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Taper and individual tree volume equations of Eucalyptus varieties under contrasting irrigation regimes

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Abstract

Background: Compatible taper and volume equations are key for traditional growth and yield and current process-based or hybrid models. However, most equations do not consider variables such as genotype, water regime and their interaction, limiting the development of general equations for species or regions. Our research investigated taper and individual tree volume equations for eight Eucalyptus genotypes (*E. nitens*, *E. badjensis*, *E. smithii*, *E. camaldulensis x globulus* and two varieties of low and high productivity of *E. globulus* and *E. nitens x globulus*), all materials are growing under summer irrigated vs. no irrigated conditions.

Methods: A 7-year old Eucalyptus plantation experiment was sampled considering four representative trees per genotype x water regime combination treatment. Four non-linear taper equations were evaluated: Kozak (2004), Kozak et al. (1969), Ormerod (1973) and Max and Burkhart (1976). In addition, total and merchantable volume was evaluated with the Schumacher and Hall (1933) equation. The effect of genotype, irrigation regime and interaction were evaluated for each equation. Then, the best taper equation was selected from adjusted coefficient of determination, mean square error, and AIC and BIC parameters. Finally, the validation of evaluations was carried out with the Leave-One-Out Jackknife method.

Results: Genotype, irrigation regime, or the interaction were not statistically significant for all evaluated taper - volume equations and a generalised model equation was obtained. The best taper equation was Kozak (2004) which showed the best fit and adaptation to irregular boles. Regarding volume equations, all showed a trend to underestimate volume (total and merchantable) in trees with a volume greater than 0.22 m^3. Validation of the equations showed reduced bias suggesting that the equations can be used to predict taper and volume regardless of Eucalyptus genotype x irrigation regimen combinations.

Conclusions: Our results suggest a negligible or minor effect of irrigation (water resource availability) and genotype (for tested taxas and genotypes) on taper and individual tree volume equations. A generalised taper and volume equation (total and merchantable) may be used for all tested genotypes, regardless of water regime (site water availability). This generalised model would simplify Eucalyptus estimates required for stand management and projection.

Keywords: non-linear equations, model, water availability, allometrics, tree improvement.

Introduction

The development of equations that describe the shape of a tree bole is essential for estimating wood volume, carbon sequestration and genetic selection of varieties with the best form for industry needs (Vallejos et al. 2010; Arias-Aguilar et al. 2020). Taper equations have been developed for estimating individual tree diameter at different heights and have been based on simple independent variables such as total height, heights of interest, and diameter at breast height (DBH, at

1.3 m), allowing us to mathematically represent the shape of a tree bole (Husch et al. 1993; Nogueira et al. 2008). Furthermore, taper equations may to comprise linear and non-linear models (Goodwin 2009). Linear models are characterised by their simplicity in application but lack precision (Garber & Maguire 2003). On the other hand, non-linear models have been widely implemented because they can be adapted to species with irregular bole shapes, and their mathematical relationships improve model precision with unbiased parameters that increase accuracy (McTague & Weiskittel 2021).

The development of taper and volume equations is highly relevant for *Eucalyptus* given their large scale of forest plantations and industrial use worldwide (Muhairwe 1999; Son et al. 2009). The species present wide climatic adaptability (Booth 2013) and intensive cultivation of *Eucalyptus* in plantation forestry allows high timber and biomass yields for commercial purposes (Lizarralde et al. 2008). These characteristics of the species have led to the development of intensive tree improvement programs that seek continuous increases in productivity of volume or biomass (Hall et al. 2020), wood properties (Hung et al. 2015), and resistance to pests (Brennan et al. 2001). Genetic improvement programs consider that a cylindrical shape is a valuable individual trait for the robustness of volume estimates (Miguel et al. 2011) and sawtimber yield production. Shiver and Brister (1992) recommend for *Eucalyptus saligna* the use of the equations of Ormerod (1973) and Max and Burkhart (1976) for accuracy and ease of use. Instead, Osler et al. (1996) developed several studies with *Eucalyptus regnans* showing that it is possible to use non-linear equations for taper analysis, and the Kozak et al. (1969) non-linear equation successfully presented the best adjustment for juvenile trees. Son et al. (2009) found that, for *Eucalyptus pellita,* the Kozak (2004) equation produced the best taper model fits (R^2>0.90), generating individual tree volume estimates with no significant differences from destructive analyses. Studies developed by Souza et al. (2018), with three 10-year-old *Eucalyptus* clonal varieties, showed that non-linear equations had the best fit for the bole taper profile (R^2>0.88), with the Kozak (2004) equation had the best performance for all varieties.

Interestingly, taper and volume models evaluated for genotypes exposed to different soil water availability regimes in the same site are scarce, and existing studies have mainly focused on coniferous species of the genus *Pinus* (Li & Weiskittel 2010; Lu et al. 2018) or effects of water availability usually have been investigated more commonly across sites for productivity purposes but not for investigating taper. Souza et al. (2018) report that taper and volume equations must be genotype-specific since they vary with genotype. In contrast, Scolforo et al. (2019) determined that it is possible to fit generalised equations for *Eucalyptus* regardless of clone. Therefore, the objective of our study was to evaluate the effect of genotype, irrigation regime and genotype x irrigation regime interaction on taper and volume equations (total and merchantable) for highly genetically improved *Eucalyptus* genotypes, including *E. globulus* and *E. nitens x globulus* hybrids of high and low productivity and one of each *E. nitens*, *E. badjensis*, *E. smithii* genotypes and one *E. camaldulensis x globulus* hybrid.

Methods

Study site, genotypes and irrigation treatments

The study was developed at a nursery facility located in the Bio-Bio region of Chile close to Yumbel town (37°8′0.01′′ S, 72° 27′34.70′′ W) (Figure 1). The site

