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ORIGINAL PAPER

Provenance variation and genetic parameters of *Eucalyptus viminalis* in Argentina

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Abstract Genetic parameters for growth, stem straightness, pilodyn penetration, relative bark thickness and survival were estimated in a base-population of five open-pollinated provenance/progeny trials of *Eucalyptus viminalis*. The trials, located in northern, central and southern Buenos Aires Province, Argentina, comprised 148 open-pollinated families from 13 Australian native provenances and eight local Argentinean seedlots. The Australian native provenances come from a limited range of the natural distribution. Overall survival, based on the latest assessment of each trial, was 62.4%. Single-site analyses showed that statistically significant provenances differences ($p<0.05$) for at least one of the studied traits in three out of the five trials analyzed. The local land race performed inconsistently in this study. The average narrow-sense individual-tree heritability estimate $\left(\widehat{h}^2\right)$ was 0.27 for diameter and 0.17 for total height. Values of $\widehat{h}^2$ also increased with age. Pilodyn penetration, assessed at only one site, was more heritable $\left(\widehat{h}^2 = 0.32\right)$ than the average of growth traits. Estimated individual-tree heritabilities were moderate to low for stem straightness (average of 0.20) and relative bark thickness (0.16). The estimated additive genetic correlations (r_A) between diameter and height were consistently high and positive (r_A average of 0.90). High additive genetic correlations were observed between growth variables and pilodyn penetration (r_A average of 0.58). Relative bark thickness showed a negative correlation with diameter $(r_A = -0.39)$ and height $(r_A = -0.51)$. The average estimated additive genetic correlation between sites was high for diameter (0.67). The implications of all these parameter estimates for genetic improvement of *E. viminalis* in Argentina are discussed.

Keywords *Eucalyptus viminalis* · Heritability · Additive genetic correlation · Genotype by environmental interactions · Tree breeding

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Introduction

Eucalyptus viminalis Labill ssp. *viminalis* (hereafter *E. viminalis*) is a forest tree native to Australia. It occurs over a wide range of rainfall conditions and soil types in south-eastern Australia from the eastern half Tasmania (43°S) to the border of New South Wales and Queensland (28°S) and its latitude ranging from 143ºE to 153ºE. Its altitude goes from near sea level to 1,300 m above sea level (masl) in the northern New South Wales (Boland et al. 2006). Across its range, the mean maximum temperature of the hottest month ranges from 18°C to 32°C, while the mean minimum of the coldest month from −3°C to −7°C. The mean annual rainfall varies from roughly 500 to 1,700 mm per year, which grades from a winter- or winter-spring maximum in the southern areas, to a more or less even distribution in central New South Wales, and to a moderate summer maximum farther north (Boland et al. 2006). Frost frequency varies widely from nil in the coastal and low-altitude sites to more than 100 days per year in the high altitude tableland areas.

E. viminalis was of interest for early introductions in many countries around the globe because of this combination of good growth and frost tolerance (Eldridge et al. 1993). In Argentina, *E. viminalis* grows well between 33°S and 39°S latitude in the Pampeana Region, which includes the provinces of Buenos Aires, eastern of La Pampa, southern of Córdoba and Santa Fe (Moschini et al. 2000), largely due to their good soil and climatic conditions. Although this area includes about 3.5 million hectares potentially available for plantations, only 10,000 hectares of *E. viminalis* across Buenos Aires province have been planted with annual mean increments varying between 25 and 35 $m^3 ha^{-1} years^{-1}$ according to soil quality. In a trial with 100 of *Eucalyptus* species tested in the north of the Buenos Aires province, Mendonza and Alliani (1983) showed that *E. viminalis* ranked in the top seven species in terms of volume increment per year after 9 years, just outperformed by *Eucalyptus fastigata* and *Eucalyptus nitens* among other species. They highlight *E. viminalis* as the best species in the region due to the quality of the wood, survival, and good form. The first provenance/progeny trials of *E. viminalis* were planted in 1971 by the Instituto Nacional de Tecnología Agropecuaria (INTA) at two sites in the north of Buenos Aires province: Ramallo and Alsina. These trials included 22 Australian provenances, covering most of the *E. viminalis* native range and including 19 open-pollinated (OP) families from selected trees within the Argentinean land race. Provenance performance was evaluated at the age of 3 years at Ramallo and ages 9 and 15 years at Alsina. Although there were statistically significant differences among provenances, there was no evidence of a geographic pattern in the height at 3 years of the Australian provenances in the Ramallo trial (Mendonza 1974). In this trial, the best provenances came from Victoria (Cann River Area, Warburton, and Yarram) though some provenances from New South Wales (e.g., Tumut and Urriara Forest) also performed well; meanwhile, the South Australian provenances were clearly inferior. The provenance Warburton (Victoria) had the best growth, stem form, and self-pruning at Alsina and ranked second at Ramallo (Gea and Alliani 1988) after Uriarra Forest (New South Wales).

Given the good growth rates, adequate frost resistance, and high-quality wood for pulp and fiber board, *E. viminalis* has become a favorite species for planting in the Pampeana Region. In the year 1995, INTA began a tree breeding program to accommodate the general interest in this species. Considering the information obtained from previous trials, a more intensive re-sampling within better provenances areas was undertaken. This new genetic material included 148 OP families from 13 Australian provenances and local selections of *E. viminalis*. From 1998 to 2000, seven provenance/progeny trials with this genetic material were established across the Buenos Aires province. The objectives of these trials were not only to provide a base-population for selection of plus trees for breeding, but also to produce improved seed for new plantings, through converting progeny trials into seedling seed orchards, as suggested by Barnes (1995).

Knowledge of genetic parameters is required to formulate breeding strategies, as well as estimated breeding values and gains from selection (White 1996). Most studies of genetic parameters in *Eucalyptus* have focused on species such as *Eucalyptus globulus* (e.g., Lopez et al. 2002; Costa e Silva et al. 2009), *Eucalyptus grandis* (e.g., Marco and White 2002), *E. nitens* (reviewed in Hamilton and Potts 2008), and *Eucalyptus urophylla* (e.g., Kien et al. 2008). Nevertheless, information on genetic parameters of *E. viminalis* is extremely limited, and published reports are based on only small numbers of families (i.e., ≤13 OP families; Otegbeye and Kellison 1980; Resende et al. 1990).

In the present study, we used data of growth traits, tree stem straightness, pilodyn penetration, bark thickness, and survival, to estimate: (1) differences among the 15 provenances and (2) genetic parameters including heritabilities, additive genetic coefficients of variation, and additive genetic correlations between traits within and across-sites in a base-population of five OP provenance/progeny trials of *E. viminalis*. Additionally, this information will be used to discuss the implications and selection strategies for genetic tree improvement of *E. viminalis* in Argentina.

Materials and methods

Genetic material

The genetic materials used in this study were obtained from OP seedlots of 148 native-forest families: 132 originated in Victoria collected by Kylisa Seeds Pty Ltd and 16 in New South Wales collected by CSIRO Australian Tree Seed Centre. The eight Argentinean OP families were derived from trees phenotypically selected for growth and form in a commercial plantation at Ramallo, northern Buenos Aires province. Additionally, the Argentinean land race was represented by four commercial bulks from Bordenave, Junín, Sierra de la Ventana, and 25 de Mayo. The number of families sampled (i.e., seedlots) varied from four to nine in five provenances and over ten for the rest. The number of families planted per trial ranged from 77 to 157. Details of the genetic material used in this study can be found in the Table 1.

