Leaf area estimation from tree allometrics in *Eucalyptus globulus* plantations

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Abstract: Data from five studies on the relationships between dendrometric measurements and leaf area of *Eucalyptus globulus* Labill. plantations were pooled and analyzed to develop regression models for the estimation of leaf area of individual trees. The data, collected at two sites in west-central and southwestern Portugal, varied in age from 2 to 19 years and in plant density from 481 to 1560 trees/ha and included both first and second rotation coppice stands. A total of 29 nonlinear regression models were tested and ranked with a multicriteria evaluation (MCE) procedure, based on goodness-of-fit statistics, predictive ability statistics, and collinearity diagnostics. The best models were validated using an independent data set. The final model selection was based on comparisons of prediction residuals data, statistical tests, and silvicultural and physiological considerations. One model is proposed as adequate for leaf area estimation of *E. globulus* plantation trees. This model contains four parameters and independent variables that quantify stem diameter, crown size, and stand density.

Résumé : Les données de cinq études sur les relations entre les mesures dendrométriques et la surface foliaire dans des plantations de *Eucalyptus globulus* Labill. furent regroupées et analysées dans le but de développer des modèles de régression capable d'estimer la surface foliaire des arbres pris individuellement. Les données collectées dans deux sites du centre-ouest et du sud-ouest du Portugal variaient pour l'âge de 2 à 19 ans et pour la densité de 481 à 1560 tiges/ha et provenaient de taillis à leur première ou seconde révolution. Au total, 29 modèles de régression non linéaire furent testés et classés à l'aide d'une procédure d'évaluation multi-critères basée sur le coefficient de détermination, la capacité de prédiction et la colinéarité. Les meilleurs modèles ont été validés avec un groupe de données indépendantes. La sélection finale du modèle a été faite sur la base de comparaisons de données résiduelles de prédiction, de tests statistiques et de critères sylvicoles et physiologiques. Un modèle adéquat pour estimer la surface foliaire de *E. globulus* en plantation est proposé. Ce modèle contient quatre paramètres et variables indépendantes qui quantifient le diamètre de la tige, la dimension du couvert et la densité.
[Traduit par la Rédaction]

Introduction

Leaf area index (LAI), defined as the projected or silhouette area of leaves per unit area of ground (Monteith and Unsworth 1990), is a fundamental parameter of canopy structure because of the strong links to primary productivity, through light interception and evapotranspiration, as well as through rainfall and pollutant interception (Gholz 1982; Marshall and Waring 1986). Direct measurements of leaf area (LA) are destructive and impractical for systematic use in forest canopies. Therefore, estimation of tree and stand LA is often based on dimension analysis equations that describe biometric relations between easily measured plant dimensions and foliage area or biomass of trees (Bonham 1989; Woods et al. 1991).

Commonly used predictors for LA and foliar biomass are tree diameter at breast height (Snell and Brown 1978; Marshall and Waring 1986; Gazarini et al. 1990; Gholz et al. 1991; Woods et al. 1991; Shelburne et al. 1993), diameter or cross-sectional area at the base of the live crown (Hungerford 1987; Shelburne et al. 1993), and sapwood area (SA) measured at various heights in the stem (Grier and Waring 1974; Snell and Brown 1978; Whitehead 1978; Kaufmann and Troendle 1981; Waring et al. 1982; Marshall and Waring 1986; West and Wells 1990; Robichaud and Methven 1992; Hees and Bartelink 1993), including sapwood permeability determination (Shelburne et al. 1993). Other individual tree measures used as LA predictors are the height of the base of the live crown (Shelburne et al. 1993), total tree height and crown length (Hungerford 1987), and tree age (West and Wells 1990). Dean and Long (1986) and Smith and Long (1989) estimated LA using both sapwood area and the distance from the SA cross section to midway into the crown.

Stand-level parameters have also been included in some empirical models of LA estimation, such as basal area (Hungerford 1987; Gholz et al. 1991) and stem density (Woods et al. 1991). The influence of various stand characteristics on relationships between individual tree predictors and LA has also been analyzed. Hungerford (1987) determined that for lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stand densities ranging from 2900 to 17 800 stems/ha, differences in the ratio of foliage area to sapwood area were not significant. Shelburne et al. (1993) analyzed the effects of site index, stand density, and sapwood permeability on the relationship between leaf area and sapwood area in four loblolly pine (*Pinus taeda* L.) stands. They found that regression equations that predicted leaf area from sapwood area differed

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Table 1. Summary of the data from the five *E. globulus* leaf area studies.

