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Modelling growing space requirements for some tropical forest tree species

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Abstract

The importance of crown data in improving the reliability of growth models for stand management has long been established, but such data are scarce for tropical forests. This paper reports studies of crown diameter–bole diameter relationships of five mixed tropical forest species by regression methods. The regression explained 77% of the variation in crown diameter. Growing space was associated with crown size, and models were developed from which growing space, limiting stocking and stand basal area density can be predicted. The paper demonstrates, e.g., that trees of 60 cm bole diameter would each require 0.009 ha of growing space with a density of about 107 stems ha^{-1}. Stand basal area converges around 31 m^2 ha^{-1}. In silvicultural practice, the baseline information provided by this study could serve as a guide for planting distances and crop density in industrial plantations of similar indigenous mixed tropical forest species.
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Keywords: Crown diameter; Stand basal area; Stocking; Plantation

1. Introduction

Growing space refers to the availability of all resources needed by a tree to exist on a given site. A deficiency of any of these resources may limit the growing space (Smith, 1986), and hence affect tree growth. For individual trees, growing space is often defined in terms of the horizontal dimensions of available ground surface area or crown projection area (Spurr, 1952; Assmann, 1970; O'Hara, 1988). O'Hara (1988) indicates that this is roughly proportional to spacing in single species stands. Each individual tree in a stand, therefore, requires a definite amount of growing space. The extent of the growing space is limited by the ground surface available, and the tree's direct neighbours restrict lateral growth.

Small gaps may exist in the canopy of unthinned stands because of the close contact between crowns. Assmann (1970) suggests that this space may be considered as the available growing space, apportioned out among the immediately surrounding trees. He refers to the vertical projection of this growing space as the area potentially available or nominally available. The mean area nominally available is inversely proportional to the number of trees (Kuuluvainen, 1991), such that the

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greater the stocking per hectare, the smaller is the average space nominally available.

These growing space concepts have been employed in growth modelling studies, based not only on its measure as the ground area or resources available to the individual tree, but also as an index of competition. For example, measurements on open-grown trees have been widely used to predict potential increments in stem diameter (e.g., Krajicek et al., 1961; Apsey, 1962; Curtin, 1964; Faber, 1991). In addition, models have been developed which use spatial co-ordinates and inventory data to calculate a range of competition indices for growth prediction. These indices are basically related to a tree's zone of influence, indicated by growing space occupation in relation to its competitors. The works of Hegyi (1974) and Ek and Monserud (1974) exemplify such models.

Reports by previous researchers indicate that the use of tree crown size as a variable in growth models has only recently gained currency (e.g., Parde, 1980; Kanazawa et al., 1982; Lim, 1988; Whitesell et al., 1988; Wadsworth et al., 1989; Fownes and Harrington, 1990). However, the relationships between tree crown diameter and bole diameter and their applicability in forest management have long been established for many temperate species (e.g., Minor, 1951; Krajicek et al., 1961; Francis, 1966; Ayhan, 1973) and a few tropical species (e.g., Dawkins, 1963).

Recent studies confirm the importance of crown size and its potential in improving the degree of accuracy and reliability of growth predictions. However, as pointed out by Maguire and Hahn (1990), long-term studies of crown dynamics are generally lacking and data from which crown development sub-models can be constructed are scarce. This general lack of information on tree crowns and their application in tree growth modelling is even more pronounced for tropical forests.

It is important, therefore, to be able to establish a relationship between crown diameter and tree diameter, as this can provide a guide to optimum planting distance and possible crop density. Specifically, the growing space requirements and the possibility of defining the limiting stocking of a stand in terms of total occupancy by tree crowns (Dawkins, 1963; Krajicek et al., 1961) can be defined for specific species in plantation work.

In Ghana, as in many other countries in Africa with similar species and forest types, such knowledge would greatly enhance the establishment and proper management of future industrial plantations. This study was, therefore, carried out with a view to providing such baseline information to facilitate the development of growth models and enhance management of indigenous species plantations in the future.

2. Source of data and methods

2.1. The study area

The study was carried out in Ghana in the Bobiri Forest Reserve which, prior to logging was diverse in its species composition, but with an emergent layer composed primarily of *Celtis* species and *Triplochiton scleroxylon* K. Schum (Foggie, 1947). Hall and Swaine (1976) classify it as Moist Semi-Deciduous (south-east) sub-type. It lies between latitudes 64° and 6°44′N and longitudes 1°15′ and 1°22′W. The topography is gently undulating between 183 and 248 m above sea level. The slope lies north-west to south-east, which is the general direction of flow of all the streams in the reserve.

