



Balancing wood production and water use efficiency in the selection of open-pollinated families of *Gmelina arborea*

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Abstract

Global climate crisis and severe water scarcity worldwide demand alternative genotypes that allow an adequate balance between production and water use while ensuring benefits for foresters. The genetic improvement of water use efficiency (WUE) in forest plantations could reduce water use without compromising yield. Above-ground biomass (AGB), saw-wood volume up to small-end diameter of 15 cm (V15), wood density (WD) and intrinsic WUE (WUE_i) from wood carbon isotopic discrimination was evaluated in forty open-pollinated families of *G. arborea* grown in a tropical dry forest known as a water-limited environment, to select superior genotypes considering a balance in wood production and water use. Heritability of open-pollinated family means were moderate with values of $h^2_f=0.554$ for AGB, $h^2_f=0.541$ for V15, $h^2_f=0.608$ for WD and $h^2_f=0.495$ for WUE_i . Significant genetic correlations between both WD and WUE_i and production traits ($p<0.05$) and a nonsignificant genetic correlation between WD and WUE_i were found. Although production traits and WUE_i showed moderate narrow-sense and family means heritabilities, considerable responses to selection of up to 13.7% in AGB, 15.5% in V15, 2.5% in WD and 3.0% in WUE_i could be achieved from intensive selection of superior families. Our results showed that it may be possible balancing wood production and WUE by selecting open-pollinated families of *G. arborea* with higher V15 and WUE_i . The deployment of these superior families can be used as a forest management strategy to adapt the species to future drought scenarios associated with global climate change.

Keywords Forest genetic improvement · Tropical dry forest · Forest plantations · Forest biomass

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Introduction

Colombia has a growing forestry sector based on the establishment of commercial forest plantations (Martínez et al. 2022), the latest report on the area covered with forest plantations shows that there are 538,000 hectares planted throughout the country (MADR 2022). Among the planted tree species, *Gmelina arborea* Roxb. is one of the most important species for areas of tropical dry forest. The species covers approximately 20,000 hectares, located mainly on the plains of the Caribbean coast and the interior of the inter-Andean valleys. Currently, *G. arborea* is the second broadleaf tree species with the highest growth rates after some species of the genus *Eucalyptus* (MADR 2022).

Gmelina arborea is a tree species belonging to the Lamiaceae family (De Kok 2012; Hernández et al. 2013), native in the humid to dry habitats of India, Bangladesh, Sri Lanka, Myanmar, Thailand, and part of the Asian continent, among others (Dvorak 2004). This species has been introduced to many countries of Central and South America, including Colombia (Osorio 2004). In Colombia, this exotic tree species has been planted since 1980, with genetic material coming mostly from a provenance trial established in the southwest of the country (Dvorak 2004). Provenances from India, Myanmar and Thailand and landraces from Colombia and Costa Rica were evaluated at three years of age, and the best results were obtained by a landrace from Costa Rica (Osorio 2004), demonstrating that the species has adapted to the environmental conditions of the American tropics and has given rise to promising landraces for commercial reforestation programs.

The genetic improvement of *G. arborea* has focused on increasing the stem volume and the stem straightness (Hodge and Dvorak 2004; Balcorta and Vargas 2004; Espitia et al. 2016). However, currently it is important to consider new traits in the selection of genotypes that allow the identification of genotypes with high efficiency in the use of resources (Bouvet et al. 2020). Climate change has had effects on the supply of essential resources for life (e.g. water availability) leading to society to impose constraints on the use of that resources, for this reason, a balance between production and conservation is currently required and the efficient use of resources is promoted (United Nations 2015).

Water availability is the main limiting factor for forestry production (Medrano et al. 2007; Bhattacharya 2019; Hakamada et al. 2020). A lower water availability has the potential to cause a significant decrease in biomass production and, in extreme cases, contribute to tree death (Guedes et al. 2018). Therefore, it is necessary to understand how biomass production can be improved (or maintained) by optimizing water use. The relationship between these two traits is known as water use efficiency (WUE) (Ehleringer et al. 1993; Bramley et al. 2013).

In general terms, the water use efficiency (WUE) is defined as the relationship between the biomass produced and the water consumed. At the leaf level, the WUE relates the amount of net CO₂ assimilated to stomatal conductance, so it is not influenced by climatic conditions (e.g. vapor pressure deficit) at the time of measurement (Bhattacharya 2019), this is known as intrinsic WUE (WUE_i). Therefore, its measurement allows to identify intrinsic differences in WUE regardless of site-specific environmental conditions and measurement time (Wullschleger et al. 1998; Barbour et al. 2010; Bramley et al. 2013).

Intrinsic WUE can also be estimated using the discrimination of stable carbon isotopes ($\delta^{13}\text{C}$) incorporated into leaves, stems, or other plant tissues (Farquhar et al. 1982; Battie-Laclau et al. 2016). Farquhar et al. (1982) demonstrated that $\delta^{13}\text{C}$ in plant tissues of C₃

plants provides a reliable index of WUE, because both WUE and $\delta^{13}\text{C}$ are controlled by intercellular CO_2 levels. Previous studies have shown a strong positive correlation between $\delta^{13}\text{C}$ and WUE_i in trees (Cernusak et al. 2006; Monclus et al. 2006; Delrot et al. 2010).