Source	Stand	No. of trees sampled	Density (trees/ha)	Age (years)	Rotation
		Fitting data set			
Pedro 1991	1	9	950	6	1st
J.Tomé[a]	1	9	981	7	1st
Pereira et al. 1989	C88[b]	10	1102	2	1st
Pereira et al 1989	C89[b]	10	1102	3	1st
M.Tomé[a]	AV01, AV02	10	1395, 1560	18	1st
M.Tomé[a]	AV03, AV04	10	981, 1070	18	1st
M.Tomé[a]	AV05, AV06	10	745, 807	18	1st
M.Tomé[a]	AV07, AV08	10	590, 601	18	1st
M.Tomé[a]	AV09, AV10	10	481, 487	18	1st
		Validation data set			
Pereira et al. 1989	F88[b]	10	1079	2	1st
Pereira et al. 1989	F89[b]	10	1084	3	1st
Fabião 1986	BC	10	1111[c]	5	1st
Fabião 1986	EC	10	1111[c]	10	1st
Fabião 1986	AV	8	1111[c]	19	1st
Fabião 1986	AVF80	20	1111[c]	4	2nd
Fabião 1986	AVJ81	20	1111[c]	3	2nd
Fabião 1986	AVJ82	20	1111[c]	2	2nd

[a] Unpublished data.

[b] C and F are control and fertilized stands. C88 and C89, F88 and F89 are plots for measurements taken in 1988 and 1989, respectively.

[c] Initial density.

in terms of stand basal area but were insensitive to site-quality variations. Inclusion of sapwood permeability measurements did not significantly improve model fitting.

The purpose of the present work was to develop practical, easy to implement regression models to estimate LA of *Eucalyptus globulus* Labill. plantations from standard dendrometric measurements, over a range of tree ages and stocking levels and at two locations in west-central Portugal, with the aim of obtaining a model applicable at least at a regional level. These simple requirements excluded the use of SA measurements at any height in the stem. SA was not available for any of the data analyzed, and its measurement was considered too impractical and time-consuming for extensive application. The physiological significance and predictive value of this variable in leaf area estimation studies is certainly acknowledged, although it has not been clearly established whether LA is dependent on SA, as the pipe model would predict, or whether SA is a function of LA as a result of the dependency of sapwood production on foliage area (Kaufmann and Troendle 1981; Shelburne et al. 1993).

Data and methods

Stand characteristics

Data from five studies were analyzed, all dealing with silhouette LA estimation by destructive methods in *E. globulus* plantations. These studies took place at Quinta do Furadouro, Óbidos (Fabião 1986; Pereira 1989; M. Tomé, unpublished data) and at Herdade de Espirra, Palmela (Pedro 1991; J. Tomé, unpublished data). Quinta do Furadouro is located in west-central Portugal (39°20′N, 09°15′W), about 10 km from the Atlantic Ocean. Predominant soil type is a sandy Podzol associated with Eutric Cambisols. Mean annual temperature is 15.2°C, and mean annual precipitation is 608 mm. Herdade de Espirra, located in southwestern Portugal (38°38′N, 08°36′W), has mean annual temperature of 15.6°C and mean annual precipitation of 708 mm. Eutric Cambisols are the main soil type.

As shown in Table 1, data span a relatively wide range of stand ages (2 to 19 years) and densities (481–1560 trees/ha) and include both first- and second-rotation coppice stands. All data were collected in January and February, except for those from Pedro (1991) and J. Tomé (unpublished data), who did their fieldwork in June and October, respectively. From the 196 trees available, 88 were used to fit the models and 108 trees were used for model validation purposes (plots F88 and F89 from Pereira et al. (1989) and all the data from Fabião (1986)). Table 2 shows summary statistics for the model fitting and validation data sets.

Dendrometric measurements, selection of trees, and leaf area sampling procedures

The set of dendrometric measurements common to all experiments included the following tree variables: diameter at breast height (DBH), diameter at the base of the live crown (DBC), total height (HT), and height at the base of the live crown (HCB). Crown depth (CD) was calculated as HT – HCB, and crown ratio (CR) as CD/HT. Fabião (1986) defined base of the

Table 2. Summary statistics of fitting and validation data sets.

	Fitting data (n = 88)				Validation data (n = 108)			
	Min.	Max.	Mean	CV	Min.	Max.	Mean	CV
DBH (m)	0.043	0.332	0.164	0.454	0.004	0.295	0.080	0.693
HT (m)	5.030	30.500	18.502	0.411	1.970	33.600	10.702	0.627
DBC (m)	0.034	0.245	0.093	0.426	0.007	0.216	0.059	0.613
HCB (m)	0.100	25.600	11.760	0.672	0.090	24.250	4.828	0.948
CD (m)	0.900	16.500	6.742	0.488	0.660	20.100	5.875	0.580
CR (dimensionless)	0.049	0.982	0.437	0.575	0.158	0.986	0.565	0.324
BA ($m^2 \cdot ha^{-1}$)	2.920	35.914	20.886	0.512	3.352	34.690	10.350	0.580
LA (m^2)	2.220	99.280	24.961	0.731	0.122	76.024	14.112	0.991

Note: CV, coefficient of variation.

live crown as the height of insertion of the lowest live branch included in a visually defined geometrically regular crown envelope. In all subsequent sampling, the base of the live crown was defined by the presence of live branches in at least three of the four quadrants defined around the tree stem. In practice, however, both methods are, to a certain extent, subjective and were considered as equivalent. Some stand variables were also available or could be computed from raw data, namely age, density, and basal area (BA).

