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Estimation of genetic parameters for productive traits in *Eucalyptus tereticornis* and implications for breeding

Estimación de parámetros genéticos para características productivas en *Eucalyptus tereticornis* e implicancias en el mejoramiento genético

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SUMMARY

Eucalyptus tereticornis exhibits adaptation to a wide range of soils and environments, making it suitable for various protective and productive purposes throughout the territory of Uruguay. Due to the absence of a locally improved seed source, INIA began a tree breeding program in 2007 using genetic material from two sources: the natural distribution area of the species and local plantations. The performance of the genetic pool was evaluated at different sites over a nine-year growth period. The objectives of this study were to estimate genetic parameters (heritability, genetic correlations, and genotype-by-environment interaction) for growth and stem form traits and to estimate the genetic gains achievable through selection at different ages, in order to guide the breeding strategy for *E. tereticornis*. The genotype-environment interaction for volume and survival exhibited moderate to low levels, with Type B genetic correlations ranging from 0.68 to 0.82. The combined analysis of the trials revealed that heritability increased with the age of measurement for all traits, with values ranging from low to moderate for growth variables (0.04 – 0.23) and stem form (stem straightness and forking) showing low values (0.05 – 0.12). Genetic correlations between growth traits at different ages and volume at 9 years were positive and high (0.32 – 0.99), while the correlations between stem form (stem straightness and forking) and volume were low to moderate (0.30 – 0.56). The results obtained suggest that it is possible establish a single breeding unit and that through early selection, genetic gains can be maximized, evaluation costs reduced, and improved seed obtained in a shorter timeframe.

Keywords: heritability, genetic correlations, genetic gain, early selection.

RESUMEN

Eucalyptus tereticornis se adapta a una amplia variedad de suelos y ambientes, utilizado en todo el territorio uruguayo con fines protectores y productivos. Dada la inexistencia de una fuente de semilla localmente mejorada, en 2007 el INIA inició un programa de mejoramiento a partir de dos fuentes genéticas: el área de distribución natural y las plantaciones locales. Se evaluó el desempeño genético en diferentes sitios hasta el noveno año de crecimiento. Los objetivos de este estudio fueron: estimar los parámetros genéticos para las variables de crecimiento y forma del fuste, y estimar las ganancias genéticas esperadas mediante selección a diferentes edades. La interacción genotipo por medio ambiente para volumen y supervivencia fue de moderada a baja (correlaciones Tipo B entre 0,68 a 0,82). El análisis conjunto de los ensayos mostró que la heredabilidad aumentó con la edad de medición para todas las características, con valores bajos a moderados para las variables de crecimiento (0,04 a 0,23) y valores bajos (0,05 a 0,12) para la forma del fuste (rectitud y bifurcación). Las correlaciones genéticas entre las características de crecimiento a diferentes edades y el volumen a los 9 años fueron positivas y altas (0,32 a 0,99) mientras que las correlaciones entre la forma del fuste (rectitud y bifurcación) y el volumen fueron bajas a moderadas (0,30 a 0,56). Los resultados obtenidos sugieren que es posible manejar una sola unidad de mejoramiento y a través de la selección temprana maximizar las ganancias genéticas, reducir costos de evaluación y obtener semilla mejorada en menor tiempo.

Palabras claves: heredabilidad, correlaciones genéticas, ganancia genética, selección temprana.

INTRODUCTION

Among the forest species, *Eucalyptus tereticornis* Sm is a highly rustic species known for its wood of high density, hardness and durability. It adapts well to a wide variety of soils and environmental conditions, displaying tolerance to drought, frost and periodic waterlogging. It features reddish or reddish-brown heartwood that is hard, heavy, and durable, with a density (when air-dried) ranging from 950 to 1,100 kg m^{-3}. Its wood is suitable for various purposes, including construction, columns, sleepers, boards, furniture, and also serves as high-quality fuel

(Brussa 1994). Thanks to its excellent wood properties and remarkable versatility, this species presents an interesting alternative for diversifying both forest and livestock farm production.

Eucalyptus tereticornis has the largest natural distribution range among eucalypt species, spanning from Papua New Guinea to South Australia (6-38º S), and at elevations from sea level to 1,000 m in Australia to 1,800 m in Papua New Guinea. It is found in coastal and continental regions with diverse climates, ranging from tropical at its northern extent to cold temperate in the south. Average maximum temperatures typically range from 24-36 ºC, while minimum temperatures vary from 1-19 ºC, experiencing up to 30 frosts per year. Annual rainfall ranges from 500 to 3,000 mm, with varying patterns such as monsoons in Papua New Guinea, summer rains in Queensland, evenly distributed rains in New South Wales, and winter rains in Victoria (Eldridge *et al.* 1994).