The genetic improvement of water use efficiency in forest plantations could reduce water use without compromising yield (Bassett et al. 2011). Previous studies have shown a trade-off between growth rates and WUE (Dixit et al. 2022) and that higher WUE is not always genetically related to lower growth (Marguerit et al. 2014). Bouvet et al. (2020) found that positive genetic gains could be obtained by using WUE_i , derived from wood stem carbon isotope composition, in combination with wood production traits for selecting *Eucalyptus urophylla* $\times$ *Eucalyptus grandis* genotypes. Past research has shown there are opportunities for genetic improvement of WUE of tree species, and this would be of importance mainly for those growing in environments with lower water availability.

In this study, we examined the genetic variation of wood production traits and WUE_i in forty open-pollinated families of *Gmelina arborea*, an interesting tree species for reforestation in dry areas in Colombia, to select superior genotypes considering a balance in wood production and water use. The specific objectives of this study were (i) to estimate the genetic variance and heritabilities of biomass and wood production, wood density, and WUE_i for open-pollinated families of *Gmelina arborea*, (ii) to determine genetic correlations among evaluated traits and (iii) to estimate the response to selection for evaluated traits, individually and balancing wood production and water use efficiency.

Materials and methods

Parent selection and progeny trial

Open pollinated seeds from forty selected plus trees of *Gmelina arborea* were collected and nursed to obtain seedlings. The plus trees were selected from commercial plantations at least 7 years of age located in the Caribbean plains and in the interior of the inter-Andean valleys of Colombia. The plus trees selected belong to four provenances (landraces) corresponding to municipalities of the two regions (Fig. 1; Table 1). The plus tree selection process consisted of comparing each candidate tree with the five best neighboring trees within a 20 m radius. The traits considered were straightness, height, diameter, stem volume, crown size, branch diameter and insertion branch angles (Rodríguez et al. 2011).

An open-pollinated progeny trial was established with the nursed seedlings during March 2011 using a planting spacing of 3×3 m (1111 trees ha^{-1}). The soil was prepared by subsoiling to a depth of 60 cm in the planting lines, allowing a better expression of the genotype due to the homogenization of the land (Rodríguez et al. 2011). A randomized complete block experimental design with 30 blocks and 40 open-pollinated families (treatments) was used, with the experimental unit being each tree (Single Tree Plot), so that the total experiment consisted of 1200 trees.

The progeny trial is located in the inter-Andean valleys of Colombia, at the coordinates $5^{\circ}00'52.10''$ latitude $-74^{\circ}54'36''$ longitude. The site has an elevation of 280 m asl, belongs to the tropical dry forest (Holdridge 1947). The geomorphology of the landscape is piedmont with a fan-terrace relief type with low slopes of 0–3% and sandy clay loam textural class soils. Data for the period 2011–2020 of a weather station 2 km from the trial



Fig. 1 Geographical location of the progeny trial in the inter-Andean valleys (red point) and of the provenances (landraces) of *G. arborea* in Colombia (blue and red points). The green shaded region shows the area where *G. arborea* forest plantations are normally established

showed an inter-annual mean precipitation of 1728.5 mm ranging from 983.1 mm (2015) to 2104.3 mm, a mean temperature of 28.7 °C, with a minimum temperature of 22.9 °C and maximum temperature of 34.1 °C. Precipitation has a bimodal behavior with a first rainy period from March to May and a second from September to November (Fig. 2). As shown in Fig. 2, there are two dry periods where potential evapotranspiration (PET) exceeds precipitation, causing water deficit for much of the year.

Measured traits

Measurements were taken in February 2020 when the trial was 9 years old. Tree dimensional variables were measured for all trees, such as diameter at 1.3 m (Dbh) using a diameter tape, and total height (Th) using a laser hypsometer. The sawn wood volume of the stem up to a small-end diameter of 15 cm under bark (V15) was calculated using a taper model fitted by Niño et al. (2018) to sample trees harvested in the study area. Above-ground biomass (AGB) was estimated using the following equation derived from Obando (2004) and Rodríguez (2013):

Table 1 List of provenances (landraces) and open-pollinated families selected within the provenance and environmental characteristics of the selection sites of *Gmelina arborea* plus trees in Colombia

Provenance (landrace)	Region	Average elevation (m asl)	Average precipitation (mm year ⁻¹)	Annual temperature (°C)			Total open-pollinated families selected	Open-pollinated families
				Mean	Maximum	Minimum		
Za	Caribbean plains	26	1427.1	28.0	35.7	20.8	27	1 to 27
Ep	Caribbean plains	16	1372.2	28.0	35.7	20.8	7	28 to 34
Sa	Caribbean plains	70	1188.2	27.7	36.2	22.3	2	35 and 36
Ar	Inter-Andean valleys	280	1788.3	28.2	35.3	20.7	4	37 to 40

Note: Precipitation and temperature values correspond to averages between 1981 and 2010 (IDEAM, 2023)

$$AGB = -2.6832 + \frac{(1156.7223 + 2.6832)}{\left(1 + e^{\frac{34.8699 - Dbh}{6.4150}}\right)} \quad (1)$$