All seedlings for all trials of *E. viminalis* were produced at INTA Castelar Research Station nursery. Seeds were first sown by individual family along with the bulk seedlot in nursery beds and germinated in 7–10 days. The seedlings were individually pricked out into 290 cm^3 black plastic bags filled with a mix of soil, humus, and perlite in equal

Table 1 Details of provenance latitude (Lat., S), longitude (Long., E), altitude (Alt., masl) and number of open-pollinated (OP) families and bulk seed collections from native stand and local source included in each trial

Provenance[a]	Lat.	Long.	Alt.	Trials					Total
				GUAM	MAYO	CAST	PRIN	VALL	
Bald Hills, VIC	37º 12′	148º 11′	980	11	14	5	12	9	14
Bonang, VIC Kylisa	37º 10′	148º 53′	955	8	10	3	9	4	10
Bonang, VIC CSIRO	37º 16′	148º 44′	720	5	9	4	9	7	9
Bonang River, VIC	37º 15′	148º 45′	850	4	8	5	7	5	8
Errinundra Road, VIC	37º 26′	148º 52′	360	6	12	5	12	4	12
Federation Road, VIC	37º 28′	146º 00′	640	12	14	2	12	6	14
Martins Creek, VIC	37º 28′	148º 33′	160	7	14	7	11	7	14
Mt. Sunday, VIC	37º 20′	146º 26′	960	3	6	1	6	2	6
Mt. Baldhead, VIC	37º 26′	147º 39′	750	5	10	3	10	6	10
Noojee, VIC	37º 54′	145º 58′	320	5	25	6	21	10	25
Rockton, NSW	37º 13′	149º 27′	460	5	6	3	2	–	6
Timbarra River, VIC	37º 22′	148º 08′	380	7	9	3	6	6	10
Uriarra S.F., NSW	35º 18	148º 55′	625	6	9	4	8	3	10
Argentina OP, Bs. As.				7	7	3	6	5	8
Argentina bulk, Bs. As.				3	4	2	4	3	4
Total				94	157	56	135	77	160

Abbreviations used for the trials are described in the text

[a] *VIC* Victoria, *NSW* New South Wales, *Bs. As.* Buenos Aires

proportions about 20 days after emergence. The seedlings were grown without any replicated layout in the nursery for 4–6 months until they reached 20–25 cm height and were shipped for trial establishment.

Trial description

The successful five trials in the north, center, and south of the Buenos Aires Province, Argentina, were measured for this study (Table 2, Fig. 1). The sites were identified as GUAM, MAYO, CAST, PRIN, and VALL. Four trials were planted in the spring of 1998, 1999, and 2000, and one trial was planted in autumn of 2000. The field experimental design was the same at all locations, a randomized complete block design with single-tree plots. Each trial contained from 15 to 25 replicates. The spacing was 3 m×3 m, except for VALL which was 5 m×2 m spacing. Details of the five trials and the sites characteristics are summarized in Table 2.

Traits evaluated

Growth traits, tree stem straightness, pilodyn penetration, bark thickness, and survival were scheduled for measurement at the ages of 2, 3, 5, and 6 years in all surviving trees. However, measurements were not available at all ages for all trials. Diameter at breast height (1.3 m, DBH) was measured in centimeters at 3 (DBH3), 4 (DBH4), 5 (DBH5), and 6 (DBH6) years after planting. Total height was measured in m at 2 (HT2) and 3 (HT3) years of age. The tree stem straightness (STR) was assessed on a 1 to 4 subjective scale with 1 indicating the "crookedest" trees and 4 indicating the straightest trees at ages 3 (STR3) and 4 (STR4) years and with the frequency of 1 to 4 scores approaching normality. Thus, the stem straightness scores were approximately normally distributed and untransformed individual STR score were used in subsequent analysis. The trait STR were scored within each site, consequently, the straightness scored at one site not necessarily represent the same degree of stem straightness at another site. Pilodyn penetration (PILO) was measured in mm using a 6 J Forest Pilodyn with a 2 mm diameter pin, in an east to west direction and without bark (a small section of bark at 1.3 m above the ground was removed prior to the PILO readings being taken). Bark thickness at breast height was measured right after Pilodyn penetration measurement, but only at the GUAM trial site, at age 5 years. The trait relative bark thickness (RBK) was calculated as the proportion of total DBH occupied by the bark, thus assuming a linear relationship between bark thickness and DBH that goes through the origin. Survival (SUR) was determined based on the oldest assessment for each trial: age 3 years for PRIN, age 5 years for GUAM, and age 6 years for MAYO, CAST, and VALL. The full list of traits is given in Table 3.

Table 2 Location, sites characteristics, date of planting, and experimental design data for each of the five trials

Trial[a]	GUAM	MAYO	CAST	PRIN	VALL
Location	Guaminí	25 de Mayo	Castelar	Cn. Pringles	Del Valle
Latitude	37°6′42″	35°32′59″	34°36′47″	38º03′64″	35°51′88″
Longitude	62°26′70″	60°6′24″	58°39′68″	61º15′20″	60°43′64″
Altitude (m)	297	46	12	331	297
Soil texture	Clay loam	Sandy loam	Clay loam	Sandy clay loam	Sandy
Drainage class	Good	Somewhat excessive	Good	Moderate	Somewhat excessive
AMP (mm)	784.0	1057.7	1034.3	796.8	963.00
AMT (°C)/AbMT (°C)	13.8/−9.5	16.4/−7.9	17.0/−6.2	14.7/−11.5	15.8/−14.5
Days/year with screen frost	42	15	12	22	23
Planting date	23/12/1998	23/09/1999	25/04/2000	15/09/2000	09/10/2000
Experimental design	RCB	RCB	RCB	RCB	RCB
Number of replicates	15	25	23	21	16
Spacing (m×m)	3×3	3×3	3×3	3×3	5×2
Initial number of trees	1,440	3,925	1,288	3,240	1,216

[a] AMP annual mean precipitation, AMT annual mean temperature, AbMT absolute minimum temperature, RCB randomized complete block

Statistical analysis

Statistical analysis was conducted in three stages. First, each trial was analyzed separately to estimate univariate genetic parameters. Second, the covariances between two different traits measured in the same individual were estimated for each trial. Third, paired-site analysis included data from GUAM, MAYO, CAST, PRIN, and VALL 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.

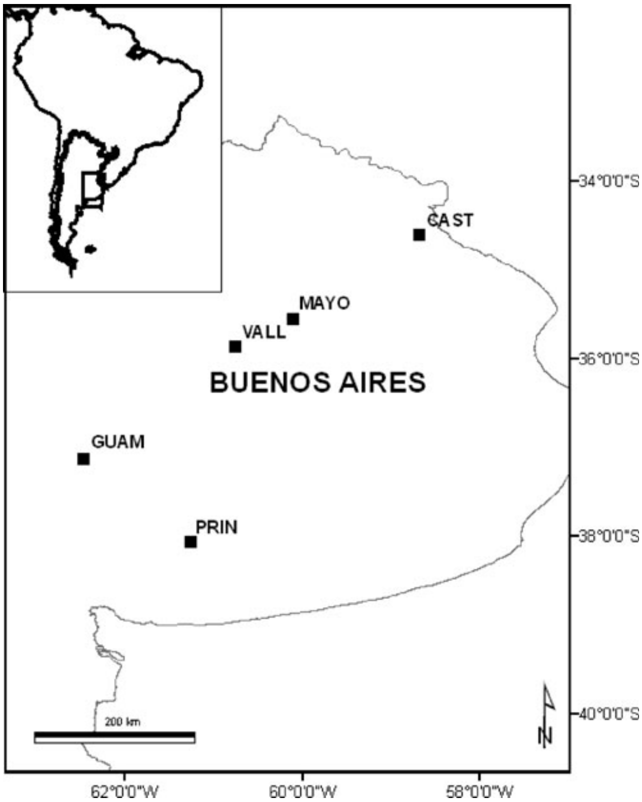

Fig. 1 Location of the five trials in Argentina. Abbreviations used for the trials are described in the text