Alder (1993) reports that the reserve suffered severe forest fires from time to time, particularly in 1961 and 1983, causing local patches of destruction or gaps. This may have resulted in a reduction in under-storey stocking, but there does not seem to be a gross effect on the larger trees in the stand. In addition, the trees from which data were collected were mostly regenerated stock following the earlier treatments imposed on the stand.

2.2. General layout and previous research

The reserve is made up of 37 compartments. Approximately 1092 ha of the total area of the forest was managed under the tropical shelterwood system (TSS), and other experimental silvicultural systems such as post-exploitation system (PES), and the diameter limit selection system (DLS) (Alder, 1993). The PES and TSS had similar features. The main difference was that no treatments were performed in the PES prior to exploitation, whereas the TSS included graded canopy openings and cleaning to initiate regeneration under a shelterwood.

Under these earlier experiments 36 girth increment sample plots (GISPs) were established in 22 compartments and subjected to the various silvicultural treatments. Each GISP measures 1 ha in area and is sub-divided into 25 subplots (quadrats). These quadrats, each measuring $20\,m \times 20\,m$ (0.4 ha), are numbered back and forth along the principal axes following procedures described by Baidoe (1968) and Alder and Synnott (1992) to facilitate data collection and analysis.

The principal objective of the experiments conducted under the tropical shelterwood system was to obtain, by natural regeneration, an even-aged high forest of valuable species. In addition, attempts were made to obtain information on the growth rates of the more economically valuable species. The post-exploitation system was carried out to establish whether sufficient regeneration could be achieved by opening the canopy after exploitation (Alder, 1993; Foli, 1993). After logging, all species that were considered uneconomical were removed by poisoning, along with the cutting of climbers and other vegetation that would impede the growth of the favoured regeneration. The result was a fairly uniform forest comprising only the desirable species that had been favoured through regeneration.

For the purposes of this study, nine GISPs were randomly selected. Measurements were carried out on tree crown diameter and bole diameter for all species (Table 1). But in this paper emphasis has been placed on five species, which were well represented in terms of sample size, to determine the relationship between crown diameter and bole diameter and obtain estimates of the species' growing space requirements. The species are *Entandrophragma angolense* (Welw.), *Guarea cedrata* A. Chev., *Khaya ivorensis* A. Chev., *Mansonia altissima* A. Chev. and *T. scleroxylon* K. Schum. The data represent a subjective subset of the randomly located plots. The sample nevertheless gives a general picture of the forest (Table 1) and adequately describes the characteristics of the trees measured.

3. Measurement procedures and data analysis

3.1. Crown diameter

Crown measurements were based on the assumption that the vertical projection of a tree crown is roughly circular (Krajicek et al., 1961; Strub et al., 1975; Cailliez, 1980; Nance et al., 1987). Cailliez (1980) recommends that at least four, but preferably eight radii should be measured, and in directions forming equal angles. Curtin (1964), Hamilton (1969) and Noordin (1973) have reported preference for six radii measurements, but Ayhan (1973) calculated crown diameter from four radii.

In this study, four crown radii were measured along four axes at right angles. Three persons were required

Table 1
Size-class distribution of 14 economically important timber species recorded in nine randomly selected GISPs in Bobiri Forest Reserve

Species	No. stems in diameter class					Total
	5–20 cm	20–40 cm	40–60 cm	60–80 cm	80–100 cm	
Antiaris toxicara	4	2	1	0	0	7
E. angolense	75	27	3	0	0	105
Entandrophragma cylindricum	3	3	5	0	0	11
Entandrophragma candollei	5	2	1	0	0	8
Entandrophragma utile	7	3	2	0	0	12
Guarea cedreta	59	30	2	0	0	91
K. ivorensis	12	20	11	4	0	47
Lovoa trichiloides	1	4	1	0	0	6
M. altissima	23	23	0	0	0	46
Nauclea diderrichii	0	1	0	1	0	2
Nesogordonia papaverifera	0	13	3	0	0	16
Piptadeniastrum africanum	1	1	3	6	2	13
Terminalia ivorensis	0	3	4	0	0	7
T. scleroxylon	0	21	48	42	8	119
Total	190	153	84	53	10	490

Table 2
Summary statistics on stem and crown diameter measurements (D) from the five species (C_d is the projected crown diameter (m))