A 5.15 mm diameter and 5 cm long increment core was extracted from the trees of 15 systematically selected blocks, choosing the odd blocks. The fresh volume of each increment core was determined geometrically by taking the dimensions of the cores. The increment cores were dried in an oven at 103 °C for 24 h. The basic wood density (WD) of each increment core was determined as the ratio between oven-dried weight and the fresh volume. The sapwood was extracted from each increment core and finely ground and packed in Eppendorf tubes for the determination of carbon isotopes. The wood samples were analyzed on a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced with a NC2500 elemental analyzer at Cornell Isotope Laboratory (Cornell University, USA). The result of the relationship between the stable ^{13}C and ^{12}C isotopes was determined, reported in parts per mil (‰), using the following equation (Farquhar et al. 1982):

$$\delta^{13}\text{C} = \left(\frac{\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{sample}}}{\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{standard}}} - 1 \right) \times 1000\text{‰} \quad (2)$$

where the standard is an established reference material (Vienna Pee Dee Belemnite). An estimate of the intrinsic water use efficiency (WUE_i) was obtained from isotopic discrimination as (Saurer and Siegwolf 2007):

$$\text{WUE}_i = c_a \frac{b - \delta^{13}\text{C}_a + \delta^{13}\text{C}_p}{1.6(b - a)} \quad (3)$$

where $\delta^{13}\text{C}_a$ and $\delta^{13}\text{C}_p$ is the $\delta^{13}\text{C}$ value of air ($\sim 8\text{‰}$) and plant tissue, respectively. The a term is the fractionation caused by CO_2 diffusion across the stoma ($a = 4.4\text{‰}$), b is the fractionation associated with CO_2 fixation ($b = 27\text{‰}$), and c_a are the CO_2 concentration in the atmosphere ($c_a = 400$ ppm) (Brugnoli et al. 1988; Marshall et al. 2007; Weiwei et al. 2018).

Data analysis

The individual tree data from the trial were analyzed using the following linear mixed effects model:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e} \quad (4)$$

where $\mathbf{y}$ is a vector of data, $\mathbf{b}$ is vector of fixed effects due to general mean, the provenance (landrace) and blocks, $\mathbf{X}$ is the design matrix for fixed effects, $\mathbf{u}$ is a vector of random genetic effects due to open-pollinated families ($\mathbf{u} \sim \text{N}(0, \mathbf{G})$) where $\mathbf{G}$ is the variance-covariance matrix for the random effects, $\mathbf{Z}$ is the design matrix for random effects and $\mathbf{e}$ is a vector of residuals ($\mathbf{e} \sim \text{N}(0, \sigma_e^2 \mathbf{I})$) where σ_e^2 is the residual variance, and $\mathbf{I}$ is an identity matrix. The basic linear mixed effects model fitted with ‘breedR’ assumes residuals with

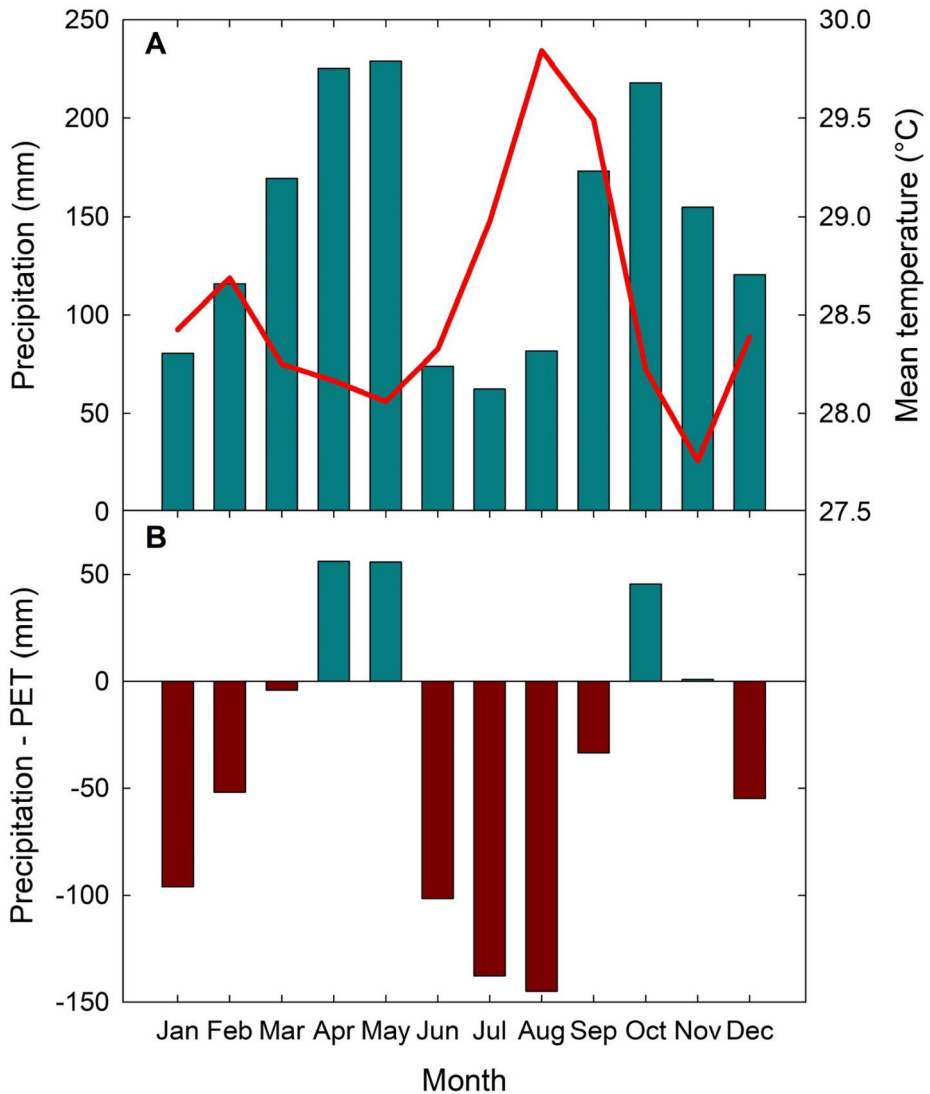


Fig. 2 Monthly precipitation and mean temperature and meteorological water deficit calculated as precipitation minus potential evapotranspiration