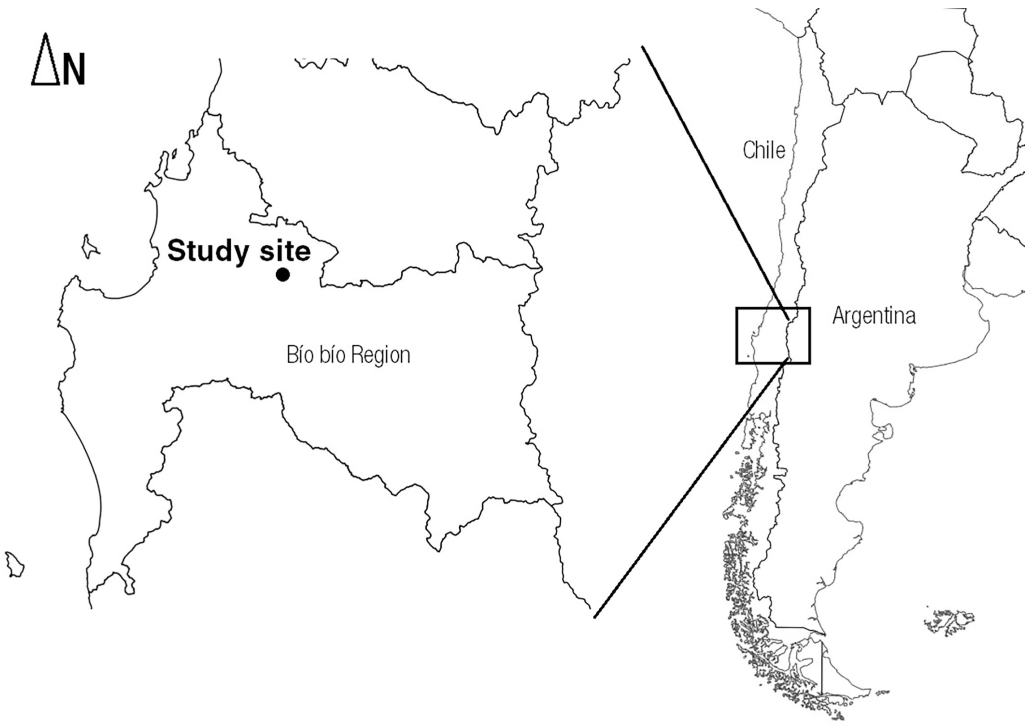

FIGURE 1: Location of the study site.

has an average annual temperature of 13.8°C, with a yearly rainfall of 1252 mm. The topography is flat, soils are classified as Dystric Xeropsamments (CIREN 1999), and the previous land use was a *Pinus radiata* D.Don nursery hedge area. The site was planted from July to August 2013 after subsoiling to 80 cm deep. The site was established with a factorial design with three replicates; the first factor was the water regime (high irrigation vs. a low irrigation treatment). The second factor consisted of the genotypes (30 top-ranking selected from CMPC and ARAUCO genetic improvement programs). Finally, the combination of factors within each replica was randomly distributed according to Rubilar et al. (2020) (30 genotypes x 2 irrigation treatments x 3 replicates). Trees were planted at a 3 x 2 m (1666 trees ha^{-1}) spacing, and genotype plots consisted of 5 x 5 trees, with an internal measurement plot of 3 x 3 trees. A summary of annual rainfall from a weather station located at the site and annual additions from each irrigation treatment before first harvesting sampling at the site are presented in Table 1. A complete description of the site and silvicultural treatments are described in Rubilar et al. (2020).

To fulfil the purpose of our study, considering budget and operational limitations, only a subset of eight genotypes in both irrigation treatments from the 30 available genotypes initially established in the experiment were sampled and considered in our study. The final selected genotypes included two *Eucalyptus globulus* (high yield-EgH vs low yield EgL), two *E. nitens x globulus* hybrids (high yield EngH vs low yield EngL), and one of each *E. nitens* (En), *E. camedulensis x globulus* (Ecg), *E. badjensis* (Eb) and *E. smithii* (Es) genotypes. Cumulative stand growth at age 7 (March 2020) for each selected genotype is presented in Figure 2. Genotypes selection was based on their operational use and high level of productivity, as detailed in Rubilar et al. (2020).

TABLE 1: Annual rainfall and irrigation regime treatments water additions in mm year^{-1} at the experimental site from 2014 to 2019.

Year	Rainfall (mm year^{-1})	Low Irrigation (mm year^{-1})	High Irrigation (mm year^{-1})
2014	1302	18	55
2015	1102	83	384
2016	782	195	552
2017	972	50	837
2018	1162	68	295
2019	833	97	163

Individual tree sampling

Individual tree sampling was carried out in January 2020 with three trees per genotype and irrigation treatment selected and 2021 when one additional tree per genotype and irrigation treatment was selected. Individual trees were selected to represent the diameter distribution of each selected genotype under each irrigation treatment

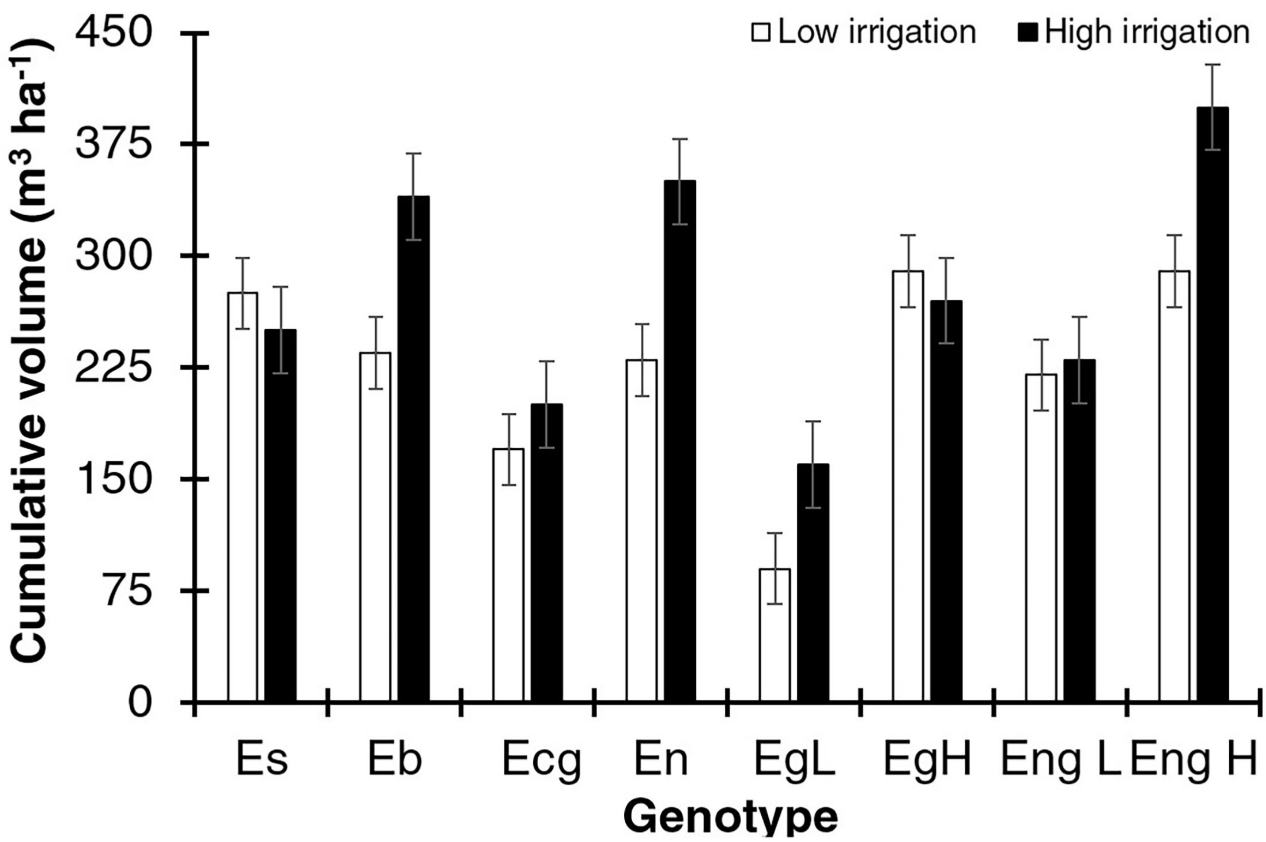

FIGURE 2: Cumulative mean stand volume of selected eight genotypes for each irrigation treatment before first sampling.

