DF), likelihood ratio significance test (LRT).

	Fixed effect			Random effect			
	Age			Family		Family x Age	
Trait[1]	DF	*F-value*	P>*F*	*LRT*	P>χ^2	*LRT*	P>χ^2
BD	1, 59.41	554.93	***	18.13	***	0.17	n.s.
MOE_d	1, 60.12	1 224.90	***	22.63	***	0.09	n.s.

[1] With the 60 families common to all progeny trials;

BD: Basic density, MOE_d: Dynamic modulus of elasticity;

*: p-value < 0.05; **: p-value <0.01; ***: p-value < 0.001; n.s.: not significant

3.3 Juvenile-mature correlations for wood quality traits

The absence of family × site and family ×age interactions for both wood quality traits (Table 3, Table 4) made it possible to calculate the juvenile-mature correlation ($r_{j\text{-}m}$) for different trees of the same family (Williams and Megraw 1994; Harfouche 2003; Zas et al. 2004). The $r_{j\text{-}m}$ values were positive for BD and MOE_d (0.51, p-value< 0.001 and 0.57, p-value< 0.001, respectively) (Figure 1). We found that 7 of the 60 families analyzed presented positive BLUPs for both traits at both ages (Group 1, Figure 1); 12 families showed positive BLUPs for BD only at both ages (Group 2); 12 families showed positive BLUPs for MOE_d only at both ages (Group 3); 17 families did not highlighted in any trait at both ages (Group 4); and another 12 families had negative BLUPs for both traits at both ages (Group 5).

3.4 Correlations between wood quality and yield-related traits

Both wood quality traits showed positive genetic (r_g) and phenotypic (r_p) correlations between them (0.21, p-value < 0.05 and 0.40, p-value < 0.001, respectively) at 12 years. Both correlations increased at 24 years (r_g= 0.46, p-value < 0.001 and r_p= 0.43, p-value <0.001, respectively, Figure 2).

All the correlations between MOE_d and yield-related traits were significant at the phenotypic level. MOE_d correlated positively with TS: the higher the MOE_d, the greater the tree slenderness. However, MOE_d correlated negatively with S and V: the higher the MOE_d, the lower the values of straightness and volume. At the genotypic level, only MOE_d and TS had a significant correlation and it was positive, as in the phenotypic correlation. In contrast, we found no significant genetic correlation between BD and yield-related traits. BD only showed a significant phenotypic correlation with V and it was negative, indicating that trees with greater volume presented lower basic density (Figure 2).

3.5 *Genetic gain*

The estimated genetic gains (ΔG) from selecting the best family for each trait at the younger age were 31.7 % for MOE_d, 10.5 % for BD, 21.0 % for V, 12.4 % for S and 5.6 % for TS. It should be noted that families with negative BLUPs for S and TS are straighter and more cylindrical than those with positive BLUPs, since lower values imply better traits. However, to make the graphs more understandable and consistent with the meaning of BV and ΔG, we inverted the sign of the BV and ΔG values for S and TS.

The correlated response for non-selected traits varies according to the selected trait. For example, by selecting the six best families (5 % of all families) for BD, we would observe an increase of 9.4% in BD, 6.5% in MOE_d, 2.2% in V, and negligible variation in S and TS. Alternatively, if we selected the top 24 families (20 % of all families) for MOE_d, we would obtain a 14.2% increase for MOE_d and the other traits would scarcely be affected. However, selecting the 24 best families for V would generate a 12.6% increase in V, a 1.6% loss in MOE_d, a 1.7% improvement in TS and negligible effects on BD and S (Figure 3).

Finally, five families showed positive breeding values for all the wood quality and yield-related traits considered. Selecting those families would result in an increment of 7.3 % for MOE_d, 3.5 % for BD, 3.9 % for V, 4.1 % for S and 1.8 % for TS (Figure 4).

4. Discussion

Our study shows high genetic variation for two wood quality traits, basic density and dynamic modulus of elasticity, among families in the Galician *P. pinaster* breeding population. The absence of genotype by environment interactions allowed us to study juvenile-mature correlations, which were high for both traits. Our results agree with those of other authors (Bouffier et al. 2008a; Hong et al. 2015), since early selection for both traits is feasible and efficient, they can be evaluated at young ages. BLUPs correlations showed almost no interaction between wood quality and yield-related traits at the genetic level. After examining different selection scenarios based on the selected trait, basic density, dynamic modulus of elasticity and volume, we suggest that including wood quality traits as selection criteria in the breeding program would be a viable option.

