FUNDAMENTAL RESEARCH

For. Sci. XX(XX):1–14
doi: 10.1093/forsci/fxy021

genetics & tree improvement

Genetic Parameters for Growth, Stem Straightness, and Branch Quality for *Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis* F_1 Hybrid in Argentina

Ector C. Belaber, María E. Gauchat, Hugo D. Reis, Nuno M. Borralho, and Eduardo P. Cappa

Genetic parameters for growth, stem straightness, and branch quality were estimated in five progeny trials of *Pinus elliottii* var. *elliottii* (PEE) × *Pinus caribaea* var. *hondurensis* (PCH) F_1 hybrid measured at ages three, five, and seven years. The trials comprised 133 full-sib families from the tree breeding program initiated by the National Institute of Agricultural Technology. Single-site analyses showed that the average individual-tree narrow- and broad-sense heritability estimates were respectively 0.24 and 0.53 for diameter and 0.34 and 0.47 for total height. Average estimated heritabilities were low to moderate for stem straightness (< 0.18), branch diameter (< 0.26), and branch angle (from 0.28 to 0.33). Bivariate analyses showed that the estimated additive and family genetic correlations between diameter and height were consistently high and positive (> 0.84). However, genetic correlations between growth variables and stem straightness, branch diameter, and branch angle were not significant in general. The average estimated additive genetic correlation between sites was high for growth trait and stem straightness (> 0.70), while for branch diameter and angle, the correlations between sites ranged from 0.19 to 0.99. The implications of these results for genetic improvement strategies based on PEE × PCH F_1 hybrid in Argentina are discussed.

Keywords: hybrid pine, heritability, additive genetic correlation, genotype-environment interaction, tree breeding

In Argentina, over 80 percent of the area planted with *Pinus* spp. is in the provinces of Misiones and Corrientes (Ministry of Agriculture-Industry, Secretariat of Agriculture, Livestock and Fisheries [MAGyP] 2016), with *Pinus taeda* L. (PT) and *Pinus elliottii* var. *elliottii* Engelm (PEE) as the most widely used species. However, in the last few years, the area planted with the interspecific F_1 hybrid between PEE and *Pinus caribaea* var. *hondurensis* (Sénécl) Barrett and Golfari (PCH) (hereafter PEE × PCH hybrid) has increased considerably, amounting to almost 21,000 hectares. Thus, this hybrid has become one of the three most commonly used conifers in the Argentinean northeast, replacing PEE in many areas, and the most highly recommended taxon for silvopastoral system. In general, growth of the PEE × PCH hybrid was superior to its parental species and commercial controls in tropical and subtropical countries (Nikles 1991, 1996 and 2000). For instance, it has shown excellent growth and wood quality properties in Zimbabwe (Gwaze 1999), Australia (Powell and Nikles 1996, Brawner et al. 2003), the United States (Rockwood and Nikles 2000), and China (Zheng 2000).

The first PEE × PCH F_1 hybrid pine trial in Argentina was planted in 1981 on a well-drained site in the northeastern province

Manuscript received July 3, 2017; accepted April 17, 2018; published online XXXX XX, XXXX.

Affiliations: *Ector C. Belaber (belaber.ector@inta.gob.ar), María Elena Gauchat (gauchat.maria@inta.gob.ar), National Institute of Agricultural Technology (INTA), Montecarlo experimental station. Av. El Libertador 2472, 3384, Montecarlo, Misiones, Argentina. Hugo D. Reis (hugoreis@pindosa.com.ar), PINDO S.A. Juan Domingo Perón 303, N3378BUA, Pto. Esperanza, Misiones, Argentina. Nuno M. Borralho (nunoborralho@sapo.pt), Private Consultant, Urb S Francisco 18, 2070–220 Cartaxo, Portugal and Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade Técnica de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal. Eduardo P. Cappa (cappa.eduardo@inta.gob.ar), National Institute of Agricultural Technology (INTA), Biological Resources Institute, Center for Natural Resource Research, De Los Reseros and Dr. Nicolás Repetto n/n, 1686, Hurlingham, Buenos Aires, Argentina and National Scientific and Technical Research Council (CONICET), Argentina.*

Acknowledgements: *This research was partially supported by National Institute of Agricultural Technology (Project PNFOR-1104062; MSNES-1242204/5) and UCAR-Project "Natural Resource Sustainable Management BIRF 7520, Component 2: Sustainable Forest Plantations" (PROMEF). The authors are grateful to the company PINDO S.A. for providing the land for the trials and logistical and monetary support. The authors also thank Diego Bogado, Lucas Gimenez, and Cristian Schoffen who assisted with field work and data collection. Finally, they also wish to thank the anonymous associate editor and two referees for their insightful comments on an earlier version of this manuscript.*

of Corrientes, as part of a series of collaborative trials sponsored by the then Queensland Forestry Research Institute (Barrett et al. 1991). This and subsequent trials (Pahr et al. 2002, Schenone and Pezzutti 2003, Bunse 2003, Cappa et al. 2012) have shown this hybrid was well adapted to the Argentinean Mesopotamia region. Furthermore, Pahr et al. (2002) showed a better growth of PEE × PCH F_1 and F_2 Australian hybrid than PEE and some PT sources in the province of Misiones. Likewise, when assessing trials planted in the northeast of the province of Corrientes, Schenone and Pezzutti (2003) and Bunse (2003) reported that F_2 hybrid grew better than PEE and PT from Marion (Florida, USA). Similar results were reported by Cappa et al. (2012), who also observed high growth potential, outstanding stem straightness, and branch diameter qualities in Australian F_1 and F_2 compared with the different *Pinus* taxa traditionally planted in the Argentinean Mesopotamia.

Given an increasing interest in this hybrid in Argentina and the high cost to purchase seeds from Australian seed orchards, the National Institute of Agricultural Technology (INTA), through an agreement with the company PINDO S.A., started a program in 2004 for the generation of F_1 hybrids between PEE and PCH (Rodríguez et al. 2005). The program currently comprises 12 trials of hybrid progenies, five of which are reported here. These five trials comprise 133 hybrid families, generated in three hybridization campaigns involving a total of 16 PEE mothers and 21 PCH fathers. This paper incorporates data for age five, previously reported for two of the sites by Gauchat et al. (2013), with new measurements taken from the other three sites for traits such as growth, stem straightness, and branches characters at three, five, and seven years from planting.

Knowledge of genetic parameters obtained from such trials is required to formulate adequate hybrid breeding strategies and estimate breeding values and expected gains from selections (White 1996). A number of studies have reported genetic parameters for interspecies *Pinus* hybrids, covering a variety of growth, stem, and crown traits (Dieters et al.1996, Dieters et al. 1997, López-Upton et al. 1999, Gwaze et al. 2000, Brawner et al. 2003, Blada 2013, Gauchat et al. 2013, Mutete et al. 2015) and wood properties (Rockwood et al. 1991, Kain 2003). Nevertheless, there are relatively few published reports presenting genetic parameters for growth and stem straightness specifically for the PEE × PCH hybrid cross (examples include Dieters et al.1996, Dungey et al. 2000, Gauchat et al. 2013), and even fewer for branch qualities (Gauchat et al. 2013). These last authors reported, based on two of the sites studied here, narrow-sense individual heritability estimates of 0.38, 0.15, and 0.39 for volume (VOL), stem straightness normal score (NSTR), and mean number of branches per whorl (NRPV), respectively; they also reported additive genetic correlations between VOL and NSTR of 0.14, between VOL and NRPV of 0.29, and between NSTR and NRPV of -0.20, and additive genetic correlations between the two sites greater than 0.7.

Our objective was to estimate genetic parameters including additive and family genetic variances, heritabilities, and additive and family genetic correlations between traits within and across sites in five progeny trials of PEE × PCH hybrid pine. Additionally, the implications of all these parameter estimates are discussed in terms of the selection strategies for genetic improvement of PEE × PCH F_1 hybrid in Argentina.

Materials and Methods

Genetic Material

The 133 F_1 hybrid families used in this study were obtained from controlled crosses made in 2004, 2006, and 2007. Hybridizations were performed in the Clonal Seed Orchard (CSO) of PEE located in the National Institute of Agricultural Technology (INTA), San Antonio, Misiones, Argentina. Sixteen PEE mothers were crossed with 21 PCH fathers to form one 13 PEE × 8 PCH and two seven PEE × 8 PCH factorial arrays. Four PCH parents were selected from two provenance trials planted by INTA in the east-center and southwest of Misiones province, while the remaining 17 parents correspond to selections from commercial plantations belonging to PINDO S.A. of unknown native origins. The number of parents, families, and full-sib and half-sib progenies in common among the trials are shown in the Supplementary Material (Tables S1 and S2). A local commercial bulk seed-lot of PEE from the CSO of INTA San Antonio (Misiones) was established at the five trials as a common control. The trials planted in 2007 included the following additional control seed-lots: PEE from CSO of INTA Cerro Azul (Misiones), PCH from Brazil, PEE × PCH F_2 hybrid from the Queensland Forestry Research Institute (QFRI, Australia), and PT Marion from CSO of Alto Parana S.A. (Puerto Libertad, Misiones). The trials established in 2011 have the following checks: PCH from commercial plantations of Puerto Esperanza (Misiones), cuttings of PEE × PCH F_1 hybrid from controlled crossbreeding of APSA Company, PEE × PCH F_2 hybrid from Villa Olivari (Corrientes), and cuttings of PT Marion from controlled crossbreeding of APSA Company.

Trial Description

Five trials, all located in the northwest of the province of Misiones, Argentina, were included in this study (Figure 1). Two trials were planted in 2007 (trials one and two), and three trials were planted in 2011 (trials three, four, and five). The experimental design was in randomized complete blocks, with five-tree row plots for trials planted in 2007, and single-tree plots for trials planted in

Management and Policy Implications

The present study assists tree breeders in planning improvement of growth and stem and branch quality of *Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis* hybrids grown in Argentina and other tropical and subtropical regions. Indirectly, this study also assists forest managers with stand management by identifying methods to obtain specific wood products in less time. According to the information in this study, managers should adjust thinning and pruning practices to the growth rhythm and crown structure of this taxon. In a broader sense, the need to increase global food production has led landowners to implement mixed and more complex production systems including livestock and afforestation. Since 1990, Argentina has implemented mixed systems where *Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis* hybrid pines are the tree component of these agroforestry systems. The contributions of the present study may be relevant for government policies in relation to the suggestion of genetic material to landowners if the focus is increased productivity of these systems and the improvement of the economic status of these farmers, especially for small farmers.

2011. All trials were established at a 3 meters × 3 meters spacing. Details of the five trials and the site characteristics are summarized in Table 1.

Trait Evaluated

Growth, tree stem straightness, and crown traits were measured at ages three, five, and seven in all surviving trees. However, measurements for every trait and age were not taken at all sites (Table 2). Diameter at breast height (1.3 meters, DBH) was measured in centimeters, and total height was measured in meters (TH). Tree stem straightness (STR), branch diameter (BD), and branch angle (BA) were assessed using a four-point subjective score, with one indicating the most crooked trees, steep branch angle, or thick branch diameter, and four indicating the straightest trees, flattest branch angle, or thin branch diameter. These ordered categorical traits were scored within each site. Consequently, the straightness, branch diameter, and branch angle scored at one site do not necessarily represent the same degree of stem straightness, branch diameter, and branch angle at another site.

