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Distance-dependent competition measures for eucalyptus plantations in Portugal

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Abstract – Data from permanent plots and spacing trials of *Eucalyptus globulus* Labill. were used to study distance-dependent competition measures. The data were divided into three subsets representing different stages of stand development and therefore different levels of competition. Different formulations of each type of index were tested. The rules for the selection of competitors as well as the mathematical formulation of each index were considered in the analysis. The linear relationship between the dbh and the distance to which a tree can compete – characteristic of the selection of competitors based on the basal area factor – was not consistent over time. Rules defined as asymptotically restricted non-linear functions of tree size were designed to overcome this problem. The use of a fixed number of competitors was also tested. The evaluation of the prediction ability of each index was based mainly on its performance in multiple linear regression functions for the prediction of the tree basal area annual increment. The results showed the superiority of the indices based on the Richards' function for selecting competitors. This supremacy was more evident when trees in the lower diameter classes were not suppressed. When the asymmetric competition was evident the area potentially available indices showed the best performance. (© Inra/Elsevier, Paris.)

distance-dependent indices / selection of competitors / prediction ability / stand development / *Eucalyptus globulus* Labill. / plantations

Résumé – Indices de compétition dépendants de la distance pour plantations d'eucalyptus au Portugal. Pour étudier des indices de compétition dépendants des distances, on utilise des données des parcelles permanentes et d'essais d'espacement d'*Eucalyptus globulus* Labill. Les données, divisées en trois sous-groupes, représentent différentes étapes de développement du peuplement, donc, différents niveaux de compétition. Diverses formulations de chaque type d'indice de compétition sont testées. Les règles pour la sélection des compétiteurs ainsi que la formulation mathématique de chaque indice sont testées dans cette analyse. La relation linéaire établie entre le diamètre et la distance jusqu'à laquelle chaque arbre peut concurrencer n'est pas consistante dans le temps. Aussi, on propose des règles basées sur des fonctions non linéaires restreintes par une asymptote supérieure. L'utilisation d'un nombre fixe de compétiteurs est aussi testé. L'évaluation de la capacité de prédiction de chaque indice est basée sur sa performance en fonction d'une régression multilinéaire pour la prédiction de l'accroissement annuel en surface terrière au niveau individuel. Les résultats mettent en évidence la supériorité des indices de compétition basés sur la fonction de Richard pour la sélection des compétiteurs. Cette suprématie est plus évidente au moment où les arbres des classes de diamètre le plus bas ne sont pas supprimés naturellement. Lorsque la compétition asymétrique est évidente, les indices basés sur le polygone de Voronoï montrent une meilleure performance. (© Inra/Elsevier, Paris.)

indices dépendants de la distance / sélection des compétiteurs / capacité de prédiction / développement du peuplement / *Eucalyptus globulus* Labill. / plantations

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1. Introduction

Competition may be defined as an interaction between individuals brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survival, growth and/or reproduction of the individual concerned [2]. The effect of competition on growth of individual trees has long been studied in an attempt to predict tree growth as accurately and precisely as possible. Distance-dependent competition indices are used to predict the performance of focal individuals as a function of the interference from a localised subset of other plants [5]. These indices incorporate in a mathematical formulation the number, dimensions and location of certain neighbours that are selected as competitors according to an empirical rule. Conceptually, one would expect some improvement in precision when comparing models that incorporate distance-dependent measures as regressors against simpler models that do not use them. However, most of the comparisons between distance-dependent and distance-independent individual tree growth models do not report the expected differences in prediction ability. One of the main reasons for this poor efficiency of distance-dependent competition indices in explaining tree growth is the fact that the processes controlling inter-tree competition are not well known, making it impossible to develop biologically consistent competition indices. Generally, the competition index formulation simply implies that competition is greater if the subject tree has more neighbours (selected with an empirical rule), if these neighbours are larger and if they are close [3, 7–9, 11, 14, 16, 23]. Depending on the respective formulation, competition indices implicitly assume an asymmetric or symmetric partitioning of plant interference processes into neighbourhood effects and are then used to predict growth of trees growing in stands of different ages independently of the stage of stand development. Competition processes have been defined according to two basic models: symmetric/asymmetric and one-sided/two-sided competition [4, 18, 31, 32]. In two-sided competition resources are shared (equally or proportionally to size) by all the trees while in one-sided competition larger trees are not affected by smaller neighbours [4, 33]. When there is perfect sharing relative to size, competition is symmetric [4]. In this study one-sided competition is considered as an extreme case of asymmetric competition and two-sided competition is considered as being symmetric or asymmetric according to whether or not the sharing of resources is proportional to the size of the individuals.

Recently, some indices have used crown measures, therefore reflecting competition for light with some success [5, 14, 21, 22]. However, crown measures are not always available and, it has also been shown for some species that, in the early stages of a stand, competition for light may not be present, although the effects of competition for water and nutrients are evident. Additionally, even when competition for light is the main factor controlling individual plant growth, two-sided competition for water and nutrients also controls plant growth [24].