Various distinct procedures were used to select trees for destructive leaf area measurements. Pereira et al. (1989) grouped the trees into three DBH classes (mean DBH, ±σ) and randomly selected four trees from the central class and three trees from each of the other two classes, for a total of 10 trees per stand. Pedro (1991) divided their stands into five classes (mean DBH, ±σ, and ±2σ) and randomly selected three trees from the central class, two from each of the ±σ classes, and one from each of the ±2σ classes, for a total of nine trees. J. Tomé (unpublished data) grouped trees into 1-cm classes and randomly sampled one tree from each decile class. M.Tomé sorted all trees by DBH, divided them into five equal frequency classes, and selected the tree closest to the quadratic mean DBH of each class.

Fabião (1986), dealing with a more diverse situation, used more complex sampling procedures. For the first-rotation stands, he divided measured sectional areas into at least four classes in each stand and selected a sample of 8 to 10 trees with a sectional area distribution similar to that of the stand. Second-rotation stands presented an additional problem, as several stumps had grown multiple poles. These poles were grouped into at least four DBH classes and subsampled, again in proportion to their overall frequency. A sample of 20 poles was required, because of the high DBH variance in stands up to 4 years old, such as those reported here.

Leaf area estimation procedures followed relatively similar protocols in all of the previously mentioned experiments, varying mainly in the number of sections into which the tree crowns were divided for branch and leaf sampling. Pereira et al. (1989) divided tree crowns into 10 equal-length sections and collected a sample branch from each. The foliated length of the branch was also divided into three equal sections, and four leaves were sampled from each for specific leaf area (SLA) calculations. Total tree fresh leaf weight was measured in the field, and sample leaves of all sections were mixed together and used for the measurement of the ratio of fresh to dry weight, in the laboratory. Specific leaf area ($m^2 \cdot kg^{-1}$) was calculated from leaf areas measured with a LI-COR LI-3000A leaf area meter and dry weights (oven-drying at 80°C for at least 24 h). Total foliar dry weight was determined for each tree, and total leaf area calculated by multiplying dry weight by SLA.

J. Tomé (unpublished data) divided tree crowns into thirds and sampled 20% of all branches. Fresh weight of the foliage of the remaining 80% of branches was determined in the field. Each sample branch was divided into four equal-length sections, from which leaves were collected, weighed, and bagged. Dry weight and leaf area were determined on a 0.2-kg subsample of these leaves. Total leaf area was calculated as in Pereira et al. (1989). Pedro (1991) also divided crowns into three equal-length sections, grouped all leaves from each section, and subsampled 0.2 kg for dry weight calculation. Leaf area was measured on 20 leaves randomly sampled from each third of the crown. Both these authors used the same leaf-drying protocol as Pereira et al. (1989). M. Tomé et al. (unpublished data) did not divide the tree crown into sections, but thoroughly mixed all leaves before extracting two 0.2-kg samples for processing in the same way as the previous authors.

Fabião (1986) sectioned the stems into 2-m segments, starting at breast height and up to a stem diameter of 2.5 cm, resulting in a last segment of variable length. Leaves from the twigs attached to each segment were bagged separately and additionally divided in four age-classes: juvenile, juvenile with petiole, transitional, and adult. This was required because of the young age of the trees and marked age-dependent leaf dimorphism in *E. globulus*. Leaf samples weighing 50 to 60 g were taken from each stem segment and foliar age-class for SLA determination. Partial SLA values were multiplied by their corresponding leaf dry weight to obtain leaf area per segment. Summation over all segments resulted in total tree leaf area values.

Model fitting, selection, and validation

We initially developed a total of 41 models, of which 12 were multiple linear regression models (i.e., models with a structure linear in the parameters) and 29 were nonlinear. All nonlinear models were generalizations of the simple allometric model, which assumes proportional relative growth rates for different plant parts (Causton and Venus 1981), and will be designated as allometric models. In generalized form, an allometric model can be represented as (Causton 1985)

$$[1] \qquad Y = kX_1^{b_1} X_2^{b_2} \ldots X_n^{b_n}$$

where Y is allometrically related to variables X_i, b_i represents the allometric constants, and k depends on the initial conditions

Table 3. Subset of the overall model evaluation matrix, showing performance of the nine best models under the six evaluation criteria.