The categorical STR, BA, and BD traits were transformed into normal scores (NS; viz. Gianola and Norton 1981) to meet the requirements for normal distributions and renamed as NSTR, NSBA, and NSBD, respectively. Furthermore, prior to conducting any cross-site analysis, growth data were standardized in order to remove scale effects by subtracting the phenotypic mean and dividing each trait measurement by the square root of the phenotypic variance for each site. To differentiate the standardized traits from the nonstandardized ones, we added a letter "S" at the beginning of the acronyms used to identify each trait. For example, the nonstandardized diameter at breast height was coded as DBH, while the standardized variable was coded as SDBH.

Statistical Analysis

Statistical analysis was conducted in four stages. First, each trial was analyzed separately to estimate univariate genetic parameters. Second, covariances between two different traits measured in the same individual were estimated for each trial. Third, paired-site analysis, including data from sites one and two, were conducted in order to investigate the covariance of the same trait measured at two ages. Fourth, paired-site analysis, including data from sites one and two, and three and four, were conducted in order to investigate the genotype by environment interaction, where an environment constitutes a particular site-year combination and assuming that a trait measured in two environments represents two distinct traits.

The single-site analysis was based on the following univariate individual-tree linear mixed model:

$$y = X\beta + Z_a a + Z_f f + e \quad (1)$$

In (1), $\boldsymbol{y}$ is the vector of individual tree observations, the fixed vector $\boldsymbol{\beta}$ contained the replication effects and is associated with $\boldsymbol{y}$ by the incidence matrix $\boldsymbol{X}$. The random vector $\boldsymbol{a}$ contained the additive genetic effects (or breeding value) of individual trees and is related to $\boldsymbol{y}$ by the incidence matrix Z_a. The expectation of $\boldsymbol{a}$ is 0, and the covariance matrix is $G = A\sigma_a^2$, where A is the average numerator relationship matrix (Henderson 1984) for the trial trees and their known ancestors, and σ_a^2 is the additive genetic variance. The random vector $\boldsymbol{f}$ included family genetic effects (or specific combination ability, SCA) and is associated with $\boldsymbol{y}$ by the incidence matrix

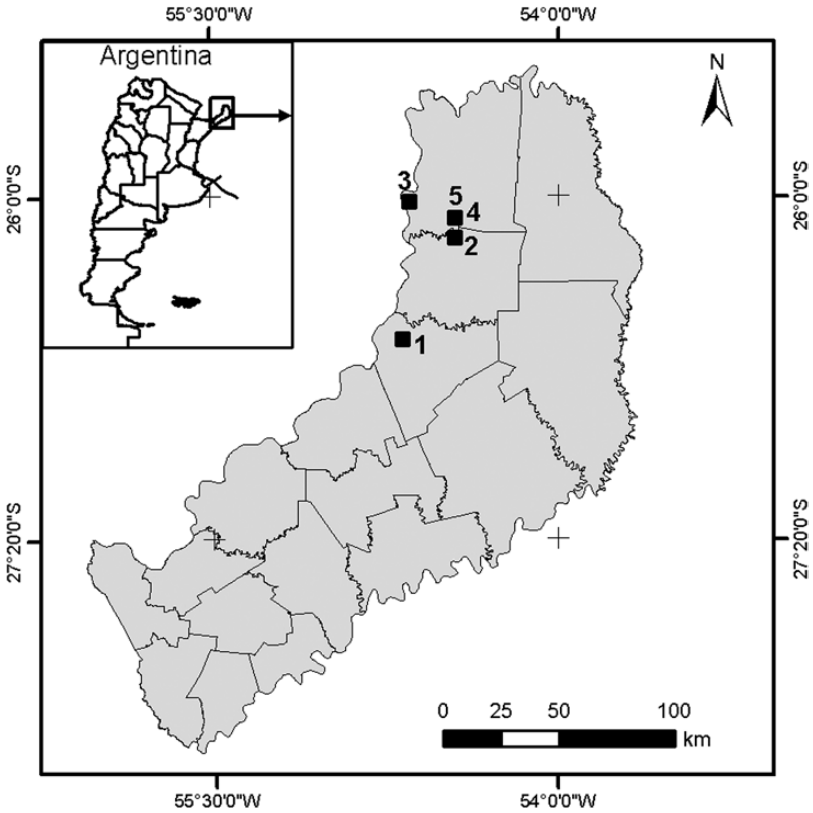

Figure 1. Approximate location of the five trials in Argentina. Abbreviations used for the trials are described in Table 1. Trials four and five are located adjacent to each other in the same site and were represented as a unique symbol (■).

Table 1. Locations and characteristics for each of the five trials.

Trial	1	2	3	4	5
Location	Pto. Laharrague	Colonia Delicia	Pto. Esperanza	Pto. Esperanza	Pto. Esperanza
Latitude (°S)	26° 33'	26° 09'	26° 01'	26° 05'	26° 05'
Longitude (°W)	54° 40'	54° 26'	54° 38'	54°26'	54°26'
Altitude (m)	174	241	222	278	278
Previous use	Native forest	Pine	Pine	Araucaria	Araucaria
Planting date	10/10/2007	26/07/2007	08/06/2011	04/07/2011	19/08/2011
Plant origin	Seed	Seed	Cutting	Cutting	Cutting
Number of trees	925	1980	875	875	875
Number of families	37	66	35	35	35
Number of replicates	5	6	25	25	25
Plot	5 Trees	5 Trees	Single tree	Single tree	Single tree
Spacing (m)	3 × 3	3 × 3	3 × 3	3 × 3	3 × 3
Survival*	94	85	95	94	87

NOTE: *Survival in the first years (percent).

Table 2. Phenotypic means (Mean), standard deviation (SD), and respective units for all traits assessed in each trial.

Year	Trait*	Unit	Trial†									
			1		2		3		4		5	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
3	**DBH**	cm	11.00	1.70	10.40	2.10	11.87	1.84	11.10	1.85	11.80	1.79
	TH	m	5.50	0.90	5.10	0.90	6.07	0.89	5.36	0.82	5.78	0.93
	STR	Scale 1–4	2.67	0.86	2.98	0.74	2.49	0.57	2.06	0.70	2.47	0.60
	BD	Scale 1–4	2.57	0.52	2.24	0.45	2.82	0.83	2.72	0.71	2.88	0.73
	BA	Scale 1–4	3.13	0.50	1.95	0.48	3.05	0.80	2.93	0.80	2.92	0.80
5	**DBH**	cm	18.20	2.70	17.60	2.60	—	—	—	—	—	—
	TH	m	10.90	1.50	10.40	1.30	—	—	—	—	—	—
	STR	Scale 1–4	2.32	0.77	2.26	0.69	—	—	—	—	—	—
7	**DBH**	cm	20.34	7.16	22.09	3.70	—	—	—	—	—	—
	TH	m	12.99	4.29	13.26	1.60	—	—	—	—	—	—
	STR	Scale 1–4	2.45	0.61	2.48	0.55	—	—	—	—	—	—
	BD	Scale 1–4	2.64	0.76	2.52	0.76	—	—	—	—	—	—
	BA	Scale 1–4	2.50	0.70	2.40	0.68	—	—	—	—	—	—

NOTE: *Diameter at breast height (DBH), total height (TH), stem straightness (STR), branch diameter (BD), and branch angle (BA).
†Abbreviations used for the trials are described in Table 1.

$\boldsymbol{Z}_f$. The expectation of $\boldsymbol{f}$ is *0* with covariance matrix $\boldsymbol{I}\sigma_f^2$, where $\boldsymbol{I}$ is the identity matrix and σ_f^2 is the family genetic variance, which estimates one-quarter of the dominance variance (σ_d^2), while epistasis is assumed to be negligible (see discussion section). For trials with linear plots (trials one and two), model (1) also included a random vector $\boldsymbol{p}$ with plot effects, associated with $\boldsymbol{y}$ by an incidence matrix $\boldsymbol{Z}_p$. The expectation of $\boldsymbol{p}$ is *0*, and the covariance matrix is $\boldsymbol{I}\sigma_p^2$, where σ_p^2 is plot variance. Finally, random residual terms are included in the vector $\boldsymbol{e}$, which is distributed as $\boldsymbol{e} \sim N(0, \boldsymbol{I}\sigma_e^2)$, and σ_e^2 is the residual variance. Spatial analysis, using separable autoregressive processes of residuals (e.g., Dutkowski et al. 2002) was also performed for each trait in the first step of the single-site analyses. In general, spatial models showed better fit and lower plot residual variance effects for the traits analyzed (see Supplementary Table S3). However, the Spearman correlation between predicted breeding values from the standard and spatial models were high: from 0.992 to 0.999 for family, from 0.952 to 1.00 for parents, and from 0.993 to 0.999 for F_1 offspring, respectively. Therefore, there was almost no gain from the spatial autoregressive model above the standard model (1), and further statistical analyses were done without considering the autoregressive residuals.

Additive and family genetic correlations between two different traits measured from the same individual, between the same trait measured at two ages, and between sites—considering measurements from different sites as different traits—were estimated based on bivariate analysis. The bivariate analysis was based on the following individual tree additive linear mixed model:

$$\begin{bmatrix} \boldsymbol{y}_i \\ \boldsymbol{y}_j \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_i & 0 \\ 0 & \boldsymbol{X}_j \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_i \\ \boldsymbol{\beta}_j \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{a_i} & 0 \\ 0 & \boldsymbol{Z}_{a_j} \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_i \\ \boldsymbol{a}_j \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{f_i} & 0 \\ 0 & \boldsymbol{Z}_{f_j} \end{bmatrix} \begin{bmatrix} \boldsymbol{f}_i \\ \boldsymbol{f}_j \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_i \\ \boldsymbol{e}_j \end{bmatrix} \quad (2)$$

where $\boldsymbol{y}_i$ and $\boldsymbol{y}_j$ are the vectors of individual tree observation for traits, ages, or sites *i* and *j*. The matrix $\boldsymbol{X}_i \oplus \boldsymbol{X}_j$, $\boldsymbol{Z}_{a_i} \oplus \boldsymbol{Z}_{a_j}$, and $\boldsymbol{Z}_{f_i} \oplus \boldsymbol{Z}_{f_j}$ related the replicates within site effects in $\left[\boldsymbol{\beta}_i' \mid \boldsymbol{\beta}_j'\right]$, the individual breeding value in $\left[\boldsymbol{a}_i' \mid \boldsymbol{a}_j'\right]$, and the genetic effects of full-sib family in $\left[\boldsymbol{f}_i' \mid \boldsymbol{f}_j'\right]$. The vector $\left[\boldsymbol{e}_i' \mid \boldsymbol{e}_j'\right]$ is the residual vector. The symbols $\oplus$ and $'$ indicate the direct sum of matrices and the transpose operation, respectively. The expectation and variance-covariance matrix for individual breeding values are respectively equal to:

