ABS ACTA BIOLOGICA SLOVENICA
LJUBLJANA 2021 Vol. 64, Št. 1: 70–90

Crown stratification ratio models for *Tectona grandis* L. f in Oluwa Forest reserve, Nigeria

Modeli razmerja stratifikacije krošnje za vrsto *Tectona grandis* L. fv gozdnem rezervatu Oluwa, Nigerija

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Abstract: This research investigated crown ratio models for *Tectona grandis* plantation in Oluwa Forest reserve (Ondo State, Nigeria) using variables of slenderness coefficient and merchantable height. With three non-linear regression functions - logistic, Chapman-Richard and exponential we showed that basal area, tree stem volume and mean tree height per hectare were of high significance. In the same vein, there were fewer tree species in the class of higher diameter and height than there were in lower class. There were also more trees in the co-dominant and intermediate classes than in the dominant and suppressed layers. The lack of emergence in the plantation reflected the past disturbance of the ecosystem. Most of the tree growth variables were significantly different in different canopy layers in the study area. Based on the evaluation models, the three functions investigated for tree crown ratio modeling gave constant and reliable results in all canopy layers considering their indices. Especially, Chapman-Richard and exponential functions gave consistent trends and good fits for crown ratio models. It is recommended to put strict measures in place to avert any level of illegalities that may likely disrupt the delicate equilibrium of the ecosystem. It is also recommended that complexity revealed in this study is sustained in the region, and encouraged in other parts of Nigeria.

Keywords: crown ratio, modeling, Oluwa forest reserve, *Tectona grandis,* tree growth

Izvleček: Raziskava preizkuša tri različne modele razmerja krošnje v nasadih vrste *Tectona grandis* v gozdnem rezervatu Oluwa (država Ondo, Nigerija) z uporabo spremenljivk koeficienta vitkosti in tržne višine. Modeli, ki temeljijo na nelinearnih regresijskih funkcijah (logistični, Chapman-Richard in eksponentni) so pokazali, da so parametri kot so bazalna površina, prostornina debel in povprečna višina drevesa na hektar zelo pomembni. V razredu višjega premera in višine je bilo manj drevesnih vrst kot v nižjem razredu. V kodominantnem in srednjem razredu je bilo tudi več dreves kot v dominantni in zavrti plasti. Omejeno pojavljanje mladih rastlin odraža pretekle motnje ekosistema. Poleg tega se je večina rastnih spremenljivk dreves v različnih plasteh krošenj na preučevanem območju bistveno razlikovala. Vsi trije modeli so glede na indekse, ki smo jih uporabili, dali zanesljive in ponovljive rezultate v vseh plasteh krošenj. Chapman-Richardova in eksponentna funkcija sta pokazali skladne trende in ujemanje. Priporočamo stroge ukrepe za kakršnekoli nezakonite posege, ki bi lahko porušili občutljivo ravnovesje ekosistema ter da se celovitost sestojev ohrani v regiji in spodbuja v drugih delih Nigerije.

Ključne besede: gozdni rezervat Oluwa modeliranje, rast drevesa, razmerje krošnje, *Tectona grandis*

Introduction

Forests are viewed, defined, assessed and valued through different points of view and from different vantage points. It can be seen as a source of timber products, an ecosystem composed of trees along with myriad forms of biological diversity, a home for indigenous people, a repository for carbon storage, a source of multiple ecosystem services, and a social-ecological system or as all of the above (Chazdon et al. 2016). Within the forest, complex layers of vegetation are common from ground cover of mosses and low flowering plants through middle layers of bushes and secondary trees (Adekunle and Ige 2006**).** According to Hardiman et al. (2011), tree crown enables net primary production. It is also known that crown ratio is the ratio of live crown length to above-ground tree height (Schomaker et al. 2007). It is often used as an important predictor variable for tree growth equation. It indicates tree vigor and is a useful parameter in forest health assessment. According to Kozlowski et al. (1991), dense and large crowns are associated with potential growth rates while sparse and small crowns may reflect unfavorable site conditions (competition, moisture, diseases).