The heritabilities observed in this work were moderate to high for both wood quality traits. The individual heritability of the dynamic modulus of elasticity at both ages studied remained stable, with intermediate values. These values are comparable to those found in other pine species (Li et al. 2007; Gapare et al. 2010; Hong et al. 2014; Hayatgheibi et al. 2019) and other conifers (Lenz et al. 2013; Chen et al. 2014; Yasuda et al.

2021). Regarding the basic density, we also found a quite high value for the individual heritability at the early age of 12 years, which then declined at age 24. By contrast, other pine species have shown higher individual heritabilities at ages close to 24 years, for example *P. radiata* (Gapare et al. 2010), as well as other coniferous species (Chen et al. 2014; Yasuda et al. 2021).This age-related decrease in heritability was also observed in *P. radiata* (Baltunis et al. 2007; Gapare et al. 2010), and *P. contorta* (Hayatgheibi et al. 2017). It might be explained by variations in the proportion of corewood to outerwood over time (Gapare et al. 2010). Corewood usually shows higher BD variation than outerwood, which tends to be more stable. The ratio of corewood to outerwood is higher in young trees than in old trees, which could lead to higher heritability at early ages (Louzada and Fonseca 2002; Burdon et al. 2004; Dungey et al. 2006; Baltunis et al. 2007).

The lack of family × site interaction for both wood quality traits in this study has been observed by several authors for other pine species (Baltunis et al. 2010; Gapare et al. 2010; Hayatgheibi et al. 2017). The lack of environmental interaction with these industrially important traits facilitates their improvement within the Galician breeding population, because fewer trials will be needed to rank and select interesting families. The significant family × site interaction for volume was negligible for breeding, since the ratio of interaction variance to additive variance was much lower than one-half (Shelbourne 1972; Zhelev et al. 2003).

To estimate the juvenile-mature correlations, we used the same families at different ages in the trials, as other authors have done (Williams and Megraw 1994; Harfouche 2003; Zas et al. 2004; Codesido et al. 2012). This approach avoids the autocorrelation bias (Williams and Megraw 1994) and is more conservative, since different environments could reduce both heritability and juvenile-mature correlations (Bentzer et al. 1989; Sonesson et al. 2002). It would probably lead to underestimation in our results, even though the juvenile-mature correlations estimated here were high for both wood quality traits.

To our knowledge, this is the first study to analyze the juvenile-mature correlation for the dynamic modulus of elasticity in *P. pinaster*. The high correlation we observed agrees with findings from other conifer studies (Chen et al. 2014; Hayatgheibi et al. 2017) and shows that it is possible to select for this trait at age 12, or earlier. Results from one study of *P. sylvestris* suggested that selection at 8 years was feasible (Hong et al. 2015). The juvenile-mature correlation obtained for basic density was high and similar to the correlation estimated for the dynamic modulus of elasticity. This corroborates the results of a ring density study on *P. pinaster* in which the relative early selection efficiency was 80% at 12 years with respect to the reference age of 30 years (Bouffier et al. 2008b). Similarly, juvenile-mature correlations with basic density were usually moderate or high in studies of other pine species, (Williams and Megraw 1994; Hong et al. 2015; Hayatgheibi et al. 2017), and other conifers (Vargas-Hernandez and Adams 1992; Chen et al. 2014).

It is interesting to highlight the strong phenotypic and genetic correlations between the two wood quality traits at both ages in this study. Our findings agree with those of other authors for other coniferous species (Baltunis et al. 2007; Lenz et al. 2013; Hong et al. 2014; McLean et al. 2016; Hayatgheibi et al. 2017; Yasuda et al. 2021). This positive genetic relationship indicates that it is possible to select families with increment value for both traits in the Galician breeding population.