homogeneous variance (Muñoz and Sanchez 2020); however, to account for the effect of intraspecific competition within the trial caused by different survival rates among families, a linear mixed model with residuals of heterogeneous variances was also used. The residuals were weighted using a distance-independent competition index that considers the ratio between the Dbh of each tree and the quadratic mean diameter of the trial (Sun et al. 2018). The quadratic mean diameter was calculated using the root of the mean of the squared diameters of the trees in the trial (Curtis and Marshall 2000). The error term was expanded to $e \sim N\left(0, w^{-1/2} \sigma_e^2 I\right)$ where w is a vector of weights (Muñoz and Sanchez 2020). The

significance of the weighted variance structure was evaluated using a likelihood ratio test (LRT).

Variance components and heritability

The variance components were estimated by restricted maximum likelihood (REML) using the ‘breedR’ and ‘breedRPlus’ packages for R software (R Development Core Team, 2023). Narrow-sense heritability (h^2_i) of each trait was calculated as (Llanos et al. 2019; Zheng et al. 2023),

$$h^2_i = \frac{\sigma^2_A}{\sigma^2_p} = \frac{4\sigma^2_f}{\sigma^2_f + \sigma^2_e} \quad (5)$$

where σ^2_A and σ^2_p are the additive genetic variance and phenotypic variance, respectively, and σ^2_f and σ^2_e are the genetic family variance and the residual variance, respectively.

The heritability of open-pollinated family means (h^2_f) was calculated as (Isik et al. 2017),

$$h^2_f = \frac{\sigma^2_f}{\sigma^2_f + \frac{\sigma^2_e}{r}} \quad (6)$$

where r is the number of repetitions (blocks).

Genetic correlation

To evaluate the relationship among evaluated traits the genetic correlation coefficients were determined with the following equation using the variance and covariance components obtained from the linear mixed effects model. The estimated genetic correlation between traits x and y is (Xu 2022),

$$r_G = \frac{\sigma_{A(x,y)}}{\sqrt{\sigma^2_{Ax} \cdot \sigma^2_{Ay}}} \quad (7)$$

where $\sigma_{A(x,y)}$, σ^2_{Ax} and σ^2_{Ay} are the additive genetic covariance and variance components of x and y traits, respectively.

The standard error of the estimated heritabilities and genetic correlation coefficients were calculated through the delta method which considers the relationship between variance-covariance included in the ‘breedRPlus’ package (Lin 2018).

Response to selection

To estimate the response to selection of *G. arborea* families, the selection differential for each trait was estimated as the mean difference of the top 10% (4 families) and 20% (8 families) of the selected families against the global mean of the forty open-pollinated fami-

lies evaluated and the response to selection (R) was estimated using the following equation (Falconer 1981):

$$R = S \cdot h_f^2 \quad (8)$$

where S is the selection differential, and h_f^2 is the heritability of open-pollinated family means.

Finally, a graphical analysis was carried out to identify the families with the best performance considering both wood production and WUE_i traits.

Results

Phenotypic characterization of the trial

The open-pollinated families show an average survival of 75% ranging from 53.3% (family 34) to 96.7% (family 8) at 9 years of age (Fig. 3; Table 2). Twenty-two open-pollinated families were above the mean of all families showing a good adaptation to the study area.

Open-pollinated families of *G. arborea* showed a mean Dbh of 22.95 cm ranging between 19.1 and 25.43 cm and a mean Th of 20.61 m ranging between 19.31 and 22.39 m (Table 2). Mean V15 ranged from 0.113 to 0.343 m³ tree⁻¹ (mean of 0.259 m³ tree⁻¹) and AGB from 103.82 to 263.09 kg tree⁻¹ (mean of 201.12 kg tree⁻¹). These two traits showed higher variability with coefficients of variation (CV) of 18.74 and 16.91%, respectively (Table 2). WD showed a lower variability ranging from 0.428 g cm⁻³ to 0.482 g cm⁻³ (CV=2.61%). Traits associated to water use efficiency as $\delta^{13}C$ ranged from -28.39‰ to -26.91‰ and WUE_i showed a mean of 59.45 $\mu\text{mol mol}^{-1}$ ranging from 52.66 to 64.45 $\mu\text{mol mol}^{-1}$ with a CV=4.65% (Table 2).

(Table 2)

As shown in Fig. 4, there is substantial variation in AGB among the forty open-pollinated families compared to the variation observed in WD and WUE_i . Family 36 stands out with

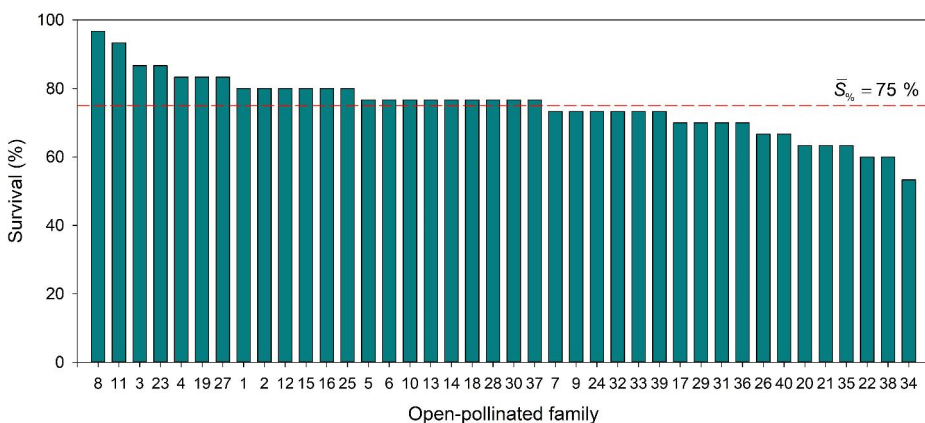


Fig. 3 Survival for forty open-pollinated families in a progeny trial of 9-years-old of *Gmelina arborea* in Colombia. The horizontal dash red line represents the mean survival of the trial (75%)

