Predicted genetic gains for growth traits and wood resistance in Pinus *maximinoi* and *Pinus tecunumanii*

Matheus Perek[1], Gary Hodge[2], Evandro Vagner Tambarussi[1], Fabricio Antonio Biernaski[3] and Juan Acosta[2*]

Abstract: *Tree breeders use traits of economic interest as productivity, stem form and wood quality, to select individuals for advanced generations. We determined the genetic control of growth volume, tree height and diameter, stem form and wood resistance, and calculated a selection index for Pinus maximinoi and P. tecunumanii, selected individuals were used to establish a seedling seed orchard (SSO). The largest genetic gain obtained in SSO for P. maximinoi was 21.48% for volume, while for P. tecunumanii it was 21.87% for stem form. There is enough genetic variability for genetic gain in future generations in tests of P. maximinoi and P. tecunumanii progenies. The selection index provided satisfactory total genetic gains for several traits, being more recommended than the BLUP method in order to support the selection and ranking of superior genetic materials in the progeny tests with greater probability of retaining favorable alleles over generations.*

Keywords: *Genetic parameters, Seed orchard, Heritability, Resistograph, Selection index*

INTRODUCTION

The genus *Pinus* ssp. has great silvicultural potential due to its wide edaphoclimatic adaptation and high productivity. Pines supply various wood products, such as sawn wood, plywood, medium density fiberboards, laminates, resins, and fibers for cellulose production (Missio et al. 2015, Braga et al. 2020). In Brazil, planted pine forests cover 1.6 million hectares, mainly in the Southern region, where edaphoclimatic conditions are favorable for the deployment of the species. Brazil led the global ranking of wood productivity in 2019, with an average of 31.5 m³ ha^{-1} yr^{-1} in pine plantations, according to information reported by the main Brazilian forestry companies (IBÁ 2020). With the high productivity and its large capacity to generate multiple products, the demand for new genotypes of the *Pinus* genus rises as breeding programs add new species aiming to increase productivity and quality (Santos et al. 2018).

In this way, the genetic characterization of germplasm from *Pinus maximinoi* H.E. Moore and *Pinus tecunumanii* F. Schwerdtf. ex Eguiluz and Perry are fundamental for the advancement of genetic improvement programs. *Pinus maximinoi* is the second most common species in Central America (Dvorak et al. 2000), usually with straight stems and total heights ranging from 20 to 35 m (Perry 1991). It is a tropical species that has been gaining prominence in the cellulose

*Corresponding author:
E-mail: jjacosta@ncsu.edu
ORCID: 0000-0002-9429-5166

[1] Universidade Estadual do Centro-Oeste, Rua Professora Maria Roza Zanon de Almeida Engenheiro, Gutierrez, 84505-677, Irati, PR, Brazil
[2] North Carolina State University, Raleigh, NC 27695, United States
[3] Klabin, Avenida Brigadeiro Faria Lima, 3600, Itaim Bibi, 04538-132, São Paulo, SP, Brazil

industries for producing good quality cellulosic pulp and growth superior to the other traditionally used commercial pine species (Santos et al. 2018). However, some provenances exhibit poor stem form with excessive crookedness and thick branches, requiring improvement in these traits (Shimizu 2008, Aguiar et al. 2011). *Pinus tecunumanii* is native to southern Mexico to central Nicaragua. Adult individuals can reach up to 50 m in height (Foelkel 2008, Aguiar et al. 2011). It is one of the most valued tropical species due to its excellent wood quality and high productivity and has great potential for reforestation in the south and southeast of Brazil. The main traits of this species include good stem form, few branches, and high adaptation to different types of soils. However, it is very susceptible to frost and may exhibit high levels of broken tops (Dvorak et al. 2000, Shimizu et al. 2008, Foelkel 2008, Aguiar et al. 2011).