At the end of the 19th century, *E. tereticornis* was introduced to different countries (Eldridge *et al.* 1994). Its cultivation has since spread widely, particularly in regions with annual rainfall ranging between 800 and 1,500 mm. However, due its adaptability, it has also been successfully planted in areas with lower precipitation levels (400 mm in India, 550 mm in Israel and 580 mm in Zimbabwe), as well as in areas of high precipitation (2,180 mm in Colombia and 3,500 mm in Papua New Guinea) (Alvarado *et al.* 2003). In India, one of the world's largest *Eucalyptus* growers, with 3.94 million hectares of plantations, *E. tereticornis* and an interspecific hybrid of this species dominate the southern plains (Varghese *et al.* 2008, Chezhian *et al.* 2010). It has been widely used in other countries, such as Zaire, Pakistan (in agroforestry systems) and Colombia (primarily along the Atlantic coast in reforestation programs involving small landowners) (Eldridge *et al.* 1994, Alvarado *et al.* 2003, Varghese *et al.* 2008, López *et al.* 2015). Introduced to Uruguay in 1853, *E. tereticornis* quickly gained popularity due to its adaptability to a wide range of soils. Until the mid-20th century, it was one of the most cultivated species in the country, primarily for providing shade and shelter for livestock but also as a source of energy (firewood and charcoal) and for various productive purposes including poles, carpentry, and flooring.

Given the significant variability of environments where this species occurs naturally, the existence of important differences among provenances is entirely expected. Indeed, considerable differences in growth rate and stem form among provenances have been documented in various countries (Ferreira *et al.* 1987, Otegbeye 1990, Balmelli and Resquín 1998, Ginwal *et al.* 2004). Due to the lack of information and the absence of a locally improved seed source, in 2007 the Forestry Program of INIA (National Institute of Agricultural Research) initiated a tree improvement plan for *E. tereticornis* with the aim of producing seeds characterized by fast growth and favorable stem form (Resquín and Balmelli 2008).

In tree-breeding programs, the accurate assessment of genetic parameters is critical for developing successful breeding strategies (Svensson *et al.* 1999). Estimating components of variance and heritability serves to compare expected gains from selection using various selection schemes. Heritability can vary among populations, among traits of interest, and with tree age. Determining genetic parameters at different ages allows helps pinpoint the optimal selection age (Dean *et al.* 1986). Methods aimed at improving the accuracy of early selection at the individual level hold considerable importance in maximizing genetic gains per unit of time (Modhumita *et al*. 2021). Genotype by environment interaction (GEI) refers to the fact that genotypes which are superior in one environment may not be similarly superior in another. Identifying GEI effects necessitates conducting genetic tests across multiple environments. When genotypes are evaluated in a single location, GEI effects can become "confounded" with genetic effects, potentially leading to overestimation of genetic parameters (Burdon 1989).

Recent research has yielded results on various topics, including provenance performance, quality indexes for paper and cellulose, and nanofiber characterization (González *et al.* 2021, Amorim *et al.* 2021, Raju *et al.* 2023), but information on genetic parameters in *E. tereticornis* remains scarce. Therefore, this study aims to estimate genetic parameters in *E. tereticornis* populations in Uruguay. The specific objectives are as follows: (1) to estimate heritabilities for growth and stem form traits up to 9 years of age, (2) to determine the genetic correlations between each trait and individual tree volume at 9 years, (3) to assess the magnitude of genotype by environment interaction, and (4) to estimate the genetic gains in individual tree volume achievable through selection at different ages.

METHODS

Genetic material and field trials. The data analyzed in this study were sourced from the breeding population of *E. tereticornis* at INIA (National Institute of Agricultural Research), Uruguay, which comprises genetic material from two sources: native forests and Uruguayan commercial plantations. The first source consists of 100 open-pollinated families gathered from 20 provenances that encompass a substantial portion of the species' natural distribution. These resources were originally introduced from CSIRO (Commonwealth Scientific and Industrial Research Organization) in Australia (table 1). The local seed pool comprises 113 open-pollinated families, with mothers selected based on growth and stem form criteria in 18 local plantations situated in northern, central and eastern regions of Uruguay (table 1). Additionally, five open-pollinated families were included from the tree improvement program of CIEF (Centro de Investigación y Experimentación Forestal) in Argentina.