$$\mathrm{E}\begin{bmatrix} \boldsymbol{a}_i \\ \boldsymbol{a}_j \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \mathrm{Var}\begin{bmatrix} \boldsymbol{a}_i \\ \boldsymbol{a}_j \end{bmatrix} = \begin{bmatrix} \sigma_{a_{i,i}}^2 A & \sigma_{a_{i,j}} A \\ \sigma_{a_{j,i}} A & \sigma_{a_{j,j}}^2 A \end{bmatrix} = \begin{bmatrix} \sigma_{a_{i,i}}^2 & \sigma_{a_{i,j}} \\ \sigma_{a_{j,i}} & \sigma_{a_{j,j}}^2 \end{bmatrix} \otimes A = \boldsymbol{G}_0 \otimes A \quad (3)$$

where $\sigma^2_{a_{i,i}}$ and $\sigma^2_{a_{j,j}}$ are the additive genetic variances for the traits, ages, or sites i and j, respectively, whereas $\sigma_{a_{i,j}}$ is the additive covariance between traits, ages, or sites i and j. The symbol $\otimes$ indicates the Kronecker products of matrices. The expectation and covariance matrix for family genetic effects are respectively equal to:

$$\mathrm{E}\begin{bmatrix} f_i \\ f_j \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \mathrm{Var}\begin{bmatrix} f_i \\ f_j \end{bmatrix} = \begin{bmatrix} \sigma^2_{f_{i,i}} I & \sigma_{f_{i,j}} I \\ \sigma_{f_{j,i}} I & \sigma^2_{f_{j,j}} I \end{bmatrix} = \begin{bmatrix} \sigma^2_{f_{i,i}} & \sigma_{f_{i,j}} \\ \sigma_{f_{j,i}} & \sigma^2_{f_{j,j}} \end{bmatrix} \otimes I = G_f \otimes I \quad (4)$$

where $\sigma^2_{f_{i,i}}$ and $\sigma^2_{f_{j,j}}$ are the family variances for traits, ages, and sites i and j, respectively, and $\sigma_{f_{i,j}}$ is the family covariance between traits, ages, and sites i and j. For trials with five-tree row plots, model (2) also included the random vectors p_i and p_j with plot effects, associated with y_i and y_j by the incidence matrices $Z_{p_i} \oplus Z_{p_j}$. The expectation and covariance matrix for plot effects are equal to:

$$\mathrm{E}\begin{bmatrix} p_i \\ p_j \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \mathrm{Var}\begin{bmatrix} p_i \\ p_j \end{bmatrix} = \begin{bmatrix} \sigma^2_{p_{i,i}} I & 0 \\ 0 & \sigma^2_{p_{j,j}} I \end{bmatrix} = \begin{bmatrix} \sigma^2_{p_{i,i}} & 0 \\ 0 & \sigma^2_{p_{j,j}} \end{bmatrix} \otimes I = P \otimes I \quad (5)$$

where $\sigma^2_{p_{i,i}}$ and $\sigma^2_{p_{j,j}}$ are plot variance effects for traits, ages, or sites i and j, respectively. The expected value and covariance matrix of e are respectively equal to:

$$\mathrm{E}\begin{bmatrix} e_i \\ e_j \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \mathrm{Var}\begin{bmatrix} e_i \\ e_j \end{bmatrix} = \begin{bmatrix} \sigma^2_{e_{i,i}} I & \sigma_{e_{i,j}} I \\ \sigma_{e_{j,i}} I & \sigma^2_{e_{j,j}} I \end{bmatrix} = \begin{bmatrix} \sigma^2_{e_{i,i}} & \sigma_{e_{i,j}} \\ \sigma_{e_{j,i}} & \sigma^2_{e_{j,j}} \end{bmatrix} \otimes I = R_0 \otimes I \quad (6)$$

where the residual variances for the traits or ages i and j are $\sigma^2_{e_{i,i}}$ and $\sigma^2_{e_{j,j}}$, respectively, and $\sigma_{e_{i,j}}$ is the residual covariance between the two traits or ages. Given that the sites were assessed separately, the residual covariances across sites are assumed to be zero.

Genetic Parameters

Restricted maximum likelihood (REML, Patterson and Thompson 1971) was used to estimate variances and covariances for the random effects in the mixed models (1) and (2) and were obtained with the ASREML program (Gilmour et al. 2006), which uses the average information algorithm described by Gilmour et al. (1995).

The single-site individual narrow- and broad-sense heritability ($\hat{h}^2$ and $\hat{H}^2$, respectively) was estimated as:

$$\hat{h}^2 = \frac{\hat{\sigma}^2_a}{\hat{\sigma}^2_a + \hat{\sigma}^2_f + \hat{\sigma}^2_e}; \quad \hat{H}^2 = \frac{\hat{\sigma}^2_a + \hat{\sigma}^2_d}{\hat{\sigma}^2_a + \hat{\sigma}^2_f + \hat{\sigma}^2_e}$$

where $\hat{\sigma}^2_a$ is the estimated additive genetic variance, $\hat{\sigma}^2_d$ is the estimated dominance genetic variance, $\hat{\sigma}^2_f$ is the estimated family genetic variance, and $\hat{\sigma}^2_e$ is the estimated residual genetic variance. Dominance variance was estimated as $4 \times \hat{\sigma}^2_f$. The additive and family genetic correlations ($\hat{r}_a$ and $\hat{r}_f$, respectively) between traits, ages, or sites were calculated as:

$$\hat{r}_a = \frac{\hat{\sigma}_{a_{i,j}}}{\sqrt{\hat{\sigma}^2_{a_i} \times \hat{\sigma}^2_{a_j}}}; \quad \hat{r}_f = \frac{\hat{\sigma}_{f_{i,j}}}{\sqrt{\hat{\sigma}^2_{f_i} \times \hat{\sigma}^2_{f_j}}}$$

where $\hat{\sigma}^2_{a_i}$ and $\hat{\sigma}^2_{a_j}$ are the estimated additive genetic variances for the traits, ages, or sites i and j, respectively; $\hat{\sigma}_{a_{i,j}}$ is the estimated additive covariance between traits, ages, or sites i and j; $\hat{\sigma}^2_{f_i}$ and $\hat{\sigma}^2_{f_j}$ are the estimated family genetic variances for the traits, ages, or sites i and j, respectively; and $\hat{\sigma}_{f_{i,j}}$ is the estimated family covariance between traits, ages or sites i and j in (2). We failed to receive model convergence or obtain relative high estimated standard errors for the additive and family genetic correlation between sites; thus, these correlations were estimated only for pairs of sites with 35 or more hybrid families in common (i.e., between sites one and two, and sites three and four) (Supplementary Table S1).

An important limitation of the REML (co)variance estimates is that their distribution is unknown. Only an approximate measure of precision of the estimates based on asymptotic or large-sample theory can be calculated. Approximate standard errors of the heritabilities and genetic correlations were computed with the "delta method." This asymptotic approach based on the Taylor expansion (Lynch and Walsh 1998) forces the confidence limits for (co)variance ratios to be symmetric and was calculated using an ASREML post-processing program (Gilmour et al. 2009).

The significances of variances and genetic correlations were evaluated by the likelihood ratio test (LRT, Stram and Lee 1994). A two-tailed LRT with one degree of freedom (Costa e Silva et al. 2005, Gilmour et al. 2009) was used for the genetic variances, correlations between traits, and between ages. However, a unilateral LRT was used to judge the significance of the genetic correlations between sites from +1 (Costa e Silva et al. 2009) with 0.5 degrees of freedom (Stram and Lee 1994).

Finally, to illustrate the relationship between DBH growth (one of the most economically important traits) and the other traits evaluated, the correlated responses of each trait at age seven (approximately one-third of the rotation age for pines in the region) for sites one and two—using individual selection—were calculated following closely Falconer and Mackay (1996; p. 317, equation 19.6). Genetic gain was considered at two selection intensities (i): the top 1 percent (i = 2.06) and 5 percent (i = 2.67) of ranked individuals. Genetic gain for DBH was determined by the tree-breeding values from the univariate model (1) for each site.

Results and Discussion

Estimates of Trait Means

The overall survival across sites was 91 percent, with the highest value in site three (95 percent) and the lowest value in site two (85 percent) (Table 1). The most important cause of death at site two was the lack of rainfall recorded in the two months after planting. Moreover, site two showed less growth at ages three and five (Table 2), which could be linked to water stress suffered during the first months of this trial, but also to the successive replantings needed to keep an acceptable level of survival. However, at age seven, this situation reversed, and site two recorded a higher growth than site one. Overall means for STR, BD, and BA were similar between trials and assessment ages (Table 2).

Genetic Variances and Heritability Estimates

Table 3 shows the estimated residual variance ($\hat{\sigma}_e^2$), additive ($\hat{\sigma}_a^2$) and dominance ($\hat{\sigma}_d^2$) genetic variances, and narrow- and broad-sense heritabilities ($\hat{h}^2$ and $\hat{H}^2$, respectively) derived from the individual-tree mixed model (1) for all the variables evaluated across trials and ages. In general, statistically significant levels of additive and dominance genetic variation were detected for all traits. However, $\hat{\sigma}_a^2$ was not statistically significant (P-value > 0.05) for NSTR at age three in trials two, three, and four. The estimated dominance variance was not statistically significant for TH at age three in trials two and five and, in general, was not significant for NSBD, NSBA, and NSTR. The only nonsignificant $\hat{\sigma}_d^2$ at age five was for NSTR at site two, which recorded a standard error four times larger than the estimation (not shown). At age seven, $\hat{\sigma}_d^2$ was not significant at site two for TH and NSTR and at sites one and two for NSBA (Table 3).

In general, this study showed a higher level of $\hat{\sigma}_a^2$ than $\hat{\sigma}_d^2$ for growth traits (DBH and TH), which in turn increases with age. The mean ratio $\hat{\sigma}_a^2 / \hat{\sigma}_d^2$ at ages three, five, and seven were 0.63, 0.88, and 1.26, respectively, for DBH, while these values were 1.30, 3.55 and 8.60 for TH. The NSTR trait showed intermediate values for the ratio $\hat{\sigma}_a^2 / \hat{\sigma}_d^2$ between DBH and TH, with mean values at ages three, five, and seven of 0.77, 1.14, and 2.60, respectively. Branch traits (NSBD and NSBA) also showed higher $\hat{\sigma}_a^2$ than $\hat{\sigma}_d^2$; however, as mentioned previously, $\hat{\sigma}_d^2$ was not statistically significant in general (P-value > 0.05) for NSBD, and it was never statistically significant for NSBA. The higher $\hat{\sigma}_a^2$ compared with $\hat{\sigma}_d^2$ is

Table 3. Number of observations (n), estimates of residual variance ($\hat{\sigma}_e^2$) additive genetic variance ($\hat{\sigma}_a^2$), dominance genetic variance ($\hat{\sigma}_d^2$), narrow- and broad-sense heritability estimates ($\hat{h}^2$ and $\hat{H}^2$, respectively) and their approximate standard errors for the variables measured across the five trials and the three years.

