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Sources of phenotypic variation of wood density and relationships with mean growth in two *Eucalyptus* species in Argentina

Pamela Alarcón[1*], María Elena Fernández[2,3,7], Gustavo Pedro Javier Oberschelp[1], Pablo Pathauer[4],
Alejandro Martínez-Meier[5,6,7]

[1]*Instituto Nacional de Tecnología Agropecuaria (INTA), EEA Concordia (Entre Ríos), Argentina.* [2]*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.* [3]*Instituto Nacional de Tecnología Agropecuaria (INTA), Grupo de Ecología Forestal, EEA Balcarce, AER Tandil, Argentina.* [4]*Instituto Nacional de Tecnología Agropecuaria (INTA), Instituto de Recursos Biológicos - CIRN EEA Castelar (Buenos Aires), Argentina.* [5]*Instituto Nacional de Tecnología Agropecuaria (INTA), EEA Bariloche (San Carlos de Bariloche), Argentina.* [6]*Instituto de Investigaciones Forestales y Agropecuarias Bariloche (IFAB), INTA - CONICET (San Carlos de Bariloche), Argentina.* [7]*Laboratorio Internacional Asociado (LIA) FORESTIA, INTA Argentina - INRAE France – UNAH, Perú.*

Abstract

Aim of study: To describe the radial patterns of wood density, and to identify their main sources of variation, and the potential tradeoffs with mean tree growth, in two *Eucalyptus* species.

Area of study: Mesopotamian (Corrientes and Entre Ríos provinces) and Pampean region (Buenos Aires province) of Argentina.

Materials and methods: Eucalyptus grandis and *Eucalyptus viminalis*, growing in genetic trials installed in two sites per species were studied. X-ray wood microdensity profiles were developed from core samples. Each profile was proportionally divided in 10 sections. Mean, maximum, minimum and the standard deviation of wood density, for each section were computed. Mean annual growth was used to study the relationships with wood microdensity variables. A linear mixed-effects model computed the significance of different sources of phenotypic variation. Pearson´s correlation computed the relationships between variables.

Main results: The pattern of radial variation in *E. grandis* showed a decrease in wood density from pith to bark, mainly due to the decrease in minimum wood density, while in *E. viminalis,* wood density increased towards the outer wood. In both species, the standard deviation of the wood density increased along the radial profile from pith to bark. Significant variation in wood density was explained by site, provenance and clone/family effects. In E. grandis mean, maximum and minimum wood density were negatively correlated with mean growth, whereas in E. viminalis correlations were positive but close to zero.

Research highlights: Both the pattern of radial variation of wood density and the relationship between wood density and mean growth were different in the studied Eucalyptus species, and they varied within species depending on the site they were growing and genetic provenance.

Keywords: wood microdensity profile; wood properties; wood products; phenotypic plasticity; Eucalyptus grandis; Eucalyptus viminalis.

Introduction

Commercial forestry production tends to a scheme of multiple wood products. The first thinning produces principally raw material suited for pulp and boards while second or commercial harvests provide wood for solid uses (López & López, 2011). Thus, it is relevant to know the physical properties of wood produced in each growth phase of the trees since they affect the wood quality required by the different industries (Zobel & Jett, 1995; Castro da Silva, 2002; Apialoza *et al.*, 2013; Burdon & Moore, 2018).

Within-tree wood variation, both longitudinal and radial, influences the quality of raw material (Downes *et al.*, 1997). In juvenile-wood, located near the pith, wood properties largely vary yearly, resulting in a lower quality material for saw timber (Castro da Silva, 2002; López & López, 2011). In contrast, adult wood has more stable and appropriate properties for this industry (Fukasawa, 1984; Evans *et al.*, 2000; Núñez, 2011). Properties that vary from juvenile to adult stage include wood density, fiber length, cell wall thickness, and chemical composition (Barnett & Jeronimidis, 2003), which depend on genetic, environmental factors and silvicultural management (Bao *et al.*, 2001; Cobas, 2012).

Wood density is one of the most studied physical properties, probably associated with its relatively easy determination, becoming the most relevant physical wood property used in genetic improvement programs (Alves *et al.*, 2020). It is an indicator of the quality and performance of wood, for both fiber and solid products (Apialoza *et al.*, 2005). The sawmill industry prefers lower radial wood density variation, either for decorative or for structural purposes (López & López, 2011). In this regard, it is possible to predict wood behaviour under different efforts from its density (Cobas *et al.*, 2014).

In addition to the within-tree variation of wood due to the cambial age, wood density shows a significant variation among trees, which is controlled by genetic effects (Zobel & Jett, 1995; Zobel & Sprague, 1998; Nabais *et al.*, 2018), and by the environmental conditions during the cells wood formation (Schweingruber, 1996). In this regard, silvicultural management may influence wood density by affecting the resources availability for the trees (Zobel & van Buijtenen, 1989). Moreover, there may be different relationships -positive, negative or neutral-between tree growth and wood density (Gonçalves *et al.*, 2004). Thus, tree selection based on growth traits could have indirect consequences on wood density (Zobel & Jett, 1995), which demands determining the possible correlations between growth and wood density.