Model	R^2	Adj. R^2	PRESS[a]	APRESS/n[b]	$\mathrm{VIF}_{\max}$[c]	NCOND[d]
15	0.83	0.82	5 845	6.09	32	205
26	0.83	0.82	6 193	6.18	107	1 069
24	0.80	0.79	7 297	6.60	81	843
13	0.78	0.77	7 554	7.01	40.7	272
33	0.80	0.79	7 530	6.88	211	1 541
14	0.76	0.76	7 569	6.78	497	2 271
35	0.79	0.78	7 484	7.05	599	5 037
41	0.84	0.82	6 516	6.35	2105	39 235
40	0.79	0.77	10 053	6.80	780	15 974

[a] Prediction residuals sum of squares.

[b] Sum of absolute prediction residuals sum of squares/sample size.

[c] Largest variance inflation factor.

[d] Condition number.

and units of the variables. Parameters k and b_i can be a function of stand characteristics.

The collection of new data, or if this is not possible, data splitting or cross-validation are important methods to determine the validity of regression models. Snee (1977) points out some reasons to prefer the validation of regression models with new data, instead of splitting. One of the main problems with data splitting is finding the best way to divide the data into two sets that cover approximately the same region of the multivariate space and have similar statistical properties (Snee 1977). A random partitioning of the data set does not always accomplish this objective. Based on these concepts, some of the data sets available were pooled into a model fitting data set, while the rest were chosen for validation. The data sets from Fabião (1986) include stands representative of different ages and also some second-rotation stands, and was considered adequate to check model robustness to extrapolation. The validation data set also includes the F88 and F89 young fertilized stands of Pereira et al. (1989).

Ordinary least squares estimation was used for linear models, and nonlinear least squares estimation, with the algorithms of the Genstat statistical software (Genstat5 Committee 1987), were used for the so-called allometric models. Model evaluation (Table 3) was performed using goodness-of-fit statistics (coefficient of determination, R^2 and adjusted R^2), predictive ability statistics (prediction residuals sum of squares, PRESS, and absolute prediction residuals sum of squares divided by sample size, APRESS/n), and diagnostic statistics of collinearity in the regressor variables (largest variance inflation factor, $\mathrm{VIF}_{\max}$, and condition number, NCOND (Myers 1986; Montgomery and Peck 1982)).

A preliminary inspection of model performance under these various evaluation criteria revealed that linear models had a consistently poorer performance than nonlinear models, which led to exclusion of the former from further consideration. Selection of the best of the 29 allometric models was accomplished with a linear additive multiple criteria evaluation (MCE) procedure. We used piecewise linear functions to standardize the different natural scales of the six statistics mentioned above to a common [0,1] value scale. Criteria weights, which must sum to 1, were assigned considering the six evaluation statistics or selection criteria grouped into three sets of two criteria each, according to whether they measure goodness of fit, predictive ability, or collinearity. Both criteria in each group were assigned equal weight. Given our main purpose of developing a predictive model for LAI, predictive ability statistics received a total weight of 0.5. Goodness-of-fit statistics were considered the next most important group of criteria, and assigned a total weight of 0.3, while collinearity criteria, primarily included to penalize overfitted models, received a total weight of 0.2.

Residual analysis was then carried out on the best ranked models in order to detect violation of the regression assumptions, namely non-normality of the model error or heterogeneity of its variance, that would affect some of the procedures selected for validation of the best models. Based on the results of this analysis, some models were discarded from further analysis, while others were refitted using more adequate procedures, as explained in the Results and discussion section.

Validation of the models retained after residual analysis was then performed, including some tests of different aspects of validation, as suggested by Soares and Tomé (1993): characterization of model error through the analysis of prediction residuals, statistical testing, and verification of model behavior from a biological standpoint. Model error characterization was based on the computation of several summary statistics for the entire data set (Table 5) and on graphical analysis of absolute prediction residuals by leaf area and age-class (Fig. 1).

Several statistical tests were performed to evaluate model bias (Table 6). Student's t-test evaluates model accuracy, based on the null hypothesis of a mean prediction residual equal to zero. The regression tests are based on the null hypothesis that when observed values are regressed over the corresponding predicted values, a regression line with unit slope and zero intercept should be obtained, if the model is unbiased. The sign test evaluates the significance of the preponderance of positive versus negative difference scores for matched-pair data. It tests the null hypothesis that each difference has a median of zero, i.e., that plus and minus signs occur with equal probability. Wilcoxon's signed-rank test uses the sign and magnitude of the rank of the differences between pairs of measurements. The formal null hypothesis for this test is that the population distribution of differences is symmetrical about zero. Details about these tests can be found in standard statistics textbooks, such as Conover (1980) and Steel and Torrie (1980).