Year	Trait*	Trial†	n	$\hat{\sigma}_e^2$	$\hat{\sigma}_a^2$	$\hat{\sigma}_d^2$	$\hat{h}^2$	$\hat{H}^2$
3	**DBH**	**1**	768	1.48	0.65**	1.04**	0.27 (0.15)	0.70 (0.19)
		2	1329	2.97	0.55**	0.80**	0.15 (0.07)	0.36 (0.11)
		3	745	2.35	0.58*	1.83**	0.17 (0.13)	0.71 (0.18)
		4	628	2.18	1.01**	0.76**	0.30 (0.14)	0.52 (0.15)
		5	748	2.41	0.40**	0.61**	0.13 (0.09)	0.34 (0.11)
	TH	**1**	771	0.27	0.44**	0.12**	0.59 (0.17)	0.76 (0.17)
		2	1329	0.46	0.19**	0.10NS	0.28 (0.10)	0.43 (0.11)
		3	749	0.58	0.12*	0.37**	0.15 (0.11)	0.62 (0.16)
		4	628	0.53	0.08**	0.10**	0.12 (0.08)	0.27 (0.11)
		5	746	0.57	0.16**	0.07NS	0.22 (0.11)	0.31 (0.11)
	NSTR	**1**	770	0.75	0.08**	0.06NS	0.09 (0.06)	0.17 (0.09)
		2	1327	0.68	0.04NS	0.03NS	0.06 (0.04)	0.10 (0.06)
		3	745	0.69	0.01NS	0.04NS	0.01 (0.03)	0.08 (0.06)
		4	628	0.75	0.02NS	0.18**	0.02 (0.06)	0.24 (0.11)
		5	746	0.64	0.09**	0.00NS	0.12 (0.06)	0.12 (0.06)
	NSBD	**1**	337	0.41	0.17**	0.06NS	0.29 (0.18)	0.40 (0.31)
		2	714	0.55	0.12**	0.05NS	0.17 (0.08)	0.25 (0.12)
		3	745	0.63	0.20**	0.02NS	0.24 (0.10)	0.26 (0.11)
		4	628	0.66	0.10**	0.18**	0.12 (0.08)	0.35 (0.13)
		5	859	0.69	0.10*	0.11*	0.13 (0.08)	0.26 (0.10)
	NSBA	**1**	337	0.37	0.37**	0.00NS	0.50 (0.16)	0.50 (0.16)
		2	714	0.42	0.30**	0.10NS	0.41 (0.13)	0.53 (0.14)
		3	745	0.53	0.25**	0.04NS	0.31 (0.12)	0.36 (0.13)
		4	628	0.44	0.35**	0.06NS	0.43 (0.15)	0.51 (0.16)
		5	859	0.72	0.12*	0.08NS	0.14 (0.09)	0.23 (0.09)
5	**DBH**	**1**	758	4.05	2.26*	3.50**	0.31 (0.16)	0.80 (0.18)
		2	1276	4.29	1.90**	1.23**	0.29 (0.10)	0.48 (0.11)
	TH	**1**	758	0.84	1.32**	0.34**	0.59 (0.17)	0.74 (0.16)
		2	1276	0.93	0.62**	0.21**	0.39 (0.12)	0.52 (0.12)
	NSTR	**1**	758	0.63	0.15**	0.19**	0.18 (0.12)	0.42 (0.13)
		2	1276	0.70	0.09**	0.02NS	0.12 (0.05)	0.14 (0.07)
7	**DBH**	**1**	829	9.23	4.64**	4.73**	0.31 (0.14)	0.62 (0.16)
		2	1412	10.07	3.23**	1.52**	0.24 (0.08)	0.35 (0.09)
	TH	**1**	828	1.63	1.62**	0.19**	0.49 (0.15)	0.55 (0.15)
		2	1402	1.87	0.53**	0.06NS	0.22 (0.08)	0.24 (0.09)
	NSTR	**1**	761	0.66	0.05**	0.03*	0.07 (0.06)	0.12 (0.09)
		2	1238	0.61	0.08**	0.02NS	0.11 (0.05)	0.14 (0.06)
	NSBD	**1**	751	0.65	0.11*	0.17**	0.13 (0.10)	0.35 (0.13)
		2	1443	0.77	0.06**	0.05*	0.07 (0.04)	0.14 (0.06)
	NSBA	**1**	751	0.42	0.27**	0.00NS	0.39 (0.14)	0.39 (0.14)
		2	1443	0.73	0.08**	0.02NS	0.10 (0.04)	0.13 (0.06)

NOTE: *Diameter at breast height (DBH, cm), total height (TH, m), stem straightness normal score (NSTR), branch diameter normal score (NSBD), and branch angle normal score (NSBA).

†Abbreviations used for the trials are described in Table 1.

Significance of effects showing difference from zero are noted as:

NSnot statistically significant ($P > 0.05$),

*statistically significant ($0.01 < P < 0.05$),

**statistically highly significant ($P < 0.01$).

consistent with other studies on *Pinus* hybrids (Dieters et al. 1997, Gwaze et al. 2000, Brawner et al. 2005, Mutete et al. 2015). For instance, Dieters et al. (1997) reported a ratio between $\hat{\sigma}_a^2$ and $\hat{\sigma}_d^2$ for DBH between 1.0 and 1.9 in hybrids among PCH, *Pinus oocarpa* Schiede (POOC), and *Pinus tecunumanii* (Schw.) Eguiluz and Perry (PTEC) at age five. In summary, the results of our work confirm the major importance of additive genetic effects, indicating that selection and breeding within hybrid populations should result in improvements in advanced generation hybrid progenies.

The low-to-moderate $\hat{h}^2$ of DBH (between 0.13 and 0.31) was comparable to those reported by other authors in PCH × POOC and PCH × PTEC hybrids. For instance, Dieters et al. (1997) found a $\hat{h}^2$ between 0.10 and 0.18 at age five, while Brawner et al. (2005) reported values ranging from 0.21 to 0.33 when assessing the same trials after 10 years. On the other hand, Dungey et al. (2000) reported lower heritability values than those found in this study for PEE × PCH at age six (from 0.09 to 0.17). The $\hat{h}^2$ for TH ranged from 0.12 to 0.59, which was similar to that reported for PEE at age six in the study by Dieters (1996) (average = 0.24) and for PCH at age 7.5 by Dean et al. (1986) (values ranging from 0.16 to 0.41.) However, our estimates of heritability for TH were above those reported by Brawner et al. (2005) in PCH × POOC and PCH × PTEC, with values between 0.11 and 0.19.

Our estimated heritability for NSTR $(\hat{h}^2)$ ranged from 0.01 to 0.18 (Table 3), which revealed a low degree of genetic control for this trait, making its improvement difficult. Our values for the heritability of NSTR were consistent with other reports. For example, Dungey et al. (2000) found heritabilities between 0.07 and 0.17 for the same hybrid used in our study, while Gwaze et al. (2000) reported heritabilities ranging from 0.08 to 0.63 in PCH × POOC and PCH × PTEC hybrids, which indicates that differences in the estimates could be environment-related. According to Williams and Lambeth (1988), the use of ordered categories to measure stem straightness overestimates additive genetic variance in trials with mostly straight trees and underestimates it in trials with mostly crooked trees. Moreover, the low number of categories used in the measurements (four, in our case) could be an additional cause of the observed low heritability in this trait (Haapanen et al. 1997).

The $\hat{h}^2$ for NSBD and NSBA (branch quality traits) ranged from 0.07 to 0.50. Even though we failed to find reports on these branch quality parameters in pine hybrids, these estimated heritabilities are in the range of those reported in pure pine species. For instance, for the PCH species, Dean et al. (1986) reported heritabilities for BD and BA of 0.38 and 0.14, respectively. Similar heritabilities were reported for *Pinus sylvestris* L. (PS) by Jansons et al. (2009) for BD (from 0.06 to 0.23), while Haapanen et al. (1997) found heritabilities between 0.00 and 0.80 for BD and between 0.12 and 0.76 for BA when assessing 16 PS trials. Zas et al. (2004), reported individual heritabilities between 0.00 and 0.10 for BD and between 0.09 and 0.22 for BA in *Pinus pinaster* Ait (PP). Adams and Morgenstern (1991) found that BA was more heritable than BD in *Pinus banksiana* Lamb., with individual heritabilities of 0.42 and 0.12, respectively. Similarly, Cumbie et al. (2012) reported mean individual heritabilities of 0.16 for BA and 0.11 for BD in four PT trials. The variation in heritability values across ages observed in our study could be due to the fact that the assessments at age three implied averaging the thickest branches with flatter angles located at the tree base and thinner branches with steeper angles at the top of the tree; assessments at ages five and seven did not include branches in the lower third of the stem, as they had been pruned. Therefore, the manner in which these categorical and subjective traits are evaluated can have an important influence on the estimates of heritabilities and thus on the expected responses from selection (Raymond and Cotterill 1990). In this sense, estimations from these traits could benefit from the use of more categories. Raymond and Cotterill (1990) proposed a six-score scale for crown traits, with three resulting in too low phenotypic and additive variances, and nine categories resulting in too high phenotypic variance. On the other hand, Meuwissen et al. (1995) suggested that the rate of genetic gain can be increased by gathering more information on the categories with the greatest incidence in the program, (i.e., dividing these categories into subcategories). This methodology could be applied to subjective assessments under the INTA-PINDO program. This method would involve increasing the number of categories from four to six, but dividing categories three and four, so that the scores would be 1, 2, 3, 3.5 (or 3+), 4, and 4.5 (or 4+).

The evaluations of trials one and two made it possible to assess heritability trends over time. In general, heritabilities increased between ages three and five but decreased between ages five and seven (Table 3). For instance, the trait with the greatest fluctuation of $\hat{H}^2$ was TH at site two, with values of 0.43, 0.52, and 0.24 for ages three, five, and seven, respectively. Similar trends were observed in the mean values of $\hat{h}^2$ and $\hat{H}^2$ for DBH, TH, and NSTR at sites one and two. For example, for DHB mean values of $\hat{h}^2$ were 0.21, 0.30, and 0.28, for ages three, five, and seven, respectively. The heritabilities of NSBD and NSBA were only estimated at ages three and seven. There was an increase in heritability with age in all cases, except $\hat{H}^2$ for NSBA at both sites. There are numerous studies reporting heritability trends over time. For instance, for the PEE species, Dieters et al. (1995) reported an increase in heritability with age, while other authors, such as Xie and Ying (1996) for *Pinus contorta* and Lambeth and Dill (2001) for PT, failed to find a clear trend. The decrease in heritabilities at age seven could be associated with the effect of competition between trees and with the use of a standard genetic model that does not account for competition additive effects. Using both simulated and empirical data for PT, Cappa et al. (2015) showed that under genetic and environmental competition, the standard model based only on direct additive effects could underestimate the additive variance and overestimate the error variance. Moreover, the competition effect increases with age (e.g., Cappa et al. 2016), resulting in large environmental variation, which would reduce heritabilities (Wu 1998). Thus, in order to better understand the behavior of heritabilities over time, new individual-tree mixed models should be used that correctly adjust for the changes of indirect genetic effects and environmental competition effects over time; this is a topic of future research. Preliminary results showed a general increase in the competition effect from age five to seven in the growth traits at sites one and two, suggesting an increase in interaction among individuals over time. For example, average correlation between direct and competition additive genetic effects for TH from the competition model became negative at age seven (results not shown).