The objective of the research described in this paper was to select a competition index for future use to model individual tree growth. Some of the existing competition indices were analysed with improvements being proposed when appropriate. Particular attention was given to the rules for the selection of competitors in order to assess their importance in the prediction ability of the indices in comparison with the index formulation. It was also our objective to test how the prediction ability of different competition indices (both formulation and rule) depends on the stage of development of the stand, i.e. if there is an overall best index applicable during all the life of the stand or not. The analysis was based on data from eucalyptus stands in Portugal, managed in plantations without thinnings and without density-dependent mortality, in relation to which a detailed study on the changes in structure, variability and relative growth rate pattern under different intraspecific competition gradients was available [24].

2. Data

Eucalyptus globulus is a fast-growing species that was introduced in Portugal 150 years ago. At present it is the third most represented forest species in Portugal, covering 20.7 % of the total forestland and occupying an area of 3 358.8 × 10^3 ha [10]. The success of eucalyptus was a consequence, in part, of good environmental conditions in a substantial part of the country for eucalyptus growth. In fact, eucalyptus species are highly productive even in areas where drought and nutrient stress occur in spite of the fact that its productivity is strongly dependent on soil water and nutrient availability [13, 19]. In Portugal, eucalyptus plantations are mainly used by the pulp industry and the trees are planted at the final density – thinning and pruning practices are not usually carried out. These stands are intensively managed as a short rotation coppice system in which the first cycle of planted seedlings (single stem) is followed by two or three coppiced stands, with an average cutting cycle of 10–12 years.

Data from permanent plots, two spacing trials and a fertilisation and irrigation experiment of *Eucalyptus globulus* Labill. in first rotation, all located in the centre coastal region of Portugal, were used. The principal criterion for the selection of these plots was the availability of tree co-ordinates or the possibility of obtaining them. This data set includes ten plots from the Alto do Vilão spacing trial with a range of densities between 500 and 1667 trees ha^{-1}. These plots were used by Tomé [27] in a study involving the evaluation of distance-dependent competition measures of different types. The permanent plots and the spacing trials were remeasured at approximately annual intervals; dbh of each tree, a sample of heights and/or dominant height were obtained in each measurement. Data about crown radius or height of the base of the live crown were not available. Dbh and height of each tree were measured in the fertilisation and irrigation experiment at monthly intervals during the first 15 months, every 2 months until the end of 1987 and twice a year thereafter. This experiment was carried out at a 3 × 3-m spacing.

Table I presents a summary of the principal variables that were gathered in the 37 plots selected. An initial set of 54 plots was available but some of them were eliminated by the use of the basal area factor (BAF) 1 m^2 ha^{-1} as a rule to define the border trees in the calculation of the distance-dependent indices. The border trees were selected for each remeasurement in every plot as a function of BAF = 1 and the maximum diameter of each remeasurement. The growth periods not corresponding to 1 year (or multiples of that) were eliminated as eucalyptus is a species characterised by free growth[1]. However, variations of 2 months were considered acceptable. After these eliminations there were 101 growth periods available and a total number of observations at the tree level of 5 409.

Figure 1 presents the site index versus age and the stand density versus tree size graphics. These provide a good summary of the site and stand conditions represented in the data base [30]. Site index was expressed as the mean height of the dominant trees (100 largest dbh trees per hectare) at a base age of 10 years and it was obtained directly by interpolation or estimated according to Tomé [28]. As can be seen in *figure 1I* there is a representative range of sites and ages in the data set. The fertilisation and irrigation experiment is well individualised corresponding to high site indices and lower ages. Most of the plots were monitored more than eight times. *Figure 1II* shows that most of the plots, excluding the spacing trials, had a similar plantation density. In fact, the pulp companies used the 3 × 3-m spacing and small variations around it during the plantation period under analysis (*table I*). At present there is a broader range of spacings and therefore new plots should be added to this database to obtain more general results. In the plots used, natural mortality (self-thinning) was not found, reflecting the under-stocking of the eucalyptus plantations in Portugal. Two plots, clearly shown in *figure 1II*, are an exception, with values of mortality of 23 % at 15 years and 40 % at 25 years.

3. Methods

3.1. Indices used

Most of the authors who analysed existing competition indices [e.g. 1, 3, 18, 29] classified them into distance-weighted size ratio functions, point density measures, area overlap indices and area potentially available. These indices as well as the unilateral version of each index and the modified version developed by Tomé and Burkhart [29] were also analysed (*table II*). The unilateral as well as the modified indices reflect one-sided competition. An analysis of the formulation of the modified indices suggests that they give an indication of the dominance of the tree in relation to its closer neighbours. The

Table I. Characterisation of the 37 plots.

variables	minimum	mean	maximum	SD
plot area (m^2)	450	1162.0	2464	630.6
year of plantation	1965	–	1986	–
age at first measurement (years)	0.9	4.6	10.1	2.2
age at last measurement (years)	4.8	14.7	24.7	5.8
number of measurements	6	10.2	25	4.4
number of trees per plot	36	118	360	70.5
altitude (m)	10	69.7	126	45.1
number of trees at plantation (ha^{-1})	500	1034	1667	268.9
site index at base age 10 years (m)	12.4	21.4	28.1	3.5

where SD is the standard deviation of the variables indicated.

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[1] free growth – "involves elongation of shoots by simultaneous initiation and elongation of new shoot components as well as expansion of performed parts. Such plants, which include eucalyptus,..., continue to expand their shoots late into the summer" [15].