Informal analysis of the validation results failed to clearly identify a preferred model, which led to a second round of MCE, this time using validation statistics as evaluation criteria. Three sets of criteria were considered: the modeling efficiency, as defined by Janssen and Heuberger (1995) (R_{p}^2), which was assigned a weight of 0.1; the set of statistical tests (Table 6), which were assigned an overall weight of 0.3, equally distributed among the five tests; and the mean of the prediction residuals (bias) and of their absolute values (precision) by leaf area and age-class, which were assigned an overall weight of 0.6, equally distributed among the 16 subcriteria. The sum of all weights equals 1. Finally, biological behavior of the best model selected with this second MCE was evaluated, by examination of the variables involved and with response surface plots of the selected model.

Table 4. Ranking, multicriteria evaluation (MCE) score, and functional form of the nine best models.

Model	No. of parameters	MCE score	Model functional form
15	4	0.99	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^2\mathrm{HCB}^{b_{10}+b_{11}\mathrm{BA}}$
26	6	0.95	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^{b_{10}+b_{11}\mathrm{BA}}\mathrm{HCB}^{b_{20}+b_{21}\mathrm{BA}}$
24	6	0.93	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^{b_{10}+b_{11}\mathrm{BA}}\mathrm{CD}^{b_{20}+b_{21}\mathrm{BA}}$
13	4	0.92	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^2\mathrm{CD}^{b_{10}+b_{11}\mathrm{BA}}$
33	6	0.91	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^{b_{10}+b_{11}\mathrm{BA}}(\mathrm{HT/HCB})^{b_{20}+b_{21}\mathrm{BA}}$
14	4	0.89	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^2\mathrm{HT}^{b_{10}+b_{11}\mathrm{BA}}$
35	6	0.87	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^{b_{10}+b_{11}\mathrm{BA}}(\mathrm{CR})^{b_{20}+b_{21}\mathrm{BA}}$
41	8	0.81	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^{b_{10}+b_{11}\mathrm{BA}}\mathrm{DBC}^{b_{20}+b_{21}\mathrm{BA}}\mathrm{HCB}^{b_{30}+b_{31}\mathrm{BA}}$
40	8	0.80	$\mathrm{LA} = (b_0 + b_1\mathrm{BA})\mathrm{DBH}^{b_{10}+b_{11}\mathrm{BA}}\mathrm{DBC}^{b_{20}+b_{21}\mathrm{BA}}\mathrm{HT}^{b_{30}+b_{31}\mathrm{BA}}$

Table 5. Summary statistics of prediction residuals for the seven models selected for the validation phase.

Model	Mean R_{P}[a]	Mean AR_{P}[b]	Max. R_{P}[c]	Min. R_{P}[d]	SSE[e]	R_{P}^2[f]
15	0.91	3.03	22.41	–17.89	3085.55	0.85
26	0.42	3.17	22.65	–17.89	3176.48	0.85
24	–1.76	4.43	21.65	–24.63	4358.06	0.79
13	1.94	4.14	33.70	–18.66	4682.04	0.78
33	0.43	3.17	17.42	–17.03	2569.43	0.88
35	–1.07	3.51	17.56	–27.51	2940.26	0.86
41	0.23	3.41	22.60	–17.16	3474.62	0.83

[a] Mean prediction residuals.
[b] Mean absolute prediction residuals.
[c] Maximum prediction residuals.
[d] Minimum prediction residuals.
[e] Sum of squared errors.
[f] Prediction coefficient of determination.

Table 6. Results of statistical tests of model validation.

Model	*t*-test ($\bar{e}$)	Regression *t*-test Intcpt.=0	Slope=1	Signs (χ^2)	Wilcoxon (z)
15	1.752	1.209	0.891	0.926	–1.738
26	0.974	–0.332	–0.540	5.333*	–0.843
24	–2.862**	–0.038	–7.454**	29.040**	–4.650**
13	3.043**	4.406**	0.287	33.330**	–4.849**
33	0.902	–2.118*	0.044	7.259**	–0.647
35	–2.126*	–4.207**	–3.550**	16.330**	–3.507**
41	0.426	–0.709	–1.450	14.810**	–1.867

*Significant at the 0.05 level.
**Significant at the 0.01 level.

Results and discussion

Multicriteria evaluation of models

The first stage of MCE, based on goodness of fit, predictive ability, and collinearity criteria, led to the identification of a set of nine best ranking models (Table 3). All these models had MCE scores equal to or larger than 0.8, and varying functional forms. The number of parameters ranged from four to eight, and the models contained different combinations of some of the available variables (Table 4). The top-ranked model was one of the simplest, having only four parameters, and the two eight-parameter models obtained the lowest scores of the preferred set. Only three individual-tree variables were present in the top four models, two of which relate to crown dimensions (HCB and CD) and one to stem diameter (DBH). Diameter at breast height was present in all nine models, but DBC appeared only in the two eight-parameter models. All successful models used information pertaining to both stem diameter and canopy size, DBH proved to be more important than DBC, and canopy size variables were more important than total tree height (HT) for the estimation of tree LA. If the sapwood cross-sectional area were the variable controlling leaf area expansion through its influence on water flow, DBC would be expected to be better related to LA than DBH, because at the base of the live crown most xylem elements would be functional, while at breast height a large proportion of the xylem is not functional.