Summary statistics	Species					
	T. scleroxylon	*E. angolense*	*K. ivorense*	*G. cedrata*	*M. altissima*	All species
Stem diameter						
No. of cases	119	105	47	91	46	408
Minimum	20.10	5.90	6.50	6.00	10.20	5.90
Maximum	89.90	49.60	73.40	50.50	39.10	89.90
Range	69.80	43.70	66.90	44.50	28.90	84.00
Mean	55.14	17.99	33.52	18.60	19.47	31.12
Standard error	1.387	0.847	2.415	0.860	0.703	1.000
Crown diameter						
No. of cases	119	105	47	91	46	408
Minimum	3.30	0.70	1.20	0.80	1.90	0.70
Maximum	21.70	11.80	16.6	10.60	11.60	21.70
Range	18.40	11.10	15.4	9.80	9.70	21.00
Mean	10.18	3.10	6.65	4.25	5.17	6.10
Standard error	0.326	0.329	0.481	0.188	0.254	0.192

for this purpose, following the method described by Alder and Synnott (1992) for measuring crown diameter in closed forests.

Average crown diameter (C_d) was then calculated by summing up the four radii and dividing by 2, thus:

$$\frac{1}{2}\sum_{i=1}^{n} r_i \qquad (1)$$

where r_i refers to the projected crown radii measured on the four axes.

3.2. Bole diameter

The morphology of tropical trees differ—some have cylindrical stems, as exemplified by species like *E. angolense*, *M. altissima* and *G. cedrata*, while others are buttressed, e.g., *T. scleroxylon* and *K. ivorensis*. Therefore, the point of measurement tends to vary depending on the presence or absence of buttresses, although conventionally stem diameter is measured at breast height (Philip, 1994; Alder and Synnott, 1992). It has been argued, however, (e.g., Assmann, 1970) that the difference in shape has the effect of introducing some fuzziness in the definition of parameters such as basal area per hectare, or reference diameter when the latter is at a variable height.

In the Bobiri Forest Reserve previous measurements of bole diameter were actually taken at two points—breast height and higher up the stem at 3.96 m (13 ft) at different measurement eras. For the present study, considering the differences in stem shape, the upper reference diameter (3.96 m) was preferred in order to standardise the point of measurement. Measurements were carried out by means of a diameter tape, facilitated by a reasonably light ladder propped up against the tree. The data are summarised in Table 2.

4. Data analysis

Dawkins (1963) has shown in his classical work on crown diameter–bole diameter relationships that the straight line adequately represents this relationship. Preliminary examination of the data for this study confirmed this observation. On the strength of this premise, crown diameter was regressed on bole diameter using SYSTAT (Wilkinson, 1990) to derive the appropriate allometric relationship between the two variables. Several curvilinear models were tested for best fit and magnitude of error associated with the regression. The models were

$$C_d = \alpha + \beta D + \varepsilon_i \qquad (2)$$

$$C_d = \alpha + \beta D^2 + \varepsilon_i \qquad (3)$$

$$C_d = \alpha + \beta \ln D + \varepsilon_i \qquad (4)$$

$$C_d = \alpha + \beta_1 D + \beta_2 D^2 + \varepsilon_i \qquad (5)$$

where C_d is the crown diameter; D the diameter at the point of measurement; and α and β the regression coefficients.

The best model was selected based on the goodness of fit, the magnitude of the errors associated with the regressions and from analysis of the studentized residuals as discussed by Alder (1980, 1995), and Vanclay (1994). Equations were developed for the determination of growing space and limiting stocking of the species from the selected model. The models were basically self-validated using residual analysis and graphical comparisons, as suggested by Alder (1980, 1995). This is acceptable for simple models involving one or two functions (Alder, 1995).

5. Results and discussion

Altogether 408 individual crown and bole diameter records were obtained for the five species as summarised in Table 2. The regression analysis (Table 3) showed that crown diameter was better correlated with tree diameter in model (2), although there were no significant differences between models (2), (3) and (5) when data for all species were combined.

Model (5) was marginally better than (2), but the β_2 coefficient was generally not significant in the former. Indeed, the shape of the curve from (5) is likely to depend on random variation in the data, and might, therefore, prove less suitable as a predictor than model (2). A comparison of the residuals tended to favour model (2), which had a more homogeneous variance, with the studentized residuals conforming to the behavioural expectations postulated by Cook (1977, 1979), Alder (1980, 1995), Draper and Smith (1980) and Vanclay (1994). The standard error of the estimate of crown diameter was low enough to make the model sufficiently reliable for predicting crown diameter from bole diameter. It also explained the variation in crown diameter adequately, with $R^2 = 0.77$.