The genus *Eucalyptus* is one of the main components of global forestry, with more than 20 million hectares planted in the world (Iglesias-Trabado & Wilstermann, 2009). They contribute to a large proportion of planted forests -and the industrial chains they feed- of southern South-American countries (Brazil, Chile, Uruguay and Argentina). In Argentina, approximately 27 *Eucalyptus* species have been introduced. The most relevant commercial species of this genus is *Eucalyptus grandis* (Hill. Ex Maiden) (SAGPyA, 2013), which is grown in subtropical areas. It was introduced mainly due to its rapid growth, and has reached a high degree of genetic improvement (Marco & White, 2002), with maximum growth rates around 50 m^3 ha^{-1} $year^{-1}$ and a mean wood density around 0.4 $g\,cm^{-3}$ (Barotto *et al.*, 2017). Wood from short rotations, as commonly developed in *E. grandis* for pulp production, is highly unfavourable as raw material for solid purposes due to high tensile growth stress, presence of knots and large variability of their physical and mechanical properties (Castro da Silva, 2002; Murphy *et al.*, 2005; Souza 2006; Hernández *et al.*, 2014; López *et al.*, 2018). Of lower current relevance in commercial terms but of high potentiality for its high abiotic stress tolerance is *Eucalyptus* viminalis. It combines relatively high growth and frost tolerance (Cappa *et al.*, 2010), allowing to be planted in temperate areas. This species has a lower degree of genetic improvement in Argentina, reaching mean growth rates ranging from 15 to 40 m^3 ha^{-1} $year^{-1}$ in Pampean region, where it is subjected to freezing temperatures in winter and drought conditions in summer. Its mean wood density is higher than in *E. grandis*, around 0.6 $g\,cm^{-3}$ (Barotto *et al.*, 2017). This species is currently used for the cellulose industry. However, it has been identified as the best species for veneer and plywood in Brazil (Iwakiri *et al.*, 2013) as well as for other solid uses.

Based on this background, the objectives of the present study were: a) to identify the significant sources of phenotypic variation of the wood density of *E. grandis* and *E. viminalis*, by using the non-destructive technique of densitometry by X-rays and; b) to estimate phenotypic correlations between mean growth and wood density traits, such as mean, minimum and maximum wood density, and a measure of wood density variation along the stem radius. To have a large variation in the wood density traits studied, and to disentangle the relative relevance of environmental (site) vs. genetics, different genetic origins growing in two sites per species were analysed. The major results are interpreted and compared from the point of view of the wood technological implications and the prospects of genetic improvement of both species.

Materials and Methods

Study material

Two increment cores per tree were mechanically collected with a Pressler increment borer, but only one 5.15 mm diameter-sample per tree was analysed for this study purpose. The samples were taken at breast height (1.30 m) perpendicular to the stem, in south-north

orientation, in two experimental trials of each *E. grandis* and *E. viminalis* (Table 1). In *E. grandis*, the samples were collected in 2016 from two clonal trials installed in 2008 and 2010 in the Mesopotamian region of Argentina. In *E. viminalis* two provenance/half-sibs family trials were sampled in 2015, corresponding to a network installed from 1998 to 2000 in the Pampa region. In both species, the trials were installed by the Instituto Nacional de Tecnología Agropecuaria (INTA) of Argentina as part of its tree genetic improvement program.

Five to 15 trees were sampled per clon/family in *E. grandis* and *E. viminalis*, respectively (Table S1 [suppl.]). In *E. grandis*, provenance effect was grouped in "Local" ("*Loc*"), considering clones selected in Concordia (Entre Ríos, Argentina) from a local landrace of unknown provenance, and "Introduced" ("*Int*") considering newly introduced materials from four provenances of Australia (Table S1 [suppl.]). Due to the low number of individuals of each Int provenance, they were analysed together ("*Loc*" *vs* "*Int*", with around 90 individuals in each group, Table S1 [suppl.]). In *E. viminalis*, five provenances were also studied (one local and four more recently introduced from Australia, Table S1 [suppl.]). In this species, since we had a balanced number of samples, we could analyse the effect of each individual provenance on the studied variables. In total, 184 and 582 increment cores were collected in *E. grandis* and *E. viminalis*, respectively.

X ray densitometry: wood microdensity

Increment cores were cut lengthwise, perpendicularly to the fiber. A 2 mm thickness lamina per core was dried to moisture equilibrium and subsequently analysed by indirect X-ray densitometry (Polge, 1966). The resulting X-ray films were scanned and the digital images were processed with the WinDENDRO® software (Guay *et al.*, 1992), obtaining a spatial resolution of 25 μm. The variation of shades of grey in each lamina was contrasted with a scale (different thickness) radiographed with the samples for which it is known its density, allowing to transform the grey pattern of each lamina in density values.