Additive and Family Genetic Correlations between Traits

Genetic correlations between traits are important for determining how selection on one trait will affect the means and genetic variation in another. Estimated additive and family genetic correlations ($\hat{r}_a$ and $\hat{r}_f$, respectively) between growth, tree stem straightness, and branch angle and diameter traits within each site are listed for ages three, five, and seven in Table 4. The $\hat{r}_a$ and $\hat{r}_f$ between DBH and TH were statistically significant (P-value < 0.05), positive, and generally high (from 0.64 to 1.00), which showed that selection based on any of these traits could lead to a high correlated response in the other. In addition, the correlated responses for TH when selection was based on DBH ranged from 11.11 percent to 31.22 percent for sites one and two and two selection intensities (the top 1 percent and 5 percent of ranked individuals; Supplementary Table S4). According to White et al. (2007), one of the reasons why different growth measurements in plants show a strong and positive correlation is that these traits are functionally related. Similar correlation values between DBH and TH were reported by Gwaze et al. (2000) for PCH × POOC hybrids (from 0.80 to 0.82) and lower for PCH × PTEC (from 0.47 to 0.61). Moreover, other studies reported comparable values of $\hat{r}_a$ in pure pine species at a similar age. For instance in PEE, Dieters (1996) reported an $\hat{r}_a$ value of 0.60 between DBH and TH traits at age 10, and Hodge and Withe (1992) showed an $\hat{r}_a$ value of 0.82 between the same growth traits at age five. In PT, Cumbie et al. (2012) reported $\hat{r}_a$ values from 0.87 to 0.97 between growth traits at age six. In *Pinus brutia* TEN, Isik et al. (1999) reported an $\hat{r}_a$ value of 0.89 between DBH and TH at age 13.

The $\hat{r}_a$ and $\hat{r}_f$ between the growth and NSTR traits in general were not statistically significant (P-value > 0.05), with values between −1.00 and 0.92, but most of them were associated with very large standard errors (Table 4). These genetic correlations indicated uncertainty for the improvement of growth and NSTR traits at the same time. This result was reinforced by the correlated

Table 4. Estimated additive genetic correlations (above diagonal) and family genetic correlations (below diagonal) and their approximate standard errors between different traits within sites and years from pairwise bivariate analysis of the five trials and the three years.

Year	Trial††	Trait†	DBH	TH	NSTR	NSBD	NSBA
3	**1**	**DBH**	—	0.84 (0.12)**	−0.12 (0.46)NS	−0.24 (0.33)NS	−0.17 (0.36)NS
		TH	1.00 (0.07)**	—	0.36 (0.36)NS	−0.44 (0.40)NS	−0.29 (0.27)NS
		NSTR	−0.93 (0.61)*	−0.77 (0.69)NS	—	−0.97 (0.23)**	−0.20 (0.39)NS
		NSBD	0.98 (0.49)**	0.85 (0.63)**	−0.99 (0.73)**	—	0.36 (0.36)NS
		NSBA	0.89 (1.20)NS	−0.00 (0.00)NS	0.82 (1.45)NS	0.00 (0.00)NS	—
	2	**DBH**	—	0.80 (0.12)**	0.40 (0.38)NS	0.10 (0.35)NS	−0.58 (0.25)*
		TH	0.97 (0.05)**	—	0.31 (0.32)NS	−0.15 (0.32)NS	−0.39 (0.25)*
		NSTR	0.28 (0.60)NS	0.60 (0.71)NS	—	−0.12 (0.38)NS	0.08 (0.82)NS
		NSBD	0.93 (0.60)**	1.00 (0.51)*	−0.66 (1.18)NS	—	0.30 (0.28)NS
		NSBA	−0.13 (0.42)NS	−0.24 (0.40)NS	−0.74 (0.82)NS	0.81 (0.56)NS	—
	3	**DBH**	—	0.61 (0.31)NS	-1.00 (1.12)NS	−0.11 (0.41)NS	0.69 (0.30)*
		TH	0.92 (0.06)**	—	-0.94 (1.46)NS	0.19 (0.42)NS	0.52 (0.36)NS
		NSTR	0.48 (0.49)NS	0.49 (0.43)NS	—	0.93 (0.22)**	0.88 (1.80)NS
		NSBD	−0.53 (0.91)NS	−0.68 (1.12)NS	−0.40 (4.06)NS	—	0.49 (0.25)*
		NSBA	0.33 (0.50)NS	0.42 (0.50)NS	−0.56 (0.92)NS	0.08 (1.40)NS	—
	4	**DBH**	—	0.89 (0.11)**	−0.51 (0.81)NS	0.16 (0.47)NS	0.72 (0.21)**
		TH	0.85 (0.16)**	—	−0.42 (0.76)NS	0.39 (0.48)NS	0.63 (0.29)**
		NSTR	−0.31 (0.42)NS	−0.50 (0.51)NS	—	0.83 (0.97)NS	−0.02 (0.72)NS
		NSBD	−0.60 (0.31)*	−0.08 (0.45)NS	0.01 (0.44)NS	—	0.50 (0.32)NS
		NSBA	−0.64 (0.57)NS	−0.81 (0.63)*	−0.17 (0.57)NS	0.57 (0.42)NS	—
	5	**DBH**	—	0.36 (0.38)NS	−0.52 (0.36)NS	0.45 (0.58)NS	0.63 (0.43)NS
		TH	0.97 (0.16)**	—	0.37 (0.35)NS	0.57 (0.55)NS	0.09 (0.43)NS
		NSTR	0.53 (2.05)NS	−0.58 (2.44)NS	—	0.11 (0.41)NS	−0.41 (0.42)NS
		NSBD	−0.97 (0.27)**	−0.94 (0.37)**	0.00 (0.00)NS	—	0.77 (0.22)*
		NSBA	−0.66 (0.45)NS	−0.66 (0.59)NS	0.97 (3.57)NS	0.77 (0.32)NS	—
5	**1**	**DBH**	—	0.80 (0.14)**	−0.01 (0.43)NS	—	—
		TH	0.93 (0.13)**	—	0.35 (0.32)NS	—	—
		NSTR	−0.48 (0.35)NS	−0.29 (0.49)NS	—	—	—
	2	**DBH**	—	0.77 (0.12)**	0.13 (0.31)NS	—	—
		TH	0.64 (0.20)**	—	0.21 (0.28)NS	—	—
		NSTR	−0.43 (0.75)NS	0.27 (0.66)NS	—	—	—
7	**1**	**DBH**	—	0.91 (0.09)*	−0.56 (1.14)NS	0.23 (0.82)NS	0.14 (0.45)NS
		TH	0.98 (0.03)**	—	-0.69 (4.09)NS	0.00 (0.00)NS	0.22 (0.42)NS
		NSTR	0.38 (0.59)NS	0.85 (0.28)**	—	0.02 (0.59)NS	−0.22 (0.50)NS
		NSBD	−1.00 (0.13)**	−1.00 (0.32)**	0.98 (0.92)NS	—	0.00 (0.43)NS
		NSBA	−0.78 (1.74)NS	−0.33 (2.52)NS	0. 89 (1.34)NS	0.99 (0.81)NS	—
	2	**DBH**	—	0.84 (0.09)**	0.15 (0.30)NS	-0.30 (0.29)NS	0.17 (0.29)NS
		TH	0.94 (0.54)*	—	0.20 (0.29)NS	−0.08 (0.32)NS	0.44 (0.25)*
		NSTR	−0.32 (0.74)NS	0.92 (1.11)NS	—	0.22 (0.33)NS	0.48 (0.26)*
		NSBD	−0.57 (0.36)NS	0.77 (1.28)NS	0.96 (0.76)**	—	0.24 (0.33)NS
		NSBA	0.24 (0.61)NS	0.90 (0.77)*	0.99 (1.47)NS	0.04 (0.84)NS	—

NOTE: *Diameter at breast height (DBH, cm), total height (TH, m), stem straightness normal score (NSTR), branch diameter normal score (NSBD), and branch angle normal score (NSBA).

†Abbreviations used for the trials are described in Table 1.

Significance of effects showing difference from zero are noted as:

NSnot statistically significant ($P > 0.05$),

*statistically significant ($0.01 < P < 0.05$),

**statistically highly significant ($P < 0.01$).

responses for STR when selection was based on DBH (from −2.98 percent to 0.79 percent, Table S4). The values found in this work have a broader range than those of other reports. For instance, for pine hybrids, Dungey et al. (2000) found correlations between 0.17 and 0.78, while Gwaze et al. (2000) presented values ranging from −0.73 to 0.34. Dieters (1996) reported correlations for PEE which were weak and negative in general, when assessing stem straightness in a four-category scale, though they were low and inconsistent in a seven-category scale. Dean et al. (1986) reported adverse correlations between growth and stem straightness traits in PCH, mainly in poorly drained sites, with no consistency found in well-drained sites. In the same way, Adams and Morgenstern (1991) reported a genetic correlation between TH and straightness of −0.49 in *Pinus banksiana* Lamb. In sum, there is a great variation of genetic correlations between growth and stem straightness traits, although conclusions are hampered by poor accuracy of the estimates. In general, authors attribute the low correlation to the methodology used to evaluate stem straightness or to a site environmental defect, such as poor drainage. The soils and general environments at the sites planted for this study were of good quality and relatively homogeneous, so the lack of clarity in these correlations could be in part related to the methodology used to assess stem straightness or to the fact that there may be no genetic correlation between the traits.

Similarly, no clear trends were observed in the genetic correlations between growth traits and NSBA or NSBD (from −0.58 to 0.72 for $\hat{r}_a$ and from −1.00 to 1.00 for $\hat{r}_f$), and in general, they were not significantly different from zero (P-value > 0.05; Table 4). This implies that selecting based on growth would not lead to changes in these traits, although caution should be used given the large standard error of the estimates. These results were further confirmed by the correlated responses in BD from selection for DBH (values from −2.38 percent to 2.69 percent); however, the correlated responses for BA ranged from 1.05 percent to 2.54 percent. We found no previous reports of correlations between stem straightness and branch quality traits in PEE × PCH, though some have been published for pure pine species. For instance in PS, Jansons et al. (2009) reported negative genetic correlations between branch thickness and TH and DBH, arguing that rapid-growth genotypes would also develop fast shadowing of lower branches, which would lead to a slower growth in their thickness, thus the correlation. For PCH, Dean et al. (1986) reported negative correlations between TH and BD (average = −0.37), although like in our work, correlations between TH and BA were inconsistent (from −0.48 to 0.59). However for PP, Zas et al. (2004) found, in general, positive correlations between growth and BD but negative ones with BA. Likewise for PT, Cumbie et al. (2012) reported positive correlations between growth traits and BD (average = 0.55) and negative correlations between growth traits and BA (average = −0.20), and Adams and Morgenstern (1991) showed negative correlations between TH and BA ($\hat{r}_a$ = −0.37) and TH and BD ($\hat{r}_a$ = −0.53).