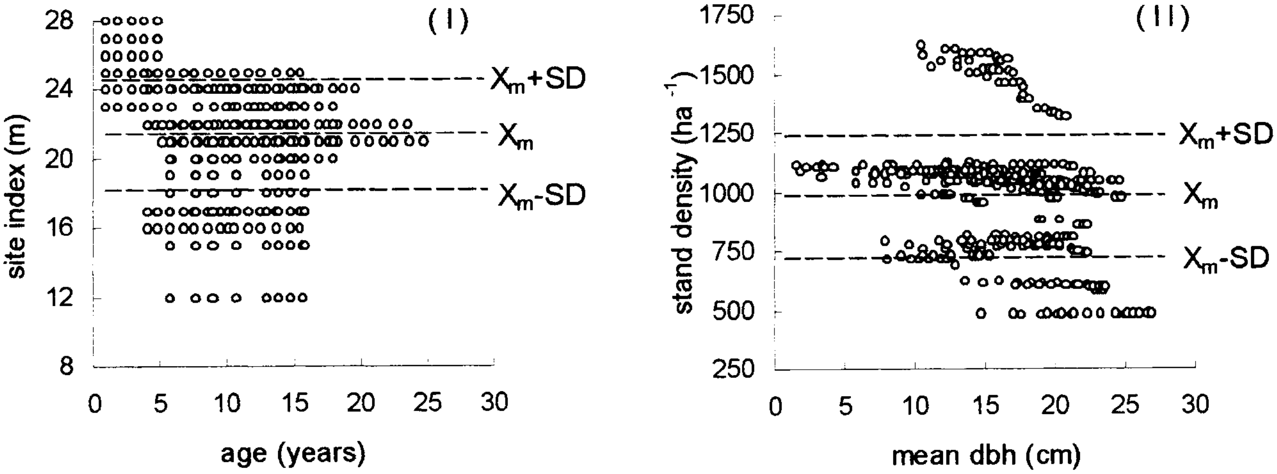

Figure 1. Relation between site index and age (I) and between stand density and mean tree size (II) for the plots used in this study. X_m and SD are the mean value and the standard deviation for the Y-variables.

usual area overlap and distance-weighted size ratio indices are typically two-sided while the area potentially available can be considered as assuming a two-sided asymmetric competition, the level of asymmetry depending on the weight given to the tree size in the definition of the area potentially available.

One aspect taken into consideration in the study of distance-dependent competition measures is the definition of border trees. Two different approaches can be used: 1) to simulate the border trees, which involves the reflection or translation of the trees inside the plot to form a border strip with trees similar in size and distribution with the plot; 2) to define the border trees from the trees on the plot and close to the plot limit. In the first case, approaches based on the linear expansion method can also be utilised [17]. In fact, the use of these simulation methodologies on applications of the competition indices can be accepted but when the objective is the comparison of the prediction ability of alternative indices these methodologies may bias the results. In that case the measurement of real border trees should be considered. Accordingly, in this study the border trees were selected from the trees inside the plots so that every subject tree's possible neighbours had been measured.

3.2. Rules to select competitor trees

To analyse the influence of the rules to select competitors on the ability of the index to predict growth some traditional rules and new rules were tested. The rules to select competitors are usually based on a fixed distance or a fixed number of trees, on overlap areas or on basal area factors, depending on the type of competition index used.

The area potentially available index represents the area of the smaller polygon built with the perpendiculars relative to the subject tree and its neighbours, and selects as competitors the trees whose perpendiculars contribute to the definition of this polygon. In this study a maximum of 35 trees was used as potential competitors. The tree basal area and its square were tested (APA2 and APA4, respectively). The APA4 gives a larger proportion of space to bigger trees than APA2.

The distance-weighted size ratio functions and point density measures were calculated for BAF 1 and 4 $m^2 ha^{-1}$. BAF 1 is associated with a greater number of competitors when compared with BAF 4. From the two modalities of point density measures presented by Spurr [26], including and excluding the subject tree, the second was consistently better in our data.

As crown measurements were not available, the area overlap indices had to be calculated using two empirical definitions of radius of influence area (0.125 × dbh; 0.25 × dbh). The first definition corresponds approximately to a BAF of 4 and the second to a BAF of 1. The rules to select competitors based on BAF define a linear positive relationship between the distance and the size of the tree. For instance, a tree with 40-cm diameter, for BAF = 1, competes until a distance of 20 m and is therefore associated with a high number of competitors (*figure 2I*). In practice, and in plantations, it is not probable that one tree has a strong effect on the growth of neighbours that are 20 m away (more than six rows apart for a 3 × 3-m spacing).

Table II. Distance dependent competition indices.