The evaluation of productive performance was conducted through four progeny tests established in representative sites across the country in 2008 and 2009. These sites share a similar climate but vary in soil characteristics (table 2). The trials were organized using a randomized complete block design, with single tree plots and 19 to 21 replications per site. Soil preparation involved tillage in bands, and trees were planted at a spacing of 4 x 2.5 meters (1,000 trees ha^{-1}) in all sites.

Assessed traits. Survival, diameter at breast height, total height, individual tree volume, stem form and incidence of forkings were measured at ages 1, 3, 5 and 9 years. All surviving trees were assessed for diameter at breast height (DBH) using a diametric tape, total height (HT) measured with a hypsometer (Vertex IV HS 102), stem straightness was evaluated on a visual scale ranging from 1 (straight stem) to 4 (twisted stem), and forking was assessed using a visual scale ranging from 0 (no forks) to 2 (more than one fork). The total stem volume, including bark (VOL), for each tree was calculated using the general equation [1]:

$$VOL = Pi / 4 * DBH^2 * HT * FF \qquad [1]$$

Where FF is the form factor with a value of 0.4.

Data analysis and estimation of genetic parameter. Data were analyzed without transformation, both separately for each test site and in a combined analysis of all sites. Variance components for each trait were estimated using the following mixed linear model for the combined analysis [2] in R 3.4.1 software (R Core Team 2015):

$$Y_{ijklm} = \mu + SITE_i + REPj_{(i)} + POP_k + PROV_{l(k)} + FAM_{m(kl)} + SITE.PROV_{il(k)} + SITE.FAM_{im(kl)} + \varepsilon_{ijklm} \qquad [2]$$

In this model, Y_{ijklm} represents the observed trait value in the j-th replication at the i-th site, associated with the k-th population (source of seed), from the l-th provenance within the m-th family. μ represents the overall mean value, $SITE_i$ signifies the effect of the i-th site, $REP_{j(i)}$ represents the effect of the j-th replication within the i-th site, POP_k denotes the effect of the k-th population (seed sources from Australia and Uruguay), $PROV_{l(k)}$ signifies the effect of the l-th provenance within the k-th population, $FAM_{m(kj)}$ represents the effect of the m-th family within the k-th population within the l-th provenance, $SITE.PROV_{il(k)}$ indicates the interaction effect between the i-th site and the l-th provenance, $SITE.FAM_{im(kl)}$ represents the interaction effect between the i-th site and the m-th family, and ε_{ijklm} accounts for the random error. Site and population effects were treated as fixed factors, while the other factors were considered as random factors. In individual site-specific analysis, the same model was used without including the site effect and its interactions with other factors.

Additive variance was determined as 2.5 times the family variance, assuming a selfing rate of 30 % (Volker *et al.* 1990). Individual tree heritability for each trait was separately estimated for each site [3] and in the combined analysis [4] using the following equations, respectively:

$$h^2 = 2.5\ \sigma^2F / \sigma^2F + \sigma^2\ \varepsilon \qquad [3]$$

$$h^2 = 2.5\ \sigma^2F / \sigma^2F + \sigma^2SF + \sigma^2\varepsilon \qquad [4]$$

Where σ^2F is the variance of the family effect, σ^2SF is the variance corresponding to the site by family interaction effect, and $\sigma^2\varepsilon$ is the residual variance.

Phenotypic and genetic correlations between different traits and ages and individual volume at 9 years of age were calculated using ASReml with the combined analysis using the equation [2].

The family by site interaction was estimated using Type B genetic correlations [5] for volume and survival at 9 years from the combined analysis, using Burdon's (1977) equation:

$$\text{Type B } r_g = (\sigma^2F) / (\sigma^2F + \sigma^2SF) \qquad [5]$$

Here, σ^2F represents the variance of the family effect, and σ^2SF represents the variance of the site by family interaction effect.

Genetic gain (ΔG) for volume at 3, 5 and 9 years was calculated using the genetic gain equation [6] (Falconer and Mackay 1996):

$$\Delta G = h^2 * \sigma_y * i \qquad [6]$$

Where h^2 is the individual tree heritability, σ_y is the phenotypic standard deviation, and i represents selection intensity. The selection intensity was set at 1.159, equivalent to selecting the top 30 % of the population.