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

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Za} + \boldsymbol{e} \qquad (1)$$

In Eq. 1, $\boldsymbol{y}$ is the vector of individual-tree observations, β is the vector of fixed effects associated to $\boldsymbol{y}$ by the incidence matrix $\boldsymbol{X}$, and such that the matrix $\boldsymbol{X}$ is of full column rank. For each trial, the fixed effects were: overall means, replicates, and genetic group to account for the means of the different provenances of parent trees. Fifteen genetic groups were formed according to provenance (see above, Table 1). The random vector $\boldsymbol{a}$ contained the additive genetic effects (or breeding values) of individual trees and is related to $\boldsymbol{y}$ by the incidence matrix $\boldsymbol{Z}$. The expectation of $\boldsymbol{a}$ is $\boldsymbol{0}$, and the covariance matrix is $\boldsymbol{A}\ \sigma_A^2$ where $\boldsymbol{A}$ is the additive tree-level relationship matrix (Henderson 1984) for the trial trees and their known ancestors, and σ_A^2 is the additive genetic variance. The $\boldsymbol{A}$ matrix was modified to take into account 25% average selfing in *E. viminalis* (see below genetic parameters). There were only a maximum of 80 bulk trees (assumed to be unrelated) for the variable HT2 in the MAYO trial, so no extra independent additive variance was assumed for these individuals and were included in $\boldsymbol{A}$ with their parents unknown (i.e., males and

Table 3 Phenotypic means (mean), standard deviation (SD), and respective units for all traits assessed from each trial

Trait	Unit	Trial									
		GUAM		MAYO		CAST		PRIN		VALL	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
DBH3	cm	–	–	–	–	8.66	3.21	6.27	2.60	7.60	2.35
DBH4	cm	–	–	11.99	2.83	11.48	4.33	–	–	12.75	3.12
DBH5	cm	9.11	3.74	–	–	15.07	5.17	–	–	–	–
DBH6	cm	–	–	19.35	4.47	16.94	5.68	–	–	21.10	5.58
HT2	m	2.25	1.05	1.05	0.41	–	–	–	–	–	–
HT3	m	–	–	–	–	8.78	2.49	4.90	1.73	–	–
STR3	Scale 1–4	–	–	–	–	–	–	1.99	0.72	–	–
STR4	Scale 1–4	–	–	1.84	0.75	–	–	–	–	–	–
PILO5	mm	12.08	1.78	–	–	–	–	–	–	–	–
RBK5	% of DBH	10.86	2.37	–	–	–	–	–	–	–	–
SUR3	%	–	–	–	–	–	–	0.51	0.50	–	–
SUR5	%	0.76	0.43	–	–	–	–	–	–	–	–
SUR6	%	–	–	0.65	0.48	0.58	0.49	–	–	0.62	0.49

The trait diameter at breast height (DBH), total height (HT), tree stem straightness (STR), pilodyn penetration (PILO), relative bark thickness (RBK), and survival (SUR) are followed by a number denoting the age of measurement in years. Abbreviations used for the trials are described in the text

females). Finally, random error terms are included in the vector $\boldsymbol{e}$, which is distributed as $\boldsymbol{e} \sim N\left(\boldsymbol{0}, \boldsymbol{I}\boldsymbol{\sigma}_e^2\right)$ and σ_e^2 is the error variance.

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

$$\begin{bmatrix} \boldsymbol{y}_i \\ \boldsymbol{y}_j \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_i & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X}_j \end{bmatrix} \begin{bmatrix} \beta_i \\ \beta_j \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_i & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z}_j \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_i \\ \boldsymbol{a}_j \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_i \\ \boldsymbol{e}_j \end{bmatrix} \qquad (2)$$

where $\boldsymbol{y_i}$ and $\boldsymbol{y_j}$ are, respectively, the vectors of individual-tree observations on trait or site i and j. Matrices $\boldsymbol{X}_i \oplus \boldsymbol{X}_j$ and $\boldsymbol{Z}_i \oplus \boldsymbol{Z}_j$ relate observations to elements of $\left[\boldsymbol{\beta}_i' | \boldsymbol{\beta}_j'\right]$ and breeding values in $\left[\boldsymbol{a}_i' | \boldsymbol{a}_j'\right]$, respectively, and $\left[\boldsymbol{e}_i' | \boldsymbol{e}_j'\right]$ is the error vector. The symbols $\oplus$ and ' indicate the direct sum of matrices and transpose operation, respectively. Finally, the expectation and variance-covariance matrix for model 2 are respectively equal to:

$$\mathrm{E}\begin{bmatrix} \boldsymbol{a}_i \\ \boldsymbol{a}_j \end{bmatrix} = \begin{bmatrix} \boldsymbol{0} \\ \boldsymbol{0} \end{bmatrix} \quad Var\begin{bmatrix} \boldsymbol{a}_i \\ \boldsymbol{a}_j \end{bmatrix} = \begin{bmatrix} \boldsymbol{\sigma}^2_{Ai,i}\boldsymbol{A} & \boldsymbol{\sigma}_{Ai,j}\boldsymbol{A} \\ \boldsymbol{\sigma}_{Aj,i}\boldsymbol{A} & \boldsymbol{\sigma}^2_{Aj,j}\boldsymbol{A} \end{bmatrix}$$

$$= \begin{bmatrix} \boldsymbol{\sigma}^2_{Ai,i} & \boldsymbol{\sigma}_{Ai,j} \\ \boldsymbol{\sigma}_{Aj,i} & \boldsymbol{\sigma}^2_{Aj,j} \end{bmatrix} \otimes \boldsymbol{A} = \boldsymbol{G}_0 \otimes \boldsymbol{A}$$

where $\sigma^2_{Ai,i}$ and $\sigma^2_{Aj,j}$ are the additive genetic variances for the traits or sites i and j, respectively, whereas $\sigma_{Ai,j}$ is the additive covariance between traits or sites i and j. The symbol $\otimes$ indicates the Kronecker products of matrices. The expected value and variance-covariance matrix of $\boldsymbol{e}$ are respectively equal to:

$$\mathrm{E}\begin{bmatrix} \boldsymbol{e}_i \\ \boldsymbol{e}_j \end{bmatrix} = 0 \quad Var\begin{bmatrix} \boldsymbol{e}_i \\ \boldsymbol{e}_j \end{bmatrix} = \begin{bmatrix} \boldsymbol{\sigma}^2_{ei,i}\boldsymbol{I} & \boldsymbol{\sigma}_{ei,j}\boldsymbol{I} \\ \boldsymbol{\sigma}_{ej,i}\boldsymbol{I} & \boldsymbol{\sigma}^2_{ej,j}\boldsymbol{I} \end{bmatrix} = \begin{bmatrix} \boldsymbol{\sigma}^2_{ei,i} & \boldsymbol{\sigma}_{ei,j} \\ \boldsymbol{\sigma}_{ej,i} & \boldsymbol{\sigma}^2_{ej,j} \end{bmatrix}$$

$$\otimes \boldsymbol{I} = \boldsymbol{R}_0 \otimes \boldsymbol{I}$$

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

A binomial model was fitted to absence/presence (SUR, 0/1) at each site and the probit transformation as link function.