From the statistical standpoint, there are not very large differences in performance between the best and the poorest models according to the goodness-of-fit and the predictive ability criteria. For example, eighth-ranked model 41 had an adjusted R^2 equal to that of the best model, and PRESS and APRESS scores comparable to those of the second-best model. Collinearity criteria, however, are quite selective and penalized heavily the two eight-parameter models, especially model 41. Second-ranked model 26 had higher levels of collinearity than third- and fourth-ranked models 24 and 13, respectively, but this was compensated by good scores on the heavily weighted predictive ability criteria. Model 15 performed best in all criteria except R^2, and thus came close to being the ideal model out of the set of available alternatives.

The residual analysis that was carried out on the nine best ranked models gave indication of non-normal errors in models 14 and 40 (according to analysis of normal plots of the residuals and confirmed by the Shapiro–Wilk's test (Shapiro and Wilk 1965)). As these models had not been ranked among the best, it was decided to exclude them from further analysis. Furthermore, the residual analysis gave evidence of heterogeneous variance for all the other seven models assessed by the Goldfeld–Quandt test described, for instance, in Johnston (1984). These models were then refitted using weighted nonlinear regression techniques (weight = $1/\mathrm{DBH}^2$, for all models). The performance of the models was then deemed sufficiently satisfactory to deserve validation with independent data.

Model validation produced very good results, especially considering that there are clear differences between the model fitting and validation data sets, ensuring true independence

Fig. 1. Absolute prediction residuals by (A) LA class and (B) age-class for the seven models selected for the validation stage. There are only four trees in the 40–80 m^2 class, and none in the 10–15 year age-class.

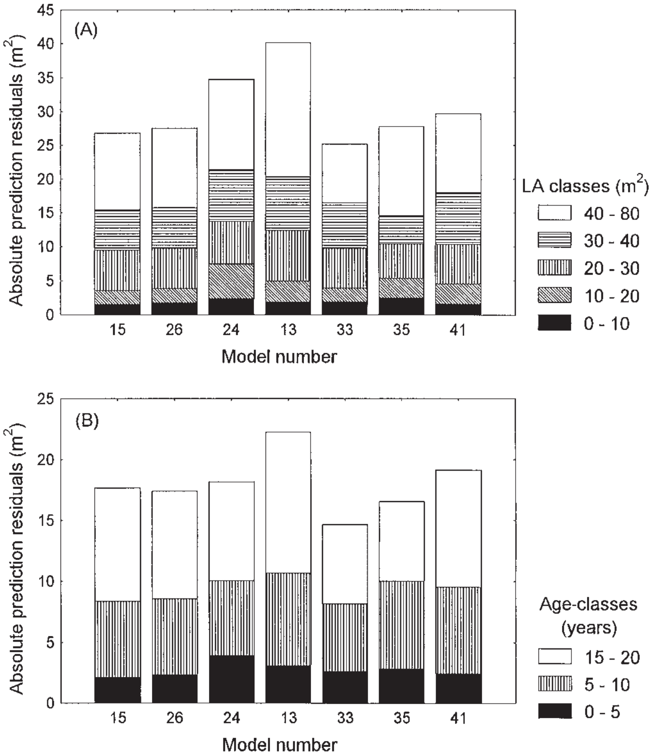
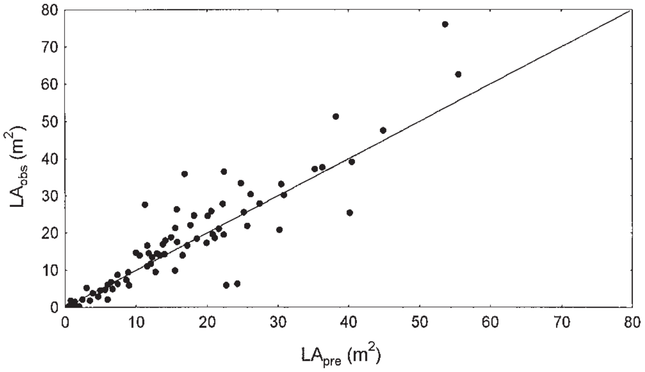


Table 7. Final ranking and evaluation scores resulting from the second stage of multicriteria evaluation (MCE), based on validation results for the seven models previously selected.