(4 trees x 8 genotypes x 2 irrigation treatments = 64 trees). Individual tree diameter was measured at 1.3 m above ground level (DBH) for each sampled tree before harvesting. Subsequently, each tree was cut as close as possible to the ground level, and all its branches were removed, and diameter was measured from the base of the tree and every two metres increments along the bole up to its maximum height until a minimum diameter of 5 cm.

Analysis of cumulative DBH, height and volume for selected genotypes and irrigation treatments

An initial analysis of variance (ANOVA) was carried out to determine if there were significant differences among genotypes and irrigation regimes for DBH, total height and total and merchantable volume (estimated with the Smalian formula, see detail in the next section). In addition, ANOVA analyses were carried out using a Tukey test to test for differences among treatments for each variable. The analyses were conducted in R software version 4.1.1 (R Core Team 2021).

A bole profile analysis was conducted for each genotype x irrigation regime interaction, for which the relative diameter (d/D, is the ratio between any particular diameter at a specific height and DBH) and relative height (h/H, is the ratio between any specific height and total height). Analysis of the d/D and h/H relationship were made according to what has been proposed by Li and Weiskittel (2010) using Origin pro 2020 software (OriginLab 2021).

Taper equations

The methodology proposed by Scolforo et al. (2008) was used to estimate coefficients of the taper and volume equations using the nlme package version 3.1-153 developed by Pinheiro et al. (2016) and implemented for linear and non-linear mixed effects models. In addition, the first-order continuous autocorrelation function (CAR1) and the power variance function were used to eliminate the total within-bole correlation and heteroskedasticity effects. The compatibility between volume and taper equations (it was carried out with the best taper equation) used a system of independent equations with simultaneous estimation of parameters by seemingly unrelated regression (SUR), according to the methodology of Diéguez-Aranda et al. (2006) and Zhao et al. (2019), the analysis used systemfit package version 1.1-24 (Henningsen et al. 2019). All analyses were conducted in R.

For all analyses, four non-linear taper equations were evaluated considering previous studies by Son et al. (2009), Hall et al. (2020) and Hirigoyen et al. (2021) for Eucalyptus (Table 2) that used the single equation of Ormerod (1973) and Kozak et al. (1969), the segmented equations of Max and Burkhart (1976) and the variable form equation of Kozak (2004).

For total and merchantable volume estimation, the Schumacher and Hall (1933) equation was implemented (Eq. 1), given that this equation has been widely used with *Eucalyptus* in previous studies (Trincado &

TABLE 2: Evaluated taper equations.

Reference	Equation
Kozak (2004)	$d_i = \alpha_0 DBH^{\alpha_1} H^{\alpha_2} X_i^{\beta_0 z_i^4 + \beta_1[1/e^{DBH/H}] + \beta_2 X_i^{0.1} + \beta_3[1/DBH] + \beta_4 H^{Q_i} + \beta_5 X_i}$ Where, $X_i = [1.0 - (h_i/H)^{1/3}]/[1.0 - p^{1/3}]$ $Q_i = [1.0 - (h_i/H)^{1/3}]$ $p = 1.3/H$
Kozak et al. (1969)	$d_i^2 = DBH^2 \left[\beta_0 \left(\frac{h}{H} - 1\right) + \beta_1 \left(\left(\frac{h}{H}\right)^2 - 1\right)\right]$
Max & Burkhart (1976)	$d_i^2 = DBH^2 \left(\beta_0 \left(\frac{h}{H} - 1\right) + \beta_1 \left(\frac{h^2}{H^2} - 1\right) + \beta_2 \left(\alpha_1 - \frac{h}{H}\right)^2 I_1 + \beta_3 \left(\alpha_2 - \frac{h}{H}\right)^2 I_2\right)$ Where, $I_1 = 1$ if $\frac{h}{H} \le \alpha_1$ and $I_1 = 0$ otherwise $I_2 = 1$ if $\frac{h}{H} \le \alpha_2$ and $I_2 = 0$ otherwise
Ormerod (1973)	$d_i^2 = DBH^2 \left(\frac{H-h}{H-1.3}\right)^{2\beta_0}$ Where, $\beta_0 > 0$

Where: d is the diameter to be estimated (cm); h is the reference height (m); H is the total height of the tree (m); DBH is the diameter at 1.3 m above the ground (cm); h_{st} is the stump height (m); α_0, α_1, β_0, β_1, β_2, β_3 are the parameters to be estimated.

Burkhart 2006; de Souza Vismara et al. 2016). According to Scolforo et al. (2019), a minimum merchantable diameter of 6 cm is adequate for merchantable volume estimation.

$$V = \beta_0 DBH^{\beta_1} H^{\beta_2} \quad (1)$$

Where: V is the total or merchantable volume per individual tree (m^3 $tree^{-1}$), DBH is the diameter at 1.3 m (cm), H is the total height or merchantable height (m) and β_0, β_1 and β_2 are the parameters to estimate.

After model adjustment, a 1:1 relationship between predicted and observed data was observed to evaluate potential under or overestimate individual tree volume (total and merchantable) estimates. The distribution of residuals was also analysed to evaluate their uniformity and bias.

Evaluation of genotype, irrigation regime and interaction effects

Indicator variables were used in each taper and volume equation to evaluate whether there was an effect of the genotype x irrigation regime interaction (scenario 1), genotype effect (scenario 2) or irrigation regime effect (scenario 3) and each scenario was analysed independently. Indicator variables were implemented according to Quiñonez-Barraza et al. (2014) where I_j=1 if *factor=j*; 0 otherwise, and where I_j represents each factor analysed. For scenario 1 (genotype x irrigation regime interaction); *j*=2 for EngH-High, *j*=3 for EgL-High, *j*=4 for EngL-High, *j*=5 for En-High, *j*= 6 for Eb-High and *j*= 7 for Es-High, *j*=8 for EgH-Low, *j*=9 for EngH-Low, *j*=10 for EgL-Low, *j*=11 for EngL-Low, *j*=11 for En-Low, *j*= 12 for Eb-Low and *j*= 13 for Es-Low (EgH-High was the reference). For Scenario 2 (genotype); *j*=2 for EngH, *j*=3 for EgL, *j*=4 for EngL, *j*=5 for En, *j*= 6 for Eb and *j*= 7 for Es (EnH was the reference). Finally, Scenario 3 (Irrigation regime); *j*= 2 for Low (High was the reference).