Hasenauer and Monserud (1996) suggested that crown ratio is a useful indicator of tree vigor, wood quality (Kershaw et al. 1990), resistance against wind (Navaratil 1997), stand density (Clutter et al. 1983) and it is important in management of many non-timber resources including wildlife habitat and recreation (Mcgraughey 1997). Crown dimensions can be important components of forest growth and yield models, and are used in many tree and crown level growth–modeling systems (Cole and Lorimer 1994). For instance, tree crown parameters can be considered when simple competition indices are not able to adequately predict recovery from competition when a competitor is removed (e.g. by thinning) (Vanclay 1994). Tree crown parameters were used as predictor variables in diameter and height growth equations (Monserud and Sterba 1996). Similarly, stand crown parameters were used to distinguish different stages of stand development (Soares 1999).

Within a forest stand, there are different forms of canopy layers. These canopy layers provide protection from strong winds and storms, while also intercepting sunlight and precipitation, leading to a relatively sparse vegetated understory layer (Lowman and Moffett 1993). The canopy of a rainforest is typically about 10m thick, and intercepts around 95% of sunlight. The canopy is below the emergent layer - a sparse layer of very tall trees that are typically very rare, one or two per hectare. With high availability of water and a near ideal temperature in rainforests, light and nutrients are two factors that limit tree growth from the understory to the canopy.

A canopy layer presents the horizontal and vertical distribution of tree crowns in a forest stand. Vertical canopy arrangement is often simplified by dividing canopy cover into height layers while horizontal canopy is commonly quantified as the vertically-projected percentage of cover of plant canopies, and the abundance and size of canopy gaps. According to Fiala (2003), additional attributes that are used to describe tree crown, include the number and height of vertical canopy layers and the proportions of cover contributed by different species groups.

Forest canopy is strongly influenced by stand density due to changing competitive interactions among the individual trees and in turn directly influences stem-wood volume production. Stand density also influenced the amount and distribution of leaf area in the forest stands. It is a measure of the stocking of a stand of trees based on the number of trees per unit area and diameter at breast height of the tree of average basal area. Stand density index is usually well correlated with stand volume and growth, and several variable-density yield tables have been created using this index (Chazdon et al. 2016).

The most commonly cited stand development model is Oliver's (1981) four-stage model, which comprises stand-initiation, stem-exclusion, understory re-initiation, and old-growth phases, all of which include canopy cover criteria. Franklin et al. (2002) proposed an alternative stand development model for natural stands. Their model highlights eight commonly encountered development stages: disturbance and legacy creation, cohort establishment, canopy closure, biomass accumulation/competitive exclusion, maturation, vertical diversification, horizontal diversification, and pioneer cohort loss, with canopy attributes described for each of these stages. Quantifying canopy structure attributes across forest stands of different ages can aid in evaluating these stand development models. The development of understory plant communities is usually related to changes in the over-story (Henderson 1981, Oliver 1981, Zamora 1981, Stewart 1988, Franklin et al. 2002, Naesset and Okland 2002). According to Connell and Slatyer (1977) "tolerance" model of succession, shade-tolerant species are generally present in all stages of succession, but invade the understory and increase in their abundance across the gradient of development stages.

Waide (2008) noted that very little of the World's tropical rainforest area can be considered to be under effective management including Nigerian forests. Clear-cut logging, tree planting, and short stand rotation lengths have greatly reduced the structural variability of forests (Smith 1988). Moreover, it is generally understood that tree canopy changes as forests develop with age (Oliver 1981, Van Pelt and Franklin 2000, Bond and Franklin 2002, Franklin et al. 2002), but these changes have rarely been quantified. The lack of data and the difficulty of accurately measuring the height to the live crown base which is even more pronounced in species with asymmetric crowns may however justify the relatively little research done on modeling crown parameters (Soares and Tome 2001).