Genetic correlations between NSBD and NSBA were positive but variable, ranging from low to high, although estimates had quite large standard errors: a correlation of 85.7 percent not significantly different from zero (P-value > 0.05; Table 4). In the same manner, Adams and Morgenstern (1991) showed positive correlations between BA and BD (average = 0.28) in *Pinus banksiana* Lamb. However, Haapanen et al. (1997) reported a small negative correlation for PS between branch diameter and angle. Similarly, Cumbie et al. (2012) reported negative genetic correlations (average = −0.46) between BA and BD for PT. Moreover, Dean et al. (1986) reported inconsistent correlations between these traits (from −0.25 to 0.25). In general, the genetic correlations of NSTR with NSBA and NSBD were not statistically significantly different from zero (from −0.97 to 0.93 for $\hat{r}_a$ and from −0.99 to 0.99 for $\hat{r}_f$), again with high estimation errors (Table 4). Unlike in the present study, Dean et al. (1986) reported positive correlations between the STR trait and BD (average = 0.37) and negative between STR and BA (average = −0.48). Adams and Morgenstern (1991) showed positive correlations between stem straightness and BD (average = 0.72) and negative correlations between straightness and BA (average = −0.11). The inconsistent genetic correlation observed in our study for NSTR with NSBA and NSBD indicates uncertainty for joint improvement of these traits.

Finally, as we mentioned previously, the disparity in results reported here and elsewhere for genetic correlations between traits related to branch quality could be associated to differences in the evaluation methodology, the age at which the evaluation was performed, forestry treatments, and the species. For instance, PEE had thicker branches and flatter branch angles than PCH, so the branches of the PEE × PCH hybrids were more like those of PCH than PEE.

Additive and Family Genetic Correlations between Ages

Accurate selection is important because it maximizes gains per time unit, resulting in the rapid capture of gains and reduction of the breeding cycle. In this sense, knowing the magnitude of age-age correlations is highly useful. Genetic correlations between measurements of the same trait at different ages yielded values between 0.50 and 1.00, with low estimation errors. They were statistically different from zero (P-values < 0.01), except for the $\hat{r}_f$ for NSTR at site two between ages three and seven and ages five and seven (Table 5). As expected, genetic correlations exhibited the highest values between ages closer to each other. High age-age correlations for the growth traits indicated that these traits can be reliably used for selection at age three. Other researchers investigating pure pine species and hybrids reported high correlations between early and late ages for growth traits. For instance in PEE, Dieters et al. (1995) reported correlations close to 1.00 for the volume trait measured three years apart, between 0.70 and 0.80 when the difference between measurement ages was six years and approximately 0.60 when the difference was nine years. When studying 23 provenances of PCH, Hodge and Dvorak (2001) reported genetic correlations for volume of 0.88 between ages three and five, 0.53 between ages three and 8, and 0.93 between ages five and eight. Brawner et al. (2005) reported genetic correlations for the DBH trait between ages five and 10 of more than 0.96 in hybrids of PCH with POOC and PTEC, suggesting that at age five, it is possible to make accurate predictions of DBH at later ages. The high age-age correlations found in this work could be due in part to the small difference between estimation ages (four years at most). Age seven represents approximately one-third of the rotation age, so further evaluations at later ages would be needed to confirm these results. However, in later ages, there is a greater degree of variation in trials (e.g., competition or thinning), which could lead to a decrease in heritability and correlations between characters (Wu 1998). Therefore, to avoid part of this problem, we suggest fitting a new mixed model that identifies and quantifies competition effects and environmental heterogeneity as addressed by Cappa et al. (2016).

Table 5. Estimate of additive and family age-age genetic correlations (and their approximate standard errors) for the same trait within trials 1 and 2.

Trait*	DBH		TH		NSTR	
Age of Correlation (Years)	Additive	Family	Additive	Family	Additive	Family
	Trial 1†					
3–5	0.91 (0.08)**	0.96 (0.04)**	0.98 (0.02)**	0.99 (0.13)**	0.95 (0.16)**	0.78 (0.28)**
5–7	1.00 (0.05)**	0.98 (0.02)**	0.97 (0.10)**	0.99 (0.05)**	0.97 (0.15)**	0.99 (0.33)**
3–7	0.77 (0.16)**	0.93 (0.06)**	0.74 (0.23)**	1.00 (0.14)**	0.96 (0.26)**	0.99 (0.33)**
	Trial 2†					
3–5	0.90 (0.08)**	0.96 (0.05)**	0.91 (0.05)**	0.95 (0.07)**	0.80 (0.20)**	0.98 (0.43)**
5–7	0.99 (0.01)**	0.98 (0.06)**	0.99 (0.02)**	0.92 (0.16)**	0.99 (0.09)**	0.56 (1.20)^{NS}
3–7	0.86 (0.13)**	0.89 (0.14)**	0.88 (0.08)**	0.74 (0.26)**	0.78 (0.21)**	0.50 (1.65)^{NS}

NOTE: *Diameter at breast height (DBH, cm), total height (TH, m), and stem straightness normal score (NSTR).
†Abbreviations used for the trials are described in Table 1.
Significance of effects showing difference from zero are noted as:
^{NS}not statistically significant ($P > 0.05$),
*statistically significant ($0.01 < P < 0.05$),
**statistically highly significant ($P < 0.01$).

In spite of the subjective nature of the STR scoring method and the difficulty in assessing it given that trees were not pruned, high age-age correlations were found between ages for this trait (Table 5), which indicates that early assessment of straightness might be a robust indication of later estimates. The high age-age correlations we observed for NSTR may have been affected by the deep, well-drained soils at the study sites. High quality soils ensure a good development of the root system and keeps the tree from leaning and developing bends that could be mistaken for poor stem straightness later on. By contrast, Gwaze (1997) reported low correlations in PT (0.06) for stem straightness between ages 1.5 and 9.5, arguing that these values would be in part due to the difficulty in measuring stem straightness at early ages. Accordingly, the same author found high correlations between ages 13.5 and 22.5 (0.55).

Additive and Family Genetic Correlations across Sites

Multi-site forest genetic trials make it possible to study the magnitude and importance of genotype-environment interactions. The importance of such interactions can be measured by the genetic correlations among pairs of environments, considering the same trait in two environments as two distinct traits (viz. Falconer and Mackay 1996). Getting to know the differential performance of genotypes based on site-environment combinations makes it possible to select and develop genetic materials which are better suited to a given region or to choose those genotypes with greater flexibility to environmental changes. Rank-change interaction is reflected in departures of genetic correlation between sites from +1. The available estimates of additive ($\hat{r}_a$) and family ($\hat{r}_f$) genetic correlations from pairs of traits across sites with 35 or more full-sib families in common (i.e., between sites one and two, and sites three and four) for growth, stem straightness, and branch quality traits are presented in Table 6. In general, these correlations were not significantly different from +1 (P-value > 0.05), except for the additive correlation between sites one and two for SDBH and NSBA traits, mainly reflecting a relatively homogeneous genetic behavior of the hybrid material across the environments studied for growth and stem straightness traits.

The $\hat{r}_a$ between sites for growth and NSTR traits varied from 0.74 to 0.99; these values were similar to $\hat{r}_f$ (from 0.70 to 0.99). These high correlations between sites reflect the fact that trials were established within a restricted area (from 26º04′ to 26º33′ south latitude and from 54º24′ to 54º40′ west longitude), with similar soil and weather conditions (Figure 1 and Table 1). However, these estimated genetic correlations (i.e., $\hat{r}_a$ and $\hat{r}_f$) across sites were similar to those reported by Brawner et al. (2003) in F_1 PEE × PCH hybrids, with values ranging from 0.80 to 0.87 for growth traits at age 11 and 0.84 for stem straightness at age six. Dieters et al. (1997) studied PCH × POOC and PCH × PTEC hybrids and found that DBH genetic correlations based on the mothers ranged from 0.95 to 0.84, while those based on the fathers were between 0.84 and 0.36. These authors suggested that the lower correlations based on PTEC could be due to the low number of fathers used or to PTEC's sensitivity to the genotype-environment interaction. In the same hybrids studied by Dieters et al. (1997), Brawner et al. (2005) also reported high values of $\hat{r}_a$ across sites for DBH (0.83) and TH (0.87) at age 10. However, the $\hat{r}_f$ for the same traits, estimated separately and independently estimated for the mother and father lines, ranged from 0.55 to 0.85. These authors attributed these results to an overestimation of additive genetic covariance due to the imbalance between the number of mothers and fathers or to the hybrid's own nature. On the other hand, Dungey (2001) suggests that the overestimation of genetic parameters in hybrids could result from the use of an inadequate genetic model.

In this work, we used an individual-tree mixed model with additive and family genetic effects. Identifying which genetic model provides the best description of a forest hybrid is a challenge (Dungey 2001), as the assumptions of the infinitesimal model may not be appropriate (Kain 2003). In spite of this, various reports of genetic parameters in hybrids use the individual-tree mixed model (Gwaze et al. 2000, Dieters and Dungey 2000) or the parent mixed model (Dieters et al. 1997, Brawner et al. 2005), with some papers comparing both models (Mutete et al. 2015). However, Mutete et al. (2015) failed to endorse any one model, due to the low number of studied fathers (11 × 6 factorial arrays). Our study presents a similar situation, with the largest factorial being a 13 × 8 crossing. In such case, a parent model (with a separate variance for each parental species) would not provide a better estimate of the combined genetic variance for the hybrid progeny. The individual-tree mixed model used here assumes that the alleles controlling the traits would be common to PEE and PCH parental lines, that epistasis is

Table 6. Estimated additive (above diagonal) and family (below diagonal) genetic correlations and their approximate standard errors between trials with at least 35 hybrid families in common.

Trait*	Trial†	1	2	3	4
SDBH	**1**	—	0.74 (0.16)**	—	—
	2	0.99 (0.28)^{NS}	—	—	—
	3	—	—	—	0.96 (0.14)^{NS}
	4	—	—	0.70 (0.25)^{NS}	—
STH	**1**	—	0.95 (0.06)^{NS}	—	—
	2	0.99 (1.35)^{NS}	—	—	—
	3	—	—	—	0.88 (0.13)^{NS}
	4	—	—	0.99 (0.22)^{NS}	—
NSTR	**1**	—	0.99 (0.26)^{NS}	—	—
	2	0.99 (1.66)^{NS}	—	—	—
	3	—	—	—	0.99 (0.57)^{NS}
	4	—	—	0.99 (1.03)^{NS}	—
NSBD	**1**	—	0.19 (0.50)^{NS}	—	—
	2	0.99 (0.42)^{NS}	—	—	—
	3	—	—	—	0.99 (0.19)^{NS}
	4	—	—	0.99 (0.58)^{NS}	—
NSBA	**1**	—	0.64 (0.23)**	—	—
	2	0.99 (2.52)^{NS}	—	—	—
	3	—	—	—	0.99 (0.05)^{NS}
	4	—	—	0.36 (0.66)^{NS}	—

NOTE: *Standardized diameter at breast height (SDBH), standardized total height (STH), stem straightness normal score (NSTR), branch diameter normal score (NSBD), and branch angle normal score (NSBA).
†Abbreviations used for the trials are described in Table 1.
Significance of effects showing difference from one are noted as:
^{NS}not statistically significant ($P > 0.05$),
*statistically significant ($0.01 < P < 0.05$),
**statistically highly significant ($P < 0.01$).

negligible, and that the segregation of the additive genetic variance is similar in the F_1 of PEE × PCH. These assumptions are based on the idea that there could be a close relation of kinship between parents (i.e., PEE and PCH), which in a way confirms the findings of Dvorak et al. (2000), who suggest that the Mesoamerican *Oocarpae* and *Australes* pines could share a common ancestor.