*New technologies, such as non-destructive evaluation of wood drilling resistance, are becoming more popular in tree improvement programs. One important tool is the IML-Resistograph (*IML 2020)*, which measures the resistance of wood to penetration with a thin drill. This resistance is directly proportional to the basic density of the wood, guaranteeing quality using quick evaluations of the trait of interest (Henriques et al. 2011, CAMCORE 2017). Currently, most breeding programs make selections based on multiple traits to obtain superior genotypes. S*election indexes (SI) allow the combination multiple information into a single trait, which provides operational advantages and simplicity to breeders (Hazel 1943, Resende et al. 1990). Most tree improvement programs with these two species are in their first breeding cycle with few commercial scale plantations. However, they have shown an increase in tree volume and good wood quality. One limitation of these species is their low seed production when planted in exotic environments* (Isik and Li 2003, Biernaski et al. 2019), making it essential to establish seedling seed orchards with selections of superior genetic quality (Shimizu et al. 2008). The first objective of this research was to estimate genetic parameters and to predict genotypic values and genetic gains through a selection index from two open-pollinated progeny tests of *P. maximinoi* and *P. tecunumanii*. Finally, we aim to establish a seedling seed orchard with sufficient genetic variability for advanced generations of genetic improvement.

MATERIAL AND METHODS

Study site and plant material

The genetic material tested originated from first-generation open-pollinated progeny of *P. maximinoi* and *P. tecunumanii* established using seed provided by Camcore, an international gene conservation and tree-breeding program based at North Carolina State University, USA. Progeny tests were established contiguously by the forestry company Klabin S.A. in the municipality of Telêmaco Borba, Paraná state, Brazil. This area has average annual precipitation of 1,646 mm, average temperature of 18.6 °C, and an altitude of about 800 m (IAPAR 2019). The progeny test of *P. maximinoi* consists of 78 open-pollination families (39 from Colombia, 24 from South Africa and 15 from Brazil) and four commercial progenies of *Pinus taeda* L., classified as controls. The progeny test of *P. tecunumanii* was composed of 59 open-pollination families (43 from Colombia and 16 from South Africa), with five control seedlots of *P. maximinoi* and four control seedlots of *P. taeda*. The experiments followed a randomized complete block design, with single tree plots and 20 blocks. The progeny tests of *P. maximinoi* and *P. tecunumanii* were established with 1,640 and 1,360 plants, respectively, in February 2013.

Traits assessment

Diameter at breast height (*DBH*) and height (*HT*) were measured at 69 months (5.8 years) after planting, and then we estimated stem volume (*VOL*) using the following equation for both species (Ladrach 1986): $VOL = 0.00003 * DBH^2 * HT$ (Equation 1)

Stem form (SF) and branch arrangement (BA) were assessed by visual evaluation using an assignment of score ranging from 1 to 4 (Table 1). Wood drilling resistance (WDR) was measured using the IML *Resistograph*®. Drilling resistance is considered to be directly related to

Table 1. Criteria for classifying individuals as to stem form and branch arrangement for Pinus maximinoi and Pinus tecunumanii

Criteria	Stem form and branch arrangement
SF1	Stem with serious problems, forked or fox-tail
SF2	Very crooked or twisted stem
SF3	Stem with slight crookedness
SF4	Straight stem
BA1	Many branches, thick and twisted
BA2	Twisted and thick branches
BA3	Slightly twisted and thin branches
BA4	Well-defined crown with thin branches

SF: Steam form; BA: branch arrangement.

wood density. WDR measurements were taken at breast height (1.3 meters). The resulting graphs display resistance amplitudes, whereas oscillations along the transverse profile represent density variations from pith to bark and from early wood to late wood. The wood resistance amplitudes were converted to Disc resistance units (weighted circular mean resistance) using the R software (R Core Team 2019). R scripts were developed by Camcore researchers at North Carolina State University, to extract wood drilling resistance (WDR). All data were transformed to homogenize variation across the whole test $Z = \frac{x - \mu}{\sigma}$ (Equation 2), where x is the trait value, μ is the mean, and σ is the standard deviation.