The last step of data processing used a computer routine written in R language (R Development CoreTeam, 2015). Since the studied *Eucalyptus* do not present well-defined growth rings, each microdensity profile was divided proportionally in 10 sections of equal length, from pith to bark. The section length of each individual sample depended on the whole sample length (Fig. S1 [suppl.]). The following microdensity variables were computed from each section: Mean wood density (Meds), maximum wood density (Maxs), minimum wood density (Mins), and standard deviation (Stds) representing the variability of wood density values for each section. Likewise, the corresponding values for the complete microdensity profile were estimated: Med_r, Max_r Min_r and Std_r. Finally, the diameter at breast height (DBH, cm) was measured to estimate the mean annual growth (MAG, cm year^{-1}) of each tree by dividing the DBH by the tree age (DBH/age).

Statistical analysis

A linear mixed-effects model computed in R (R Development CoreTeam, 2015) allows estimating the significance of different sources of phenotypic wood density

Table 1. Sampled sites of *E. grandis*: Caá Catí (CAAC, Corrientes province) and Concordia (CONC, Entre Ríos province) and *E. viminalis*: Guaminí (GUAM), and Del Valle (VALL), both in Buenos Aires province

Species	*E. grandis*		*E. viminalis*	
Site	Caá Catí	Concordia	Guaminí	Del Valle
[a]Age	6	8	17	15
[b]DBH	20.9	23.1	25.9	30.1
Latitude	-27º 47' 04"	-31º 21' 55"	-37° 06' 42"	-35° 51' 53"
Longitude	-57º 41' 06"	-58º 07' 20"	-62° 26 '70"	-60° 43' 34"
Soil	Loam-clay-sandy	Sandy	Clay loam	Sandy
[c]MAP	1279.7	1429.1	735.6	959.9
[d]MAT	21.7	19.2	13.8	16.9
[e]MinAbsT	-1.1	-4.8	-13.5	-7.9

[a] Age: from planting to sampling year, [b]DBH: diameter at breast height mean (cm), [c] MAP: Mean Annual Precipitation (mm), [d] MAT: Mean Annual Temperature (ºC), [e] MinAbsT: Minimum Absolute Temperature (ºC). Period from: 2008 to 2016 and 1998 to 2015 for *E. grandis* and *E. viminalis,* respectively.

Fuente: Instituto del Clima y Agua, Instituto Nacional de Tecnología Agropecuaria (Argentina)

variation. All sections of a tree were considered as repeated measurements of wood density upon the same tree, describing the radial wood density variation (Faraway, 2006; Bates, 2010). The maximum restricted likelihood method (REML) was computed to estimate values in the following lmer function:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \tau_k + \beta_j \, m_k + a_{l(k)} + b_{i(m(l))} + e_{ijklm}$$

Where,

$Y_{ijkl} = {}_{ijkl}$ observed wood microdensity value (mean, maximum, minimum and standard deviation) corresponding to the $_{ijkl}$-section

μ = overall mean

α_i = fixed effect of the $_i$-section

β_j = fixed effect of the $_j$-site

τ_k = fixed effect of the $_k$-provenance

$\beta_j \, \tau_k$ = interaction site by provenance

$a_{l(k)}$ = random effect of the $_l$-clon/family nested in the $_k$-provenance

$b_{i(m(l))}$ = microdensity value of the $_i$-section of the $_m$-tree nested in the $_l$-clon/family, of the $_k$-provenance nested in the $_j$-site

e_{ijklm} = random error

In both species, provenance was considered a fixed factor. In the case *E. grandis* because only two levels were taken into account ("*Loc*" and "*Int*"), and in *E. viminalis*, even when all the provenances were considered, they corresponded to a second cycle of introduced genetic plant materials from a restricted region of the natural distribution area of the species, selected by their growth performance.

Significance of fixed levels was determined using the Satterthwaite Approximation method (Bates, 2010). Random levels significance was computed using the likelihood ratio test ($P < 0.05$), comparing the complete model with a reduced model without the factor.

Pearson's correlation coefficients ($p < 0.05$) were computed between MAG and wood density variables (Med$_r$, Max$_r$, Min$_r$ and Std$_r$) at tree level. The function corr.test of the R software was used for this purpose (R Development CoreTeam, 2015). The *r* values interpretations were done considering sign (positive or negative) and grade or force (low: $0.10 < r \; 0.30$; moderate: $0.30 < r \; 0.50$; and hight: > 0.50) (Vinuesa, 2016).

Results

Descriptive statistics

Mean wood density in *E. grandis* and *E. viminalis* was 0.43 g cm^{-3} and 0.55 g cm^{-3} respectively, ranging from 0.31 g cm^{-3} to 0.61 g cm^{-3} and from 0.43 g cm^{-3} to 0.77 g cm^{-3} in *E. grandis* and *E. viminalis*, respectively (all sources of variation). MAG and wood density variables described for both species in each site (mean values and their standard error) are shown in Table 2. To see the mean values of each clone or family per site and species, please refer to the Figs. S2 and S3 [suppl.] provided as supplementary material.

Considering both sites, in *E. grandis*, Med$_r$ was similar in *Loc* and *Int* provenances (0.43 g cm^{-3} ± 0.04 g cm^{-3}). Similar values for Max$_r$, Min$_r$ and Std$_r$ were computed in CAAC for both provenances, while Med$_r$ and Max$_r$ were higher in CONC for *Loc* in relation to *Int* (0.45 g cm^{-3} *vs* 0.43 g cm^{-3}, and 0.542 g cm^{-3} *vs* 0.52 g cm^{-3}, respectively).