Our results indicate a significantly low and negative correlation between basic density and volume at the phenotypic level. These results differ from two previous studies involving the French (Bouffier et al. 2009) and

Portuguese (Gaspar et al. 2009) *P. pinaster* breeding programs. While Bouffier et al. (2009) found no phenotypic correlations between basic density and growth traits, Gaspar et al. (2009) reported a positive correlation between those traits and ring density. Nevertheless, both studies support our findings of non-significant genetic correlations between basic density and yield-related traits. In breeding populations of the Australian *P. pinaster* breeding program, volume also increased while basic density remained stable (Hill 2000). As with density, the dynamic modulus of elasticity and volume presented a significant negative phenotypic correlation and no genetic correlation. Other studies report diverse relationships between the dynamic modulus of elasticity and volume, depending on the species. For example, the dynamic modulus of elasticity correlated positively with growth traits in *P. sylvestris* (Šilinskas et al. 2020) and *L. kaempferi* (Fukatsu et al. 2015) but negatively in *P. radiata* (Gapare et al. 2009). Despite the negative phenotypic correlations between volume and wood quality traits, the lack of genetic correlation suggests that selecting by volume would not have a negative impact on wood quality.

Tree slenderness showed no correlation with basic density but correlated positively with the modulus of elasticity at the genetic and phenotypic level in our study, which agrees with findings from other authors (Lasserre et al. 2008; Lenz et al. 2013; Merlo et al. 2014; Watt and Trincado 2019). This means that trees with greater slenderness have higher dynamic modulus of elasticity, possibly because when trees reach a critical height their dynamic modulus of elasticity increases to prevent Euler buckling (Merlo et al. 2014).

Selecting by volume barely influenced the two wood quality traits evaluated here, though the literature contains examples in the literature of selection by volume that affect both traits positively (Perek et al. 2022) and negatively (Hayatgheibi et al. 2017). In our work, we identified a minimum number of families to select based on either wood quality or volume, to avoid decreases in non-selected traits. In fact, selecting more than 5% of families based on basic density or more than 20 % based on the dynamic modulus of elasticity is enough to avoid influencing the volume. Similarly, selecting 20% of the families based on volume would not affect either wood quality trait. These scenarios had a negligible influence on straightness and tree slenderness. Thus, wood density and yield-related traits appear to be independent of each other, or weakly correlated at best.

It is possible to select specific families with interesting breeding values for all traits, regardless of whether they had the best breeding value rankings. This strategy has been studied by some authors, who report positive genetic gains for all selected and non-selected traits (Xiao et al. 2021). Other available strategies such as the selection index could prove interesting to study in future works (Isik et al. 2017; Perek et al. 2022).

As a practical application, establishing basic forest materials with high wood quality to obtain forest reproduction materials for plantations in the Galician territory is a real possibility. Seed orchards or parents of families could be included in the Spanish National Catalogue of Basic Materials to meet demand by forest industries and landowners. Seeds from these basic materials would improve both wood quality and yield traits.

New research lines could unravel how selecting by wood quality traits affects resistance to diseases, such as the dreaded pine wilt disease. (Steffenrem et al. 2016; Chen et al. 2018; Ishiguri et al. 2021).

5. Conclusion

This work supports the possibility and potential advantage of adding the wood quality traits of basic density and the dynamic modulus of elasticity as selection criteria in the *P. pinaster* Galician breeding program. Selection at the tree age of 12 years is feasible for both traits, and genetic correlations indicate that both wood quality traits can be improved by choosing just one of them. Selecting a minimum number of families based on wood quality traits or volume minimizes genetic loss in non-selected traits. Moreover, selection of specific families can lead to positive genetic gains for all traits.

Declarations

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Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Ethical approval

Not applicable.

Consent to participate (include appropriate statements)

Not applicable.

Consent for publication (include appropriate statements)

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

Availability of data and material (data transparency)

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

Code availability

The custom code generated during the current study are available from the corresponding author on reasonable request.

Authors' contributions

Conceptualization: R.D.; methodology: R.D. and E.P.; investigation: E.T.S. and E.P.; data curation: E.T.S.; formal analysis: E.T.S.; writing - original draft preparation: E.T.S.; writing - review and editing: E.T.S., E.P. and R.D.; funding acquisition: R.D. and E.P.; supervision: R.D. All the authors read and approved the final manuscript.