Table 2 Descriptive statistics for measured traits for forty open-pollinated families in a progeny trial of 9-years-old of *Gmelina arborea* in Colombia

Trait	Number of trees evaluated	Mean	Minimum	Maximum	Standard deviation	Coefficient of variation (%)
Survival (%)	1200	75.0	53.3	96.7	8.83	11.78
Dbh (cm)	900	22.95	19.10	25.43	1.38	6.01
Th (m)	900	20.61	19.31	22.39	0.70	3.42
AGB (kg tree ⁻¹)	900	201.12	103.82	263.09	34.02	16.91
V15 (m ³ tree ⁻¹)	900	0.259	0.113	0.343	0.05	18.74
WD (g cm ⁻³)	430	0.454	0.428	0.482	0.01	2.61
$\delta^{13}\text{C}$ (‰)	430	-27.53	-28.39	-26.91	NA	NA
WUEi ($\mu\text{mol mol}^{-1}$)	430	59.45	52.66	64.45	4.40	4.65

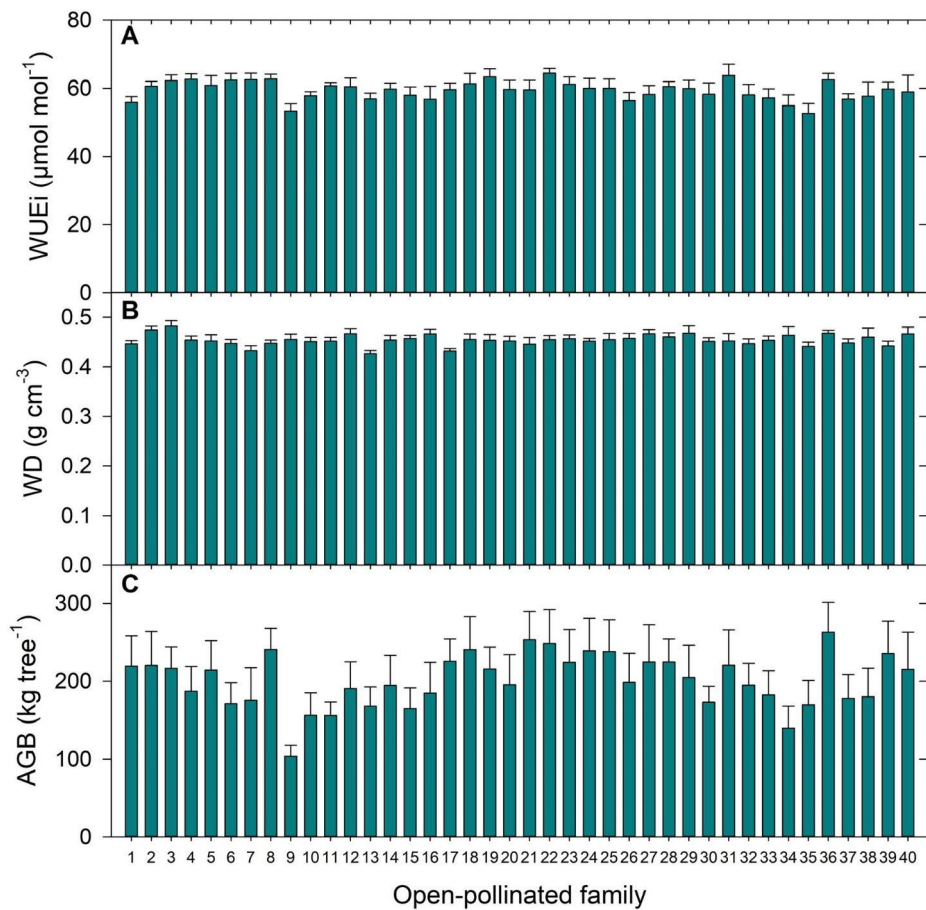
**Fig. 4** Variation of WUEi, WD and AGB among forty open-pollinated of families of *Gmelina arborea*

Table 3 Variance components and narrow-sense heritabilities for evaluated traits for open-pollinated families of 9-years-old *Gmelina arborea* in Colombia

Trait	σ^2_f	σ^2_e	σ^2_p	LRT	h^2_i	h^2_f
AGB	1352.00 (679.71)	32606.0 (1264.70)	33958.0 (1344.00)	370.85***	0.15926 (0.07792)	0.55436 (0.12588)
V15	0.0021825 (0.0011307)	0.0555960 (0.0022376)	0.0577785 (0.002351)	271.41***	0.15109 (0.07637)	0.54080 (0.13044)
WD	0.000093294 (0.000043306)	0.000902340 (0.000061331)	0.000995634 (0.00006855)	36.396***	0.37481 (0.16314)	0.60798 (0.11447)
WUE _i	3.166 (1.9432)	48.503 (3.5337)	51.669 (3.64)	25.742***	0.24510 (0.14568)	0.49472 (0.15828)