type of index	version	mathematical formulation
distance weighted size ratio functions	traditional (DR)	$\sum_{j=1}^{n} \frac{d_j}{d_i} \times f(dist_{ij})$
	unilateral (DRU)*	$\sum_{j=1}^{n_1} \frac{d_j}{d_i} \times f(dist_{ij}),\ d_j > d_i$
	modified (DRM)**	$\sum_{j=1}^{n_1} \left(\frac{d_j}{d_i} \times f(dist_{ij})\right) - \sum_{j=1}^{n_2} \left(\frac{d_i}{d_j} \times f(dist_{ij})\right) - \sum_{j=1}^{m} \left(\frac{d_j}{d_{j0}} \times f(dist_{ij})\right)$ (dominant neighbours)–(dominated neighbours)–(dead neighbours)
	modified (DD)**	$\sum_{j=1}^{n} (d_j - d_i) \times f(dist_{ij}) + \sum_{j=1}^{m} (d_{j0} - d_i) \times f(dist_{ij})$ (dominant neighbours)–(dominated neighbours)–(dead neighbours)
point density measures	traditional (PD)	$\frac{2500}{n} \times \left(\sum_{j=1}^{n} (j - 0.5) \times \left(\frac{d_j}{dist_{ij}}\right)^2 \right)$, not considering the subject tree $\frac{2500}{n} \times \left(\sum_{j=1}^{n} (j + 0.5) \times \left(\frac{d_j}{dist_{ij}}\right)^2 \right)$, considering the subject tree
	unilateral (PDU)*	$\frac{2500}{n} \times \left(\sum_{j=1}^{n_1} (j - 0.5) \times \left(\frac{d_j}{dist_{ij}}\right)^2 \right)$, not considering the subject tree, $d_j > d_i$ $\frac{2500}{n} \times \left(\sum_{j=1}^{n_1} (j + 0.5) \times \left(\frac{d_j}{dist_{ij}}\right)^2 \right)$, considering the subject tree
area overlap indices	traditional (AO)	$\sum_{j=1}^{n} \left(\frac{a_{ij}}{A_i} \times \left(\frac{d_j}{d_i}\right)^{k1} \right)$
	unilateral (AOU)*	$\sum_{j=1}^{n_1} \left(\frac{a_{ij}}{A_i} \times \left(\frac{d_j}{d_i}\right)^{k1} \right),\ d_j > d_i$
	modified (AOM)**	$\sum_{j=1}^{n_1} \left(\frac{a_{ij}}{A_i} \times \left(\frac{d_j}{d_i}\right)^{2} \right) - \sum_{j=1}^{n_2} \left(\frac{a_{ij}}{A_i} \times \left(\frac{d_i}{d_j}\right)^{2} \right) - \sum_{j=1}^{m} \left(\frac{a_{ij}}{A_i} \times \left(\frac{d_i}{d_{j0}}\right)^{2} \right)$ (dominant neighbours)–(dominated neighbours)–(dead neighbours)
area potentially available	traditional	$w_k = \frac{d_i^k}{d_i^k + d_j^k}$, in its weighted version with k = 2 (APA2) and k = 4 (APA4)

* larger trees are not affected by smaller neighbours; ** neighbours larger than the subject tree place it at a competitive disadvantage and smaller neighbours place it at a competitive advantage [29]; d, dimension; n, total number of competitors ($n = n_1 + n_2$); n_1, number of dominant neighbours; n_2, number of dominated neighbours; m, number of dead neighbours; i, subject tree; j, competitor; j_0, dead neighbour; $f(dist_{ij})$, distance function between the subject tree i and the competitor j; a_{ij}, overlap area between the subject tree i and the competitor j; A_j, area of influence of the subject tree defined as a function of its dimension.

Each selected competitor has its own contribution to the value of the index and this contribution must decrease when the distance increases or the size decreases. New rules based on asymptotically restricted non-linear functions of tree size are proposed in this paper. These rules are specific for the distance-weighted size ratio function indices and point density measures both in their traditional and modified formulations. The selected functions were hyperbolic and monomolecular and Richards' function (see mathematical formulations in *figure 2I, II, III*, respectively). The monomolecular function is a particular case of Richards' function when m = 0. This selection was based on the graphical form of these functions in their integral formulation and on the existence of a superior asymptote. Each of these functions has two to three parameters: one of them being the asymptote A and the others (k, m) being shape parameters (*figure 2*). Based on the results of a previous study by Soares and Tomé [25], a value of 7 m for the asymptote was used. This distance is a function of tree size and, for the bigger trees, it approaches 7 m. The asymptote of 7 m was found to be the more appropriate based on a previous study in which different asymptotes were tested. This value refers only to eucalyptus trees in plantation (densities ranging from 1 000 to 1 600 trees per hectare). Both functions were restricted to obtain null coordinates in the origin. Different values were tested for the m and k parameters. A fixed number of competitors (four or eight) were also tested.

The consistency of the different rules that were tested, as well as the selection of the parameters in the asymptotically restricted non-linear functions of tree size (testing one value of asymptote and several values for the k and m parameters), was mainly based on the number of selected competitors for a particular rule in different age classes.

3.3. Definition of stages of stand development

The study of evidence and intensity of competition present in the selected data at different moments in time was analysed. For that, and based on Perry [20], the data were initially divided into three subsets representing different competition stages of stand development: 1) small trees present larger relative growth rate (RGR) than large ones – correlation coefficient between RGR and dbh