In *E. viminalis*, also at the provenances level, mean and maximum wood density were higher in Err: 0.58 g cm^{-3} (± 0.05 g cm^{-3}) and 0.74 g cm^{-3} (± 0.06 g cm^{-3}), respectively, being Bon the provenance with the lowest values for Med$_r$, Max$_r$ y Min$_r$: 0.53 g cm^{-3} (± 0.04 g cm^{-3}); 0.68 g cm^{-3} (± 0.06 g cm^{-3}) and 0.40 g cm^{-3} (± 0.04 g cm^{-3}), respectively. Std$_r$ was higher for the provenances *Bal, Err* and *Fed*: 0.07 g cm^{-3} (±0.01 g cm^{-3}) *vs* 0.06 g cm^{-3} ± (0.01 g cm^{-3}) in *Arg* and *Bon*.

In both species, the coefficient of variation was higher for MAG (22% and 35% for *E. grandis* and *E. viminalis*, respectively) than for Med$_r$, Max$_r$ and Min$_r$, which were lower and similar between species and traits: 10% in Med$_r$, 9% in Max$_r$ and 12 % Min$_r$. In the case of Std$_r$, the coefficient of variation was higher than the other density variables (24% and 17% in *E. grandis* and *E. viminalis*, respectively).

Table 2. Mean and standard error (in brackets) of MAG (cm year^{-1}), Med$_r$, Max$_r$, Min$_r$ and St$_d$ (g cm^{-3}) in *E. grandis* at Caá Catí (CAAC) and Concordia (CONC), and *E. viminalis* in Guaminí (GUAM), and Del Valle (VALL).

Site	*E. grandis*				
	MAG	Med$_r$	Max$_r$	Min$_r$	Std$_r$
CAAC	4.18-(± 0.55)	0.42 (± 0.04)	0.48 (± 0.04)	0.36 (± 0.04)	0.03 (±0.01)
CONC	2.89 (± 0.32)	0.44 (± 0.04)	0.53 (± 0.05)	0.37 (± 0.04)	0.04 (±0.01)
	E. viminalis				
	MAG	Med$_r$	Max$_r$	Min$_r$	Std$_r$
GUAM	1.44 (± 0.46)	0.55 (± 0.07)	0.73 (± 0.06)	0.42 (± 0.05)	0.07 (±0.01)
VALL	1.88 (± 0.61)	0.55 (± 0.06)	0.69 (± 0.06)	0.43 (± 0.05)	0.06 (±0.01)

Significant sources of phenotypic variation: longitudinal model with repeated measures

The mean values estimated for the fixed effects and their statistical significance, as well as the components of variance for random effects expressed in terms of standard deviation, are presented in Tables 3 and 4 for *E. grandis* and *E. viminalis*, respectively.

The estimated mean wood density in *E. grandis* was 0.45 g cm^{-3}. Wood density significantly decreased along the radius of the tree (section effect), both for mean and minimum wood density: -0.004 g cm^{-3} and -0.006 g cm^{-3} per section, respectively, from pith to bark. However, the variability of wood density through the section increased in the same direction. The radial decrease of the maximum density was not significant, so it seems that the decrease in mean wood density along the radius in *E. grandis* could be associated with the decrease in the minimum wood density (see Table 3 and Fig. 1).

Significant differences could also be established in *E. grandis* (Table 3) between sites for mean, maximum and standard deviation of wood density, while the effect of provenance (*Loc vs Int*, indicated "*Loc*" as reference value in Table 3) was not significant in any of the microdensity variables. However, the interaction site x provenance was significant for maximum wood density. This is the consequence of an increase in maximum wood density of *Loc* in CONC, even when this increase was not associated to a significant difference among provenances.

Regarding random effects, even when the major contribution to the total phenotypic variance was related to the individual trees, only clone level was statistically significant for all studied wood density traits (Med$_r$, Max$_r$ and Min$_r$), except for standard deviation (Table 3).

In *E. viminalis* (Table 4), the radial variation was significant for all wood density traits analysed. Unlike the patterns observed in *E. grandis*, wood density traits (mean, maximum, minimum) increased throughout the radius of *E. viminalis* stems (Fig. 1). For each 10% of radial section, mean density increased 0.02 g cm^{-3}, and the same was observed for maximum (0.03 g cm^{-3} per section) and minimum wood density (0.01 g cm^{-3} per section). The radial variability of wood density values, measured as the standard deviation, increased from pith to bark similarly to *E. grandis* (Fig. 1). However, in *E. viminalis* increased fourfold (Fig. 1).