Model (2) was, therefore, selected based on its superiority in past research (e.g., Krajicek et al., 1961; Dawkins, 1963; Curtin, 1964; Newnham, 1966; Leech, 1984; Farr et al., 1989; Smith et al., 1992) and ease of application. The regressions for individual species were all statistically significant.

Generally, the scatter of the data points in the crown diameter–bole diameter relationships gave no evidence of non-linearity, the curves for individual species conforming mostly to Dawkins' (1963) type 2 behaviour, i.e. straight line with a positive intercept (α coefficient). Only *E. angolense* exhibited the type 3 behaviour described by Dawkins, namely a straight line with a negative intercept. This negative value of the intercept was, however, not significantly different from zero.

Smith et al. (1992) contend that crown diameter–bole diameter equations should have positive intercepts. Also, as pointed out by Dawkins, the positive intercept suggests that crown diameter–bole diameter ratio decreases with tree size, implying that in plantation management stand basal area can be allowed to rise towards maturity, as is generally indicated in yield tables.

The variability of the α term across the species may also be ascribed to the ecology of the species and the relative position of the crowns within the canopy (Swaine et al., 1987) and their tolerance to crown density and basal area density. This follows from the theories advanced by other researchers in previous work relating crown size to tree size and growth, and the competitive interactions amongst trees in mixed-species stands (e.g., Dawkins, 1963; Assmann, 1970; Grier and Waring, 1974; Kigomo, 1980).

Although the data points for *M. altissima* tended to cluster, a linear trend was obvious. The weak relationship for *M. altissima* may be attributable to the sample size and the fact that almost all the sample trees were small-sized with relatively small crowns (see Tables 1 and 2). In general, good fits were obtained (Table 3).

Further examination of the regressions by Bartlett's test (Snedecor and Cochran, 1989; Clarke, 1990; Freese, 1990) suggested that a general linear model would adequately represent all the species (Table 4).

Combining data for all species, therefore (Fig. 1), the following model was derived:

$$C_d = 0.829 + 0.168D \quad (6)$$

The growing space of each tree was then expressed as a function of diameter, thus:

$$S = k(\alpha + \beta D)^2 \quad (7)$$

where S denotes growing space required by the tree, α and β the regression coefficients of Eq. (2) and k the constant $\pi/40\,000$ (conversion of crown diameter in metres to area in hectares). From this, it can be

Table 3
Parameter estimates and coefficients for regressions of crown diameter on tree diameter (R^2 and $\sigma_{(y)}$ are coefficient of determination and standard error of the estimate, respectively; α and β are regression coefficients)

Species	Statistic	Model			
		$C_d = \alpha + \beta D$	$C_d = \alpha + \beta D^2$	$C_d = \alpha + \beta \ln D$	$C_d = \alpha + \beta_1 D + \beta_2 D^2$
E. angolense	R^2	0.606	0.622	0.504	0.625
	α	−0.005 ns[a]	1.715***	−5.691***	1.229**
	β_1	0.172***	0.003***	3.144***	0.047*
	β_2	–	–	–	0.003**
	$\sigma_{(y)}$	1.209	1.184	1.357	1.186
G. cedrata	R^2	0.359	0.348	0.317	0.360
	α	1.812***	3.204***	−2.743**	2.179**
	β_1	0.131***	0.003***	2.465**	0.095*
	β_2	–	–	–	0.001 ns
	$\sigma_{(y)}$	1.448	1.460	1.508	1.454
K. ivorensis	R^2	0.669	0.619	0.607	0.669
	α	1.187*	3.853***	−8.620***	1.005*
	β_1	0.163***	0.002***	4.525***	0.175**
	β_2	–	–	–	−0.001 ns
	$\sigma_{(y)}$	1.918	2.056	2.089	1.939
M. altissima	R^2	0.254	0.315	0.183	0.351
	α	1.625*	3.142***	−3.948*	6.692***
	β_1	0.182***	0.004***	3.101***	−0.297*
	β_2	–	–	–	0.011**
	$\sigma_{(y)}$	1.506	1.443	1.576	1.421
T. scleroxylon	R^2	0.555	0.565	0.495	0.565
	α	0.402 ns	4.994***	−23.223***	3.764*
	β_1	0.175***	0.002***	8.390***	0.046 ns
	β_2	–	–	–	0.001*
	$\sigma_{(y)}$	2.382	2.358	2.538	2.365
All species combined	R^2	0.770	0.742	0.698	0.771
	α	0.829***	3.339***	−10.180***	1.202***
	β_1	0.168***	0.002***	5.023***	0.142***
	β_2	–	–	–	0.001 ns
	$\sigma_{(y)}$	1.857	1.970	2.135	1.855

[a] Not significant.
* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$.

deduced, e.g., that a dominant free-growing tree of diameter 60 cm would require a growing space of 0.009 ha (Table 5). Curtin (1964) used a similar approach for establishing a stand density index (SDI) for even-aged Messmate (*Eucalyptus obligua*) stands. It is noteworthy, however, that he included tree total height in the formula in determining SDI for Messmate.