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Figures

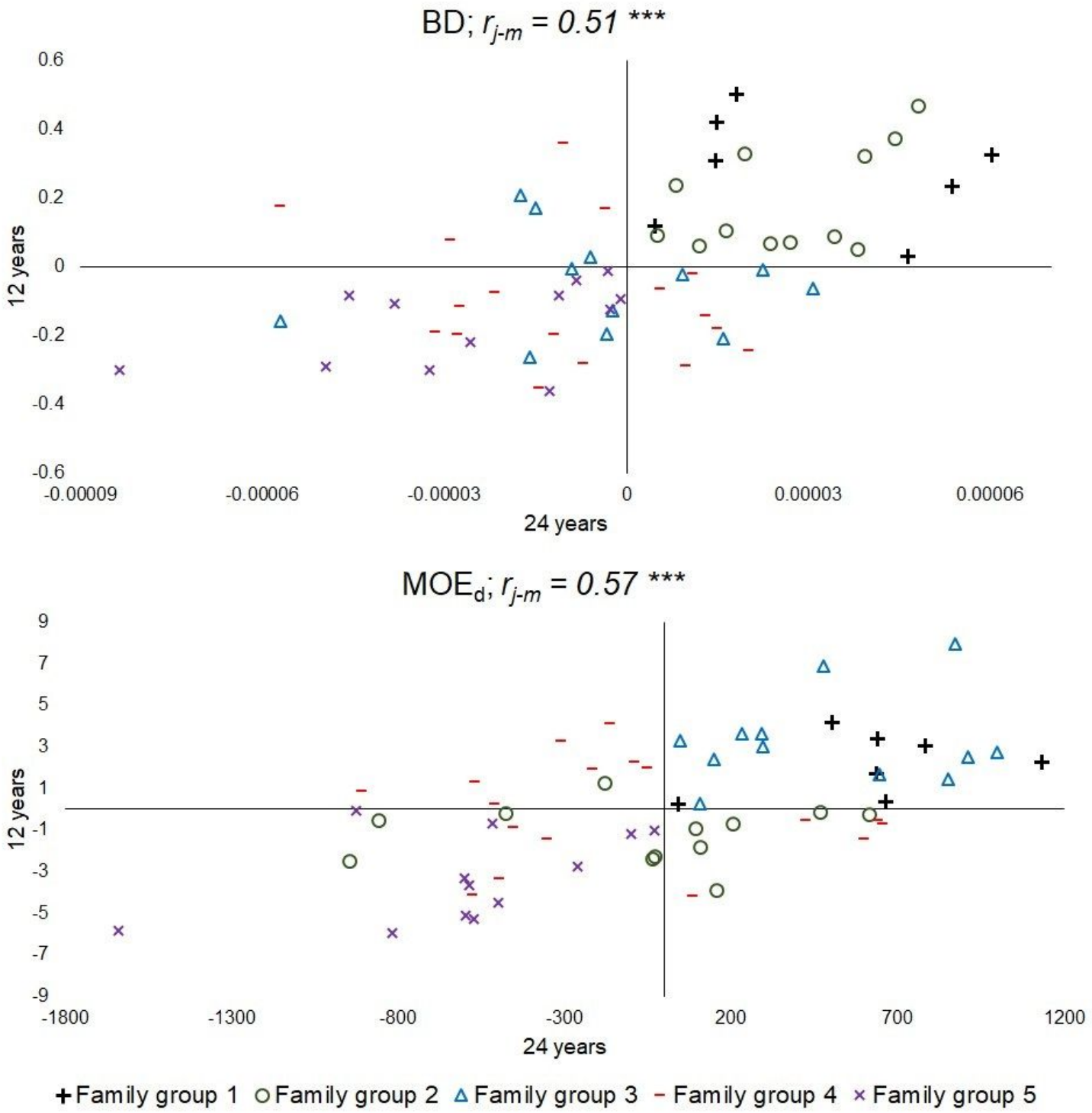

Figure 1

Juvenile-mature correlations (r_{j-m}) between ages 12 and 24 years for: a) BD and b) MOE$_d$. Family Group 1 (black crosses) includes families with positive BLUPs for both wood quality traits at both ages; Family Group 2 (green circles) includes families with positive BLUPs for BD at both ages; Family Group 3 (blue triangles) includes families with positive BLUPs for MOE$_d$ at both ages; Family Group 4 (red hyphens) includes families which did not highlighted in any trait at both ages. Family Group 5 (purple crosses), includes families with

negative BLUPs for both wood quality traits at both ages. BD: basic density; MOE_d: dynamic modulus of elasticity; ***: p-value < 0.001.