Though much is known about how forests change in the number and size and identity of their stems (e.g. Oliver and Larson 1990), scanty information is available on the forest canopy (Aber 1979, Brown and Parker 1994) and almost nothing is known of the development of canopy layers in a forest stand (Parker 1995). This presents a problem since numerous functional characteristics of forests are linked to developmental stages (Waring and Schlesinger 1985). Thus, lack of information on the development of the outer canopy precludes the prediction of some stand functional characteristics from remote information. The shape of the outer canopy as well as the different levels below is important for several reasons. This part of a forest is the interface of atmospheric interactions. The extent, shape and disposition of this surface have implications for the penetration of light and heat, and for the extent of turbulent mixing, among other properties. Furthermore, the shape of the outer canopy necessarily constrains some aspects of the internal structure included below that surface. In addition, changes in the canopy reflect the development of the forest.

Tree crown research contributes to several key forest ecosystem attributes: biodiversity, productivity, forest management, forest environment, and wildlife. Crown ratio is used as an input variable to estimate growth and mortality of individual trees and also to display changes in the appearances of stands over time for habitat suitability and visual changes (Avery and Burkhart 2001). The crown leaves capture radiant energy for photosynthesis. The size of a tree crown has a marked effect and strong correlation with the growth of the tree and its various parts (Temesgen et al. 2005). Thus, measurement of a tree crown is often used to estimate the tree growth (Kozlowski et al. 1991).

No single model can be expected to be best for all purposes. It is therefore important to consider forest crown under different canopy layers to provide useful alternative model for management decisions. Many authors have based crown ratio equation on logistic functions (Hasenauer and Monserud 1996, Temesgen et al. 2005), exponential function (Holdaway 1986, Dyer and Burhart 1987) or Chapman Richard function (Soares and Tome 2001, Adesoye and Oluwadare 2008). However, most of these models were formulated for either even aged single species stands, or multi-species stands comprising of different ages or mixed stand with two or more species. These statistical functions have been tested on even aged stand consisting of different canopy layers (Popoola and Adesoye 2012), but none or rare in Oluwa Forest reserve.

The purpose of this study was to enhance understanding of canopy structure at different strata across different ages of forest stands using inventory data. Specifically, horizontal and vertical canopies were compared under different layers and the impact on the growth at different ages were quantified and assessed in Oluwa Forest reserve in Ondo State of Nigeria, as well as the determination of stand density indices.

Materials and methods

Study area

This study was carried out in Oluwa Forest reserve located in Odigbo Local government area, the southern part of Ondo State, Nigeria (Figs. 1 and 2). Four stands of different ages (39, 34, 30 and 26 years) which covered a total area of 2000 ha were investigated for the study. The forest is under the management of the Department of Forestry of the Ondo State Government of Nigeria. Oluwa Forest reserve covers 828 km^2 in area. It is located along the Lagos-Benin expressway and it is the largest forest reserve in the state. Most

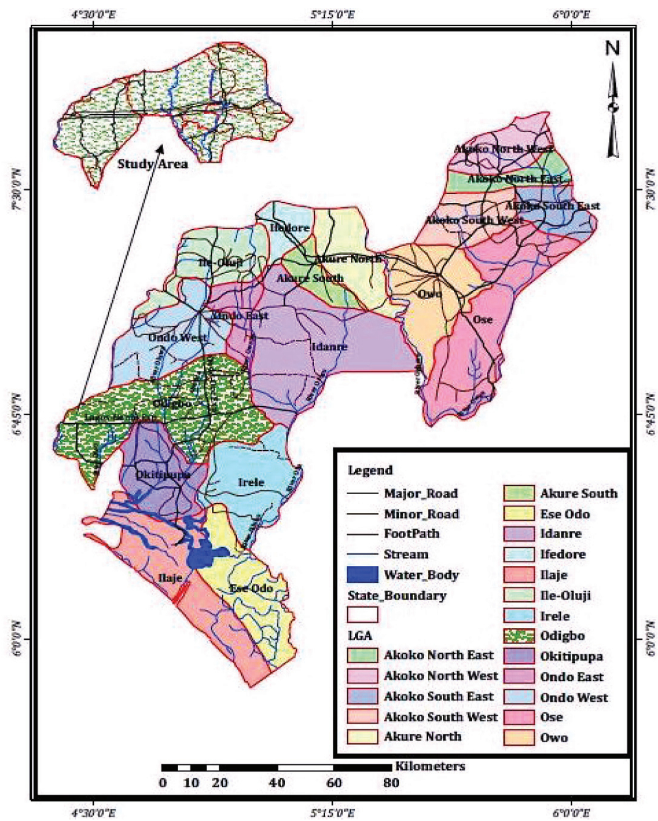


Figure 1: Administrative map of Ondo State showing the study area (Oluwa Forest reserve). Source**:** Ministry of Land and Housing, Akure, Ondo State, Nigeria.