The model parameters were rewritten based on indicator variables, so that α_i and β_i could be represented as $\alpha_i = \alpha_{i1} + \alpha_{i2}I_2 + ... + \alpha_{in}I_n$ and $\beta_i = \beta_{i1} + \beta_{i2}I_2 + ... + b_{in}I_n$. Each full model with indicator variables only comprised the significant parameters different from zero at a significance level of 5% (α = 0.05). In order to assess the genotype x irrigation regime interaction, the genotype or irrigation regime effect significantly affect the taper and volume equations; the likelihood ratio test (LRT) (Eq. 2) was used to test the full versus reduced equation.

$$LRT = -2(LogL_a - LogL_b) \quad (2)$$

Where: LRT is likelihood ratio test, L_a is maximum likelihood of L_a (equation of each scenario) and L_b is likelihood of L_b (reduced equation).

The test was performed using a mixed Chi-square distribution of (n-1), where n is genotype x irrigation regime x repetitions. The null hypothesis analysed that there are no differences between the reduced equation model and the equation model with the indicator variable (each evaluated scenario).

Selection of best taper equation

To select the best taper equation, we used the approach proposed by Scolforo et al. (2018) and Hirigoyen et al. (2021), considering: the adjusted coefficient of determination (Adj-R^2) (Eq. 3), the root mean squared error (RMSE) (Eq. 4), the Akaike Information Criterion (AIC) (Eq. 5) and the Bayesian Information Criterion (BIC) (Eq. 6). Additionally, final equations were ranked using the methodology proposed by Hirigoyen et al. (2021) in which the results of the variables Adj-R^2, RMSE, AIC and BIC were used.

$$R^2_{adj} = 1 - \left[\frac{(1-R^2)(n-1)}{n-p-1}\right] \quad (3)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(Y_i - \hat{Y}_i)^2}{n}} \quad (4)$$

$$AIC = -2\log(M) + 2k \quad (5)$$

$$BIC = -2\log(M) + w\ log(n) \quad (6)$$

Where, *n* denotes the number of observations; *p* is the number of independent regressors; R^2 is the coefficient of determination; Y_i is an observed value of diameter. $\hat{Y}_i$ is a predicted value of diameter; *M* is the maximum likelihood; *k* is the number of independently adjusted Parameters within the equation and *w* is the free parameters to be estimated.

Validation of taper and volume equations

Since it was impossible to obtain an independent validation data set, the Leave-One-Out Jackknife method was used to test equations (Yang & Kung 1983; Rodríguez et al. 2013). The following criteria were evaluated: mean bias error (Bias) (Eq. 7), percentage mean bias error ($Bias_{\%}$) (Eq. 8), standard error of the estimate (SEE) (Eq.9) and percentage standard error of the estimate ($SEE_{\%}$) (Eq.10). Also, the bias variation at different heights was analysed in the best taper equation; 10 relative height classes were created (ej. 0-10, 10-20, ... 90-10) that grouped all the trees. Finally, with the total and merchantable volume equations, the bias variation analysis was performed according to DBH, for which 10 DBH classes were used (ej. 8, 10, ... 26), that aggregated all the observations.

$$Bias = \frac{1}{n}\sum_{i=1}^{n}(Y_i - \hat{Y}_i) \quad (7)$$

$$Bias_{\%} = \frac{Bias}{\bar{Y}} 100 \quad (8)$$

$$SEE = \sqrt{\frac{\sum_{i=1}^{n}(Y_i - \hat{Y}_i)^2}{n-k}} \quad (9)$$

$$SEE_{\%} = \frac{SEE}{\bar{Y}} 100 \quad (10)$$

Where, Y_i is an observed value of diameter or bole volume. $\hat{Y}_i$ is a predicted value of diameter or bole volume. $\bar{Y}$ is the mean of the observed values of diameter or volume. n is the number of observations, k is the number of parameters in the equation. Bias is the mean bias error and SEE is the standard error of the estimate .

Results

Individual tree characteristics for selected genotypes under irrigation treatments

Mean cumulative growth estimates of selected trees for each genotype are presented in Table 3. The DBH data ranged from 11.97 to 22.17 cm and five genotypes (Eb, En, EngH, EgH and EngL) did not show statistical DBH differences by irrigation regime. Contrastingly, Es, Ecg and Ecg genotypes showed smaller DBH at the low irrigation regime. For H, values ranged from 14.15 to 20.70 m, and only Es, Ecg, EgL and EngL genotypes showed a significant decrease in height for the low irrigation regime treatment. Finally, total and commercial volume values ranged from 0.074 to 0.334 m^3 $tree^{-1}$ for the high irrigation and from 0.029 to 0.223 m^3 $tree^{-1}$, for the low irrigation regime. All genotypes showed decreased individual tree volume under low irrigation, being EngL and EgH those that showed the largest response to irrigation.

Regarding the bole form (Figure 3), the same inverse relationship between d/D and h/H was determined for the eight genotypes and irrigation regime treatments. These relationships showed wide variation in-ground line diameter of the evaluated trees (h/H close to zero), and d/D variability decreased as h/H variability increased in both irrigation regimes for the four evaluated equations.

Effects of genotype and irrigation on taper and volume equations

No significant effects of genotype x irrigation regimes interaction, genotypes and irrigation regimes on taper equations were found (Table 4). The LRT test showed p-values greater than 0.22 for the four evaluated equations, and simplified reduced equations independent of genotype and/or irrigation regime are viable. The same results were observed for total and commercial volume equations (Table 4). Therefore, using a generalised equation is optimal since the variables analysed did not generate a gain in accuracy.

TABLE 3: Mean of diameter (DBH), total height (H), total volume (TV) and merchantable volume (MT) characterisation of the eight selected *Eucalyptus* genotypes in contrasting irrigation regimes (Standard deviation for each parameter in parenthesis; Different letters indicate significant differences at 0.05).