Significant differences were also found between sites in *E. viminalis*, but not in the mean wood density (Table 4). In Del Valle site (VALL) the maximum wood density and the variability of wood density were lower, while the minimum wood density was higher, than in Guaminí site (GUAM). In relation to the provenances effect, mean and minimum wood density were significantly lower for *Bald Hills (Bal), Federation Road (Fed)* and *Bonang (Bon) provenances than for Argentina (Arg)* (reference value in the model), but no differences were observed between *Argentina* and *Errinundra Road (Err)*. For maximum wood density, only significant differences were found between *Bonang* or *Errinundra Road* and *Argentina*. All introduced provenances showed higher standard deviation than *Argentina*, although these results need to be interpreted site by site given that all provenances, but *Errinundra Road,* showed lower standard deviation in Del Valle than Guaminí.

Statistically significant contributions were established for families and tree levels in *E. viminalis* for the four variables studied (mean, maximum and minimum wood density and the standard deviation). A major contribution to the variance was computed for maximum wood density, both at family (0.02 g cm^{-3}) and tree levels (0.07 g cm^{-3}).

Table 3. Estimated mean values of fixed effects and the corresponding standard error, and the components of variance for the random effects, expressed in terms of standard deviation for *E. grandis*. The reference site for the model was CAAC and the reference provenance was *Int*.

	Mean density	Maximum density	Minimum density	Standard deviation
Fixed effects				
Overall mean	0.448 (0.009)	0.489 (0.009)	0.400 (0.009)	0.022 (0.001)
Section	-0.004 (0.001) **	-0.001 (0.001) ns	-0.006 (0.001) ***	0.001 (0.0001) ***
CONC	0.006 (0.007) *	0.034 (0.009) ***	-0.006 (0.008) ns	0.006 (0.001) ***
Loc	0.012 (0.011) ns	-0.013 (0.012) ns	-0.005 (0.011) ns	-0.001 (0.0001) ns
CONC x *Loc*	0.021 (0.011) ns	0.028 (0.013) *	0.011 (0.011) ns	0.003 (0.002) ns
Random effects				
Clone	0.025 ***	0.025 ***	0.024 ***	0.002 ns
Tree	0.054 ns	0.056 ns	0.055 ns	0.008 ns
Residual	0.029	0.044	0.028	0.010

Mean density, Maximum density and Minimum density are expressed in g cm^{-3}; CONC: Concordia; *Loc*: Local provenance. Standard error in parentheses. Level of significance: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant
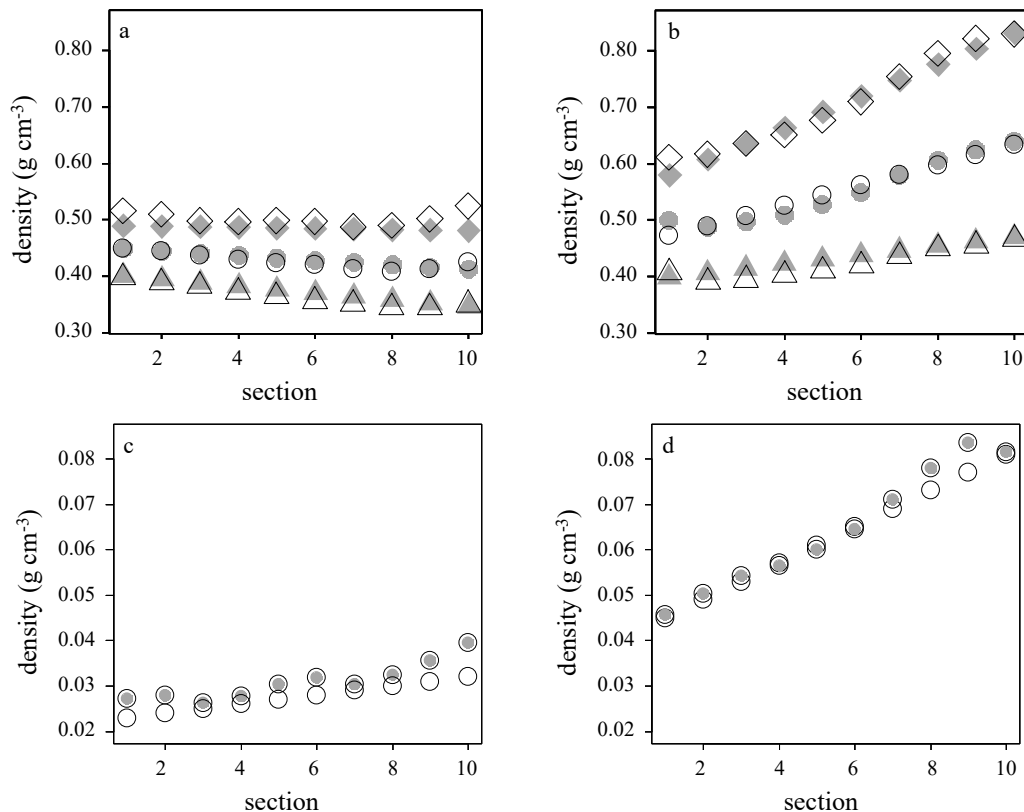
Figure 1. Wood density observed values (grey points) and estimated (white points) by the linear mixed model in a) *E. grandis* and b) *E. viminalis* for Med$_r$ (circles), Max$_r$ (diamonds) and Min$_r$ triangles). The points (each point represents a radial section) can be observed quite-distorted or perfectly overlapped to the modelled values. In figure c) and d) the standard deviation (Std$_r$) variable, a measure of the variability in wood density values within each section, is represented for *E. grandis* (c) and E. viminalis (d).