To determine the optimal age for individual volume selection and to maximize genetic gain per year, three ages of selection were simulated (3, 5 and 9 years) using the following equation [7] (adapted from Falconer and Mackay 1996):

$$\Delta G = h_x * h_y * r_{gxy} * \sigma_y * i / t \qquad [7]$$

In this equation, h_x represents the square root of the heritability of volume at 3 or 5 years, h_y represents the square root of the heritability of volume at 9 years, r_{gxy} signifies the genetic correlation between x and y (volume at 3 or 5 years and volume at 9 years), σ_y is the phenotypic standard deviation for volume at 9 years, i is the selection intensity (selection differential in standard deviations), and t represents the age of selection (3, 5 or 9 years).

Table 1. Australian and local provenances of *Eucalyptus tereticornis* and number of mother trees from each provenance under evaluation. QLD: Queensland, VIC: Victoria, NSW: New South Wales.

Procedencias australianas y locales de *Eucalyptus tereticornis* y número de árboles madre de cada procedencia en evaluación. QLD: Queensland, VIC: Victoria, NSW: Nueva Gales del Sur.

Location	State	Nº mother trees	Latitude (S)	Longitude (*)	Altitude (m a.s.l.)
Mill Stream Archer Creek	QLD[1]	4	17° 39’	145° 21’	670
MT Garnet	QLD[1]	6	17° 40’	145° 00’	640
Cardwell	QLD[1]	5	18° 10’	145° 58’	84
SW of Mount Garnet	QLD[1]	1	18° 24’	144° 45’	890
Burdekin River	QLD[1]	8	19° 48’	146° 04’	291
Crediton SF	QLD[1]	9	21° 17’	148° 31’	730
Marlborough	QLD[1]	5	22° 52’	149° 48’	100
Raglan Creek	QLD[1]	5	23° 43’	150° 52’	20
Calliope River	QLD[1]	5	23° 57’	151° 09’	30
Kalpower	QLD[1]	5	24° 40’	151° 19’	350
Bunya SF	QLD[1]	1	26° 48’	151° 35’	440
W of Warwick	QLD[1]	3	28° 11’	151° 39’	485
Warwick	QLD[1]	5	28° 15’	152° 05’	450
Maryland	NSW[1]	8	28° 29’	152° 05’	750
Selection Flat SF559	NSW[1]	10	29° 10’	152° 58’	40
N of Woolgoolga	NSW[1]	1	29° 55’	153° 12’	30
Buckenbowra SF	NSW[1]	5	35° 40’	150° 07’	110
Yurammie SF	NSW[1]	4	36° 49’	149° 45’	170
S of Loch Sport	VIC[1]	8	38° 03’	147° 01’	2
Loch Sport	VIC[1]	2	38° 03’	147° 36’	5
Villasboas	Durazno[2]	22	33º 07’	56º 24’	138
Ruta 5, Km 414	Tacurembó[2]	3	31º 35’	55º 46’	210
Iporá	Tacuarembó[2]	8	31º 39’	55º 58’	165
Camino a Grutas	Tacurembó[2]	14	31º 40’	55º 59’	173
Camino a Grutas	Tacuarembó[2]	1	31º 39’	56º 19’	176
Paso del Cerro	Tacuarembó[2]	3	31º 35’	55º 51’	185
Santa María	Rivera[2]	5	31º 16’	55º 36’	214
La Negra	Río Negro[2]	1	32º 26’	57º 25’	125
La Portuguesa	Río Negro[2]	5	32º 33’	57º 41’	71
Ruta 59	Tacuarembó[2]	2	31º 57’	55º 48’	158
Nueva Esperanza	Rivera[2]	7	31º 00’	55º 37’	194
La Palma	Paysandú[2]	6	31º 46’	56º 16’	320
Santa Magdalena	Paysandú[2]	4	31º 46’	56º 20’	291
La Rosada	Tacuarembó[2]	7	32º 17’	55º 27’	95
La Teja	Durazno[2]	2	32º 37’	55º 32’	115
La Chirimoya	Paysandú[2]	7	32º 32’	56º 50’	174
Algorta	Río Negro[2]	9	32º 26’	57º 25’	130
El Tabaré	Río Negro[2]	7	32º 48’	57º 55’	52

(*) Longitude East in Australia and West in Uruguay. [1] Australian provenances, [2] Uruguayan provenances.

RESULTS

Important differences in heritability values were identified in the analysis of individual sites (table 3). Generally, the highest heritability values for growth traits were observed in the Reyles trial (0.41, 0.38 and 0.39 for height, DBH and individual volume, respectively), while the lowest values were recorded in Rivera. Survival and stem straightness exhibited higher heritabilities in El Carmen (0.34 and 0.18, respectively), whereas forking had the

Table 2. Location of *Eucalyptus tereticornis* progeny tests and main characteristics of the sites.