Irrigation	Genotype	DBH (cm)	H (m)	TV (m^3 $tree^{-1}$)	MV (m^3 $tree^{-1}$)
High	Eb	19.35^{AB} (1.95)	18.95^{A} (0.28)	0.282^{B} (0.018)	0.185^{B} (0.024)
	Ecg	16.05^{B}(1.84)	15.84^{B} (0.13)	0.139^{D} (0.082)	0.082^{D} (0.068)
	EgH	16.85^{B}(1.45)	19.45^{A} (0.21)	0.210^{BC} (0.012)	0.132^{BC} (0.073)
	EgL	12.82^{C}(1.40)	15.40^{B} (0.09)	0.091^{E} (0.044)	0.044^{E} (0.022)
	En	22.17^{A} (2.70)	20.70^{A} (0.33)	0.334^{A} (0.022)	0.223^{A} (0.012)
	EngH	19.45^{AB} (1.57)	18.57^{A} (0.24)	0.245^{B} (0.015)	0.179^{B} (0.089)
	EngL	17.50^{B} (1.52)	16.52^{B} (0.17)	0.179^{B} (0.012)	0.142^{B} (0.092)
	Es	19.27^{AB} (1.97)	17.97^{AB} (0.24)	0.241^{B} (0.015)	0.155^{B} (0.084)
	Average	17.93 (1.92)	17.92 (0.21)	0.215 (0.013)	0.137 (0.067)
Low	Eb	18.55^{AB} (1.06)	18.06^{A} (0.20)	0.201^{BC} (0.033)	0.133^{BC} (0.097)
	Ecg	14.70^{C}(1.80)	15.80^{C} (0.11)	0.117^{D} (0.063)	0.063^{D} (0.050)
	EgH	16.97^{B}(1.77)	16.77^{AB} (0.16)	0.164^{C} (0.060)	0.105^{C} (0.045)
	EgL	11.97^{C}(1.15)	14.15^{C} (0.07)	0.074^{E} (0.089)	0.029^{E} (0.064)
	En	21.37^{A} (1.38)	19.38^{A} (0.33)	0.337^{A} (0.095)	0.225^{A} (0.077)
	EngH	21.55^{A} (1.81)	18.81^{A} (0.32)	0.326^{A} (0.069)	0.219^{A} (0.056)
	EngL	15.62^{C}(1.85)	15.85^{C} (0.14)	0.141^{D} (0.085)	0.085^{D} (0.063)
	Es	17.6^{B}(1.93)	15.93^{C} (0.19)	0.195^{B} (0.012)	0.125^{B} (0.056)
	Average	17.29 (1.84)	16.84 (0.19)	0.194 (0.012)	0.123 (0.080)

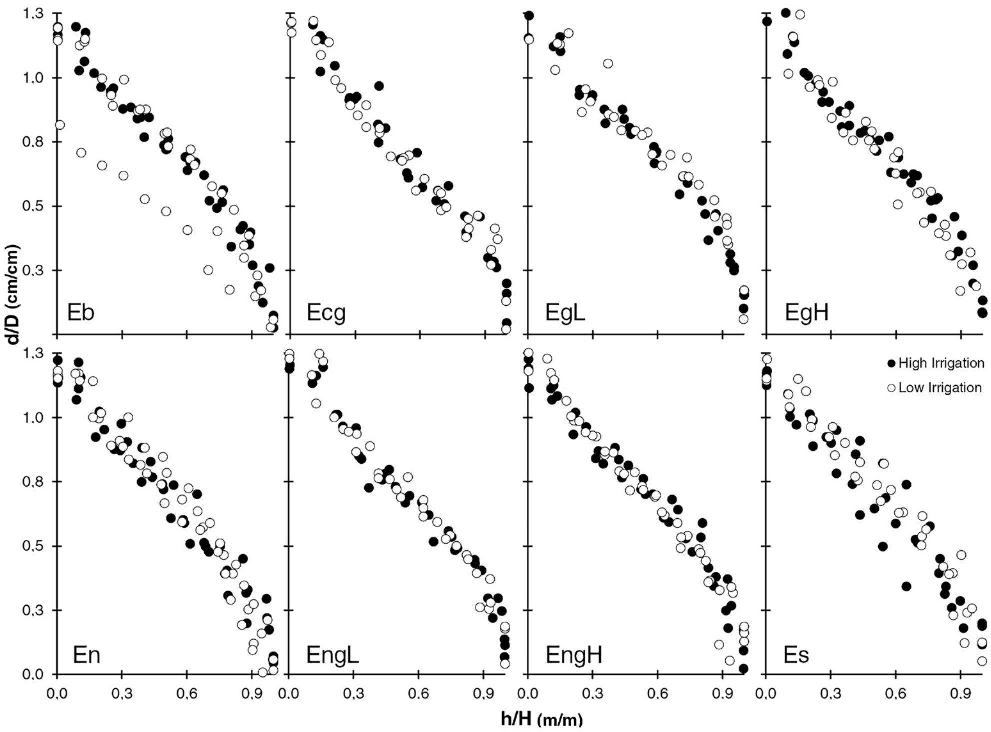

FIGURE 3: Relationship between relative diameter ratio (d/D) and relative height ratio (h/H) for all evaluated Eucalyptus genotypes under both irrigated treatments.

Taper equation selection

All adjusted parameters of the four equations analysed were significant (Table 5). The equation with the best fit was Kozak's (2004) model with the lowest RMSE, AIC and BIC in comparison to other models, and presented the best accuracy and smallest residual distribution range (±1.4%) (Figure 4a). The second-best equation was Kozak et al.'s (1969) model, that showed a good Adj-R^2 (0.960) and RMSE, AIC, and BIC values slightly higher than those of Kozak's (2004) model. However, its residual distribution (Figure 4b) showed a larger dispersion (±4%) but still maintained a uniform distribution. The Ormerod (1973) equation showed intermediate RMSE, AIC and BIC values suggesting a lower quality fit compared to Kozak's (2004) and Kozak et al.'s (1969) models and a broader but uniform residual distribution range compared to Kozak (2004) or Kozak et al. (1969) models (Figure 4c). Finally, the Max and Burkhart (1976) equation presented the poorest fit from all models with the lowest Adj-R^2 values and the highest RMSE, AIC, BIC, and MAD estimates. Also, its residual distributions showed the highest heteroscedasticity of all four equations (Figure 4d).

TABLE 4: Likelihood ratio test (LRT) and their respective P-Value (*p*) for genotype, irrigation regime and genotype x irrigation regime interaction effects on taper and volume equations.

Equation	Variable					
	Genotype x Irrigation		Genotype		Irrigation	
	LRT	*p*	LRT	*p*	LRT	*p*
Taper						
Kozak (2004)	2.02	0.09^{ns}	1.33	0.12^{ns}	0.44	0.33^{ns}
Kozak et al. (1969)	1.33	0.12^{ns}	0.45	0.33^{ns}	0.32	0.25^{ns}
Max and Burkhart (1976)	0.34	0.25^{ns}	0.22	0.50^{ns}	0.24	0.52^{ns}
Sharmar and Oderwald (2001)	0.45	0.33^{ns}	0.22	0.50^{ns}	0.23	0.52^{ns}
Ormerod (1973)	1.46	0.10^{ns}	0.43	0.35^{ns}	0.30	0.27^{ns}
Volume						
Total	1.94	0.10^{ns}	1.10	0.20^{ns}	0.40	0.41^{ns}
Merchantable	1.90	0.11^{ns}	0.99	0.36^{ns}	0.38	0.40^{ns}

note: ^{ns} not significant, * significant at 0.05.