Slika 1: Zemljevid pokrajine Ondo s prikazom območja proučevanja (gozdni rezervat Oluwa). Vir: Ministrstvo za okolje in stanovanjske zadeve, Akure, pokrajina Ondo, Nigerija.

part of the reserve lies north of the road while a minor part (about one-sixth of the total area) lies south of the road. Its eastern border is very close to the Ondo road, a major road that leads to both Ondo and Akure towns (Figs. 1 and 2). The area is part of the western plains of Nigeria. According to Iloeje (1981), the experimental site lies approximately between latitudes 635’ N and 720’ N, and longitudes 345’ E and 432’ E with much of it lying approximately between 300 and 600 m above the sea level. Most rivers and streams draining this area originated at the southern part of the study area. Important rivers are Oni, Oluwa, Ominla and Owena rivers. The study area is under the influence of Koppens humid tropical rain forest climate. Mean annual rainfall according to the observations of the Nigerian Meteorological Society (2007) ranges from 1,200 mm to 1,450 mm and temperatures are high throughout the year with a mean of about 27 °C with annual range of 3 °C. Natural vegetation of the area is tropical rainforest, characterized by multiple canopies and lianas. Some of the most commonly found trees in the area are: *Melicia excels* C.C Berg (Welw.), *Afzelia bipindensis* Harms, *Antiaris africana* Lesch, *Brachystegia nigerica* Hoyle & A.P.D Jones, *Lophira alata* Banks ex C.F. Gaertn, *Lovoa trichilioides* Harms, *Terminalia ivorensis* A. Chev, *T. superba* Engl. & Diels and *Triplochiton scleroxylon* K. Schum. However, the natural vegetation of the area, with the exception of the areas within the forest reserve had been reduced to secondary re-growth forest thickets and fallow re-growth in various stages of development, or was replaced by perennial and annual crops (Osunade 1991). These perennial crops include cocoa, kola and citrus. Most of the rural settlements in the study area had been established between 1920 and 1950 and by 1970 human colonization of the area was completed (Adejuwon 1971). Oluwa Forest reserve used to be contiguous with Omo Forest reserve in Ogun State of Nigeria. However, along the western border, the area is now densely populated.

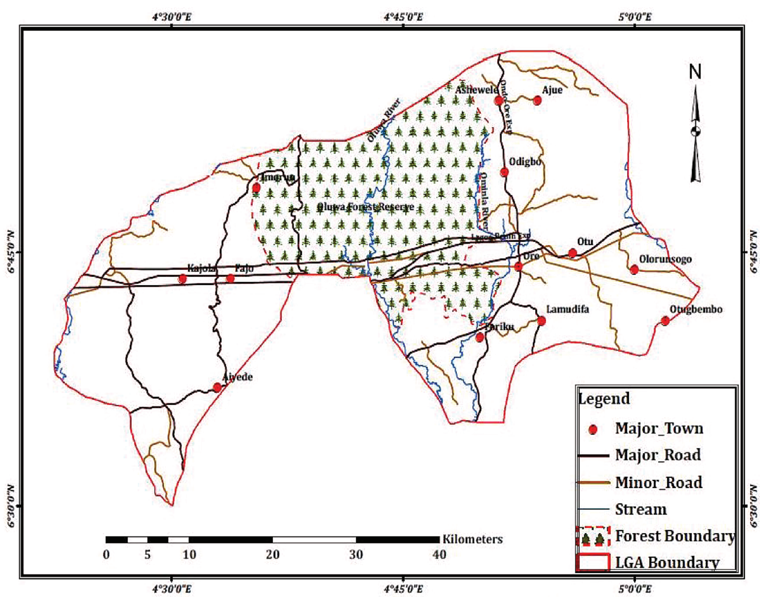


Figure 2: Odigbo Local government area showing Oluwa Forest reserve and road network pattern.
Slika 2: Zemljevid območja Odigbo z gozdnim rezervatom Oluwa in cestnim omrežjem.