For each trait: Values in parentheses are the standard error for variance components and heritabilities; ***, significant at $p < 0.001$

Table 4 Genetic correlations among evaluated traits for open-pollinated families of 9-years-old *Gmelina arborea*

Trait	AGB	V15	WD	WUE _i
AGB	1	0.988*** (0.010)	0.635* (0.339)	0.506* (0.315)
V15		1	0.557* (0.336)	0.502* (0.304)
WD			1	0.144 ^{ns} (0.369)
WUE _i				1

For each trait: Values in parentheses are the standard error for genetic correlation coefficients; ***, significant at $p < 0.001$; *, significant at $p < 0.05$; ^{ns}, nonsignificant

the highest AGB (263.09 kg tree⁻¹), family 22 the highest WUE_i (64.45 (μmol mol⁻¹) and family 3 with highest WD (0.482 g cm⁻³).

Variance components and narrow sense heritabilities

The variance components estimated by REML using a weighted variance structure proved to be significant for all evaluated traits ($p < 0.001$, Table 3). For all traits, the main source of variation in the trial was the residual variance, followed by the genetic family variance. Production traits and WUE_i showed moderate narrow-sense heritabilities. Considering heritability of open-pollinated family means, production traits showed $h^2_f=0.55436$ for AGB, $h^2_f=0.54080$ for V15 and $h^2_f=0.60798$ for WD and WUE_i showed a moderate $h^2_f=0.49472$ (Table 3).

Genetic correlation among traits

Genetic correlations among traits are shown in Table 4, as expected, genetic correlation analysis revealed that AGB and V15 showed a high genetic correlation ($r_G = 0.988$, $p < 0.001$). WD showed significant positive genetic correlation with AGB ($r_G = 0.635$, $p < 0.05$) and V15 ($r_G = 0.557$, $p < 0.05$) and nonsignificant correlation with WUE_i ($p > 0.05$) and, interestingly, both AGB and V15 showed a significant genetic correlation with WUE_i ($r_G = 0.502$, $p < 0.05$).

Response to selection

Table 5 shows the response to selection for each trait considering the selection of 10% (4 families) and 20% (8 families) of the superior open-pollinated families of *G. arborea*. The greatest response to selection would be obtained in V15 and AGB, varying from 0.040 m³ tree⁻¹ (15.5%) to 0.033 m³ tree⁻¹ (12.7%) and from 27.571 kg tree⁻¹ (13.7%) to 23.290 kg tree⁻¹ (11.6%) by selecting 10 or 20% of the superior families, respectively. Although WD showed the highest h^2_f among evaluated traits, this trait showed a low selection differential resulting in a modest genetic gain of 2.5% or 2.1% by selecting 10 or 20% of the superior families, respectively. Finally, the response to selection for WUE_i showed minor gains ranging from 3.0% (4 families selected) to 2.9% (8 families selected) (Table 5).

Family selection for wood production and WUE_i

Sawn wood volume (V15) was chosen as the target wood production trait because it showed a significant genetic correlation with AGB and, moreover, a higher response to selection than AGB. In Fig. 5 the 20% of superior families for V15 and WUE_i are represented by green dashed lines. As shown in Fig. 5, we can balance the objectives of genetic selection by selecting the top families considering both wood production and WUE_i, in this case, only families 8, 22 and 36 would be selected. By selecting these three top families the genetic gain in V15 would be 0.0361 m³ tree⁻¹, corresponding to 13.9% and the genetic gain in WUE_i would be 1.8409 μmol mol⁻¹ corresponding to 3.1%.

Discussion

Production traits and water use efficiency were evaluated in forty open-pollinated families of *G. arborea* grown in a tropical dry forest known as a water-limited environment. This study provides evidence about the opportunities for tree genetic improvement of trees, reconciling the objectives of wood production and water use efficiency. Intrinsic water use efficiency (WUE_i) was derived from the carbon isotopic discrimination of wood samples which is considered as an important indicator of tree adaptability to the climate change (Weiwei et al. 2018).

The open-pollinated families of *G. arborea* exhibited satisfactory growth with an average diameter of 22.95 cm and height of 20.61 m at 9 years. The average volume V15 was 0.259 m³

Table 5 Response to selection for open-pollinated families of 9-years-old *Gmelina arborea* in Colombia

Trait	Popula- tion mean	h^2_f	10% Superior			20% Superior		
			Mean	S	R	Mean	S	R
AGB (kg tree ⁻¹)	201.116	0.554	250.851	49.735	27.571 (13.7) [‡]	243.128	42.012	23.290 (11.6) [‡]
V15 (m ³ tree ⁻¹)	0.259	0.541	0.333	0.074	0.040 (15.5)	0.320	0.061	0.033 (12.7)
WD (g cm ⁻³)	0.454	0.608	0.473	0.019	0.012 (2.5)	0.470	0.016	0.010 (2.1)
WUE _i (μmol mol ⁻¹)	59.451	0.495	63.114	3.663	1.812 (3.0)	62.963	3.512	1.737 (2.9)

[‡] For each trait the response of selection (R) in percentage is presented in parentheses