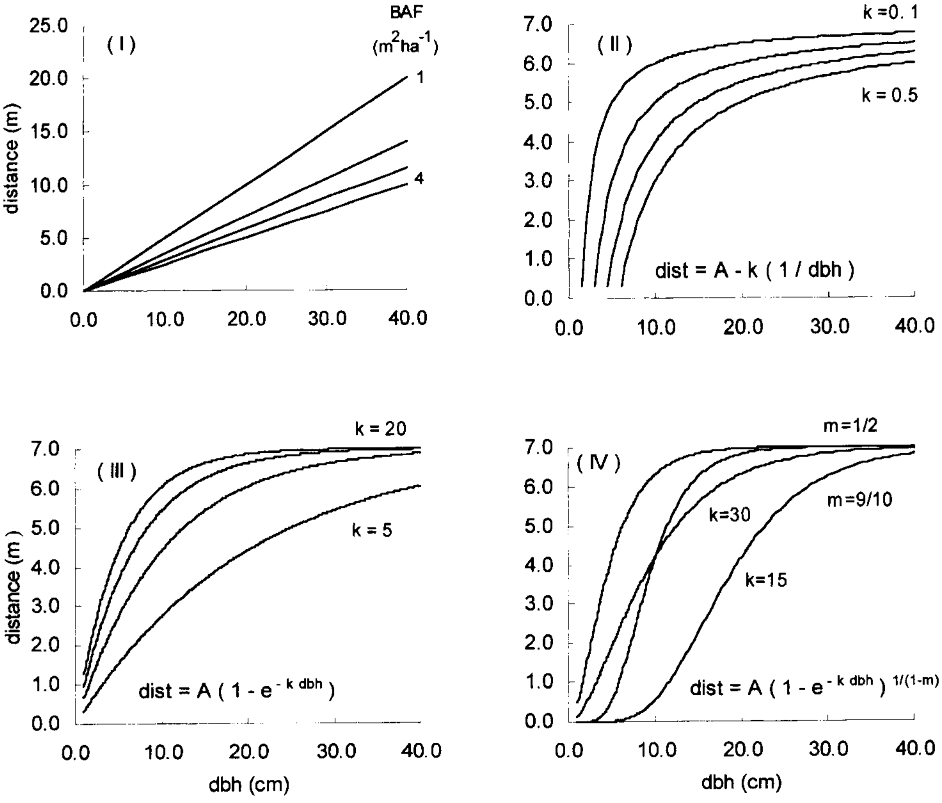

Figure 2. (I) Relation between the distance of competition and the size of a tree for BAF: 1, 2, 3 and 4 $m^2.ha^{-1}$; (II) hyperbolic function; (III) Monomolecular function; (IV) Richard's function. An asymptote of 7 meters was assumed for all the functions. A: asymptote; k and m shape parameters.

negative and significantly different from zero; 2) RGR differs little among social classes – correlation coefficient not significantly different from zero; 3) trees in the lower diameter classes are suppressed – correlation coefficient between RGR and dbh positive and significantly different from zero.

The characterisation of the data subsets is presented in *table III*. It was anticipated that the two-sided oriented indices would give better predictions for subset 1 while the unilateral or asymmetric versions would be more appropriate to predict growth in subsets 2 and 3.

3.4. Prediction ability

The growth of individual trees on particular sites is influenced by a number of factors such as tree characteristics (size and age), microenvironment, genetic characteristics and competitive status [29]. One of the most important predictors of how a tree grows is its own size [20] because past competitive interactions are integrated in current tree size and also because variability is introduced as a consequence of genotypic differences in response to competition and of environmental heterogeneity [6]. Stand density expresses differences in tree growth among different stands, the relative dimension of the tree expresses the dominance of a tree in relation to other trees in the stand and competition indices express local competition among a tree and its neighbours.

The study of the prediction ability of distance-dependent indices was based both on:

– simple correlation of each index with tree basal area growth for each one of the data subsets considered;

– performance in a multiple linear regression equation to predict the annual increment of tree basal area where variables characterising the stand and the individual tree were present:

$$i_b = a_0 + a_1 S_{h,t} + a_2 \, TD + a_3 \, RTD + a_4 \, SC$$

where i_b is the annual increment in tree basal area; $S_{h,t}$, represents a measure of site productivity (site index); TD expresses tree initial characteristics (diameter, dbh; tree basal area, b); RTD is a measure of the relative tree dimension (ratio between tree basal area and stand basal area, RBM; ratio between dbh and the quadratic mean dbh, RDM); and SC expresses the competition at stand level (number of trees per hectare, N; basal area per hectare, G; the inverse of each of these variables, 1/N, 1/G).

An all possible regression algorithm was used to select the best model out of a large set of tree and stand variables representing site index, initial tree size, stand density and relative tree size. The selection of the model was based on measures of multiple linear regression quality and prediction ability: adjusted R^2, residual mean square (RMS), prediction sum of squares (PRESS) and sum of absolute prediction errors (APRESS). The presence of colinearity in the models was analysed through the values of the variance inflation factors (VIF). This study was carried out separately for each one of the data subsets. The contribution of each index to the selected model was analysed based on the value of the F-statistic.

Table III. Characterisation of the data subsets.

data set (Nobs)		age (years)	Nmed	Npha	$S_{h,t}$	dbh (cm)
	minimum	4.7	2	500	12.4	0.2
total	mean	10.8	9.0	1094	22.6	13.6
(5409)	maximum	17.9	25	1667	28.1	31.5
	minimum	0.9	2	1087	21.9	0.2
(1)	mean	2.1	13.1	1110	25.0	7.0
(1136)	maximum	6.8	22	1111	28.1	18.3
	minimum	1.8	2	500	12.4	1.5
(2)	mean	5.4	13.3	1020	22.2	12.1
(911)	maximum	15.8	25	1125	28.1	27.2
	minimum	2.8	2	500	15.6	1.1
(3)	mean	10.4	6.5	1109	21.9	16.3
(3362)	maximum	17.9	25	1667	28.1	31.5

where Nobs is the number of observations; Nmed is the number of measurements; Npha is the number of trees at plantation; $S_{h,t}$ represents the site index at base age 10; dbh is the diameter at breast height; (1), (2) and (3) are as explained in the text, point 3.3.