Genetic parameters

We used restricted maximum likelihood (REML) to estimate variance components, and best linear unbiased prediction (BLUP) to estimate random effects. Using the lme4 R package in R (Bates et al. 2015, R Core Team 2020), the following linear mixed model was applied: $y = X_\beta + Z_g + e$ (Equation 3), where: X_β is the vector of fixed effects associated with blocks; Z_g is the vector of random effects associated with progenies; and e is the experimental error. Afterward, we estimated the individual narrow sense heritability (h_a^2), within-family heritability (h_w^2) and heritability of family means (h_m^2) using the following equations:

$$h_a^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_e^2} \text{ (Equation 4)}, \quad h_w^2 = \frac{3\sigma_f^2}{\sigma_e^2} \text{ (Equation 5) and } \quad h_m^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_e^2}{bn}} \text{ (Equation 6)}, \text{ where: } \sigma_f^2 \text{ is the family variance,}$$

σ_e^2 is the error variance, b is the number of block, and n is the number of plants per plot.

The estimates of the coefficient genetic variation ($CV_g(\%)$) and the coefficient of error variation ($CV_g(\%)$) were obtained using the following equations: $CV_g(\%) = \frac{\sqrt{\sigma_a^2}}{\bar{x}} 100$ (Equation 7) and $CV_e(\%) = \frac{\sqrt{\sigma_e^2}}{\bar{x}} 100$ (Equation 8), where: σ_a^2 is the additive genetic variance. The accuracy of the family general combining ability (GCA) predictions was estimated as $r_{aa} = \sqrt{h_a^2}$ (Equation 9). Additionally, genetic gain was estimated using the equation: $BV = GCA + ds_w h_w^2$ (Equation 10). The individual BLUPs of each tree (BV) were predicted as the sum of the parental BLUPs (GCA) plus the genetic deviation within the family, where ds_w is the individual tree deviation from the block and family mean, multiplied h_w^2. Using this approach, the average BV of all trees in test progeny was obtained, and then the average BV of the population after thinning was used to estimate the genetic gain of the test of progeny. For the estimation of the effective population size, we used the equation: $N_e = \frac{4N_f \bar{K}_f}{\bar{K}_f + 3 + \left(\frac{\sigma_{kf}^2}{K_f} \right)}$ (Equation 11), where N_e is the effective population size; N_f is the number of progenies sampled; $\bar{K}_f$ is the average number of individuals selected by progenies; σ_{kf}^2 is the variance in the number of individuals selected by progenies. This equation is defined for selection in experimental populations with several numbers of individuals selected by family of half-sibs (Resende and Bertolucci 1995).

Selection Index

We calculated a selection index with different degrees of importance for the traits DBH (45%), HT (10%), SF (20%), BA (10%) and WDR (15%) after obtaining the BLUPs for all traits. The relative weights were defined by the breeder based on company goals. The selection indices were calculated using the expression proposed by Hazel (1943):

$$SI = [(a_1 BV_{DBH}) + (a_2 BV_{HT}) + (a_3 BV_{SF}) + (a_4 BV_{BA}) + (a_5 BV_{WDR})] \text{ (Equation 12)},$$

Where SI is a linear function; BV represents the predicted breeding values (BLUPs) for each of the traits, and a is the value of the percentage importance for the breeding program considering the trait. We ranked genetic materials using the SI. For comparison, we ranked the genetic materials based on volume BLUPs alone, as is commonly done. We also estimated the genetic gains from selection and compared results using the SI and BV_S for volume. After ranking and selecting the best genotypes, thinning of the progeny test was performed, removing the progenies with lower performance to create a Seedling Seed Orchard (SSO). For this practice, after ranking the best genotypes in the office, phenotypic verification of these individuals in the field was performed for a more accurate selection. Thus, the materials that were to remain after thinning were selected and marked. The selection was carried between and within families seeking to maintain at least one genetically superior individual per family to preserve the genetic diversity.