The significance of fixed effects was assessed using F-tests. F-statistics were calculated to examine if significant differences among provenances existed using error degrees of freedom derived from the family within-provenance term.

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 Eqs. 1 and 2 and were obtained with the ASREML program (Gilmour et al. 2006), which use the average information algorithm described by Gilmour et al. (1995).

Single-site narrow-sense individual heritability $\left(\widehat{h}^2\right)$ and additive genetic correlations (r_{A}) were estimated as:

$$\widehat{h}^2 = \frac{\widehat{\sigma}_A^2}{\widehat{\sigma}_A^2 + \widehat{\sigma}_e^2};\ r_A = \frac{\widehat{\sigma}_{Ai,j}}{\widehat{\sigma}_{Ai,i}^2 + \widehat{\sigma}_{Ai,j}^2}$$

where $\widehat{\sigma}_A^2$ is the estimated additive genetic variance, $\widehat{\sigma}_e^2$ is the estimated error variance in Eq. 1, $\widehat{\sigma}_{Ai,i}^2$ and $\widehat{\sigma}_{Aj,j}^2$ are the estimated additive genetic variances for the traits or sites i and j, respectively, and $\widehat{\sigma}_{Ai,j}$ is the estimated additive covariance between traits or sites i and j in Eq. 2. The heritability estimates of survival, on the underlying unobservable continuous scale, was estimated with the same equation and assumed that $\widehat{\sigma}_e^2$ was equal to 1.0. 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)variances ratios to be symmetric and was calculated using an ASREML post-processing program (Gilmour et al. 2006).

Eucalypts have a mixed mating system setting inbred, originating from selfing and matings between close relatives, as well as outcrossed seed. The mating system of *E. viminalis* has not yet been specifically documented well; however, outcrossing rates of OP families from other *Eucalyptus* species and their natural populations averaged 74% (range of 59–84%; Eldridge et al. 1993; Table 19.2). Self-fertilization in *Eucalyptus* species may result in inflated heritability estimates (Griffin and Cotterill 1988; Hodge et al. 1996; Lopez et al. 2002) and biased additive genetic correlation estimates across ages and sites (Hodge et al. 1996), without proper consideration of the mixed mating system. Depending on the proportion of offspring generated by self-pollination, a particular OP family will have a mixture of relatedness among individuals ranging from selfs to half-sibs. Assuming that parental trees were not inbred, the additive genetic relationship between two individuals generated by self-pollination would be 1 (Cockerham 1984); 0.5 if two individuals are full-sibs through a common father and the mother tree, and 0.25 if both trees have different fathers (with unrelated pollen), thus being maternal half-sibs. Therefore, multiplying each case by its probability of occurrence, the average relationship between individuals of the same family (a) would be

$$a = s^2 + 2s(1-s)1/2 + (1-s)^2 1/4$$

where s is the self-pollination rate. This average relationship between trees could be used instead of 0.25 to modify the additive relationship matrix $\boldsymbol{A}$. Different authors have used different coefficients of relationship in the same or different *Eucalyptus* species, ranging from 0.25 to 0.54 (see Hodge et al. 1996; Table 2, p. 56). Alternatively, using a and the average inbreeding coefficient $(F = 0.5 \times s)$ adjusted heritability estimates $\left(\widehat{h}_0^2\right)$ can be calculated from the heritability estimate calculated assuming a coefficient of relationship of 0.25 and no inbreeding $\left(\widehat{h}^2\right)$ as (Soria et al. 1998):

$$\widehat{h}_0^2 = 0.25\widehat{h}^2/a - 0.25\widehat{h}^2 F$$

In this study, the coefficient of additive relationship between two individuals in $\boldsymbol{A}$ matrix were modified using the pedigree file qualifier SELF, in the *.as* ASReml file. SELF qualifier allows incorporate a self-pollination rate (i.e., s) when a progeny come from a cross where the male parent is unknown, assuming to be from selfing with probability s and from outcrossing with probability $1-s$ (Gilmour and Dutkowski 2004). Given that we do not have the differences in outcrossing rates between the plantation and natural forest families, an average selfing rate of 25% was used in both cases. We also assumed that families did not differ in the levels of susceptibility to inbreeding depression.

Houle (1992) argued that comparison of genetic variances between different traits should be made by a standardized measure. To compare the absolute level of additive genetic variance across the trials, for each trait and trial, the additive genetic coefficient of variation $\left(\widehat{C}V_A\right)$ was calculated as the ratio between the additive genetic standard deviation $(\widehat{\sigma}_A)$ and the population phenotypic mean $(\overline{x})$:

$$\widehat{C}V_A = 100 \times \frac{\widehat{\sigma}_A}{\overline{x}}.$$

Results and discussion

Estimates of trait means

General phenotypic means and standard deviations for all traits observed at each site are presented in Table 3. The overall survival at the sites assessed was 62.4%. However, survivals at the sites CAST at age 3 years and PRIN at age 6 years were 58% and 51%, respectively. The major cause of mortality at these sites (i.e., CAST and PRIN) was largely due to atypical establishment problems, i.e., foliage damage by ants and flooding by an excessive rainfall, respectively, therefore we did not consider this variation in survival due to adaptive traits important for this area of Argentina.

The trial at CAST had faster initial growth (DBH3), but growth declined in relation to VALL over the next few years (i.e., DBH4 and DBH6), likely caused by the difficulties of a clay loam soil at CAST. Under similar clay loam soils the site GUAM had the worst overall performance at 5 years (DBH5), possibly due to a subsuperficial petrocalcic horizon with variable depth. By the age of 6 years (DBH6), VALL showed the best growth (21.10 cm) followed by MAYO (19.35 cm), both sites having well-drained and sandy soils. The better growth on sandy soils agrees with the soil preference of this species in its native distribution (Boland et al. 2006; Ladiges and Ashton 1974). The height means at age 2 years were 1.05 and 2.25 m in the trials MAYO and GUAM, respectively, whereas at age 3 years the means were 4.90 and 8.78 m in the trial PRIN and CAST, respectively.

Similar means for tree form score (i.e., STR) were recorded at MAYO (1.84) and PRIN (1.99). The traits PILO and RBK were assessed only at age 5 years in the south-western site GUAM where the trial means were 12.08 mm and 10.86%, respectively. The mean PILO penetration for *E. viminalis* at age 5 years was similar to that measured at age 4 years from base-population trials of *E. globulus* grown in Argentina (12.60 mm); however, mean RBK was slightly lower (8.00%, Lopez et al. 2001) than in the present study.

Growth performance and provenance differences

Least-squares means for provenances for DBH are presented for the five trials in Table 4. For the three sites that had significant provenance effects (i.e., GUAM, MAYO, and VALL), Errinundra Road (VIC) was one of the best Australian provenances for growth (ranked second, first, and first, respectively) and was well-represented by 12 families from natural forest. Meanwhile, the neighboring Mt. Baldhead (VIC) was the one of the slowest-growing provenances on the three sites, ranking 15th, 14th and 11th at GUAM, MAYO, and VALL, respectively. Another provenance with good growth performance in the trials GUAM and MAYO was Timbarra River (VIC) which ranked third and second, respectively. Although the provenances tested in these trails come from a limited part of the species' natural range, multiple linear regressions of diameter least-squares means at breast height (centimeters) on latitude, longitude, and altitude (masl), on the three sites with significant provenance variation and for all the Australian provenances represented by three or more families, were studied. Only altitude was statistically significant at GUAM and MAYO ($p<0.05$). However, adjusted R^2 were moderate to low (from 0.60 to 0.31, Fig. 2), which suggests that altitude of origin does have a small but significant negative effect on growth in *E. viminalis*. Similar trends due to altitude have been observed for growth traits (height and diameter) in other *Eucalyptus* provenance studies (Eldridge et al. 1993; Tripiana et al. 2007). Survival among provenances across-sites varied from 30% (Mt. Sunday, VIC) to 87% (Argentina OP, Buenos Aires), based on the latest assessment for each trial. However, multiple linear regressions of survival rate on latitude, longitude, and altitude for the two sites with significant provenance variation (i.e., PRIN and MAYO), showed no statistically significant effect ($p>0.05$) for the three independent variables studied (i.e., latitude, longitude, and altitude).