Growing space calculation for the species in the present study was founded on the assumption that the tree crowns are circular and do not overlap. In practice, however, this is not entirely true, except in monocultures. Tropical forests are characteristically diverse in species composition, and the different species have peculiar growth habits. Some are light-demanders, others are shade bearing; some are fast-growers while others are slow growing (Halle et al., 1978; Hawthorne, 1990). Consequently, the canopy is layered, and the crowns overlap. Nevertheless, in the study area the contribution of under-storey trees to the

Table 4

Statistics from tests for differences in the individual crown diameter–stem diameter regressions for *E. angolense* (Ea), *T. scleroxylon* (Tri), *M. Altissima* (Man), *K. ivorensis* (Ki) and *G. cedrata* (Gc) (as indicated by the calculated *F* values, neither the difference in slopes nor the levels of the regressions differ significantly at the 0.01 level)

	n	d.f.	$\sum y^2$	$\sum xy$	$\sum x^2$	Residuals		
						d.f.	SS	MS
Species								
Ea	105	104	382.3539	1347.5539	7834.8939	103	150.5829	1.4620
Tri	119	118	1492.8975	4734.4688	27032.8431	117	663.7134	5.6728
Man	46	45	133.7933	186.2876	1022.4611	44	99.8525	2.2694
Ki	47	46	499.7762	2052.5809	12607.9043	45	165.6137	3.6803
Gc	91	90	290.7468	794.5895	6056.6196	89	186.5018	2.0955
Pooled residuals						398	1266.2643	3.1816
Difference for testing different slopes						4	10.2088	2.5522
Common slope	408	403	2799.5677	9115.4807	54554.7130	402	1276.4731	3.1753
$F_{(cal)}$ from test for common slopes = 0.8022								
Difference for testing levels of the regressions						4	98	24.5267
Single regression	408	407	7625.9125	35465.7680	201208.4100	405	1374.5799	
$F_{(cal)}$ from test of differences in the levels of the regressions = 7.7242								

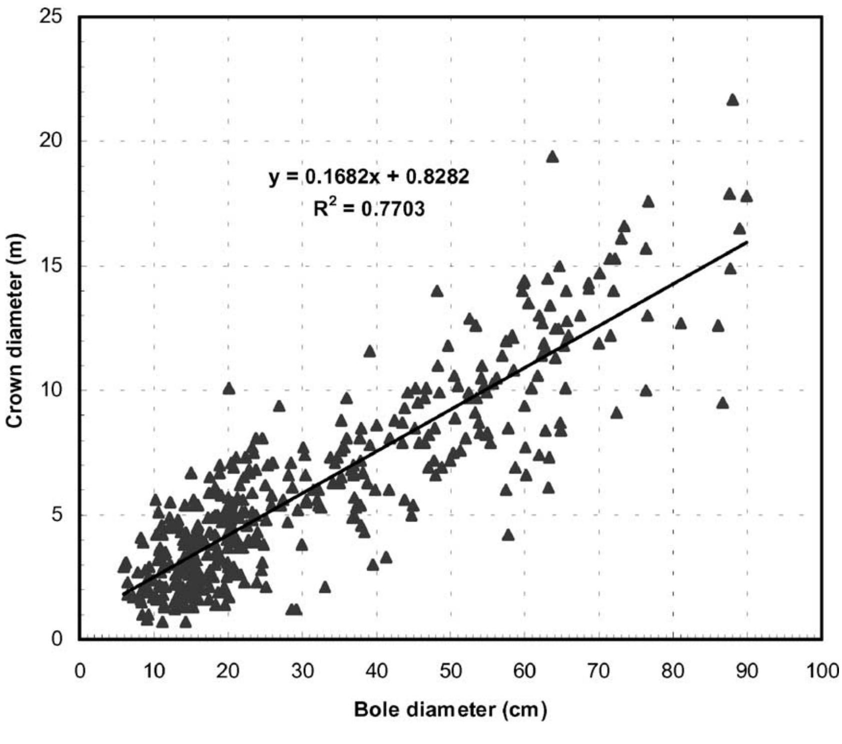

Fig. 1. Relationship between crown diameter and bole diameter.