RESULTS AND DISCUSSION

The lowest heritabilities at the level of individuals (h^2_a) and within progenies (h^2_w) were obtained for height (HT) . The h^2_a and h^2_w values were 0.14 and 0.11 for *P. maximinoi* and 0.25 and 0.20 and for *P. tecunumani*, respectively. For diameter at breast height (DBH), volume (VOL), stem form (SF) and branch arrangement (BA) we found moderate heritabilities values for *P. maximinoi,* ranging from 0.28 to 0.37 for h^2_a and from 0.23 to 0.30 for h^2_w (Table 2). However, for wood drilling resistance (WDR) in *P. tecunumani* the h^2_a was 0.55 and h^2_w was 0.48. The h^2_w values were close to the h^2_a values, but slightly lower for all traits in both progeny tests, as it is expected when dealing with within-family values (Resende 2002, Ziegler and Tambarussi 2022).

The median values for narrow- sense heritability (h^2_a) and heritability within family (h^2_w) were similar to the values previously reported for the tree species, indicating that a large part of the genetic traits will be transferred to the next generation after selection. These heritability values are in agreement with those normally found in pine species (Aguiar et al. 2010, Hodge and Dvorak 2012), and indicate the potential for genetic gain after the selection of the best genotypes. In a study with *P. maximinoi* measured at five and eight years of age in Brazil, h^2_a ranged from 0.08 to 0.29 for BA and SF respectively (Gapare et al. 2001), similar values to those obtained in our research for these traits. In an experiment with *P. tecunumanii*, Hodge and Dvorak (1999) found lower heritability than those obtained in the present study for the traits VOL, BA and SF at five and eight years of age, and this fact may be due to the age of the experiment, which consists of a variation of environmental effect and can influence the estimation of heritability. The average family mean heritability values were considered moderate to high ($h^2_m \geq 0.42$) for all traits evaluated, indicating that those traits can be used in breeding programs for selection of superior individuals.

The coefficient of genetic variation (CV_g) expresses the magnitude of the genetic variation in relation to the trait average (Ziegler and Tambarussi 2022). The coefficients of genetic variation were high for VOL, SF and BA ranged from 11.35% to 12.75% for *P. maximinoi* and 12.51% to 13.67 for *P. tecunumanii*, respectively. For HT, DBH and WDR traits this parameter was low, with values ranging from 2.24% to 5,08% for *P. maximinoi* and 2.99% to 5,64% for *P. tecunumanii* (Table 2).

According to Ziegler and Tambarussi (2022), values between 4.80% and 14% for DBH and HT are considered moderate and indicate the presence of genetic variability to be explored over generations. The highest values of CV_g were observed for SF and BA, which indicates substantial genetic variation for these traits. This suggests it should be possible to get

Table 2. Estimates of genetic parameters for growth and quality traits for progeny tests of *Pinus maximinoi* and *Pinus tecunumanii* at five years old

Pinus maximinoi									
Traits	σ^2_f	σ^2_e	σ^2_p	h^2_a	h^2_w	h^2_m	CV_g (%)	CV_e (%)	r_{aa}
DBH	25.81	337.47	363.28	0.28 ± 0.080	0.23	0.60	5.08	18.37	0.53
HT	5.01	139.30	144.31	0.14 ± 0.056	0.11	0.42	2.24	11.80	0.37
VOL	128.92	1645.72	1774.64	0.29 ± 0.080	0.23	0.61	11.35	40.57	0.54
SF	163.49	1855.00	2018.48	0.32 ± 0.086	0.27	0.64	12.75	41.98	0.57
BA	154.98	1876.31	2031.29	0.30 ± 0.085	0.24	0.62	12.44	43.31	0.55
WDR	11.15	108.84	119.98	0.37 ± 0.025	0.30	0.67	3.38	10.43	0.61
Pinus tecunumanii									
Traits	σ^2_f	σ^2_e	σ^2_p	h^2_a	h^2_w	h^2_m	CV_g (%)	CV_e (%)	r_{aa}
DBH	31.92	330.42	362.34	0.35 ± 0.1026	0.28	0.66	5.64	18.17	0.59
HT	8.99	135.36	144.35	0.25 ± 0.086	0.20	0.57	2.99	11.64	0.50
VOL	156.60	1612.59	1769.18	0.35 ± 0.1010	0.29	0.66	12.51	40.15	0.59
SF	187.10	1844.57	2031.67	0.37 ± 0.1052	0.30	0.67	13.67	42.94	0.61
BA	163.15	1865.95	2029.10	0.32 ± 0.0984	0.26	0.64	12.73	43.19	0.57
WDR	16.72	104.22	120.94	0.55 ± 0.1006	0.48	0.76	4.08	10.20	0.74