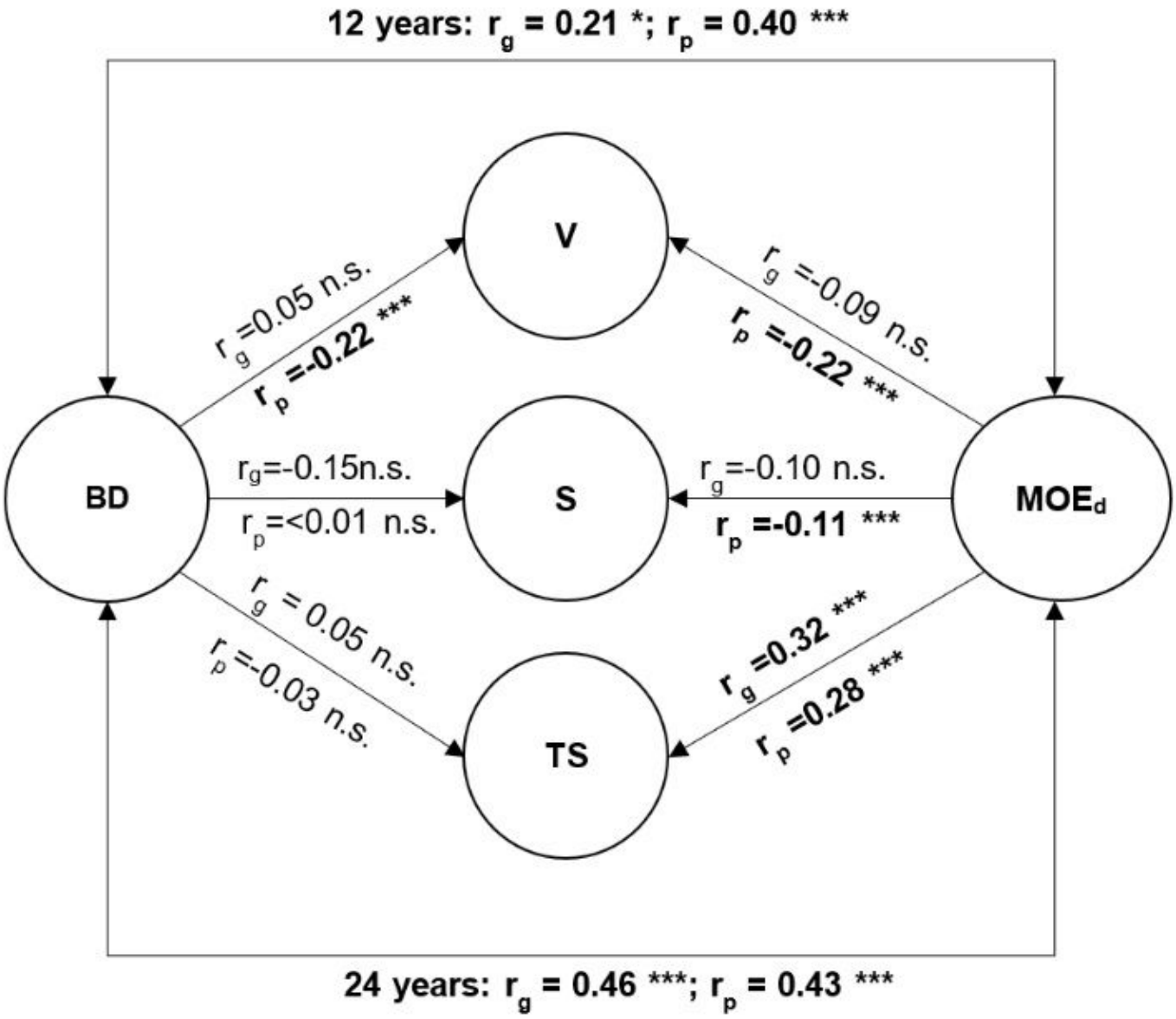

Figure 2

Genetic correlations (r_g, above the arrows) and phenotypic correlations (r_p, below the arrows) between wood quality traits and yield-related traits at age 12. BD: Basic density; MOE_d: Dynamic modulus of elasticity; S: Straightness; TS: Tree Slenderness; V: Volume. *: p-value <0.05; **: p-value < 0.01; ***: p-value < 0.001; n.s.: not significant.