Ubicación de las pruebas de progenie de *Eucalyptus tereticornis* y principales características de los sitios.

	Site 1	Site 2	Site 3	Site 4
Location (department)	Ruta 5, km 438 (Rivera)	El Carmen (Durazno)	Carlos Reyles (Durazno)	Vergara (Treinta y Tres)
Latitude	31° 25.419’ S	33° 19.616’ S	33° 5.291’ S	32° 45.747’ S
Longitude	55° 39.703’ W	56° 6.313’ W	57° 4.621’ W	54° 0.869’ W
Mean min. annual temp.	13.5 ºC	11.3 ºC	11.3 ºC	12.1 ºC
Mean annual temp.	18.6 ºC	17.2 ºC	17.2 ºC	17.7 ºC
Mean max. annual temp.	23.7 ºC	23.1 ºC	23.1 ºC	23.4 ºC
Mean annual rainfall	1,558 mm	1,159 mm	1,159 mm	1,409 mm
Soil characteristics				
Depth	Deep	Deep	Shallow to moderately Deep	Shallow
Drainage	Good	Good	Moderately Good	Poor
Fertility	Low	Low to medium	Medium	Low
Texture	Sandy loam	Sandy loam	Clay loam	Loam

Table 3. Individual narrow-sense heritability estimates and standard error (in parentheses) for different traits and measurement ages in *Eucalyptus tereticornis*, calculated separately for each site and in the combined analysis.

Estimaciones individuales de heredabilidad en sentido estricto y error estándar (entre paréntesis) para diferentes características y edades de medición en *Eucalyptus tereticornis*, estimadas para cada sitio por separado y para el análisis conjunto.

Trait and age	Rivera	Reyles	Vergara	Carmen	Joint análisis
Height 1	0.11 (0.03)	0.41 (0.06)	0.06 (0.03)	-	0.04 (0.02)
Height 3	0.16 (0.03)	0.35 (0.06)	0.19 (0.04)	0.25 (0.04)	0.16 (0.02)
Height 5	0.12 (0.03)	0.28 (0.05)	-	-	0.13 (0.03)
Height 9	0.14 (0.03)	0.32 (0.06)	0.26 (0.05)	0.25 (0.04)	0.19 (0.02)
DBH 3	0.17 (0.03)	0.38 (0.06)	0.12 (0.04)	0.22 (0.04)	0.13 (0.02)
DBH 5	0.17 (0.03)	0.34 (0.06)	-	-	0.19 (0.03)
DBH 9	0.21 (0.04)	0.33 (0.06)	0.33 (0.06)	0.27 (0.04)	0.23 (0.03)
Volume 3	0.16 (0.03)	0.39 (0.06)	0.07 (0.04)	0.22 (0.04)	0.10 (0.02)
Volume 5	0.16 (0.03)	0.34 (0.06)	-	-	0.15 (0.03)
Volume 9	0.19 (0.03)	0.30 (0.05)	0.28 (0.05)	0.27 (0.04)	0.20 (0.03)
Stem straightness 5	0.10 (0.03)	0.09 (0.03)	-	-	0.05 (0.02)
Stem straightness 9	0.11 (0.03)	0.12 (0.04)	0.15 (0.04)	0.18 (0.03)	0.12 (0.02)
Forking 9	0.08 (0.03)	0.10 (0.04)	0.11 (0.03)	0.06 (0.02)	0.06 (0.01)
Survival 9	0.15 (0.03)	0.23 (0.06)	0.28 (0.05)	0.34 (0.05)	0.16 (0.03)

highest heritability value in Vergara (0.11). As expected, the estimated heritabilities in individual sites exceeded those calculated in the pooled analysis. This is because at each site, the genotype by environment interaction, or GEI effect, is integrated into the family effect. In other words, the estimated heritability in an individual site is inflated by the GEI effect.

In the combined analysis, the heritability values for growth traits increased with age: from 0.04 to 0.19 for height, from 0.13 to 0.23 for DBH, and from 0.10 to 0.20 for individual volume. Among these traits, DBH at 9 years exhibited the highest heritability in the combined analysis (0.23), varying between 0.21 and 0.33 in the site-specific analyses. Generally, tree height displayed lower heritability values compared to DBH. The heritability of individual volume at 9 years was estimated at 0.20 in the combined analysis, with values varying between 0.19 and 0.30 in the site-specific analyses. Survival at 9 years demonstrated a heritability of 0.16, with values varying between 0.15 and 0.34 in the site-specific analyses. In contrast, traits related to stem form, such as straightness and forking, exhibited low heritabilities of 0.12 and 0.06, respectively, at 9 years in the combined analysis.