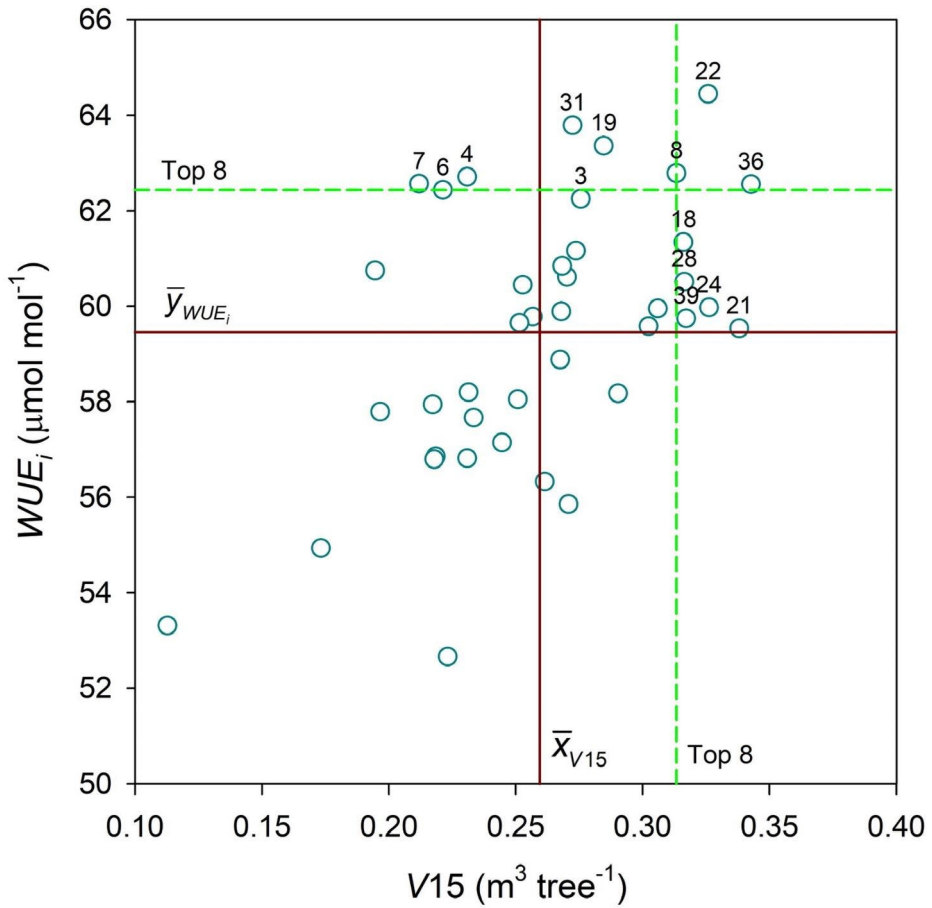


Fig. 5 Phenotypic relationship between V15 and WUEi for open-pollinated *G. arborea* family selection

tree⁻¹, slightly lower than the volume (0.359 m³ tree⁻¹) reported by Onyekwelu et al. (2006) for 10-year-old trees in forest plantations in Nigeria and the average AGB of 201.12 kg tree⁻¹ is similar to the AGB of 226.08 kg tree⁻¹ reported in Costa Rica by (Fonseca et al. 2021) for trees with an average diameter of 18 cm.

The open-pollinated families of *G. arborea* showed a mean survival of 75% at 9-years old, which is close to the rotation age. Traditionally, these forest plantations have been harvested for pulpwood and sawn wood at 6 and 15 years old, respectively. In higher site indices the rotation age could be reduced to 12 years (Martinez et al. 2015). This result suggests that the species is well adapted to the environmental conditions of the study area and that, the tropical dry forest partially fulfills the species environmental requirements. Lamprecht (1990) and Dvorak (2004) reported that *G. arborea* requires an annual rainfall between 1500 and 2300 mm, a defined dry season of 3 to 5 months, and an average temperature between 18 and 35 °C.

Heritability of open-pollinated family means were modest for all traits, $h^2_i=0.554$ for AGB, $h^2_i=0.541$ for V15, $h^2_i=0.608$ for WD and $h^2_i=0.495$ for WUE_i . However, previous studies have reported lower results for this broadleaf species, Hodge and Dvorak (2004) reported moderate heritabilities for height, diameter and volume in provenance/progeny trials with values around $h^2_i=0.10$. Heritabilities for WUE_i of *Gmelina arborea* have not been reported to date, but for other broadleaf species this trait has shown higher heritabilities. Bouvet et al. (2020) reported for WUE_i a narrow sense heritability $h^2=0.704$ for *Eucalyptus urophylla* × *Eucalyptus grandis* clones in the Republic of the Congo. For pines, heritabilities of $\delta^{13}C$ (WUE_i) from 0.14 to 0.41 have been reported (Baltunis et al. 2008; Marguerit et al. 2014).

This study reports significant positive genetic correlations between WD and production traits ($p<0.05$) and a nonsignificant genetic correlation with WUE_i . This genetic correlation implies that the selection of families with high values of AGB, V15 and WUE_i will not reduce the WD in the next generations. Conversely, Espinoza (2003) reported negative genetic correlations ($-0.92 \geq r_G \geq -0.30$) between wood specific gravity and diameter in a provenance trials of *G. arborea* in Venezuela. As expected AGB and V15 showed a significant high genetic correlation ($r_G = 0.988$, $p<0.001$). Additionally, significant genetic correlations were found between WUE_i and production traits AGB ($r_G = 0.506$, $p<0.05$) and V15 ($r_G = 0.502$, $p<0.05$). This finding shows that some open-pollinated families of *G. arborea* can meet the production objectives while maintaining high water use efficiency. In other forest species these types of relationships have been studied but the results have not been conclusive.