The Australian native provenances included in this study come from a limited part (i.e., from 35° 18′ to 37° 54′ of latitude south and from 145° 58′ to 148° 55′ of longitude east) of the natural distribution of *E. viminalis*. However, single-site analysis showed that the provenance differences were statistically significant different ($p<0.05$) in two (GUAM and MAYO) of the five trials for all variables analyzed, except survival at PRIN (F values and significances, Table 5). The trials CAST, PRIN, and VALL did not show significant provenance differentiation ($p>0.05$) for any traits, with the exception of DBH6 at VALL (F values and significances, Table 5). The non-significant difference among the provenances at CAST, PRIN, and VALL sites may be due to the limited number of families included (CAST and VALL), as well as of some establishment problems (CAST and PRIN). Regardless, the result suggests that provenance selection from these three trials (CAST, PRIN, and VALL) would result in little genetic gain.

E. viminalis grows across a wide environmental and geographical range (Boland et al. 2006). This warrants a search for ecological races. For five central Victorian populations of *E. viminalis*, Ladiges and Ashton (1974) suggested that differences observed in seedling growth rate indicated that ecological races exist, through the natural selection in particular habitats. However, we did not find enough evidence to support this conclusion, likely due to our limited range of Australian provenances.

The Argentinean land race selections performed inconsistently across the sites, so it may not be suitable as a source of seed or breeding materials to develop plantings in the Pampas Region. The lack of outstanding performance of this land race, relative to the native Australian provenances in the trials (despite the genetic improvement typically expected by selecting desirable OP trees and bulk collections) may be due to the original selections coming from a narrow and perhaps suboptimal genetic base for this area of Argentina (Eldridge et al. 1993). Likewise, Eldridge (1995) for 11 *Eucalyptus* species in 13 different countries around the world (including the results of the first provenance/progeny trials planted in 1971 by INTA), cited the inferior performance of the land-race material to native-stand collections.

Heritability estimates and additive genetic coefficients of variation

The estimated residual and additive genetic variances and heritabilities derived from the individual-tree mixed model

Table 4 Provenance least-squares means (mean) and ranking within sites (rank) for diameter at breast height (DBH, centimeters) at age 6 years, except for GUAM (5 years) and PRIN (3 years) in the five trials

Provenance [a]	GUAM		MAYO		CAST		PRIN		VALL	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
Bald Hills, VIC	9.0	14	19.6	9	16.9	7	6.0	7	19.4	12
Bonang Kylisa, VIC	9.1	12	19.9	7	15.6	14	6.0	6	20.9	4
Bonang CSIRO, VIC	9.4	10	19.6	8	17.8	4	6.0	5	21.0	3
Bonang River, VIC	9.3	11	18.7	15	16.7	8	5.5	13	19.9	10
Errinundra Road, VIC	10.9	2	21.3	1	18.2	3	6.1	4	23.1	1
Federation Road, VIC	9.0	13	20.6	4	16.1	10	5.8	9	20.5	5
Martins Creek, VIC	10.2	6	20.5	5	18.3	2	5.9	8	21.9	2
Mt Sunday, VIC	9.5	9	19.0	12	15.8	13	4.8	15	16.7	14
Mt. Baldhead, VIC	8.8	15	18.8	14	14.5	15	5.7	11	19.5	11
Noojee, VIC	11.2	1	19.9	6	18.8	1	5.7	10	20.5	6
Rockton, NSW	9.6	8	19.0	11	16.1	11	5.5	14	–	–
Timbarra River, VIC	10.8	3	21.3	2	15.9	12	5.6	12	20.0	8
Uriarra .S.F., NSW	10.3	5	20.8	3	17.1	6	6.1	3	20.4	7
Argentina OP, Bs.As.	10.1	7	18.9	13	16.5	9	6.5	2	17.2	13
Argentina bulk, Bs. As.	10.6	4	19.3	10	17.5	5	6.9	1	20.0	9
Site mean (SE)	9.1 (0.7)*	19.4 (0.7)**	16.9 (2.0), NS	6.3 (0.4), NS	21.1 (1.5)*					
Range for provenance	8.8–11.2	18.7–21.3	14.5–18.8	4.8–6.9	16.7–23.1					
No. of provenance	15	15	15	15	14					

Site means and approximate pooled standard errors (SE) are given together with the significance of provenances differences noted as not statistically significant (*NS*; $p>0.05$), *Statistically significant $(0.01 < p < 0.05)$ and **statistically highly significant ($p<0.01$). Abbreviations used for the trials are described in the text

[a] *VIC* Victoria, *NSW* New South Wales, *Bs. As.* Buenos Aires

Eq. 1 for the variables evaluated across all trials are shown in Table 5. Certainly, a key objective trait for breeding eucalypts is the fast growth, typically measured by diameter and/or height. Estimates of narrow-sense individual-tree heritability were moderate to high for growth variables (DBH and HT), with the average estimates across the five Argentinean trials being 0.27 and 0.17, respectively. These genetic variations suggest that selection for growth traits in *E. viminalis* should be effective, even when clear gains were not evident from provenance selection in two out of the five trials analyzed. Individual-tree heritability estimates ranged from 0.12 at 3 years to 0.44 at 6 years for DBH and from 0.07 at 2 years to 0.27 at 3 years for HT. Heritabilities increased from 3 to 6 years for DBH and from 2 to 3 years

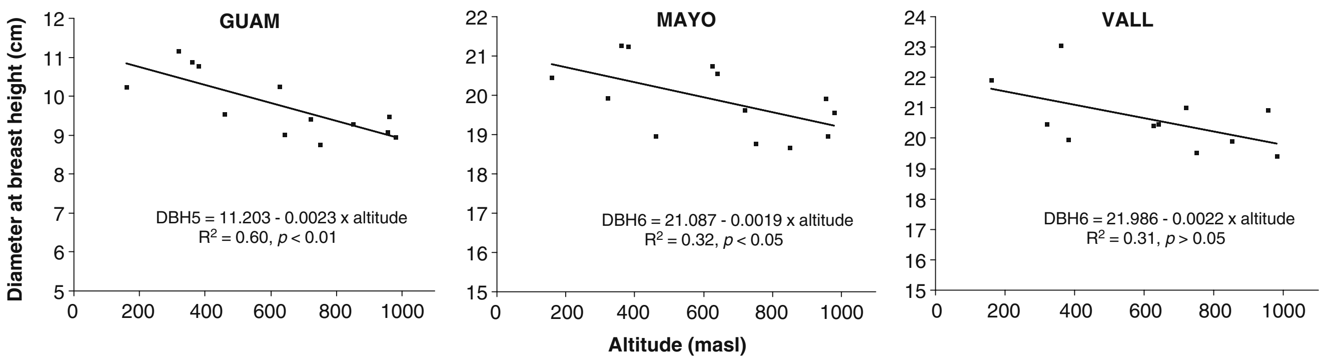

Fig. 2 Regression of diameter at breast height (DBH, centimeters) last square means on altitude (masl), for the 13 better-represented provenances in the GUAM, MAYO, and VALL open-pollinated progeny trials. The *Y*-axis is DBH at the age of 5 (GUAM) and 6 (MAYO and VALL) years and were started at 5 (GUAM) and 15 cm (MAYO and VALL). Abbreviations used for the trials are described in the text