σ^2_f: family variance; σ^2_e: error variance; σ^2_p: phenotypic variance; h^2_a: Narrow-sense heritability coefficient; h^2_w: Narrow-sense heritability within progeny family; h^2_m: average family mean heritability;CV_g: Coefficient of genetic variation; CV_e: Coefficient of error variation; r_{aa}: Selection accuracy for parent GCA values; DBH: diameter at breast height; HT: Height; VOL: Volume; SF: Stem form; BA: Branch arrangement; WDR: Wood drilling resistance.

significant genetic gain as observed in several studies with pine species (Missio et al. 2004, Sebbenn et al. 2005). The lowest values of CV_g were verified to HT. Santos et al. (2018) found similar values in a population of *P. maximinoi* they observed CV_g of 4.39% for height at five years of age in the same region as in the current study.

The estimated coefficients of error variation (CV_e) for VOL, SF and BA ranged from 40.15% (VOL, *P. tecunumanii*) to 43.31% (BA, *P.maximinoi*) (Table 2). According to the classification by Gomes and Garcia (2002), the coefficients of error variation were high for BA, SF and VOL indicating a strong environmental influence on the evaluated traits. One of the factors that could increase CV_e (%) is the mortality rate, which was 9.45% (155 trees) and 6.40% (87 trees) for *P. maximinoi* and *P. tecunumanii*, respectively. The high values for the SF and BA can be explained by the large variability in these traits. Ettori et al. (2004), also found high values of CV_e for form (41%) and arrangement of branches (36%) for *P. maximinoi*. Other studies with *Pinus* species have shown that the values of CV_g (%) varied from medium to high for all traits (Souza et al. 2016, Santos et al. 2018).

The values of selection accuracy (r_{aa}) for parent GCA were low to moderate (ranging from 0.37 to 0.61) for *P. maximinoi* and moderate to high (ranging from 0.50 to 0.74) for *P. tecunumanii* (Table 2). Using the guidelines proposed by Resende and Alves (2020): very high accuracy ($r_{aa} \geq 0.90$), high ($0.70 \leq r_{aa} < 0.90$), moderate ($0.40 < r_{aa} < 0.70$) and low ($0.10 \leq r_{aa} < 0.40$), the observed values in this study indicate moderate experimental quality and precision of GCA estimates.

For WDR, we found a mean value of 1,016.88 for *P. maximinoi*, ranging from 409.81 to 2,280.12. For *P. tecunumanii* the mean value was 1,141.21 ranging from 673.81 to 2,402.18, Indicating that the later species had greater resistance to drilling. Previous studies have shown that there is a positive and significant correlation between WDR and wood density. Isik and Li (2003) found moderated correlation values (0.65) for *P. taeda*. Similarly, Gwaze and Stevenson (2008) reported a correlation of 0.47 for *P. echinata*.