TABLE 5: Adjusted coefficients and statistical criteria values for selected taper equations considering all Eucalyptus genotypes and irrigation regimes.

Equation		Parameter	SE	P-Value	Adj-R^2	RMSE	AIC	BIC	Ranking
Kozak (2004)	α_0	1.032	0.033	0.001*	0.986	0.877	109.500	90.322	1
	α_1	0.980	0.009	0.010*					
	α_2	0.010	0.001	0.003*					
	β_0	0.312	0.002	0.007*					
	β_1	-0.722	0.010	0.001*					
	β_2	0.745	0.012	0.006*					
	β_3	2.533	0.040	0.001*					
	β_4	0.052	0.003	0.009*					
	β_5	-0.589	0.004	0.001*					
Kozak et al. (1969)	β_0	-2.092	0.250	0.005*	0.960	1.040	120.437	109.101	2
	β_1	0.820	0.076	0.003*					
Ormerod (1973)	β_0	0.582	0.045	0.001*	0.936	1.149	123.809	112.233	3
Max and Burkhart (1976)	α_1	0.822	0.012	0.001*	0.913	2.800	130.711	133.010	4
	α_2	0.285	0.034	0.002*					
	β_0	-0.793	0.089	0.003*					
	β_1	-1.066	0.233	0.004*					
	β_2	1.540	0.345	0.002*					
	β_3	0.361	0.098	0.001*					

note: ^{ns} not significant, * significant at 0.05

Volume equations

For total and merchantable volume equations all coefficients of the general model equations were significant (p-value<0.001) and an estimated error (SE) less than 0.023 (Table 6). The equations showed good fits, Adj-R^2 estimates greater than 0.98, and low RMSE, AIC and BIC values. When analyzing our generalised equation against Smalian estimates for total volume (Figure 5a), an underestimation of 3 to 8% was observed in trees with individual volumes ranging from 0.25 to 0.32 m^3 $tree^{-1}$, and underestimation increased as the volume of the tree increased. Residuals distribution (Figure 5b) showed uniformity and its variation was less than 0.3%, indicating a good accuracy level.

Similar to total volume, the merchantable volume equation (Figure 5c) showed a slight tendency to underestimate volume in trees with a merchantable volume greater than 0.22 m^3 $tree^{-1}$ and the same trend to increase underestimation as the size of the tree increased was observed but reached a maximum of 5% of

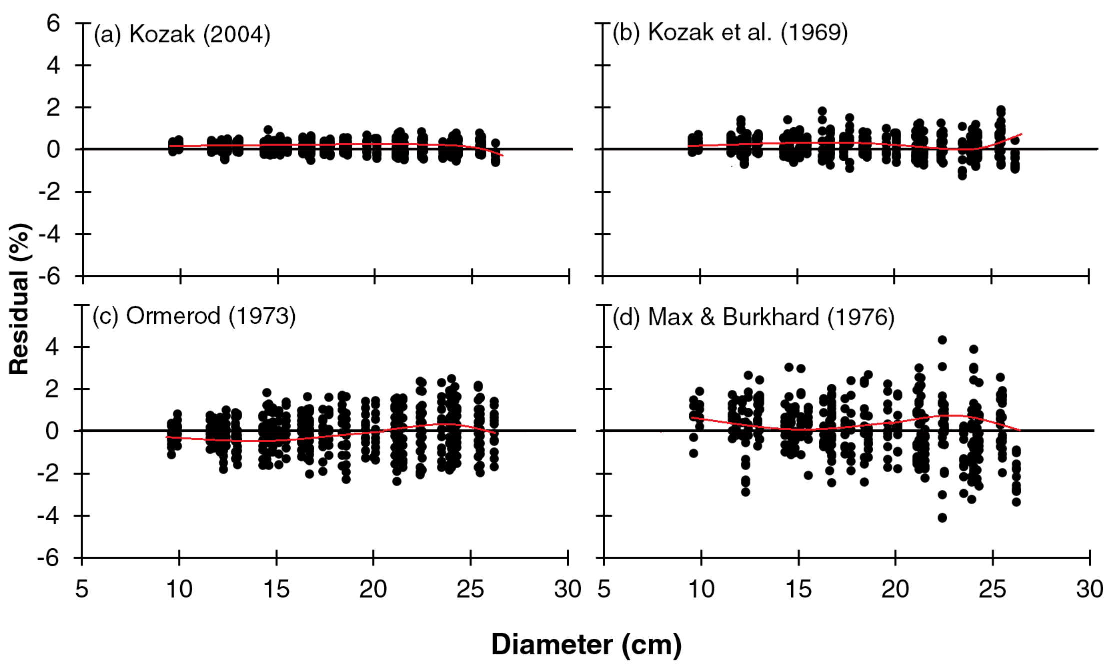

FIGURE 4: Residual plots for the generalised model equations adjusted across genotypes and irrigation regime treatments.

TABLE 6: Adjusted coefficients and statistical criteria values for total and merchantable volume equations considering all Eucalyptus genotypes and irrigation regimes.

Volume equation		Parameter	SE	P-value	Adj-R^2	RMSE	AIC	BIC
Total	β_0	2.750 x10^{-5}	>0.001	>0.001*	0.980	0.020	132.789	138.901
	β_1	2.082	0.023	0.002*				
	β_2	0.974	0.009	0.001*				
Merchantable	β_0	3.912x10^{-5}	>0.001	>0.001*	0.982	0.017	129.444	132.562
	β_1	1.71	0.019	0.002*				
	β_2	1.164	0.008	0.001*				

note: ^{ns} not significant, * significant at 0.05

underestimation. On the other hand, the distribution of the residuals (Figure 5d) was homogeneous and showed less than 0.15% variation indicating high accuracy for this equation.

Validation of equations

Validation with the Leave-One-Out Jackknife method (Table 7) showed that the selected general equations were valid for predicting the taper and volume of *Eucalyptus* boles. Kozak's (2004) taper equation showed high flexibility with a negative bias of -0.081 cm ($Bias_{\%}$ of -0.692%), the $SEE_{\%}$ was less than 4.5% (SEE of 0.509 cm), showing good precision in data estimation. Regarding bias variation in relative height classes (Figure 6a), showed a uniform bias in classes from 0 to 70%, with a mean value of -0.007 cm. In classes above 70% (relative height), the bias increased with a negative trend, with an average value of 0.210 cm.