The genetic and phenotypic correlations of growth traits with respect to the individual volume at 9 years were positive, and increased as the age of measurement increased (table 4). Among these traits, DBH exhibited the strongest correlation with volume at 9 years of age, reaching the highest phenotypic (r_p = 0.94) and genetic (r_g = 0.99) correlation values at that age. In contrast, stem straightness, evaluated at 5 and 9 years, displayed negative genetic correlations with individual volume at 9 years, with values of -0.56 and -0.30, respectively. Since the assessment scale for stem straightness assigned higher values to more crooked trees, the negative sign indicates a desirable relationship: as the volume increases, stem straightness improves. Furthermore, the presence of forks exhibited a positive and moderate genetic correlation with volume at 9 years (r_g = 0.41).

The highestmost substantial phenotypic and genetic correlations for individual volume, assessed at various ages, were observed between ages 5 and 9, with values of 0.85 and 0.95, respectively (table 5). The genetic correlation between years 3 and 5 was exceptionally high (0.93), although it decreased between years 3 and 9. Nevertheless, the correlation remained relatively high at 0.82.

The Type B genetic correlation for individual volume at 9 years was notably high and positive, measuring at 0.82. This suggests that there is minimal genotype by environment interaction for this trait. Conversely, for survival at 9 years, the Type B genetic correlation was 0.68, indicating a moderate level of genotype by environment interaction.

Table 6 presents the anticipated genetic gains for individual volume at different ages, obtained through the selection of the top 30 % of families. If selection were conducted at the third or fifth year of growth, genetic gains of 11.3 % and 12.0 %, respectively, would be realized in the subsequent generation. However, when selecting at 9 years of age, a higher genetic gain of 18.7 % is expected. Estimates of genetic gains per year, specifically for individual volume at 9 years, indicate that selecting at age 3 would yield a genetic gain 79 % greater than that achieved through direct selection at 9 years. Similarly, if the selection were made at 5 years, the expected genetic gain per year for volume at 9 years would be 51 % greater than direct selection at 9 years. These results show that, for the purpose of improving the individual volume at 9 years of age through indirect selection, the optimal selection age is 3 years.

Table 4. Phenotypic (r_p) and genetic (r_g) correlations, estimated from the combined analysis for different traits and years of measurement versus individual volume at 9 years old in *Eucalyptus tereticornis* (standard error in parentheses).

Correlaciones fenotípicas (r_p) y genéticas (r_g), estimadas a partir del análisis conjunto para diferentes características y años de medición versus volumen individual a los 9 años en *Eucalyptus tereticornis* (error estándar entre paréntesis).

	volume at 9 years old	
Trait and age	r_p (± SE)	r_g (± SE)
Height 1	0.27 (0.01)	0.32 (0.14)
Height 3	0.58 (0.01)	0.74 (0.05)
Height 5	0.65 (0.01)	0.86 (0.05)
Height 9	0.83 (0.06)	0.94 (0.01)
DBH 3	0.65 (0.01)	0.81 (0.04)
DBH 5	0.83 (0.01)	0.96 (0.02)
DBH 9	0.94 (< 0.01)	0.99 (< 0.01)
Stem straightness 5	-0.25 (0.18)	-0.56 (0.15)
Stem straightness 9	-0.15 (0.02)	-0.30 (0.10)
Forking 9	0.20 (0.02)	0.41 (0.11)

Table 5. Phenotypic (r_p) and genetic (r_g) correlations, estimated from the combined analysis, for individual volume at different ages in *Eucalyptus tereticornis* (standard error in parentheses).

Correlaciones fenotípicas (r_p) y genéticas (r_g), estimadas a partir del análisis conjunto, para volumen individual a diferentes edades en *Eucalyptus tereticornis* (error estándar entre paréntesis).

	r_p (± SE)	r_g (± SE)
Vol 3 - Vol 5	0.75 (0.01)	0.93 (< 0.01)
Vol 5 - Vol 9	0.85 (0.01)	0.95 (0.11)
Vol 3 - Vol 9	0.65 (0.10)	0.82 (0.05)

Table 6. Expected genetic gain in individual volume at different ages through direct selection of the top 30 % of families and expected genetic gain per year in individual volume at year 9 by early selection of the top 30 % of families.