Rankings using volume breeding values (BVs) and selection index, for *P. maximinoi* and *P. tecunumanii* respectively, are depicted in Figures 1 and 2. Note that there are differences between family rankings when they are sort by volume BVs and the ranking by selection index. There are a few families that are placed high in both rankings, which indicates their genetic value superiority, for example, family 46 for *P. maximinoi* and family 20 for *P. tecunumanii*. However, some families behave inconsistently, for example, family 72 *for P. maximinoi* and family 63 for *P. tecunumanii*, those families would not be transferred to the next generation if the selection was based only tree volume. Consequently, ranking families based on their SI should be a priority since it reassures that the selected families exhibit important traits for the genetic improvement of this species.
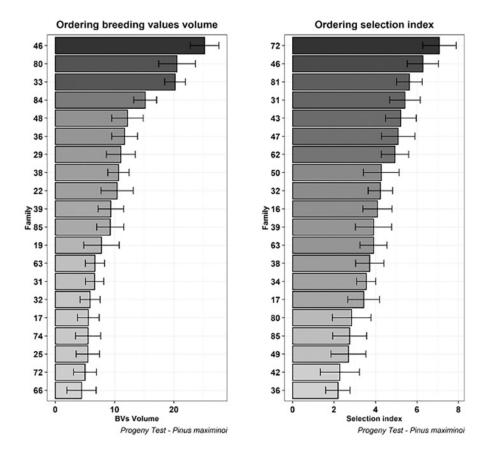
After ordering the genotypes through the SI, we removed the genetically inferior individuals to conduct the seedling orchard (SSO). After thinning, 27% of the original population was kept of *P. maximinoi*, and 31% of *P. tecunumanii* in the SSOs. The selection gains in SSO were high to moderate with both methods. However, we see that the selection index had lower gains for growth traits (DBH, HT and VOL) (Table 3). On the other hand, we observed higher genetic gains for BA, SF and WDR traits using the selection index.

As shown in Table 3, the genetic gains obtained in the SSO for *P. maximinoi* varied among traits from 2.89% (WDR) to 21.48% (VOL). In the SSO for *P. tecunumanii* gains were from 5.17% (WDR) to 21.87% (BA). The difference between the gains for the two methods was from - 7.72% to 18.41% (*P. maximinoi*) and -10.36% to 19.57% (*P. tecunumanii*) for the VOL and BA traits, respectively. After the selection of genetic materials, thinning of the lower-ranked individuals were carried out in the two progeny tests to establishing the SSO. A thinning intensity of 73% was applied in *P. maximinoi*, reducing the population of 1,640 plants. The effective population size (N_e) was reduced from 280.11 to 166.70 after thinning. For the progeny test of *P. tecunumanii* the thinning intensity was 69%, reducing the population of 1,321 plants with a N_e of 216.36, for 427 plants with a N_e of 143.93. After selecting the superior material, thinning was performed in the progeny test, maintaining an N_e adequate to retain sufficient genetic variability for future selection cycles. The N_e resulting from the SSO was 166.7 and 143.9 for *P. maximinoi* and *P. tecunumanii* respectively, being considered adequate to maintain population variability over generations of genetic improvement (Vencovsky and Crossa 2003, Aguiar et al. 2010). Because an N_e of 150 or more guarantee the maintenance of approximately 90% of the population's variability after several selection cycles (Vencovsky and Crossa 2003).

The difference between the selection order in Figures 1 and 2 demonstrates that when selection is based on the volume BVs, we would be not select some genotypes that offer important gains in other traits. For example, if we look at the ranking based on the selection index for the *P. maximinoi* test, we can see that family 72 is ranked third, but when we consider the ranking based only on volume BVs. The same family does not even appear among the top 20. On the other hand, using the selection index, we would select other families, that may contain favorable alleles for other important traits. Therefore, the use of the selection index guaranteed some genetic gain in multiple traits of interest at the same time, indicating the best individuals for the formation of the SSO, advancing the generation in the breeding program of the species.