Bouvet et al. (2020) reported a significant negative genetic correlation ($r_G = -0.26$) between WUE_i and 55-month wood volume of *Eucalyptus urophylla* × *Eucalyptus grandis* clones in the Republic of Congo. Castillo et al. (2018) found no genetic correlation between $\delta^{13}C$ and tree growth in a longleaf pine (*Pinus palustris*) genetic trial in United States. For 12 years-old maritime pine (*Pinus pinaster*), a non-significant genetic correlation between was found circumference and $\delta^{13}C$ and positive significant genetic correlations were found between $\delta^{13}C$ and height ($r_G = 0.31$) and ring width ($r_G = 0.40$), however this behavior was not constant in three evaluation sites in France (Marguerit et al. 2014).

Our results indicated that moderate responses to selection are expected in AGB and V15 by an intensive family selection, however, higher responses to selection have been reported in previous studies by Espitia et al. (2016), and Hodge and Dvorak (2004). V15 and AGB showed the highest response to selection ranging between 15.5% ($0.040 \text{ m}^3 \text{ tree}^{-1}$) and 13.7% ($27.571 \text{ kg tree}^{-1}$) to 12.7% ($0.033 \text{ m}^3 \text{ tree}^{-1}$) and 11.6% ($23.290 \text{ kg tree}^{-1}$) by selecting the best 4 and 8 families, respectively. Espitia et al. (2016) estimated genetic gains for selected *G. arborea* plus trees of 36% for stem volume in Colombia, assuming a heritability of 0.25. Balcorta and Vargas (2004) reported a selection differential of $0.056 \text{ m}^3 \text{ tree}^{-1}$ in total volume for 3 years-old *G. arborea* trees in Mexico, however, in the present study we found a higher selection differential in V15 ranging $0.061\text{--}0.074 \text{ m}^3 \text{ tree}^{-1}$, indicating the superior performance of the evaluated open-pollinated families.

Wood basic density showed a low selection differential for open-pollinated *G. arborea* families resulting in a low response to selection ranging 2.5–2.1%, despite a moderate high heritability, this implies an improved population mean ranging 0.466 to 0.464 g cm^{-3} , when selecting 10 or 20% of the best families. However, the evaluated open-pollinated families showed high mean WD (0.454 g cm^{-3} , 0.428 g cm^{-3} – 0.482 g cm^{-3}) compared to previous studies for this species by Dvorak (2004) who reported a mean of 0.410 g cm^{-3} , and to those of Espinoza (2004) who found that the WD of 7-year-old provenances varied between 0.411 and 0.440 g cm^{-3} at a site in

Venezuela and similar to Lauridsen and Kjaer (2002) who reported variations in WD between 0.350 and 0.535 g cm⁻³ (average of 0.443 g cm⁻³) for *G. arborea* provenances.

Response to selection for WUE_i ranged from 2.9 to 3.0% imply that a genetic gain of approximately ~1.7–1.8 μmol mol⁻¹ would be expected. Higher genetic additive gains of around 10.3% in WUE_i for hybrid *Eucalyptus* clones were reported by Bouvet et al. (2020) using a single-trait selection strategy.

The genetic gains found for WUE_i and the positive genetic correlation showed between this trait and AGB and V15 suggest that some open-pollinated families in which WUE_i is mainly controlled by the photosynthetic rates and not by a good stomatal control. However, past studies suggest that *G. arborea* also has a good stomatal control, during water deficit seasons the species change foliar functional traits (Melo et al. 2012) and loses all its leaves in drier sites (Rojas et al. 2012).

This study identified three open-pollinated families of *G. arborea* that were more efficient in water use. These families with higher WUE_i and V15 (families 8, 22 and 36) come from drier regions than the study site, where water deficit is experienced for most of the year. This result suggests that possibly these genotypes from the Caribbean plains have adapted and developed a better stomatal control allowing them to achieve a better balance between the photosynthesis rates and transpiration. Deploying these identified improved genotypes with high biomass production and adequate use of water will contribute to generating a more sustainable forestry as an adaptation strategy to face climate change.

However, it is important to recognize the limitation of the results obtained, since the progeny test is located in a single site, suggesting that the genotypes evaluated should be tested in other site conditions to give greater confidence to the genetic improvement program of the species in the inter-Andean valleys, also, because in the present study was considered a reduced sample of selected plus trees (open-pollinated families), for future studies it is necessary to expand the experimental samples to minimize the uncertainty in the analysis of the data and in the calculation of genetic parameters.

Conclusions

This study presents a genetic evaluation of production traits and water use efficiency derived from δ¹³C isotopic discrimination in a progeny trial of forty open-pollinated families of *G. arborea* grown in a tropical dry forest. Although production traits and WUE_i showed moderate narrow-sense and open-pollinated family means heritabilities, considerable responses to selection of up to 13.7% in AGB, 15.5% in V15, 2.5% in WD and 3.0% in WUE_i could be achieved through intensive selection of superior families. In addition, positive genetic correlations were found between production traits and WD and WUE_i showing that some open-pollinated families were more productive while using water more efficiently. This positive relationship also suggests that WUE_i of *G. arborea* is mainly controlled by the photosynthetic capacity of the species. However, further ecophysiological studies are needed to understand the drivers of WUE_i for this forest tree species. Finally, the conducted analyzes allowed to identify three superior open-pollinated families of *G. arborea* as a basis for the genetic improvement of the species aiming to achieve a balance between forest production and water use. Deploying these superior open-pollinated families can be used as a forest management strategy to adapt the species to future drought scenarios associated with global climate change.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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