Phenotypic correlations between wood density and mean stem growth

Moderate negative relationships at individual level (Table S2 [suppl.]) was established between MAG and wood density variables (Med$_r$: -0.36; Max$_r$: -0.47, Min$_r$: -0.26 and Std$_r$: -0.34) in *E. grandis*, whereas in *E. viminalis* correlations between MAG and wood density variables were low, some close to zero and positive except for Std$_r$ (Med$_r$: 0.16; Max$_r$: 0.09; Min$_r$: 0.06 and Std$_r$: -0.19). In relation to Std$_r$, the negative correlation was established with MAG in both species, being moderate in *E. grandis* and low in *E. viminalis*. Both in *E. grandis* and *E. viminalis*, correlations between pairs of the wood density traits Med$_r$, Max$_r$ and Min$_r$ were positive, with values from moderate to high, while the correlation between Min$_r$ and Std$_r$ was low and negative (Table S2 [suppl.]).

When the data were disaggregated by site (Table S3 [suppl.]), the correlations at individual level between MAG and the different wood density variables (Med$_r$, Max$_r$ and Min$_r$) in *E. grandis* were low to moderate and negative, while a correlation with positive sign was found between MAG and Std$_r$. The correlations between MAG and the wood density variables in CAAC and CONC, respectively, were as

follows: Med$_r$ (r: -0.37 and -0.25), Max$_r$ (r: -0.22 and -0.24), Min$_r$ (r: -0.45 and -0.26) and Std$_r$ (r: 0.18 and -0.13). However, at the clone level, the correlations between MAG and the wood density variables increased in CAAC in relation to the pooled data of both sites. For example, negative relationships were found (r: -0.56, -0.43 and -0.65, for Med$_r$, Max$_r$ and Min$_r$, respectively), not being significant the relations between MAG and Std$_r$. In the case of CONC, these correlations, although negative, were not significant.

Regarding *E. viminalis* results analysed by site (Table S3 [suppl.]), the correlations at individual level between MAG and the wood density traits (Med$_r$, Max$_r$ and Min$_r$), differently to *E. grandis*, were positive in both sites, while the correlation between MAG and Std$_r$ was negative in GUAM (r: -0.09) but significant only in VALL (r: 0.17). No significant correlations were established at the family level in each site between MAG and the four wood density variables (Table S3 [suppl.]).

Discussion

Mean wood density values of *E. grandis* reported in this study are in the range of values informed by other

authors. Arango & Tamayo (2008) reported mean wood density values ranging from 0.38 g cm⁻³ to 0.55 g cm⁻³ in clones of *E. grandis* (8 year-old), similar to those indicated by Castro da Silva (2002) (0.31 g cm⁻³ – 0.59 g cm⁻³). In both cases, the studies were carried out in Brazil. Values reported for different genetic trials and commercial plantations of this species in Argentina were in the range of 0.39 to 0.49 g cm⁻³ (Harrand & López, 2007; López & López, 2011; Alarcón *et al.*, 2018). However, Monteoliva *et al.* (2017) obtained mean density values higher than those reported here (0.52 g cm⁻³) in clones of *E. grandis* planted in Entre Ríos, Argentina (southwards from CONC). The estimated values are in the range considered suitable for pulp and paper production (0.40 g cm⁻³ to 0.60 g cm⁻³, Downes *et al.*, 1997), wood density values that can be obtained from juvenile wood in *E. grandis* (Núñez, 2011).

In *E. viminalis,* average wood density was 0.55 g cm⁻³ with no significant differences between sites. These values are similar than the higher values reported for *E. viminalis* by Otegbeye & Kellison (1980), Pathauer (2005) (0.40 g cm⁻³ – 0. 57 g cm⁻³) and Alarcón *et al.* (2018) for the basic wood density (0.48 g cm⁻³ – 0.52 g cm⁻³). However, our values are lower than those reported by Iwakiri *et al.* (2013) of 0.61 g cm⁻³ and Monteoliva *et al.* (2017) of 0.67 g cm⁻³ for the basic wood density, in the same plantations of this study. These differences highlight the importance of the methodological approaches to determine the basic wood density, which can lead to different results on the same materials (Alarcón *et al.*, 2018).

Sources of phenotypic variation of wood density

Significant differences among sites, provenances, clones or families have been widely reported for wood characters both in coniferous species (Zobel & Sprague, 1998; Larson *et al.*, 2001; Rigling *et al.* 2002; Martínez-Meier *et al.*, 2011; Salaya-Domínguez *et al.*, 2012; George *et al.*, 2015; Klisz *et al.*, 2016), and in broad-leaves (Arango & Tamayo, 2008; Harrand *et al.*, 2009; Cappa *et al.*, 2010; López & López, 2011; Moreno & Igartua, 2015). In *E. grandis*, López & López (2011) showed significant differences involving 12 sites for both mean wood density and radial wood density variation. In the present study, the fixed effect of site showed significant differences in *E. grandis* for mean, maximum and standard deviation of wood density. Higher values were found in CONC, representing a two-year older plantation than CAAC. CONC is a site with higher average annual precipitation and lower average annual temperature (*i.e.* a more favourable water balance) (Instituto de Clima y Agua, Instituto Nacional de Tecnologia Agropecuaria, Argentina) than CAAC. In *E. viminalis*, the site level was also statistically significant for maximum, minimum and standard deviation wood

density, but not for mean wood density, showing GUAM the higher values of maximum wood density but the lower minimum wood density, and a larger standard deviation than in VALL.