As for branch quality traits (i.e., NSBD and NSBA), significant differences were found in the values of additive and family correlations between sites one and two. In some cases, there was a high degree of interaction, while in others there was stability across sites (Table 6). Baltunis et al. (2010) evaluated *Pinus radiata* D. Don at trials planted in Australia and Tasmania Island and failed to find genotype-environment interactions ($\hat{r}_a > 0.71$) for the branch angle trait. By contrast, these authors found a certain degree of interaction for branch size trait ($\hat{r}_a = 0.55$). However, the large standard errors found by these authors for genetic correlations of branch traits scored with an arbitrary and subjective scale makes it difficult to compare the genotypes performance across the assessed environments.

Conclusions and Implications for the F_1 Hybrid Program

A higher $\hat{\sigma}^2_a$ relative to $\hat{\sigma}^2_a$, observed mainly in growth traits and increasing with age, suggests a moderate to high degree of additive genetic control in these traits. In general, growth and branch quality traits presented moderate to high broad- and narrow-sense heritabilities, which indicates that significant genetic gains could be achieved for these traits through selection, although additional gains could be captured through vegetative multiplication (cloning). Conversely, the NSTR trait generally showed lower levels of genetic variances and heritability. Genetic correlations between growth and NSTR traits were not clear, suggesting a certain degree of uncertainty for a successful combined genetic improvement. However, it is possible to identify families and individuals with high genetic value in both traits. We believe it is necessary to adjust the scoring method of the ordered categorical traits to improve its heritabilities and, thus, the resulting genetic gains. In this sense, we propose evaluating the STR, BA, and BD traits in six subjective categories, subdividing those which are most relevant to the program.

The degree of genetic correlations found between ages was generally high for growth and NSTR traits, which suggests that early selection, even at age three, could prove effective, although these results are preliminary. Our latest evaluation was at age seven, approximately one-third of the rotation age for pines in the region. This early selection age would make it possible to significantly increase gains per unit of time and reduce the program costs.

High genetic correlations were found across sites. Thus, selected materials could be used with little restrictions across the region. However, if the goal is to optimize gains, it will be important to ensure that there are enough connections between trials for individuals to be compared across sites. Moreover, it should be mentioned that, all five trials were planted in a restricted area in the northwest of the province of Misiones, so only a part of the potential region for this hybrid was effectively evaluated. For that reason, new trials should be planted in other areas of the Argentine Mesopotamia with contrasting sites to confirm the high across-site correlations.

Finally, the higher additive genetic variance of the PEE × PCH hybrids under study was due to the genes' additive effects, which suggests that selection and crossing within hybrid populations could result in cumulative improvements in advanced generation hybrid. In this case, a synthetic hybrid line would be the most effective strategy, as it would produce the greatest gains per cycle at the lowest cost (Kerr et al. 2004, Brawner et al. 2005, Mutete et al. 2015). However, in the current situation, such a synthetic strategy would be limited by the reduced number of parents currently involved

(16 PEE and 21 PCH). This would rapidly build up the levels of inbreeding in future generations (Williams and Hamrick 1996). Thus, in order to advance towards a synthetic strategy, it would be necessary to broaden the genetic variability of F_1 by including new parents. The advantage of the INTA-PINDO hybrid is its solid basis in the INTA genetic improvement program for PEE, with over 400 families planted in different sites of the Argentine Mesopotamia. By contrast for PCH, the only phenotypic selections available come from commercial plantations and trials of origins/provenances. Thus, to achieve an F_1 population that is broad enough to sustain a synthetic strategy, it would be necessary to bring in PCH materials from other genetic improvement programs. Additionally, in order to deepen our understanding of the genetics of hybrid populations, future progeny trials would benefit from including not only a wide range of F_1 and F_2 hybrid families but also pure open or controlled pollinated progenies from the same PEE and PCH parents used. This would also help obtain better estimates of heterosis and correlation between hybrids and pure breeding values, (i.e., the correlation between pure and hybrid merit as studied for PEE × PCH by Brawner et al. [2003] and Kain [2003]). In the short term, given the significant degree of genetic variation at the individual and family levels observed in growth traits and bearing in mind the available technology, two methods are suggested for mass seedling production: 1) generation of F_2 seeds through the creation of an F_1 CSO and 2) mass clonal propagation of best F_1 families.

Data Archiving Statement

We followed standard Forest Science policy. Data of trees, families, fathers, and mothers used in this study are available as electronic supplementary material to this publication (see Supplementary Table S5).

Literature Cited

Adams, G.W., and E.K. Morgenstern. 1991. Multiple-trait selection in jack pine. *Can. J. For. Res.* 21(4):439–445, doi: https://doi.org/10.1139/x91-059.

Baltunis, B.S., W.G. Gapare, and H.W. Wu. 2010. Genetic parameters and genotype by environment interaction in radiata pine for growth and wood quality traits in Australia. *Silvae Genet.* 59:2–3. doi: https://doi.org/10.1515/sg-2010-0014.

Barrett, W.H., S.M. Danner, and A. Hennig. 1991. Híbridos de *P. elliottii* var. *elliottii* × *P. caribaea* var. *hondurensis* en cultivo en el norte de Corrientes. P. 107–111, in *Proc. Jornada sobre Pinus caribaea*. Centro de Investigaciones y Experiencias Forestales, Eldorado, Misiones, Argentina

Blada, I., and Ş. Tănasie. 2013. Growth, straightness and survival at age 32 in a *Pinus strobus* × *P. wallichiana* F_1 hybrid population (Experiment 2). *Ann. For. Sci.* 56(1):15–30. doi: https://doi.org/10.15287/afr.2013.41.

Brawner, J.T., M.J. Dieters, and D.G. Nikles. 2003. Correlations between pure and hybrid combining abilities of slash pine parents. *For. Genet.* 10(3):241–248.

Brawner, J., M.J. Dieter, and D.G. Nikles. 2005. Mid-rotation performance of *Pinus caribaea* var. *hondurensis* hybrids with both *P. oocarpa* and *P. tecunumanii*: Hybrid superiority, stability of parental performance and potential for a multi-species synthetic breed. *For. Genet.* 12(1):1–13.

Bunse, G. 2003. Pinos híbridos en la provincia de Corrientes. in *Proc. Jornada Técnica Foresto-industrial Híbridos de PEE × PCH. INTA EEA*. Montecarlo, LIPSIA S.A. Puerto Esperanza, Misiones, Argentina.

Cappa, E.P., M.A. Marcó, D.G. Nikles, and I.A. Last. 2012. Performance of *Pinus elliottii*, *Pinus caribaea*, their F_1, F_2 and backcross hybrids and *Pinus taeda* to 10 years in the Mesopotamia region, Argentina. *New For.* 44:197–218. doi: https://doi.org/10.1007/s11056-012-9311-2.

Cappa, E.P., F. Muñoz, L. Sanchez, and R.J.C. Cantet. 2015. A novel individual-tree mixed model to account for competition and environmental heterogeneity: A Bayesian approach. *Tree Genet. Genomes.* 11:1–15. doi: https://doi.org/10.1007/s11295-015-0917-3.

Cappa, E.P., M.U. Stoehr, C.-Y. Xie, and A.D. Yanchuk. 2016. Identification and joint modeling of competition effects and environmental heterogeneity in three Douglas-fir trials. *Tree Genet. Genomes.* 12:102. doi: https://doi.org/10.1007/s11295-016-1061-4.

Costa e Silva, J., G.W. Dutkowski, and N.M.G. Borralho. 2005. Across-site heterogeneity of genetic and environmental variances in the genetic evaluation of *Eucalyptus globulus* trials for height growth. *Ann. For. Sci.* 62:183–191. doi: https://doi.org/10.1051/forest:2005010.

Costa e Silva, J., N.M.G. Borralho, J.A. Araújo, R.E. Vaillancourt, and B.M. Potts. 2009. Genetic parameters for growth, wood density and pulp yield in *Eucalyptus globulus*. *Tree Genet. Genomes.* 5:291–305. doi: https://doi.org/10.1007/s11295-008-0174-9.

Cumbie, W.P., F. Isik, and S.E. McKrand. 2012. Genetic improvement of sawtimber potential in loblolly pine. *For. Sci.* 58(2):168–177. doi: https://doi.org/10.1139/x95-152.

Dean, C.A., P.P. Cotterilll, and R.L. Eisemann. 1986. Genetic parameters and gains expected from selection in *Pinus caribaea* var. *hondurensis* in Northern Queensland, Australia. *Silvae Genet.* 35(5–6):229–236.

Dieters, M.J., T.L. White, and G.R. Hodge. 1995. Genetic parameter estimates for volume from full-sib tests of slash pine (*Pinus elliottii*). *Can. J. For. Res.* 25:1397–1408. doi: https://doi.org/10.1139/x95-152.

Dieters, M.J. 1996. Genetic parameters for slash pine (*Pinus elliottii*) grown in south-east Queensland, Australia: Growth, stem straightness and crown defects. *For. Genet.* 31:27–36.

Dieters, M.J., D.G. Nikles, P.G. Toon, and P. Pomroy. 1997. Genetic parameters for F_1 hybrids of *Pinus caribaea* var. *hondurensis* with both *Pinus oocarpa* and *Pinus tecunumanii*. *Can. J. For. Res.* 27(7):1024–1031. doi: https://doi.org/10.1139/x97-053.

Dieters, M.J., and H.S. Dungey. 2000. Relationship between the relative importance of nonadditive variance and the genetic correlation between hybrid and parental populations in some *Pinus* species. P. 87–92, in *proc. of QFRI/CRC-SPF hybrid breeding and genetics of forest trees*, eds. Dungey, H.S., M.J. Dieters, and D.G. Nikles, Noosa, Queensland, Australia, Department of Primary Industries, Brisbane.

Dungey, H.S., and D.G. Nikles. 2000. An international survey of interspecific hybrids in forestry. P. 419–422, in *proc. of QFRI/CRC-SPF hybrid breeding and genetics of forest trees*, eds. Dungey, H.S., M.J. Dieters, and D.G. Nikles, Noosa, Queensland, Australia, Department of Primary Industries, Brisbane.

Dungey, H.S. 2001. Pine hybrids a review of their use performance and genetics. *Forest. Ecol. Manag.* 148:243–258. doi: https://doi.org/10.1016/s0378-1127(00)00539-9.

Dutkowski, G.W., J. Costa e Silva, A.R. Gilmour, and G.A. Lopez. 2002. Spatial analysis methods for forest genetic trials. *Can. J. For. Res.* 32:2201–2214. doi: https://doi.org/10.1016/s0378-1127(00)00539-9.