Ganancia genética esperada en volumen individual a diferentes edades por selección directa del 30 % de las mejores familias y ganancia genética esperada por año en volumen individual en el año 9 por selección temprana del 30 % de las mejores familias.

Age	Genetic gain (m^3 tree^{-1})	Genetic gain (%)	ΔG/year (m^3 tree^{-1})	% base age 9
3	0.0014	11.3	0.0062	179
5	0.0081	12.0	0.0052	151
9	0.0312	18.7	0.0035	100

DISCUSSION

Genetic parameter estimates. The genetic base of *E. tereticornis* analyzed in this study exhibited significant genetic variation at the population, provenance and family levels. Generally, growth traits present moderate heritabilities, while stem form traits exhibit moderate to high values (Valera and Kageyama 1995, Santos *et al*. 2008, Vargas *et al.* 2013, Azevedo *et al.* 2015). In this study, however, growth traits demonstrated higher heritabilities compared to traits related to stem form (stem straightness and forking), suggesting that the expected responses to selection for growth rate are relatively favorable, while they are less pronounced for traits related to stem form.

In general, heritability values increased with age of measurement. However, other studies report somewhat different results. Valera and Kageyama (1995) observed in *E. saligna* that heritability for DBH tended to decrease with age. The estimated heritabilities for growth traits at 9 years in the joint analysis (0.23 for DBH and 0.19 for total height) fall within the range of values reported by other authors, such as Valera and Kageyama (1995), which varied between 0.13 to 0.28 in *E. grandis*, 0.17 to 0.25 in *E. tereticornis*, 0.24 to 0.36 in *E. urophylla* and 0.24 to 0.44 in *E. cladocalyx* (Vargas *et al.* 2013). In the joint analysis, the individual volume at 9 years old presented a heritability of 0.20, with variations between 0.19 and 0.30 in each trial. For *E. saligna* in Brazil, Valera and Kageyama 1995 estimated a heritability for individual volume at 32 months of 0.13. Similarly, for *E. urophylla* in Brazil, Rosado *et al.* (2010) reported a heritability value for individual volume at 4 years of 0.24.

In the joint analysis, the heritability of survival at 9 years was relatively low, measuring at 0.16. This contrasts with the findings of Balmelli *et al.* (2014), who reported higher heritabilities for survival until the ninth year in *E. globulus* in Uruguay, ranging between 0.33 and 0.45.

The traits related to stem form, specifically stem straightness and forking, presented low heritability values in the joint analysis at 9 years, measuring at 0.12 and 0.06, respectively. These values contrast with findings in other studies. Santos *et al.* (2008) and Azevedo *et al.* (2015) reported heritability values for stem form in *E. camaldulensis* of 0.25 and 0.16, at 3 and 21 years, respectively. Valera and Kageyama (1995) report a heritability of 0.45 in *E. saligna* at 32 months of age. Vargas *et al.* (2013) observed heritabilities for stem straightness in *E. cladocalyx* at 9 years of age of 0.29 and 0.57 for two localities in Chile, respectively. The low heritability values estimated in this study for stem straightness and forking contrast with that proposed by Zobel and Talbert (1994), who suggested that these characteristics are easily improved through selection due to their high heritability. It is worth noting that the low heritability values obtained in this study may be influenced by environmental factors, such as strong winds that could have affected the stems at early ages.

Overall, growth traits such as height, DBH, and individual volume, as well as survival, displayed moderate heritabilities across all sites. Conversely, stem form traits (straightness and forking) exhibited low heritabilities. These findings suggest that there are favorable prospects for improving growth traits (height, DBH and volume) as well as survival through selective breeding. In contrast, the limited genetic control observed for stem straightness and forking indicates that these traits are likely to exhibit a minimal response to selection.

The genetic correlations observed between the growth traits and the breeding objective (volume at 9 years) were strongly positive. DBH, in addition to its high correlation with individual volume, is an easily measurable trait, therefore its use as a selection criterion reduces evaluation costs. Conversely, genetic correlations between stem form traits (stem straightness and forking) and individual volume were low. These findings align with the results of Harrand *et al.* (2009) in *E. grandis*, who reported a negative and low genetic correlation (-0.19) between stem straightness and volume at 8.5 years of growth. In the case of forkings, the correlation with volume is unfavorable (more forkings lead to more volume), whereas for straightness, the correlation is favorable (greater straightness results in more volume). These results suggest that selection for growth is unlikely to bring about significant changes in stem traits, or in at most, there may be a slight increase in forkings and a slight improvement in stem straightness.