Significant differences among sites could be attributed partially to slight differences in age, since wood density normally increases with age (Bermúdez Alvite *et al.*, 2002; Resquin *et al.*, 2012; Moreno & Igartúa, 2015), but also to differences in environmental conditions, not only local but also as evolutionary legacies of the climate of the origin of the plant material (Hevia *et al.*, 2020). Dendroecology studies have shown the sensibility of wood density and growth to climatic conditions at inter-annual level (Schweingruber FH, 1996; Rozas *et al.*, 2016) as well as intra-annual level (*e.g.* Rozenberg *et al.*, 2001; Rozenberg & Paques, 2004; Martinez-Meier *et al.*, 2015). High rainfall, which ensures high soil water availability, stimulates the biomass production (*e.g.* Le Quéré, 2015), whereas soil water deficit would stimulate the production of high wood density (Bouriaud *et al.*, 2005). In our study, however, higher wood density was produced in the site with higher precipitation and lower mean temperature (*e.g.* better water balance, CONC site) in *E. grandis*. In the case of *E. viminalis* the differences in rainfall between sites are somewhat compensated by differences in temperature and soil conditions making difficult to know *a priori* which site has a better water balance for the plants (see Table 1). In this regard, the mean wood density did not differ between sites in this species, and maximum and minimum densities did differ in opposite direction.

Regarding the effect of mean temperature, Thomas *et al.* (2004) found a plastic response of wood density in *E. camaldulensis*, both variables being positively related. This contrasts to our results in *E. grandis*, which presented higher wood density in the site with lower temperature (CONC). In the case of *E. viminalis*, both sites largely differed in mean temperature (around 3°C), but that did not result in significant differences in mean wood density. The different responses to mean climatic conditions of the studied species -among them and compared to other studies- could be associated to the seasonal variability of climatic conditions and to the particular strategies of response to abiotic stressor agents at species level (Olivar *et al.*, 2003; Wimmer & Downes, 2003; Bouriaud *et al.*, 2005). In this sense, it has been proposed that the studied species respond differently to water deficit because of different hydraulic architectures (Barotto *et al.*, 2017).

Another source of phenotypic variation in wood density in our studied species was the genetic provenance. According to Nabais *et al.* (2018), species with a large geographic range may present high variability between provenances for traits such as wood density. In the case of *E. viminalis*, although the provenances studied in this work represent only a small portion of the natural range of the species in Australia/Oceania (a range of 15 degrees

of latitude, and from the sea level to 1,500 m altitude), they correspond to a second introduction of plant material selected for their growing performance (Cappa *et al.*, 2010). This may imply that they would maintain also significant differences for wood characteristics that can be explored further for the genetic improvement of the species. It is relevant to indicate that in the present study, a trend towards higher wood microdensity values in lower altitude provenances were observed, coincident with the plant material indicated by Cappa *et al.* (2010) as with the best growth performance in Argentina. No differences were found between provenances in *E. grandis*, probably because the genetic material was pooled at this level. However, the genetic effect at clone level showed a significant component of variance for all wood density variables, except for Std_r.

Variation in wood density was observed among individuals (in *E. viminalis*), provenances and sites within each species, but also along the radial section of the stems. The segmentation of the radial profile describing radial wood density variation, both in *E. grandis* and in *E. viminalis*, resulted from the impossibility of delimiting annual growth rings in the studied species. The 10 established sections allowed describing their variation by means of a mixed linear model. This variation was significant for the mean and minimum wood density and its standard deviation in *E. grandis* and for all the variables studied in *E. viminalis*. These results lead to conceptual patterns of radial variation showing marked differences inherent to the species. It can be attributable to the presence of only juvenile wood in *E. grandis* and juvenile-mature wood in *E. viminalis* considering the age of the sampled trees and references of wood stage for the same species (Núñez, 2011; López & López, 2011; Iwakiri *et al.*, 2013). For *E. grandis*, the pattern of variation was coincident with the type 3 modelled by Panshin & Zeeuw (1980), described for species with circular porosity of vessels, but also for *E. grandis* of diffuse porosity (Fukazawa, 1984; Arango & Tamayo, 2008; Núñez, 2011). In *E. viminalis* the significant increase in the mean, maximum and minimum wood density along the radius, from pith to bark, was coincident with the pattern 1 described by the same authors (Panshin & Zeeuw, 1980), which is described for species with diffuse porosity (Fukasawa, 1984). These changes in wood density along the radial direction, from pith to bark, are influenced by the cambial age as well as by the annual growth (Cobas, 2012), and the shape of the curves describing the radial pattern may differ when are analysed based on the growth-ring widths than with fixed sections. The type 1 form of radial variation is described by a positive exponential form with a rapid growth in the juvenile portion (near to the pith) followed by a stabilization of density values towards the bark. That general form was observed for the pooled data of *E. viminalis*. In this sense, the linear model here proposed implies a simplification