Table 5 Number of observations (n), and estimates of error variance $\left(\widehat{\sigma}_e^2\right)$, additive genetic variance $\left(\widehat{\sigma}_A^2\right)$, additive genetic coefficient of variation ($\widehat{CV}_A$in % unit), heritability $\left(\widehat{h}^2\right)$ with their approximate standard error (SE), F values (F) and significance (Sig.) of the provenance effects, for the different variables measured across the five trials

Trait	Site	n	Error variance	Additive variance		Heritability		Provenance effect	
			$\widehat{\sigma}_e^2$	$\widehat{\sigma}_A^2$	$\widehat{CV}_A$	$\widehat{h}^2$	SE	F	Sig.
DBH3	CAST	713	5.16	2.14**	17	0.29	0.11	0.90	NS
	PRIN	1,279	4.92	0.70**	13	0.12	0.05	1.44	NS
	VALL	763	4.03	1.02**	13	0.20	0.08	0.84	NS
DBH4	MAYO	2,516	6.01	0.97**	8	0.14	0.04	2.51	**
	CAST	747	8.22	3.40**	17	0.33	0.11	1.08	NS
	VALL	737	6.54	2.46**	12	0.27	0.09	1.02	NS
DBH5	GUAM	1,028	9.90	1.70**	14	0.15	0.06	1.98	*
	CAST	743	11.99	7.63**	18	0.39	0.12	0.64	NS
DBH6	MAYO	2,540	14.60	3.38**	10	0.19	0.04	2.99	**
	CAST	733	14.23	11.16**	20	0.44	0.13	0.72	NS
	VALL	751	17.25	11.20**	16	0.39	0.11	1.63	*
HT2	GUAM	1,178	0.78	0.18**	19	0.19	0.06	2.69	**
	MAYO	2,656	0.10	0.01**	8	0.07	0.03	4.04	**
HT3	CAST	712	2.35	0.86**	11	0.27	0.10	1.16	NS
	PRIN	1,414	1.93	0.40**	13	0.17	0.05	1.28	NS
STR3	PRIN	1,301	0.39	0.10**	16	0.20	0.06	1.40	NS
STR4	MAYO	2,517	0.42	0.10**	17	0.19	0.04	3.88	**
PILO5	GUAM	781	1.81	0.83**	8	0.32	0.10	3.87	**
RBK5	GUAM	770	3.97	0.71**	8	0.15	0.08	5.76	**
SUR3	PRIN	2,835	1.00	0.01, NT		0.01	0.02	4.12	**
SUR5	GUAM	1,440	1.00	0.14, NT		0.12	0.04	1.10	NS
SUR6	MAYO	3,925	1.00	0.07, NT		0.06	0.02	2.50	**
	CAST	1,288	1.00	0.21, NT		0.17	0.04	0.48	NS
	VALL	1,216	1.00	0.04, NT		0.04	0.04	1.2	NS

Significance of effects are noted as not statistically significant (*NS*; $p>0.05$), *Statistically significant ($0.01<p<0.05$) **statistically highly significant ($p<0.01$) and *NT* could not be tested. The traits diameter at breast height (DBH), total height (HT), tree stem straightness (STR), Pilodyn penetration (PILO), bark thickness (RBK) and survival (SUR) are followed by a number denoting the age of measurement in years. Abbreviations used for the trials are described in the text

for HT. For example, the heritability estimate for DBH at 6 years in trial VALL was slightly below double that at 3 years ($\widehat{h}^2 = 0.20$ to 0.39). Single-site heritability for growth traits tends to increase with age in the most widely planted *Eucalyptus* species (Bouvet and Vigneron 1995; Greaves et al. 1997; Wei and Borralho 1998; Lopez et al. 2002), and *E. viminalis* here was no exception. The estimated average individual-tree heritabilities of DBH at CAST and VALL (0.36 and 0.29, respectively) were higher than that estimated for GUAM, MAYO, and PRIN (0.15, 0.16, and 0.12, respectively). Estimated average heritability for DBH and HT across ages and sites for our OP progenies seems somewhat lower than that found for Resende et al. (1990) for ten half-sib progenies of *E. viminalis*. However, our heritability estimates were similar to the average reported for other *Eucalyptus* species. Hamilton and Potts (2008) reviewed estimates of *E. nitens* genetic parameters for growth, wood-property, tree-architecture, and fitness traits; estimated heritabilities in OP trials of that species were highly variable for DBH and HT, ranging from 0.00 to 0.78 and from 0.06 to 0.72, and averaging 0.26 and 0.23, respectively. In *E. globulus*, the heritabilities for growth traits reported for large OP trials averaged 0.21 and 0.23, which is considered typical for DBH and HT, respectively (Lopez et al. 2002).

Estimated individual-tree heritability at PRIN and MAYO were moderate to low for tree form (STR), 0.20 at 3 years and 0.19 at 4 years, and are similar to those reported by Hamilton and Potts (2008; i.e., from 0.20 to 0.24) for *E. nitens* (summarized from six studies). Similar results (0.22) obtained by Volker et al. (1990) in *E. globulus* from 45 OP families collected from 14 provenances assessed at age 6 years. However, Lopez et al. (2002) reported lower estimates (0.07 to 0.14) for four *E. globulus* trials in Buenos Aires Province, Argentina.

Breeding objectives for eucalypts are increasingly taking into account wood quality (Raymond 2002). Pilodyn penetration is an indirect measure of wood basic density (i.e., deeper pin penetration means lower density). This variable has been assessed in a large number of eucalypts species, such as *E. globulus* (McDonald et al. 1997; Muneri and Raymond 2000; Lopez et al. 2002; Costa e Silva et al. 2009); *E. nitens* (Hamilton and Potts 2008), and *E. urophylla* (Wei and Borralho 1997; Kien et al. 2008). From our study in *E. viminalis*, as in other eucalypt species, pilodyn penetration was evidently more heritable (0.32) than diameter growth at age 5 years (DBH5=0.15) and HT for age 2 years (HT2=0.19). Nevertheless, this single-site narrow-sense individual-tree heritability estimate in *E. viminalis* was lower than reported in other *Eucalyptus* species, such as in *E. globulus* (from 0.43 to 0.52, Lopez et al. 2002) and in two thinned OP progeny trials of *E. urophylla* in northern Vietnam at the ages of 8 and 9 years (0.40 and 0.43, Kien et al. 2008). Also, Hamilton and Potts (2008) highlighted that in *E. nitens* the estimates of individual-tree heritability for pilodyn penetration averaged 0.35 but varied widely (like for DBH) ranging from 0.00 to 1.00.

Relative bark thickness may be of adaptive significance, affecting the susceptibility or recovery of trees from damage by pests or environmental stress (Dutkowski and Potts 1999). Estimates of narrow-sense individual-tree heritability assessed at GUAM for relative bark thickness (RBK) were relatively low (0.15) at age 5 years. Higher estimates were obtained by Lopez et al. (2002) in *E. globulus* (0.31 and 0.33) in two trials at age 4 years and for Wei and Borralho (1997) in *E. urophylla* (0.30 to 0.55) for four progenies trials at ages between 4 and 7 years.