Dvorak, W.S., A.P. Jordon, G.P. Hodge, and J.L. Romero. 2000. Assessing evolutionary relationships of pines in the *Oocarpae* and *Australes* subsections using RAPD markers. *New For*. 20:163–192. doi: https://doi.org/10.1023/A:1006763120982.

Falconer, D.S. and T.F.C. Mackay. 1996. *Introduction to quantitative genetics*, 4th ed. Harlow, Essex, UK, Longmans Green.

Gauchat, M.E., E.C. Belaber, E.P. Cappa, R.A. Scherer, and H.D. Reis. 2013. Parámetros genéticos de Progenies híbridas F_1 entre *Pinus elliottii* var. *elliottii* y *P. caribaea* var. *hondurensis* generadas en Argentina. in *proc. of 4º congreso forestal argentino y latinoamericano*. Misiones, Argentina, Iguazú.

Gianola, D., and H.W. Norton. 1981. Scaling threshold characters. *Genetics*. 99:357–364.

Gilmour, A.R., R. Thompson, and B.R. Cullis. 1995. Average information, an efficient algorithm for REML estimation in linear mixed models. *Biometrics*. 51:1440–1450. doi: https://doi.org/10.2307/2533274.

Gilmour, A.R., B.J. Gogel, B.R. Cullis, and R. Thompson. 2009. *ASReml User Guide Release 3.0*. Hemel Hempstead, UK, VSN International Ltd.

Gwaze, D.P. 1997. *Genetic parameter estimates for height and stem straightness in Pinus taeda L. and implications for breeding*. PhD thesis, University of Edinburgh, Edinburgh, Escocia. 180 p.

Gwaze, D.P. 1999. Performance of some interspecific F_1 pine hybrids in Zimbabwe. *For. Genet.* 6:283–289.

Gwaze, D.P., H.S. Dungey, M.J. Dieters, P.G. Toon, and D.G. Nikles. 2000. Interspecific pine hybris. I. genetic parameter estimates in Australia. *For. Genet.* 7(1):11–20.

Haapanen, M., V. Pirkko, and A. Marja-Leena. 1997. Progeny trial estimates of genetic parameters for growth and quality traits in Scots pine. *Silva Fenn.* 31(1):3–12. doi: https://doi.org/10.14214/sf.a8506.

Henderson, C.R. 1984. *Applications of Linear Models in Animal Breeding*. Canada, University of Guelph, Guelph, Ont.

Hodge, G.R., and T.L. White. 1992. Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. *Silvae Genet.* 41(4):252–262.

Hodge, G.R., and W.S. Dvorak. 2001. Genetic parameters and provenance variation of *Pinus caribaea* var. *hondurensis* in 48 international trials. *Can. J. For. Res.* 31:496–511. doi: https://doi.org/10.1139/x00-189.

Isik, F., K. Isik, and S.J. Lee. 1999. Genetic variation in *Pinus brutia* TEN. in Turkey: I. Growth, biomass and stem quality traits. *For. Genet.* 6(2):89–99.

Jansons, A., I. Baumanis, and M. Haapanen. 2009. Branch traits as selection criteria in scots pine breeding in Latvia. *LLU Raksti*. 23(318):45–46.

Kain, D.P. 2003. *Genetic parameters and improvement strategies for the Pinus elliottii var. elliottii x Pinus caribaea var. hondurensis hybrid in Queensland, Australia*. Ph.D. thesis, Canberra, Australia, Australian National University. 416 p.

Kerr, R.J., M.J. Dieters, B. Tier, and H.S. Dungey. 2004. Simulation of comparative gains from four different hybrid tree breeding strategies. *Can. J. For. Res.* 34:209–220. doi: https://doi.org/10.1139/x03-180.

Lambeth, C., and L.A. Dill. 2001. Prediction models for juvenile-mature correlations for Loblolly pine growth traits within, between and across test sites. *For. Genet.* 8(2):101–108.

López-Upton, J., T.L. White, and D.A. Huber. 1999. Taxon and Family Differences in Survival, Cold Hardiness, Early Growth, and Rust Incidence of Loblolly Pine, Slash Pine and Some Pine Hybrids. *Silvae Genet.* 48:303–313.

Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sunderland, MA, Sinauer Associates, Inc.

Ministry of Agriculture-Industry, Secretariat of Agriculture, Livestock and Fisheries (MAGyP). 2016. Available online at https://www.agroindus tria.gob.ar/sitio/areas/ss_desarrollo_foresto_industrial/; last accessed May 15, 2016.

Meuwissen, T.H., B. Engel, and J.H. van der Werf. 1995. Maximizing selection efficiency for categorical traits. *J. Anim. Sci.* 73:1933–1939. doi: https://doi.org/10.2527/1995.7371933x.

Misztal, I. 1997. Estimation of variance components with large-scale dominance models. *J. Dairy Sci.* 80:965–974. doi: https://doi.org/10.3168/jds.s0022-0302(97)76021-1.

Mutete, P., R. Murepa, and W.J. Gapare. 2015. Genetic parameters in subtropical pine F_1 hybrids: Heritabilities, between-trait correlations and genotype-by-environment interactions. *Tree Genet. Genomes.* 11(93):1–16. doi: https://doi.org/10.1007/s11295-015-0926-2.

Nikles, D.G. 1991. Increasing the value of future plantations in Argentina and southern Brazil using slash × Caribbean pine hybrids developed in Queensland. P. 93–102, in *Proc. Jornada sobre Pinus caribaea*. Eldorado, Misiones, Argentina, Centro de Investigaciones y Experiencias Forestales.

Nikles, D.G. 1996. The first 50 years of the evolution of forest tree improvement in Queensland. P. 93–102, *in Proc. of QFRI-IUFRO conference, tree improvement for sustainable tropical forestry*, eds. Dieters, M.J., A.C. Matheson, D.G. Nikles, C.E. Harwood, and S.M. Walker, Caloundra, Queensland, Australia, Queensland Forestry Research Institute, Gympie.

Nikles, D.G. 2000. Experience with some *Pinus* hybrids in Queensland, Australia. P. 27–42, in *Proc. of QFRI/CRC-SPF symposium, hybrid breeding and genetics of forest trees*, eds. Dungey, H.S., M.J. Dieters, and D.G. Nikles, Noosa, Queensland, Australia, Department of Primary Industries, Brisbane.

Pahr, N.P., M.E. Gauchat, F. Sorge, and G.H. Rodríguez. 2002. Ensayo comparativo de Pinos Subtropicales Mejorados. Noreste de Misiones, Argentina. in *Proc. of 9ª Jornadas Técnicas Forestales*. Misiones, Argentina, Eldorado.

Patterson, H.D., and R. Thompson. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika.* 58:545–554. doi: https://doi.org/10.1093/biomet/58.3.545.

Powell, M.B., and D.G. Nikles. 1996. Performance of *Pinus elliottii* var. *elliottii* and *P. caribaea* var. *hondurensis*, and their F_1, F_2 and backcross hybrids across a range of sites in Queensland. P. 382–383, in *Proc. of Tree improvement for sustainable tropical forestry*, eds. Dieters, M. J., A. C. Matheson, D. G. Nikles, C. E. Harwood, and S. M. Walker Queensland, Australia.

Raymond, C., and P. Cotterill. 1990. Methods of assessing crown form of *Pinus radiata*. *Silvae Genet.* 39(2):67–71.

Rockwood, D.L., K.J. Harding, and D.G. Nikles. 1991. Variation in the wood properties of the *Pinus elliottii* × *Pinus caribaea* var. *hondurensis* F_1 hybrid, its parental species, and backcross to *Pinus elliottii* in Australia. P. 233–240, *in Proc. of the 21st Southern Forest tree improvement conference, June 17–20, Knoxville, Tennessee*. SFTIC Sponsored Publication no. 43, Springfield, VA, National Technical Information Service.

Rockwood, D., and D.G. Nikles. 2000. Performance of slash pine x Caribbean pine hybrids southern Florida, USA. P. 114–119, in *Proc. of QFRI/CRC-SPF Symposium, hybrid breeding genetics of forest trees*, eds. Dungey, H.S., M.J. Dieters, D.G. Nikles, Noosa, Queensland, Australia, Department of Primary Industries, Brisbane.

Rodríguez, G.H., M.E. Gauchat. 2005. *Sub-capítulo I: Subprograma Pinos en Región Mesopotámica Pinus elliottii, Pinus taeda. Capítulo III Subprogramas de Producción de Material de Propagación Mejorado, Mejora Genética. Mejores Árboles para más Forestadores, El programa de Producción de Material de Propagación Mejorado y el Mejoramiento Genético en el Proyecto Forestal de Desarrollo*. SAGPyA - INTA. 23–41 p.

Schenone, R.A., and R.V. Pezzutti. 2003. Productividad de progenies de *Pinus elliottii* x *Pinus caribaea* var. *hondurensis*. in *Proc. of 12º Congreso Forestal Mundial*. Québec, Canadá. Available online at http://www.fao.org/docrep/ARTICLE/WFC/XII/0023-B4.HTM; last accessed March 15, 2015.

Stram, D.O., and J.W. Lee. 1994. Variance components testing in the longitudinal mixed effects model. *Biometrics*. 50:1171–1177. doi: https://doi.org/10.2307/2533455.

White, T.L. 1996. Genetic parameter estimates and breeding value prediction: Issues and implications in tree improvement programs. P. 110–117, in *Proc. of QFRI-IUFRO Conference of Tree improvement for sustainable tropic forestry*, eds. Dieters, M.J., A.C. Matheson, D.G. Nikles, C.E. Harwood, and S.M. Walker, Caloundra, Queensland, Australia.

White, T.L., W.T. Adams, and D.B. Neale. 2007. *Forest Genetics*. Oxfordshire, CABI Publishing. doi: https://doi.org/10.1079/9781845932855.0000.

Williams, C.G., and J.L. Hamrick. 1996. Elite populations for conifer breeding and gene conservation. *Can. J. For. Res.* 26:453–461. doi: https://doi.org/10.1139/x26-051.

Williams, C.G., and C.C. Lambeth. 1988. Bole straightness measurement for advanced-generation Loblolly pine genetic tests. *Silvae Genet.* 38:5–6.

Wu, H.X. 1998. Study of early selection in tree breeding. 1. advantage of early selection through increase of selection intensity and reduction of field test size. *Silvae Genet.* 47:2–3.

Xie, C.Y., and C.C. Ying. 1996. Heritabilities, age-age correlations, and early selection in lodgepole pine. *Silvae Genet.* 45:2–3.

Zas, R., E. Merlo, and J. Fernandez-López. 2004. Genotype x environment interaction in maritime pine families in Galicia, Northwest Spain. *Silvae Genet.* 53:175–181. doi: https://doi.org/10.1515/sg-2004-0032.

Zheng, Y. 2000. Hybrid breeding of *Pinus caribaea* in China. in *Proc. of QFRI/CRC-SPF symposium, hybrid breeding and genetics of forest trees*, eds. Dungey, H.S., M. J. Dieters, and D.G. Nikles, Noosa, Queensland, Australia, Department of Primary Industries, Brisbane.