4. Results and discussion

4.1. Rules to select competitor trees

Table Iva, b shows the number of observations obtained with six different rules to select competitors in each one of the possible combinations of 'number of selected competitors/age'. To analyse these tables the stage of stand development represented by each one of the data subsets was considered. For rules based on BAF = 4 $m^2 ha^{-1}$, in 32 % of the observations in age class]36, 60] months no competitors were selected (*table IVa*). Based on the conclusions of previous studies [24], considering the age and the development of the stand, the non-existence of competition relationships between trees was not expected for these ages. In fact, if the low number of selected competitors by this rule for older stands (maximum of 12 competitors) seems logical for planted stands, the high percentage associated with no competitors in this age class is not biologically consistent. For BAF = 1 $m^2 ha^{-1}$, 41 and 84 % of the observations in the age classes]108, 132] and]132, 216] months, respectively, were associated with a number of competitors superior to 20 that seems too large from a biological standpoint.

On the selection of the parameters for the new rules to select competitors in the classes of both no competitors and age greater than 24 months as well as in the classes of more than 20 competitors, a reduced or low number of observations was required (*table IVb*). Accordingly, the following parameter values were selected: hyperbolic function k = 0.2 and 0.3; monomolecular function k = 10 and 15; Richards' function k = 15 and 30; m = 1/2 and 9/10.

Table IVa. Number of observations obtained with different rules in each one of the possible combinations of number of competitors with age.

age	number of selected competitors						
(months)	0	1–4	5–8	9–12	13–16	17–20	+20
BAF = 1 $m^2 ha^{-1}$							
]0,12]	606	4	–	–	–	–	–
]12,24]	23	327	218	8	–	–	–
]24,36]	–	2	152	153	50	5	–
]36,48]	–	–	49	117	107	58	19
]48,60]	15	180	80	100	86	48	47
]60,84]	–	87	215	475	328	120	24
]84,108]	–	9	56	145	504	441	206
]108,132]	–	1	8	64	109	351	375
]132,216]	–	–	16	12	71	94	1004
BAF = 4 $m^2 ha^{-1}$							
]0,12]	610	–	–	–	–	–	–
]12,24]	558	18	–	–	–	–	–
]24,36]	109	253	–	–	–	–	–
]36,48]	42	280	28	–	–	–	–
]48,60]	249	250	57	–	–	–	–
]60,84]	229	948	72	–	–	–	–
]84,108]	42	1037	282	–	–	–	–
]108,132]	8	489	410	1	–	–	–
]132,216]	4	220	926	47	–	–	–
area potentially available (APA)							
]0,12]	–	62	542	6	–	–	–
]12,24]	–	36	527	13	–	–	–
]24,36]	–	20	333	9	–	–	–
]36,48]	–	29	312	9	–	–	–
]48,60]	–	52	488	16	–	–	–
]60,84]	–	86	1131	32	–	–	–
]84,108]	–	110	1230	21	–	–	–
]108,132]	–	81	815	12	–	–	–
]132,216]	–	116	1060	21	–	–	–

border trees were defined by BAF = 1 $m^2 ha^{-1}$

Table IVb. Number of observations obtained with different rules in each one of the possible combinations of number of competitors with age.

age	number of selected competitors						
(months)	0	1–4	5–8	9–12	13–16	17–20	+20
			hyperbolic function, A = 7 m, k = 0.2				
]0,12]	550	60	–	–	–	–	–
]12,24]	2	168	460	–	–	–	–
]24,36]	–	2	360	–	–	–	–
]36,48]	–	–	344	6	–	–	–
]48,60]	2	150	389	15	–	–	–
]60,84]	–	118	840	232	59	–	–
]84,108]	–	73	906	198	184	–	–
]108,132]	–	26	575	177	130	–	–
]132,216]	–	4	587	473	133	–	–
			monomolecular function, A = 7 m, k = 10				
]0,12]	584	26	–	–	–	–	–
]12,24]	11	396	169	–	–	–	–
]24,36]	–	23	339	–	–	–	–
]36,48]	–	4	343	3	–	–	–
]48,60]	11	223	306	16	–	–	–
]60,84]	–	233	775	239	2	–	–
]84,108]	–	89	892	336	44	–	–
]108,132]	–	22	567	262	57	–	–
]132,216]	–	8	589	512	88	–	–
			Richards' function, A = 7 m, k = 30, m = 9/10				
]0,12]	610	–	–	–	–	–	–
]12,24]	269	246	61	–	–	–	–
]24,36]	–	68	252	42	–	–	–
]36,48]	–	21	194	123	12	–	–
]48,60]	91	168	145	119	33	–	–
]60,84]	14	201	604	394	35	1	–
]84,108]	–	39	488	594	219	21	–
]108,132]	–	7	265	378	220	38	–
]132,216]	–	13	321	396	338	125	4

border trees were defined by BAF = 1 m^2 ha^{-1}

4.2. Prediction ability

Table V presents the linear tree basal area growth models selected for the three stages of stand development considered. The best model with four variables was similar for each one of the stages of stand development considered, involving site index, dbh, RDM or RBM and basal area per hectare. In the latter stages of stand development the RBM had a better contribution to the tree basal area growth model while in the other stages the RDM was superior. This result may be justified by the fact that, for eucalyptus trees, the exponent in the allometric relationship between weight and dbh increases with age [12]. The RDM and RBM may both express, at different ages, the ratio between the subject tree biomass and the tree of mean biomass.