Similar results were obtained regarding the volume equations (total and commercial) (Table 7). Again, the bias showed negative values, less than 5.0 x10^{-3} m^3 $tree^{-1}$, with an average $Bias_{\%}$ of -3.27%, showing good accuracy for volume estimation. On the other hand, SEE was less than 8.0 x10^{-3} m^3 $tree^{-1}$ (average $SEE_{\%}$ 5.23%), showing good precision for estimating volume per tree. According to DBH classes, the bias variation analysis had a uniform bias between 8 and 22 cm (average 1.57 x10^{-3} m^3 $tree^{-1}$) for total volume (Figure 6b), and trees with a DBH ≥22 cm showed a negative increase in bias on average of -1.83 x10^{-2} m^3 $tree^{-1}$. Finally, the merchantable volume equation showed excellent accuracy in DBH classes (Figure 6c); with an average bias of -1.25 x 10^{-3} m^3 $tree^{-1}$ in classes from 8 to 18 cm, and it was in trees with DBH ≥20 cm, that bias increased with an average of -1.50 x 10^{-2} m^3 $tree^{-1}$.

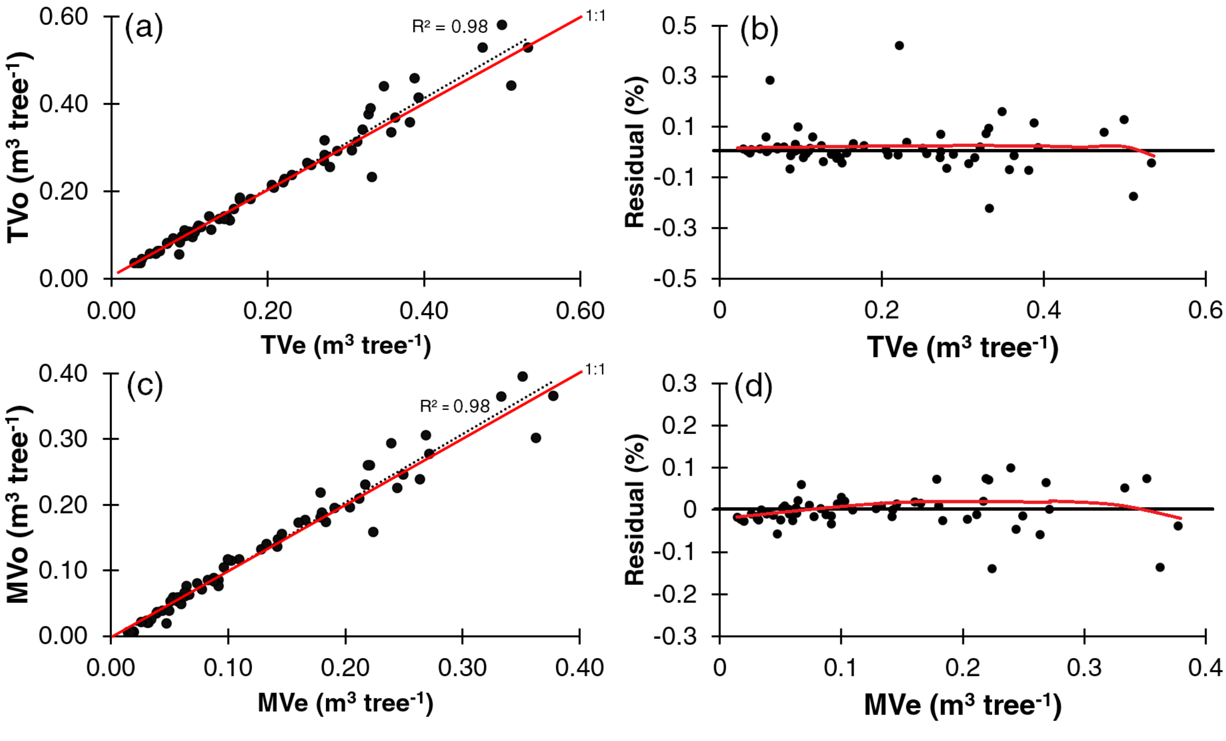

FIGURE 5: (a) (c) Predicted (Ve) versus observed (Vo) individual tree total (T) and merchantable (M) volume. (b) (d) Plot of residues distribution against individual tree total (T) and merchantable (M) volume predicted values considering a generalised model considering all genotypes and irrigation regime treatments.

TABLE 7: Statistical criteria (Bias, $Bias_{\%}$, SEE and $SEE_{\%}$) obtained to validate taper and volume (total and merchantable) equations with the Leave-One-Out Jackknife method.

Equation	Statistical criteria	Value
Taper Kozak (2004)	Bias (cm)	-0.081
	$Bias_{\%}$	-0.689
	SEE (cm)	0.509
	$SEE_{\%}$	4.351
Total volume	Bias (10^{-3} m^3 $tree^{-1}$)	-4.402
	$Bias_{\%}$	-2.268
	SEE (10^{-3} m^3 $tree^{-1}$)	8.371
	$SEE_{\%}$	4.31
Merchantable volume	Bias (10^{-3} m^3 $tree^{-1}$)	-5.250
	$Bias_{\%}$	-4.268
	SEE (10^{-3} m^3 $tree^{-1}$)	7.557
	$SEE_{\%}$	6.144

Discussion

Effects of irrigation regime and genotype on taper and volume equations

Developing individual tree taper, total and merchantable volume equations is essential to estimate and make productivity projections (Li et al. 2017) and optimise a forest crop's growth ((Scolforo et al. 2019). In our study, a generalised taper and volume equations was obtained in which the effect of the genotype, water regime and interaction of both variables was considered. Our results indicated that none of these effects affected taper and individual tree volume equations (Table 4), similar to what has been reported before by Gomat et al. (2011) and Scolforo et al. (2019) in which a single generalised model equation could be used for *Eucalyptus* regardless of genotype and climatic environment.

Gomat et al. (2011) and Scolforo et al. (2019) highlighted that irrigation regime may affect tree growth, but they found no evidence of these effects on individual tree bole shape. Binkley et al. (2017) showed that temperature and precipitation variations directly affected growth rate and transpiration but not bole profile shape for several Eucalyptus clones across a large climatic gradient. The plasticity of *Eucalyptus* growing in different water availability environments affects their productivity but does not change their individual tree shape (Hill & Hollender 2019). Studies developed by Souza et al. (2016) and Cerqueira et al. (2021) determined that taper is mainly affected by variables such as competition for space, severe water stress, or aspects associated with the spatial location of cultivation, but broad climatic factors are not significant. However, as Scolforo et al. (2018) suggested, excluding climatic variables, such as water regime, does not mean that it may not add precision to taper-volume equations for different species.

In the case of genotypes from advanced tree improvement programs, clonal material is selected to maximise productivity and other desirable characteristics, whereas taper variability is usually deployed by selecting cylindrical trees of maximum individual tree volume to optimise final harvest (Vallejos et al. 2010). This may explain why the genotype effect was not significant in our study and in practice may be omitted from taper and volume equations for a broad range of genotypes for a single species (Scolforo et al. 2019). Interestingly, our study found similar results, even for a broad range of taxa tested at this site.