Chambers and Borralho (1997) showed that survival is a very important selection trait for maximizing productivity per hectare. They suggest that in areas of significant mortality due to ground frost, drought, or specific pests, it may be more important to breed for than volume per tree. The poor survival suffered at sites PRIN (51%) and CAST (58%) was due to atypical conditions (i.e., ant attack and flood). For all our five sites, the heritability estimates for survival were low. The average of individual-tree heritabilities for *E. viminalis* survival was 0.09 across all sites with age from 3 to 6 years, with a range from 0.01 to 0.17. In contrast, Chambers et al. (1996) examined 11 *E. globulus* ssp. *globulus* progeny trials from 4 to 5 years of age in Australia and Portugal showing that early survival was under moderate to high genetic control, with heritabilities ranging between 0.19 and 0.57.

Statistically significant levels of additive genetic variation were detected for all traits (Table 5). However, where scales or magnitudes of the variance components differ between traits, the coefficient of additive genetic variance $\left(\hat{C}V_{\mathrm{A}}\right)$ may provide a more informative measure of the potential response to selection than the heritability as it reflects the amount of additive genetic variation in the population (Houle 1992). The average $\hat{C}V_{\mathrm{A}}$ across the five sites studied follows the same pattern as the heritability for DBH (14.5%) and HT (12.6%). That means that higher estimated heritabilities are associated with higher additive genetic variances. The additive genetic variation was close to 8% for PILO (7.5%) and RBK (7.8%) at the age of 5 years and 16.4% for STR. In a review of seven traits of conifers, *Eucalyptus* spp. and other broadleaf forest tree species from 67 published papers, Cornelius (1994) reported comparable values of $\hat{C}V_{\mathrm{A}}$ for DBH (9.1%), HT (11.1%), and STR (16.3%). As we did, Hamilton and Potts (2008) also observed a higher additive coefficient of variation for DBH (13.3%) compared with HT (11.3%) across a range of studies in *E. nitens*. Lower estimates of $\hat{C}V_{\mathrm{A}}$ for PILO (4.8% and 5.2%) were reported (Kien et al. 2008) in two OP progeny trials of *E. urophylla* at the age of 8 and 9 years, but these lower values perhaps were believed to be due to thinning effects.

Additive genetic correlations between traits

Additive genetic correlations between traits are important for telling how selection on one trait will affect the means and potentially additive genetic variation in other. Estimated additive genetic correlations between growth traits, tree stem straightness, pilodyn penetration, relative bark thickness, and survival traits within each site are listed in Table 6. Strong genetic correlations were observed among growth traits, indicating that selection for any one of these traits would give a high correlated response in the others. Genetic correlations between DBH and HT were consistently high and positive, r_A ranging from 0.55 to 1.00 and averaging 0.90 across the five trials, so these variables effectively behave as a single trait. These results confirm previous studies in *E. viminalis* (Resende et al. 1990) where r_A between height and DBH was 0.996 in ten OP progenies. Studies of other *Eucalyptus* species, such as *E. globulus* also gave estimates between 0.64 and 1 (Volker et al. 1990; Lopez et al. 2002), *E. nitens* an average of 0.58 from 15 estimates of different studies for OP trials (Hamilton and Potts 2008), and *E. urophylla* an estimate of 0.83 across three sites (Wei and Borralho 1998).

Growth traits were independent of tree-stem straightness or positive. The estimated genetic correlations between growth variables and tree stem straightness for age 3 and 4 years at one site (MAYO) were low and negative (from −0.02 to −0.09), with high standard errors. Another site (PRIN) had high and positive values at age of 3 years (0.70 for DBH and 0.67 for HT). It is unclear why there was such large variation among the sites for this particular correlation. Another study in *Eucalyptus* showed a similar general tendency for fast growth to be genetically correlated with good form in *E. globulus*, with estimates between 0.01 and 0.45 (Lopez et al. 2002 and Volker et al. 1990), but in *E. nitens* r_A between diameter and tree form were much higher and averaged 0.53 (Hamilton and Potts 2008).

The correlation between growth and wood density (assayed by pilodyn penetration) is a major concern in breeding for pulpwood (Borralho et al. 1993). Strong and positive genetic correlations between growth variables and pilodyn penetration were found within the site assessed (GUAM) at age 5 years, 0.67 for DBH5-PILO5 and 0.49 for HT2-PILO5. These correlations indicate that larger trees

Table 6 Estimated additive genetic correlation (approximate standard errors) between different traits within sites from pairwise bivariate analysis of the five trials

Site	Trait	DBH4	DBH5	DBH6	HT2	HT3	STR3	STR4	PILO5	RBK5	SUR^{a}
GUAM	DBH5	–	–	–	0.90** (0.06)	–	–	–	0.67** (0.18)	−0.39NS (0.28)	0.99** (0.21)
	HT2	–	–	–	–	–	–	–	0.49** (0.20)	−0.51* (0.26)	^{b}
	PILO5	–	–	–	–	–	–	–	–	−0.75** (0.20)	−0.44* (0.11)
	SUR5	–	–	–	–	–	–	–	–	−0.79** (0.13)	–
MAYO	DBH4	–	–	0.94** (0.03)	0.55** (0.16)	–	–	−0.05, NS (0.17)	–	–	^{b}
	DBH6	–	–	–	0.56** (0.16)	–	–	−0.02, NS (0.16)	–	–	0.91** (0.13)
	HT2	–	–	–	–	–	–	−0.09, NS (0.21)	–	–	^{b}
	STR4	–	–	–	–	–	–	–	–	–	−0.08, NS (0.21)
CAST	DBH3	1.00** (0.01)	1.00** (0.01)	1.00** (0.02)	–	0.92** (0.05)	–	–	–	–	0.62** (0.14)
	DBH4	–	0.99** (0.01)	0.99** (0.01)	–	0.93** (0.04)	–	–	–	–	0.55* (0.13)
	DBH5	–	–	1.00** (0.01)	–	0.93** (0.05)	–	–	–	–	0.25, NS (0.17)
	DBH6	–	–	–	–	0.94** (0.05)	–	–	–	–	−0.01, NS (0.18)
	HT3	–	–	–	–	–	–	–	–	–	0.60** (0.15)
PRIN	DBH3	–	–	–	–	0.93** (0.03)	0.70** (0.22)	–	–	–	0.57, NS (0.91)
	ALT3	–	–	–	–	–	0.67** (0.16)	–	–	–	0.18, NS (0.61)
VALL	DBH3	0.90** (0.06)	–	0.97** (0.06)	–	–	–	–	–	–	^{b}
	DBH4	–	–	1.00** (0.02)	–	–	–	–	–	–	^{b}
	DBH6	–	–	–	–	–	–	–	–	–	^{b}

The trait diameter at breast height (*DBH*), total height (*HT*), tree stem straightness (*STR*), pilodyn penetration (*PILO*), relative bark thickness (*RBK*), and survival (*SUR*) are followed by a number denoting the age of measurement in years. Abbreviations used for the trials were described in the text

[a] SUR, survival at age 3 (GUAM), 5 (PRIN), and 6 (MAYO, CAST and VALL) years

[b] Correlation and their approximate standard errors were not estimated due to convergence problems

The *p* values refer to likelihood ratio test, showing different from zero

NS not statistically significant, $p>0.05$

*Statistically significant, $0.01 < p < 0.05$

**Statistically highly significant, $p<0.01$

will have deeper penetration of the pilodyn pin and thus lower basic wood density. This adverse genetic correlation between growth traits and pilodyn penetration is consistent with results from most previous studies in *Eucalyptus* (Wei and Borralho 1997; McDonald et al. 1997; Muneri and Raymond 2000; Hamilton and Potts 2008; Volker et al. 2008; Costa e Silva et al. 2009) and suggests that selection for faster growth will give a reduced wood density. Nevertheless, two studies involving other species reported that pilodyn penetration was negatively correlated with diameter but did not differ significantly different from zero (Lopez et al. 2002; Kien et al. 2008).