Table 5
Reckoner for estimating crown diameter, growing space, stocking and stand density from bole diameter for the five study species[a]

D (cm)	C_d (m)	S (ha)	N (stems ha^{-1})	G ($m^2\ ha^{-1}$)
20.00	4.19	0.001	726	23
25.00	5.03	0.002	503	25
30.00	5.87	0.003	370	26
35.00	6.71	0.004	283	27
40.00	7.55	0.004	223	28
45.00	8.39	0.006	181	29
50.00	9.23	0.007	149	29
55.00	10.07	0.008	126	30
60.00	10.91	0.009	107	30
65.00	11.75	0.011	92	31
70.00	12.59	0.012	80	31
75.00	13.43	0.014	71	31
80.00	14.27	0.016	63	31
85.00	15.11	0.018	56	32
90.00	15.95	0.020	50	32

[a] The above table was derived from the crown diameter–bole diameter regressions, and was computed as follows—crown diameter: $C_d = 0.829 + 0.168D$; growing space: $S = C_d^2\pi/40\,000$; limiting stocking: $N = 1/S$; stand basal area: $G = D^2\pi/40\,000N$.

total stand basal area is slight, as these are usually small trees. Besides, the stand is characterised by dominants and co-dominants because of the earlier treatments imposed to create a uniform forest, as well as the effects of periodic bush fires on the smaller trees.

The results also provide a means of computing the limiting stocking per hectare (N ha^{-1}) required for producing a complete canopy or for the trees to fully occupy the site. This can be expressed as the inverse of the growing space, $1/S$ (Kuuluvainen, 1991; Philip, 1994). From Eq. (7), the limiting stocking of the stand in terms of total occupancy by tree crowns was determined. Table 5 shows that about 107 dominant trees of 60 cm diameter will fully occupy an area of 1 ha.

Furthermore, it can be shown that a simple linkage exists between the crown diameter regression and the likely maximum stand basal area. Thus stand basal area for trees of the same size in the stand, assuming full occupancy of the growing space, can be determined from the growing space and stocking from:

$$G = \frac{D^2\pi}{40\,000N} \tag{8}$$

G is the basal area per hectare; N the maximum number of stems per hectare. D the bole diameter at breast height.

Maximum stand basal area converges around 31 $m^2\ ha^{-1}$. Alder (1990) reports a maximum stand basal area of 29 $m^2\ ha^{-1}$ for TSPs from the Ghana Forest Inventory Project data set. Philip (1994) suggests that common values of stand basal area vary between 10 and 20 $m^2\ ha^{-1}$ for young plantations, with a possible maximum of 60 $m^2\ ha^{-1}$. Dawkins (1958) gives a Pan-Tropic average of 35 $m^2\ ha^{-1}$. A reckoner for determining crown size, growing space and other stand characteristics is provided in Table 5.

6. Conclusion

Generally, the crown diameter–bole diameter regressions were highly significant and showed a strong linear relationship between the two variables. This corroborates results reported by earlier researchers (e.g., Krajicek et al., 1961; Vezina, 1962; Dawkins, 1963; Bonnor, 1964; Curtin, 1964; Wong, 1966; Hetherington, 1967; Ayhan, 1973; Lamson, 1987; Smith et al., 1992). The curves for the various species mostly conformed to Dawkins' (1963) type 2 behaviour, although *E. angolense* exhibited type 3 behaviour. In interpreting the data, however, it must be pointed out that the model may not be suitable for extrapolation to extreme values, i.e. values which are very small or very large relative to the spread of the original data (Table 2).

This allometric relationship is of practical significance since crown size can be easily predicted from bole diameter. The possibility of defining the maximum crop basal area density, stand density and the growing space required by the various species for plantation work has been demonstrated. These results apply to the dominant and co-dominant trees, and in silvicultural practice can be a useful guide when considering factors such as spacing in establishing plantations of these species. It must be emphasised, however, that the use of maximum growing space and maximum crop density concepts have been based largely on the assumption of a uniform crop without taking account of competitive interactions from neighbouring trees. This assumption holds for the experimental plots from which data were collected, as a consequence of the silvicultural interventions imposed on the natural forest to create a more or less uniform crop. The essence here is to provide a guide for spacing and crop density in plantations of similar species in the tropics.

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