Model	MCE score
15	0.613
26	0.597
33	0.591
41	0.539
35	0.398
24	0.282
13	0.275

between the two. The model-fitting data set does not contain any trees from second-rotation stands, while these are the majority in the validation set. The latter also includes trees from fertilized experimental stands, which grew at much faster rates and had higher leaf area index than otherwise comparable nonfertilized stands (Pereira et al. 1989). Re-evaluation of the seven previously selected models using validation statistics as evaluation criteria altered the rankings of most of the models but not the two first-ranked models, 15 and 26, which remained in the first positions. Performance of model 15 is clearly superior concerning overall prediction residuals (Table 5) and statistical tests (Table 6). It is the only model that passed all statistical tests. Precision of the model by LA and age-class is also among the best in most classes (Fig. 1).

Fig. 2. Observed versus predicted data plots for model 15, including 1:1 line.



Next in the final ranking (Table 7) were models 26 and 33, with similar evaluation scores. Both models performed quite well overall, except that they did not pass the sign test ($\alpha = 0.05$ and 0.01, respectively) and that model 33 failed the intercept test ($\alpha = 0.05$). Model 41, although with eight parameters, performed also reasonably well, only failing the sign test. Models 35, 24, and 13 had poorer overall prediction residual statistics, failed most of the statistical tests, and had relatively large residuals by LA class.

Based on this analysis, model 15 was selected as the overall best model to predict leaf area. The parameters of model 15 were tested for significance ($\alpha = 0.05$) using Gallant's (1975) test, in an attempt to simplify its functional form. However, it was found that all the parameters were significantly different from 0. The functional form of the model is

$$[2] \quad LA = (2189.527 + 99.037BA)DBH^2 \times HCB^{0.0494-0.0300BA}$$

The regression between observed and predicted data is shown in Fig. 2. Owing again to heterogeneity of variance in the residuals, the regression was fitted using weighted linear regression techniques (weight = $1/DAP^2$). The regression is given by

$$[3] \quad LA_{obs} = 0.134 + 1.025LA_{pre}, \qquad R^2 = 0.92$$

As can be seen in Fig. 2, the amount of bias was very small.

Response surface analysis and model interpretation

Model 15 was subjected to a more in-depth analysis to establish the biological interpretability of its behavior under different circumstances. Response surfaces of model 15 are shown in Figs. 3A, 3B, and 3C, where BA is handled as a parameter that controls the generation of a family of surfaces. The gridded surfaces represent the model equation in the space of its respective variables, and the spiked points are the measured LA values from the model-fitting data set. The points plotted over each surface represent trees from actual stands with a BA range centered around the BA value used to generate the surface. For BA = 10 (Fig. 3A), actual values are $3\ m^2 \cdot ha^{-1} < BA \leq 15\ m^2 \cdot ha^{-1}$, for BA = 20 (Fig. 3B), actual values are $15\ m^2 \cdot ha^{-1} < BA \leq 25\ m^2 \cdot ha^{-1}$, and for BA = 30 (Fig. 3C), actual values are $25\ m^2 \cdot ha^{-1} < BA \leq 36\ m^2 \cdot ha^{-1}$. In terms of the stands described in Table 1, the points plotted around the surfaces for BA = 10 represent trees from the stands of Pedro (1991)