The greatest genetic progress for growth traits was found for volume (21.48% and 11.56%) in the SSO of *P. maximinoi* and *P. tecunumanii,* respectively. Sampaio et al. (2000) found similar patterns of volume gain (14.9%) for *P. caribaea* var. *hondurensis* populations at the age of five years. With multi-trait selection, obviously the gain in some traits is reduced, so the gains obtained in SF, BA, and WDR influenced the reduction in growth traits. With a selection using the SI, we lost approximately 7.72% volume gain in *P. maximinoi*, and approximately 10.36% gain for *P. tecunumanii.* For the other traits not related to tree volume, we obtained superior gains using the SI, with the biggest gains for BA (> 21%) in both SSO, the trait WDR showed the lower gain rate in comparison to the other traits.

Since the SI methodology focuses on selection for an array of traits, and is not focused on just one trait, it was possible to make genetic gain in all traits and increase the probability of retaining favorable alleles for all traits in the population. In contrast, if selection is done using only the volume BLUPs, we could have a population with slightly worse stem form, and we would risk decreasing the density of the wood, and we would miss out on selecting some genotypes, which carry

Figure 1. Ranking of the 20 best families within the progeny test of Pinus maximinoi using BVs volume (left) and the selection index (right).

traits of interest for the genetic improvement of these species. Therefore, the SI fulfills the objective of guaranteeing total gains, grouping the traits of growth, productivity, and quality in a single value, reducing the possibility of loss of favorable alleles during the selection.
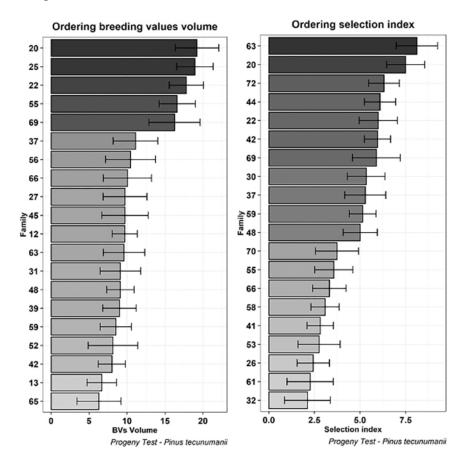

Figure 2. Ranking of the 20 best families within the progeny test of *Pinus tecunumanii* using BVs volume (left) and the selection index (right).

Table 3. Estimates of genetic gain of the selected population with the selection index (SI) and volume BLUPs for *Pinus maximinoi* and *Pinus tecunumanii* measured at five years of age, in Telêmaco Borba, PR, for each evaluated trait

Trait	Method	*P. maximinoi*		*P. tecunumanii*	
		Selection gain (%)	Gain difference (%)	Selection gain (%)	Gain difference (%)
DBH (cm)	SI	10.46	-7.39	9.17	-7.8
	BLUPs	17.85		16.97	
HT (m)	SI	18.24	-6.59	15.43	-6.24
	BLUPs	24.83		21.67	
VOL (m³)	SI	21.48	-7.72	11.56	-10.36
	BLUPs	29.2		21.92	
SF	SI	9.24	3.86	21.47	10.83
	BLUPs	5.38		10.64	
BA	SI	21.03	18.41	21.87	19.57
	BLUPs	2.62		2.3	
WDR	SI	2.89	1.14	5.17	4.48
	BLUPs	1.75		0.69	

DBH: Diameter at breast height; HT: Height; VOL: Volume; WDR: Wood drilling resistance; SF: Stem form; BA: Branch arrangement.

CONCLUSIONS

There is enough genetic variability for genetic gain in future generations in tests of *P. maximinoi* and *P. tecunumanii* progenies, mainly considering parameters such as h_m^2, CV_g (%) and r_{aa} in most of the evaluated traits. The high values of h_m^2 allow to recommend selection between and within progenies as well as phenotypic selection, considering the high degree of genetic control verified for almost all traits in both species. The selection index provided satisfactory total genetic gains for several traits, being more recommended than the BLUP method in order to support the selection and ordering of superior genetic materials in the progeny tests. We can say that the selection index method is efficient to support the formation of seedling seed orchards (SSO), ensuring the advancement of genetic improvement programs for the species and with greater probability of retaining favorable alleles over generations.

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