of the observed pattern. However, even with this simplification, the model represents a good tool to describe the general trends and their sources of variation, capturing satisfactorily most of the radial variability pattern (Fig. 1). Within-tree source of variation is indicated as the major relevance source of wood density variation for broad-leaf species with diffuse porosity (Downes *et al.*, 1997). On the other hand, although the authors do not propose it as a causal effect, the radial variation in wood density is related to the fibers-length variation in *Eucalyptus*, which increases from pith to bark (Igartúa & Monteoliva, 2010).

Given that the presence of growth stresses is a phenomenon in *Eucalyptus* genus, varying at intra and interspecific level, with several implications from the economic point of view (López *et al.*, 2018), identifying traits that can be measured by non-destructive methods renders benefits for both genetic programs and wood industry, optimizing tree selection and industrial processes. In this regard, significant relations between growth stresses and basic wood density variation from pith to bark has been described for several species, including E. dunni (Hernández *et al.*, 2014), *E. grandis* and interspecific hybrids (López *et al.*, 2018). In our study, we described the form of that variation in the studied two species, as well as how it may change due to site and genetic effects (which must be explored more in detail). The implication of these changes on the technological characteristics of the wood needs still to be explored.

Phenotypic correlations between wood density and mean stem growth

Zobel & Jett (1995) argued that a possible genetic gain in growth could have an indirect effect on wood properties due to a possible unfavourable genetic correlation between growth and wood density. Even when in this study we only explored phenotypic relationships, they were highly complex in *E. grandis*. The negative relationship between MAG and wood density (measured by x-ray densitometry) was described by Aparicio *et al.* (2011). However, the study of this relationship at the site level showed that there exists a negative correlation between MAG and density in CAAC, the site with higher mean growth, but a non-significant correlation in CONC, where growth was more limited. It is important to note that although CAAC was the site with the highest growth of both studied, it is not the best site for the species in the studied region.

In the case of *E. viminalis*, the correlations MAG-Med$_r$ and MAG-Max$_r$ although close to zero, were positive in both sites evaluated. This type of positive relationship between growth and wood density has also been described for *E. urophylla* (Kien *et al.*, 2008) and E. globulus (Igartua & Monteoliva, 2010). However, for this last species, a negative relationship has also been described for

Chilean sites (Lizana, 2006), which demonstrates that there are not unique relationships between growth and wood density even at a species level.

Conclusions

In both studied species, the results show that there is a significant variation in wood density along the radial profile (within-tree), between trees (in *E. viminalis*), between sites and between genetic entities (provenances, clones or families) for the wood density variables assessed. Despite considering only two sites for each species and a limited number of provenances, clones and families, the existence of a significant difference in relation to the common gene pool, indicates the possibility of identifying genotypes with desirable technological properties. This is particularly relevant in the frame of the genetic improvement program of *E. viminalis* considering the potentially reduced genetic basis (*i.e.* a limited representation of the large natural distribution area of the species). Depending on the requirements of the industry, whether low wood density variation is desired or high or low mean wood density values, these different wood characteristics can be explored and potentially selected in the genetic program.

Due to differences in mean growth rates, *E. grandis* supplies similar log diameters in half of the time compared to *E. viminalis*. This raw material, composed of mostly juvenile wood in the former species, has a higher wood density in the pith than closed to the bark. In contrast, probably due to differences in wood type (juvenile-mature) in *E. viminalis*, an opposite pattern was observed, with higher wood density towards the outer wood.

Although in *E. grandis* there is a negative association between stem growth and wood density, described here and in previous studies, this relation is complex and probably driven by sites or clones that allow high growth rates. This compromise seems to disappear in sites of relatively low growth potential, but that can still contribute an important proportion of the area planted with this species in Argentina. More research is needed considering growth-wood density relationships in a broad range of site qualities and plant origins (clonal vs seed-origin materials). In *E. viminalis*, even when the mean wood density was similar in both sites and no trade-off was observed with growth, the least productive site presented lower minimum but higher maximum wood density. This variability associated with site conditions could have implications in determining the quality of *E. viminalis* wood for sawmill and deserves been explored in a broader range of environmental conditions. The results also suggest that even if no differences between sites are found for mean wood density, its variation along the radial profile may differ between sites and should be taken into account to better explain wood properties related to the quality for solid uses.

Site conditions not studied here, such as the effective soil depth, soil water retention capacity, seasonal and interannual patterns of rainfall, would play a major role on wood characteristics, with a higher effect than the mean temperature. This highlights the complexity of the studied processes and the risks of extrapolating relationships between wood density and productivity from other species of the same genus, or even from the same species but of different genetic source and/or growing in other environmental conditions. Further research is needed to elucidate the effect of these environmental factors on the wood properties, in interaction with growth rates, in woody species.

Acknowledgments

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