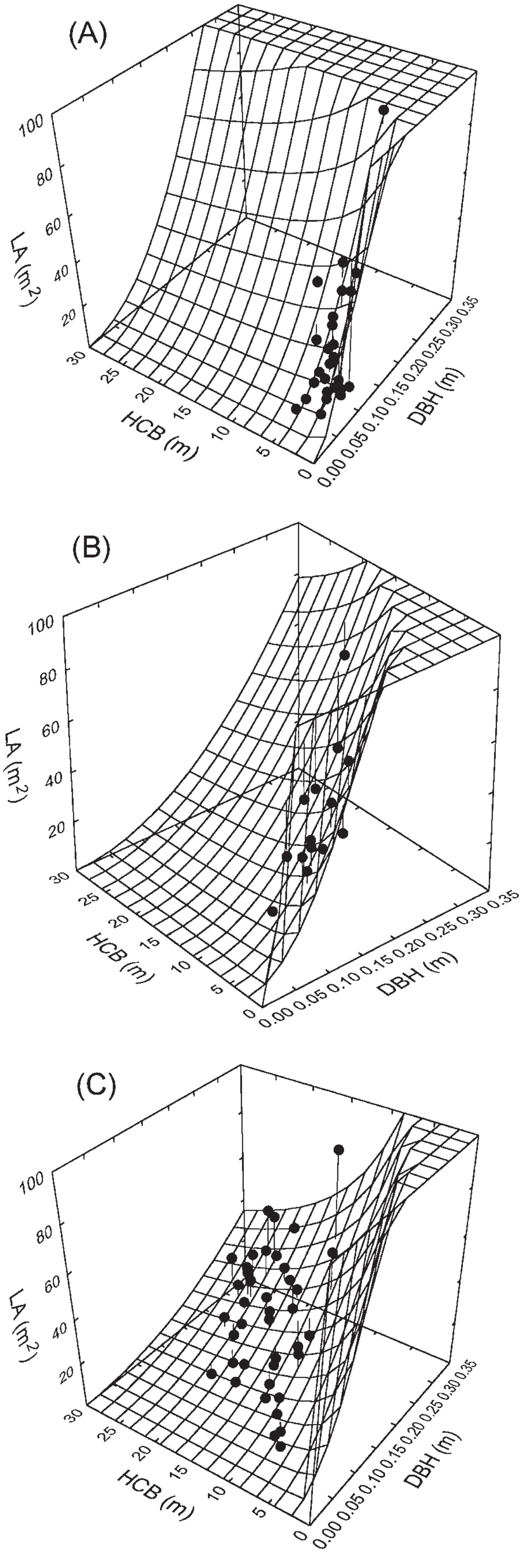


Fig. 3. Response surfaces for model 15 (eq. 2). (A) BA = 10 m^2·ha^{-1} in eq. 2. Points represent trees from actual stands with 3 m^2·ha^{-1} < BA ≤ 15 m^2·ha^{-1}. (B) BA = 20 m^2·ha^{-1} in eq. 2. Points represent trees from actual stands with 15 m^2·ha^{-1} < BA ≤ 25 m^2·ha^{-1}. (C) BA = 30m^2·ha^{-1} in eq. 2. Points represent trees from actual stands with 25 m^2·ha^{-1} < BA ≤ 36 m^2·ha^{-1}.

and stands C88 and C89 of Pereira et al. (1989). For BA = 20, the trees are from the stand of J. Tomé (unpublished data) and stand AV09 of M. Tomé (unpublished data), and for BA = 30 all trees are from the remaining stands of M. Tomé (unpublished data).

A situation of low basal area (Fig. 3A, 10 m^2·ha^{-1}) corresponds to young (2- to 6-year-old) stands, planted at intermediate densities (980 to 1100 trees/ha). HCB (Fig. 3A) was quite low for all trees. LA grew exponentially with DBH, at rates that showed little sensitivity to variations of HCB, within its respective available ranges.

Two stands had intermediate levels of basal area (Fig. 3B, 20 m^2·ha^{-1}), one with 7-year-old trees, present at an intermediate density (981 trees/ha), and one very low-density (481 trees/ha) 18-year-old stand. The relationship between variables was such that the rate of increase in LA with DBH decreased as HCB increased, i.e., LA grew faster with DBH in younger trees. This agrees with the observation that at densities of ca. 1000 trees/ha, E. globulus grows fast in the earlier years but has a much reduced growth rate at ages such as 18 years.

All stands with large basal area (Fig. 3C) were 18 years old, spanning a broad range of densities (487 to 1560 trees/ha). The behavior of the model (Fig. 3C) was similar to that shown at the intermediate levels of basal area, with an increased sensitivity to variations of HCB.

In summary, an increase in stand basal area was generally associated with an increase in HCB, and as this trend intensified, the exponential nature of the rate of increase of LA with DBH was attenuated to near linearity. These results are consistent with the observation that LAI of *E. globulus* stands should reach maximum in early years after planting, possibly when the foliage consists of a mixture of juvenile (shade tolerant and short-lived, ca. 1 year) and adult leaves (shade intolerant and longer lived, more than 1 year) (Madeira et al. 1995). In older trees with foliage completely changed to the adult type, it appears that the maximum foliage mass that can be maintained in each crown tends to be constant, decreasing the CR as HCB increases. This may result from self-pruning of shaded branches occurring as trees grow, but also from the decline in the capacity to produce new leaves and branches with age. These changes determine the reduction in the slope of the relationship between LA and DBH. Based on this analysis, model 15 (eq. 2) was found adequate to estimate leaf area of *E. globulus*. Its application requires only standard dendrometric measurements of DBH, BA, and HCB. In this case model application is simple and does not require time-consuming measurements, because DBC values are not required.

Conclusions

The multiple linear allometry model between LA and several tree and stand variables proved to be appropriate to predict individual-tree leaf area in a broad range of *E. globulus* plantations, covering stands with different ages, densities, fertilization regimes, and even coppice rotations. The most successful models included DBH (accounting for tree dimension) and CR or HCB (accounting for canopy size). DBH proved to be more important than DBC, and canopy size variables were better predictors of LA than tree height. Basal area was the most important stand-level variable, and it was present in all the best ranked models, accounting for the effect of stand density (and competition) on crown shape and dimensions. The model selected was validated with an independent data set with very good results, especially considering that there were clear differences between the fitting and validation data sets, ensuring true independence between the two. The results of the model are easily interpreted from a biological standpoint.

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