The contribution of each competition index to the tree basal area growth model is presented in *table VI*. APA indices were excluded from the analysis, as they are quite different both in the mathematical formulation and in the way the competitors are selected. The superiority of the rules to select competitors based on the Richards' function is evident from this table, particularity in the modality 2 (A = 7, k = 30 and m = 9/10). It is also evident that the contribution of a certain index formulation (mathematical expression and selection rule) is different for each stage of stand development. In the initial stages DR indices are generally non-significant with the exception of those defined by the Richards' function (namely modality 2) and, to a certain extent, BAF = 4. The AO indices are poorly significant for BAF = 1 and non-significant for BAF = 4. The contribution of PD measures is slightly better in this stage, however showing again a

Table V. Tree basal area growth models selected (i_b, cm^2) for each one of the stages of stand development considered.

stage of stand development	variables	adj-R^2	RMS 10^3	PRESS/n 10^2	APRESS/n	VIF
		models with 4 variables				
(1)	Sh,t, dbh, G, RDM	0.578	0.182	1.832	10.414	8.75
(2)	Sh,t, dbh, G, RDM	0.571	0.231	2.321	11.153	6.05
(3)	Sh,t, dbh, G, RBM	0.624	0.134	1.340	8.418	3.43

where PRESS and APRESS values are divided by the number of observations in each data set in order to make results comparable; all the other symbols are as explained in the text.

Table VI. Contribution of the competition indices to tree basal area growth models (partial-F's for the competition term).

rules to select competitors	stage of stand development	competition indices										
		DR	DRU	DRM	DD	PD	PDU	AO	AOU	AOM	APA2	APA4
hyperbole	(1)	0.1^{ns}	0.3^{ns}	1.2^{ns}	0.2^{ns}	18.5	0.9^{ns}					
A = 7 m	(2)	4.0^{ns}	0.4^{ns}	0.8^{ns}	2.7^{ns}	4.5^{ns}	18.4					
k = 0.2	(3)	7.4	5.7^{ns}	0.0^{ns}	1.6^{ns}	22.3	31.3					
hyperbole	(1)	3.4^{ns}	11.9	3.1^{ns}	13.4	12.1	0.7^{ns}					
A = 7 m	(2)	0.3^{ns}	1.9^{ns}	0.0^{ns}	6.8^{ns}	3.2^{ns}	15.9					
k = 0.3	(3)	3.2^{ns}	0.8^{ns}	0.1^{ns}	0.3^{ns}	27.7	35.2					
monomolecular	(1)	1.2^{ns}	2.0^{ns}	0.6^{ns}	6.8	20.1	0.4^{ns}					
A = 7 m	(2)	2.4^{ns}	1.1^{ns}	0.8^{ns}	3.4^{ns}	4.1^{ns}	16.8					
k = 10	(3)	8.4	4.6^{ns}	0.0^{ns}	1.4^{ns}	21.6	30.3					
monomolecular	(1)	2.4^{ns}	0.6^{ns}	3.8^{ns}	0.0^{ns}	8.8	0.6^{ns}					
A = 7 m	(2)	6.2^{ns}	0.0^{ns}	0.7^{ns}	3.5^{ns}	2.3^{ns}	18.7					
k = 15	(3)	18.2	12.9	1.7^{ns}	7.7^{ns}	17.7	25.3					
Richards	(1)	3.0^{ns}	8.0	24.0	40.7	69.8	91.7					
A = 7 m	(2)	0.8^{ns}	1.6^{ns}	29.5	42.3	0.5^{ns}	3.6^{ns}					
k = 15; m = 1/2	(3)	13.5	6.6^{ns}	26.2	75.9	40.7	3.4^{ns}					
Richards	(1)	70.5	70.7	25.1	39.1	62.4	84.5					
A = 7 m	(2)	30.3	41.0	27.1	36.1	0.2^{ns}	3.0^{ns}					
k = 30 m; m = 9/10	(3)	43.3	83.6	30.2	82.5	26.0	0.4^{ns}					
4 competitors	(1)	0.6^{ns}	2.9^{ns}	1.1^{ns}	1.6^{ns}	8.2	0.3^{ns}					
	(2)	6.2^{ns}	0.0^{ns}	0.6^{ns}	2.6^{ns}	3.5^{ns}	10.9					
	(3)	5.7^{ns}	0.8^{ns}	5.4^{ns}	8.7	24.6	38.3					
8 competitors	(1)	0.1^{ns}	1.9^{ns}	0.4^{ns}	0.7^{ns}	8.4	1.0^{ns}					
	(2)	9.1	0.1^{ns}	0.7^{ns}	3.8^{ns}	2.1^{ns}	17.8					
	(3)	7.7	1.0^{ns}	4.1^{ns}	2.6^{ns}	12.9	37.8					
BAF	(1)	3.7^{ns}	6.8	5.2^{ns}	14.8	14.6	0.1^{ns}	17.5	27.8	22.1	10.1	16.1
1 m^2 ha^{-1}	(2)	3.5^{ns}	0.1^{ns}	1.1^{ns}	1.0^{ns}	2.5^{ns}	18.4	2.5^{ns}	0.3^{ns}	0.1^{ns}	1.2^{ns}	6.5^{ns}
	(3)	24.4	16.1	3.9^{ns}	14.6	20.3	22.7	23.8	16.9	1.6^{ns}	143.4	161.5
BAF	(1)	28.9	32.5	17.0	33.6	9.2	14.4	0.0^{ns}	1.2^{ns}	5.0^{ns}		
4 m^2 ha^{-1}	(2)	0.6^{ns}	0.0^{ns}	0.0^{ns}	0.2^{ns}	0.9^{ns}	3.0^{ns}	0.2^{ns}	0.1^{ns}	1.5^{ns}		
	(3)	15.3	8.9	0.1^{ns}	3.6^{ns}	10.2	13.7	9.9	9.2	6.1^{ns}		