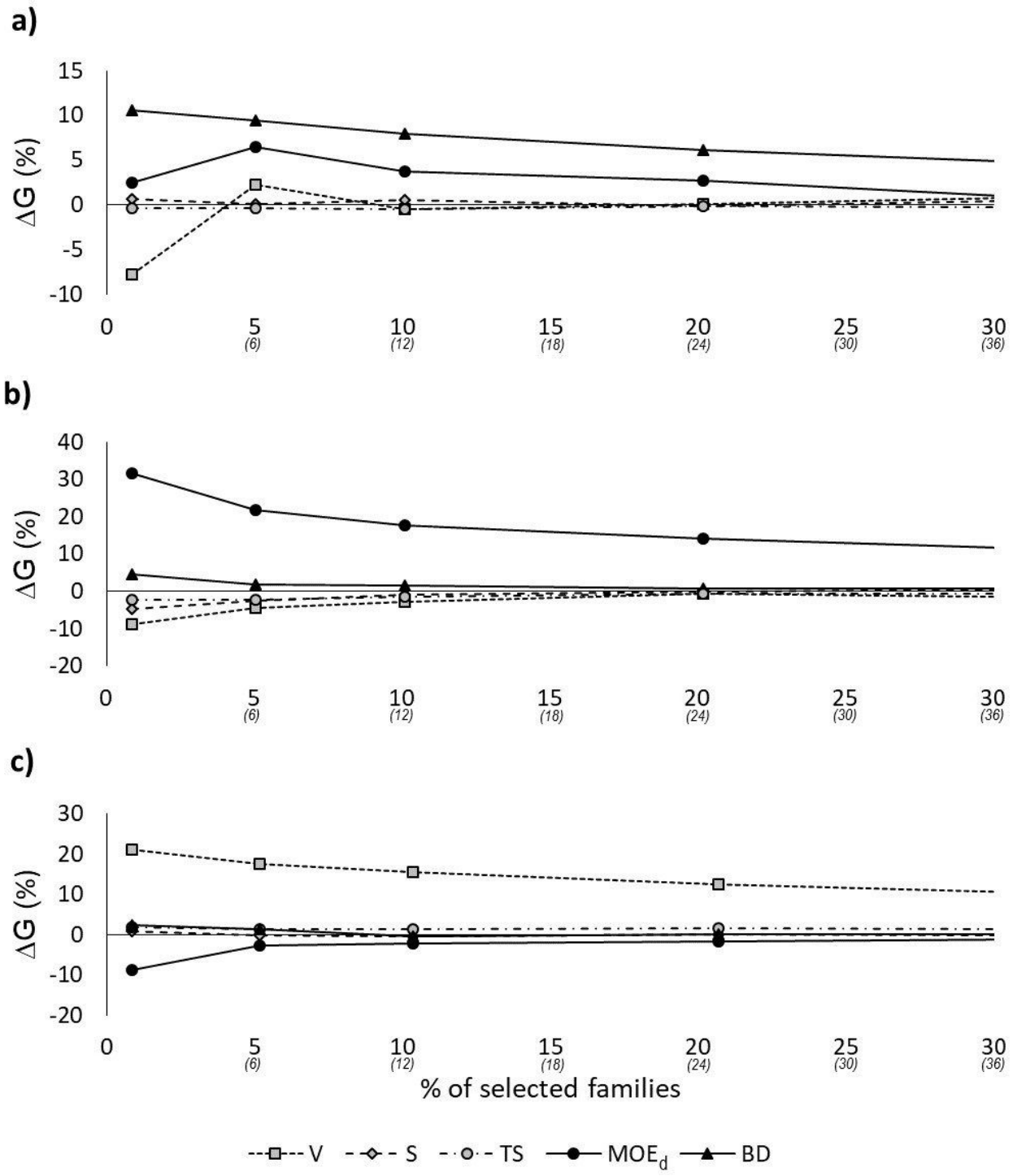

Figure 3

Estimated genetic gain (ΔG) when selecting for one trait: a) BD, b) MOE_d, c) V and correlated response of the other traits. The abscissa (x) axis represents the percentage of selected families and the number of selected families appears in parentheses. BD: basic density; MOE_d: dynamic modulus of elasticity; V: volume; S*: straightness; TS*: tree slenderness. *The sign of BV and ΔG has been changed to make the graph more understandable.