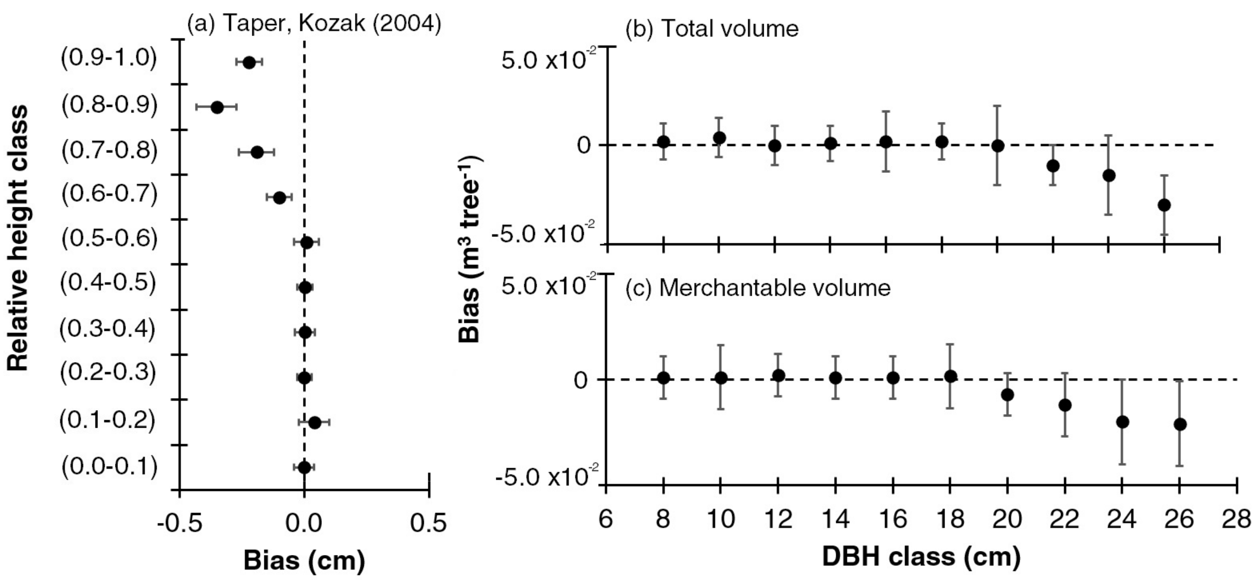

FIGURE 6: Bias variation obtained in each class analysed (relative height and DBH) in the validation of: (a) taper; (b) total; and (c) merchantable volume equations. The bars represent the 95% confidence intervals.

Selected taper equation

Kozak's (2004) equation showed the best fit in our study and many authors have considered it the optimal equation. This result is similar to previous studies carried out in different Eucalyptus species such as Son et al. (2009), Scolforo et al. (2018) and Scolforo et al. (2019), in which it was suggested that the Kozak's (2004) equation showed the best response to adaptation to the shape of *Eucalyptus* boles. Kozak's (2004) equation has the advantage of describing the lower part of the shape of the bole as a neiloid, the middle as a paraboloid and the upper part as a cone. The equation considers a bole shape transition that responds to most species that have been analysed, providing flexibility and reduced error (Rojo et al. 2005), aspects that have allowed its use on a large number of coniferous and broadleaf species (Li & Weiskittel 2010). The model allows a simple adjustment and may provide representative generalised models for taxa or geographic regions (Son et al. 2009).

Kozak et al.'s (1969) and Ormerod's (1973) equations, which are considered simple models, showed lower quality of fit compared to Kozak's (2004) equation. In addition, the simplicity of these equations does not provide a better representation of the shape of the bole generating over or underestimates (Souza et al. 2018). Muhairware (1999) indicated that simple models provide ease of estimation, are algebraically integrable but provide serious limitations for species with irregular shapes or that show transitions along the bole (de Andrade 2014), an aspect that caused the adjustment to be lower, increased variation of residuals (Figure 4), and final equations were not considered in our study.

Finally, Max & Burkhart's (1976) equation showed the poorest adjustment and most considerable bias of all the evaluated equations. Although it is a segmented model that shows biologically consistent behavior since it makes the transition from a neiloid to a paraboloid, in addition to having an algebraic simplicity of use (McTague & Weiskittel 2021); however, it had significant deficiencies in the explanation of transition in the bole shape by generating a non-continuous model (McTague & Weiskittel 2021; Salekin et al. 2021). Our results suggest that it is less functional than other models such as Kozak's (2004) model, providing the poorest adaptation to model bole shape, and it was not considered for providing a valuable final model.

Study considerations and limitations

The generalisation of equations that accurately describe the shapes of trees in different irrigation regimes and with different genotypes simplifies forest management, productivity projection, and decision-making (Miguel et al. 2011; da Silva Menezes et al. 2020), and our model contributes to this. However, two elements must be considered: Firstly, the plantation experiment comprised of middle-aged trees, comparable to studies such as Gomat et al. (2011) and Campos et al. (2014), where *Eucalyptus* after three years of age had the same bole shape although the canopy had not completely closed. Changes in stocking may affect bole shape and proposed equations need to be used with caution for more advanced stages of plantation with or without silvicultural treatments applied.

The second aspect to consider is the validation of our equations. Unfortunately, due to logistical and budget constraints and the availability of the same genotypes in a single experiment, it was impossible to validate our equations with an independent data set. Therefore, it was decided to use the Leave-one-Out Jackknife validation method, ideal for analyzing small-sized samples and avoiding overestimating the bias and standard error in the equations (Pal 2017). Furthermore, it is a safe validation method in volume and taper equations (Yang & Kung 1983; Rodríguez et al. 2013), showing a greater accuracy gain if used in equations that have been fitted with mixed models that reduce the error of estimating the coefficients of the equation compared to other methods (Trincado & Burkhart 2006). Very few studies evaluate taper and volume in large sets of genotypes grown in different water conditions, so having this information provides a first step for modeling the species in the study region. In addition, previous studies by Benbrahim and Gavaland (2003) have shown that taper studies without independent validation data sets are viable when seeking to understand new silvicultural conditions and species, such as was the case of our study.

Conclusions

No statistically significant effects of irrigation regime, genotype, and interactions of genotype with irrigation regime were found for any of the individual tree taper, total and merchantable volume equations evaluated; therefore, the use of a generalised equation regardless of the taxa or water regime may provide reliable estimates across the evaluated genotypes under contrasting water availability conditions. The Kozak (2004) equation showed the best performance of all evaluated models and equations of total and commercial volume showed a slight underestimation of individual tree volume for larger trees.

The use of a generalised equation for taper and total and commercial volume, regardless of taxa or water regime, would simplify forest modelling, management and estimates of Eucalyptus plantation productivity.

Competing interests

The authors have no competing interests.

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Author contributions

All the authors contributed to all aspects of the study and manuscript preparation.

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