Relative bark thickness at age 5 years (RBK5) showed a negative correlation with DBH5 and HT2, r_A equal to −0.39 and −0.51, respectively. This suggests a possibility to reduce bark proportion simultaneously with improved growth and is similar to the result of Wei and Borralho (1997) in *E. urophylla* (−0.15 to −0.36). However, in two trials of *E. globulus*, Lopez et al. (2002) found low correlations, which did not differ significantly from zero, between growth traits and relative bark thickness.

There was a clear trend for trees with denser wood to have proportionally thicker bark. The estimated of genetic correlation between relative bark thickness and pilodyn penetration in *E. viminalis* was strongly negative (−0.75) at age 5 years. A similar finding was reported for *E. globulus* (Dutkowski and Potts 1999; Lopez et al. 2002). The first authors suggested that this association involved a pleiotropic relationship reflecting the joint origin of wood and bark in the cambium. Interestingly, this argument is not supported by the *E. urophylla* study by Wei and Borralho (1997) where the estimated values ranged from −0.20 to 0.14.

Estimates genetic correlation between survival at age of 6 years and DBH6 ranged from virtually nil (−0.01) at CAST, to highly positive (0.91) at MAYO. However, low and negative correlations at CAST were again likely associated with establishment problems there. The high and positive genetic correlations agreed with results of Chambers et al. (1996) where survival and diameter were generally high and positively associated, ranging from 0.08 to 0.81 averaging 0.50 for ages 4 to 5 years across ten progeny trials of *E. globulus*. Estimated correlations between the binary survival trait at age 6 years and the continuous DBH or HT trait at younger ages (DBH3, DBH4, and HT2) within the sites MAYO and VALL, could not be estimated due to convergence problems.

Additive genetic correlations across sites

Multi-environment forest genetics trials allowed studying the magnitude and importance of the genotype by environment interactions. The importance of such interactions is indicated by the genetic correlations among environments, viewing a trait in two environments as two distinct traits (Falconer and Mackay 1996). Rank-change interaction is reflected in departures of r_A between sites from +1. The available estimates of additive genetic correlations from pairs of traits across-sites for growth traits at the same age are presented in Table 7. The average estimate of additive genetic correlations between pairs of sites, regardless of age for DBH, was relatively high (0.67), and seven out of the 12 estimates tested did not differ significantly from +1, indicating no additive genetic by environmental interaction. Estimated correlations were significantly lower between PRIN and VALL for DBH3 (0.38) and between CAST and VALL for DBH4 and DBH6 (i.e., 0.35 and 0.58, respectively). These last estimates, although still positive, were imprecise, but could reflect different soil characteristics (i.e., clay soil at CAST and well-drained and sandy soil at VALL). The estimated additive genetic correlation for HT between the trials at GUAM and MAYO and between CAST and PRIN, were weak and negative (−0.09) or positive (0.14) with high standard errors and differed significantly from +1. They could be partly due to establishment problems at two sites (i.e., CAST and PRIN). Therefore, the interaction (departure from r_A between sites=1) found for HT should be interpreted cautiously. Furthermore, these estimates of additive genetic correlations across-sites for DBH and HT are generally imprecise.

Table 7 Estimated additive genetic correlations (approximate standard error) between sites for diameter at breast height (DBH) and total height (HT) in the trials

Trait	Site	GUAM	MAYO	PRIN	VALL
DBH3	CAST	–	–	0.70 (0.35), NS	0.71 (0.35), NS
	VALL	–	–	0.38 (0.33)**	–
DBH4	CAST	–	0.70 (0.23), NS	–	0.35 (0.35)**
	VALL	–	0.78 (0.20), NS	–	–
DBH5	CAST	0.70 (0.34), NS	–	–	–
DBH6	CAST	–	0.80 (0.17), NS	–	0.58 (0.27)**
	VALL	–	1.00 (0.12), NS	–	–
HT2	MAYO	−0.09 (0.29)**	–	–	–
HT3	CAST	–	–	0.14 (0.38)**	–

The traits diameter at breast height (*DBH*) and total height (*HT*) are followed by a number denoting the age of measurement in years. Abbreviations used for the trials were described in the text

The p values refer to likelihood ratio test, for departures from +1

NS not statistically significant, $p>0.05$

*Statistically significant, $0.01 < p < 0.05$

**Statistically highly significant, $p<0.01$

In *E. globulus*, Muneri and Raymond (2000), Lopez et al. (2002), and Costa e Silva et al. (2006) also reported high correlation across-sites for DBH and HT. Lopez et al. (2002) reported across-sites genetic correlations from 0.79 to 0.95 for DBH and from 0.78 to 0.94 for HT. Costa e Silva et al. (2006) found slight higher average across-sites correlation (0.85) for DBH over four states of Australia.

Conclusions and implications for tree improvement in *E. viminalis*

Differences among provenances and a range of genetic parameters for growth traits, tree stem straightness, pilodyn penetration, relative bark thickness, and survival in a base-population of five OP provenance/progeny trials of *E. viminalis* established across of Buenos Aires province were studied. Provenances were statistically significant different for at least one of the studied traits in three out of the five progeny trials analyzed. Regardless, this information is useful if one needs to import seeds from Australia for plantation establishment. The local land race performed inconsistently in this study relative to the Australian provenances.

The moderate levels of genetic control for growth traits, pilodyn penetration, and form and moderate to low levels for relative bark thickness and survival indicate that one can to achieve reasonable levels of genetic gain by intensive selection, selecting the best trees from the better provenances and families. However, an initial step in the genetic improvement in *E. viminalis* here would be to convert one or more of these trials into a seedling seed orchard by selective thinning using trees' ranking for breeding values.

Growth traits were, in general, positive and highly genetically correlated, which indicate that early selection, even by age 2 years, could be effective. However, our latest growth measurement was at DBH6 which would still be considered one half of the commercial rotation age for *E. viminalis* in the region. Relative bark thickness showed a favorable negative correlation with diameter and height, indicating potential to reduce bark proportion simultaneously with selection for growth. Nevertheless, regarding traits other than growth, thicker bark may protect trees against the penetration of various insect pests, diseases, and damage from environmental stress (i.e., frost, hail, fire).

The strong adverse additive genetic correlation observed between DBH and pilodyn penetration indicates the difficulties to improve two key traits at the same time. Nevertheless, these results should be interpreted with care, since the correlation was evaluated just at one site. Furthermore, the pilodyn penetration, as an indirect measure of wood density, needs to be validated with further investigations as explained by Muneri and Raymond (2000) and Costa e Silva et al. (2009). Certainly, breeding for growth and wood density will require a selection index to identify trees that combine good breeding values for both traits.

Despite environmental differences across trials (mostly from diverse soils), growth traits on the different sites can be considered the same trait, since there were weak additive by environmental interactions across of the five trials for DBH. This study suggests that a single multi-provenances breeding population seems appropriate for *E. viminalis* in Argentina if the trial sites are representative of the planting target zone.

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