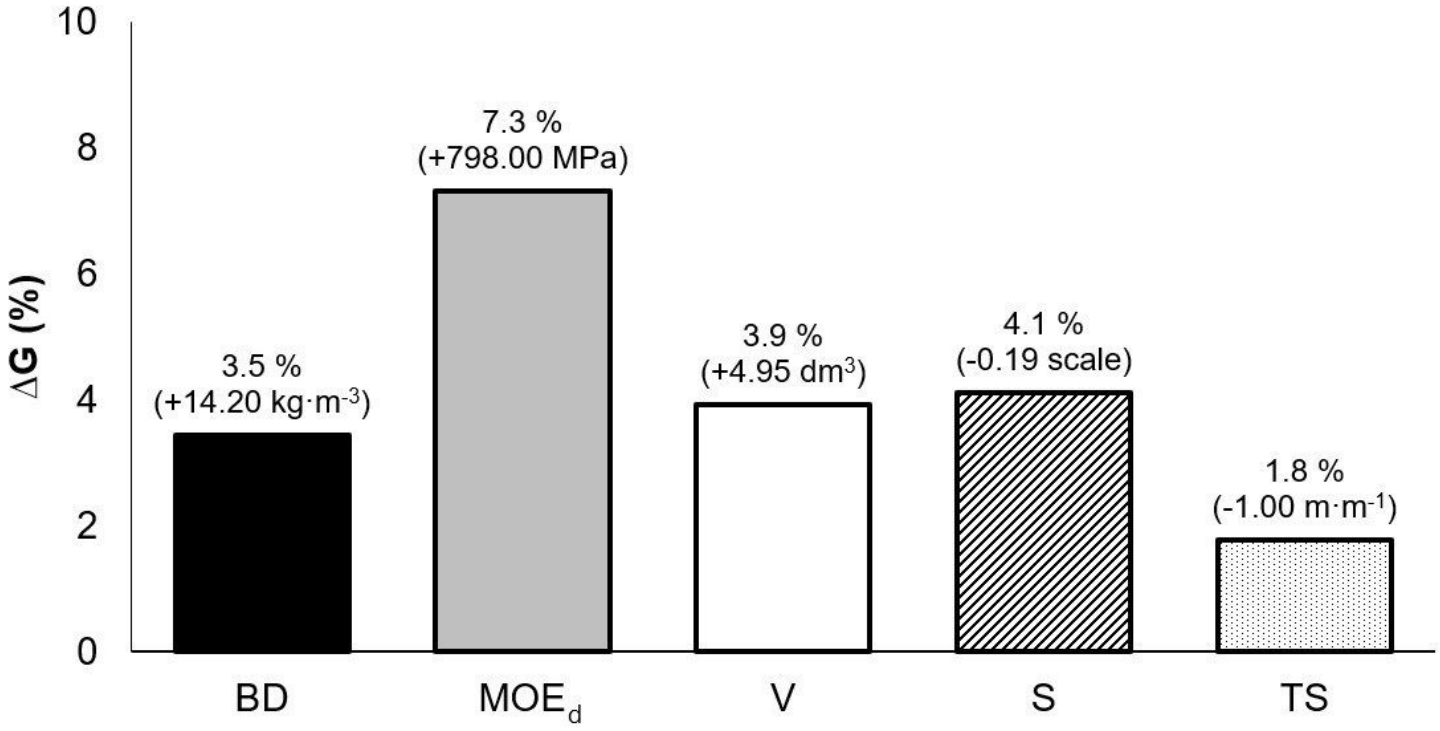

Figure 4

Estimated genetic gain (ΔG) when selecting the five families with positive BVs for BD, MOE_d, V, S and TS. BD: basic density; MOE_d: dynamic modulus of elasticity; V: volume; S*: straightness; TS*: tree slenderness. *The sign of BV and ΔG has been changed to make the graph more explicit. Values above the bars represent the genetic gain in percentage and values in parentheses represent the genetic gain in real value with respect to the mean of each trait.