All the values are significantly different from zero at $p < 0.01$ except for the values marked with ^{ns}; all the other symbols are as explained in the text and in table II.

strong superiority of the Richards' function, in particular if associated with the unilateral version. However, the expected superiority of the unilateral or modified versions of the indices is not clear. Most of the tested indices are not significant in the intermediate stage of stand development. An exception is the DR indices associated with the Richards' function, namely in the modality 2 with the unilateral and modified versions being slightly superior to the traditional one. This lack of significance of competition indices in this intermediate stage may indicate that this data set joins remeasurements that are not clearly from the initial stages of stand development nor show evidence effects of suppression of small trees. Note that this is the smallest of the three subsets. Later in stand development, when there is evidence of suppression of small trees, the unilateral and modified versions of the DR indices associated with the modality of the Richards' function were clearly superior

Finally, the superiority of the APA indices in the last stage of stand development is also evident with the APA indices showing the highest partial correlation in multiple regression with tree basal area growth. Tomé and Burkhart [29] and Tomé [27] with adult eucalyptus stands have obtained identical results. APA4, which gives more weight to larger trees, shows greater F-values reinforcing the presence of asymmetric competition in the data.

The DRU, based on Richards' function with asymptote 7, k = 30 and m = 9/10 presents the best contribution when analysed simultaneously in each subset and with all the data. In fact, the contribution of the DRU to the tree basal area growth model defined for all the data (model with four variables – $S_{h,t}$, d, G and RDM) corresponded to a partial F of 162.2, the highest partial F-value when all the data were considered as a whole (very similar to the value of 161.5 obtained with APA4).

The correlation coefficients of some competition indices with tree basal area growth are presented in *table VII*. The lack of correspondence between the values of correlation coefficients and the contribution of each index to the tree basal area growth model reinforces the scant information given by the correlation coefficients when analysed per se. For instance, in the last stage of stand development, the PDU presents the highest absolute values but this type of index has no significant contribution to the tree basal area growth model (*table VI*). This fact is a consequence of the relationship between some of the indices and the other variables already present in the model (colinearity).

As expected, all the indices indicating competitive stress present negative correlation with growth, while the APA indices expressing competitive advantages show positive correlation. Analysing the correlation between competition indices and tree basal area growth over an increased intensity of asymmetric competition – subset 1 to subset 3 – it can be observed that the correlation coefficients are small in subset 1 and increase as the asymmetric competition increases. This behaviour was not observed with the DRM and DD as well as with the APA indices.

5. Conclusion

Indices based on asymptotically restricted non-linear functions of tree size as rules for selecting competitor trees present, when compared with the BAF rule, a higher contribution to multiple linear regression models. The Richards' function defined by asymptote 7 m and shape form parameters k = 30 and m = 9/10 seems to be capable of expressing a biologically acceptable relationship between 'number of selected competitors/age'. The

Table VII. Correlation coefficients of some competition indices with tree basal area growth.

rules to select competitors	stage of stand development	competition indices							
		DR	DRU	DRM	DD	PD	PDU	APA2	APA4
Richards	(1)	–0.253	–0.314	–0.139	–0.187	–0.213	–0.244		
A = 7 m	(2)	–0.280	–0.416	–0.067	–0.155	–0.358	–0.406		
k = 15; m = 1/2	(3)	–0.446	–0.525	–0.331	–0.444	–0.444	–0.612		
Richards	(1)	–0.235	–0.237	–0.137	–0.186	–0.213	–0.245	0.526	0.536
A = 7 m	(2)	–0.429	–0.414	–0.079	–0.146	–0.344	–0.398	0.273	0.345
k = 30; m = 9/10	(3)	–0.529	–0.547	–0.334	–0.441	–0.435	–0.615	0.559	0.599

All the values are significantly different from zero at $p < 0.01$ except for the values marked with ^{ns}; all the other symbols are as explained in the text and in table II.

supremacy of the indices based on the Richards' functions was observed for all stages of stand development.

The DRU indices, based on the Richards' function, make a significant contribution to the tree basal area growth model in all of the analysed data subsets. However, later in stand development, when there is evidence of suppression of small trees, the APA4 seemed to present a better performance.

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