The heritabilities estimated at individual sites tend to be higher than those estimated from combined sites. This discrepancy arises because, in the analysis of each site, the variance component associated with the site-by-family interaction is incorporated into the family variance component. In other words, the estimated heritability for each site is inflated by the genotype by environment interaction. Understanding the magnitude of genotype by environment interaction is crucial when defining breeding units, which are specific areas targeted for the generation of selected genetic material. In this study, the magnitude of GEI, analyzed at the family level within provenances, was low, indicating a high Type B genetic correlation for individual volume and moderate GEI for survival. In a previous analysis of GEI, moderate provenance by site interaction was observed for volume, survival, and forking (González *et al.* 2021).

In a clonal trial of *E. urophylla* conducted in Mexico, Sánchez *et al.* (2005) identified a moderate Type B genetic correlation for height, diameter and volume ranging between 0.61 to 0.65. These results imply a reasonably good stability in the relative performance of the clones. Based on the values reported in this study, it appears feasible to consider a single management unit for the first generation. Furthermore, assuming a genotype by environment interaction (GEI) of similar magnitude, it may be possible to establish a single management unit for the second generation as well. This may help reduce the costs of evaluation and seed production for the breeding program.

The significant genetic correlations observed in this study between individual volume at juvenile stages (3 and 5 years) and the selection objective (individual volume at 9 years) indicate the feasibility of implementing early selection strategies. Indeed, the estimates of genetic gains expected through selection at different ages confirm that selection by volume at 3 and 5 years would yield a substantially greater genetic gain in the subsequent generation compared to direct selection for volume at 9 years.

These results indicate that the third year is the optimal selection age for improving individual volume at 9 years. Selecting at this stage yields higher genetic gains per unit of time, reduces evaluation costs, and expedites availability of improved seed stock. Lima *et al.* (2011), in their evaluation of early selection efficiency for parent and tree cloning in full-sib progeny tests of *Eucalyptus* spp., reported gains per year that were 31 % greater with selection at 30 months compared to selection at 84 months. These studies underscore the efficacy of early selection across different *Eucalyptus* species. Simultaneously, the high genetic correlations observed between DBH at different ages and volume at 9 years suggest the feasibility of selecting based on DBH at early stages without significantly compromising genetic gains in volume at 9 years. In fact, the genetic gain per year in volume at 9 years, when selecting by DBH at 5 and 3 years, exceeds that of direct selection for volume at 9 years by 34 % and 67 %, respectively. In essence, this demonstrates the feasibility of conducting indirect and early selection, reducing the evaluation period and its associated costs, while maintaining genetic gains.

Implications for breeding. The estimation of genetic parameters plays a crucial role in the management of seed orchards and provides valuable guidance for developing the evaluation and selection strategy for the next generation of improvement. The findings from this study regarding growth traits in *E. tereticornis* indicate moderate heritability and low genotype-by-environment interaction, which implies the possibility of achieving satisfactory genetic gains within a single breeding unit. Furthermore, the high age-age genetic correlations demonstrate the effectiveness of early selection in improving individual volume, thereby reducing evaluation costs and the time required to obtain improved seed.

From a practical standpoint, for breeding programs that rely on open-pollinated seed production, a two-stage parent selection approach is recommended. The first stage involves a preliminary selection with low intensity in the third year, primarily aimed at eliminating the poorest-performing families to reduce competition between trees and encourage flowering. The second stage, conducted with greater intensity in the fifth year, focuses on retaining only the best parents for commercial seed production. This two-stage selection method not only promotes flowering and increases seed production, but also provides the opportunity for a second parent evaluation, enabling more precise ranking of parents or establishing a new ranking if selection objectives change.

CONCLUSION

The heritability estimates for the assessed traits ranged from low to moderate, spanning values between 0.04 and 0.23. These heritability estimates tended to increase with age of measurement. Genetic correlations between stem form traits (straightness and forking) and individual volume were found to be low. Conversely, genetic correlations between growth traits and the breeding objective (volume at 9 years) were positive and high. The genotype by environment interaction was observed to be low for individual volume and moderate for survival, suggesting that it may be feasible to consider a single breeding unit for the second generation. Furthermore, the genetic gains per unit of time expected through selection at year 3 or 5 were greater than those expected from selection at year 9. Consequently, early selection has the potential to accelerate the breeding cycle, reduce evaluation costs, and expedite the production of improved seed.

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AUTHOR CONTRIBUTIONS

FR and GB: conception, design and performance of the experiment, MG: data collection, data analysis and manuscript preparation, GB: supervision of the work and critical revision of the manuscript.

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