Data collection

Four stands of different ages which were planted in 1982, 1987, 1991, and 1995 (ages 39, 34, 30 and 26 years, respectively) were studied in this investigation. Within each stand, five sample plots of 25 m x 25 m (0.0625 ha) were determined and surveyed for the purpose of this study. This was in a total 20 sample plots.

Within each sample plot, tree growth variables such as total height of trees (THT), merchantable height (MHT), crown length (CL) and crown diameter (CD) were measured. Similarly, diameters at breast height (DBH) were measured at 1.3 m above the ground level while diameters at the base, middle, and top of the tree were also measured with Spiegel Relascope (Relaskop). In addition, trees within each plot were classified into four canopy layers namely; dominant (height above 25 m), co-dominant (height range of 20 m to 24.9 m), intermediate (height range of 14 m to 19.9 m), and suppressed (height lower than 13.9 m) layers.

Data analysis

Data collected from tree measurements were used to estimate basal area, crown projection area at different layers, slenderness coefficient, crown ratio of individual tree, stand volume per plot, mean crown ratio and stand density index of trees at different layers. The following formulae (eq. 1-14) were used for calculations.

Basal area (eq. 1)

$$BA = \frac{\pi D^2}{4} \quad (1)$$

where: BA, basal area (m^2); D, diameter at breast height (m).

Tree slenderness coefficient (eq. 2)

$$TSC = \frac{THT}{D} \quad (2)$$

where: TSC, tree slenderness coefficient; THT, tree total height (m); D, diameter at breast height (m).

Crown projection area (eq. 3)

$$CPA = \pi \frac{CD^2}{4} \quad (3)$$

where: CPA, crown projection area; CD, crown diameter (m).

Tree volume per plot (eq. 4)

$$v = h\left[\frac{A_b + 4A_m + A_t}{6}\right] \quad (4)$$

where: v, tree volume (m^3); h, tree height (m); A_b, cross-sectional area at the base of a tree (m^3); A_m, cross-sectional area at the middle of a tree (m^3); A_t, cross-sectional area at the top of a tree (m^3).

Stand density index

The maximum density line was expressed by the equation 5 (Reineke 1933),

$$log_{10} N = -1.605\ (log_{10} D) + k \quad (5)$$

where: N, number of trees per acre; D, diameter at breast height (DBH) of the tree of average basal area; k, a constant varying with the species (a specific species constant).

When the quadratic mean diameter equals 10 inches (250 mm), the log of N equals the stand density index (SDI) in equation 6,

$$log_{10} SDI = -1.605(1) + k \quad (6)$$

which means that: $k = log_{10}SDI + 1.605$

Substituting the value of k above into the reference-curve formula gives the equation 7,

$$log_{10} N = log_{10} SDI + 1.605 - 1.605\ log_{10} D \quad (7)$$

This equation can be rewritten as equation 8:

$$log_{10} SDI = log_{10} N + 1.605\ log_{10} D - 1.605 \quad (8)$$

The above equation is an expression for computing the stand density index from the number of trees per acre and the diameter of the tree of average basal area. Estimates of stand density express the degree to which the growing space available for tree growth is utilized. Thus, stand density is a function of three elements:

i. Number of trees - which is readily determined by counting.
ii. Tree size - which involves a number of factors, e.g.:
   - Stem - characterized by diameter, height and taper
   - Crown - characterized by spread and height
   - Root - characterized by spread and depth (both difficult to measure).
iii. Spatial distribution on the ground - which is not readily determined. Generally, a square or triangular spacing is assumed.

In even-aged stands, crown closure may be proportional to basal area per ha. This relationship has led to the development of indices between estimates of crown closure obtained from aerial photographs and basal area. The value of crown closure as a variable depends on how well variation in stand volume is correlated with it.

The functional form of this relationship is (eq. 9),

$$Log_{10} N = k - 1.605 \ (Log_{10} QMD) \quad (9)$$

where: N, number of trees per hectare; k, a species-specific constant; QMD, quadratic mean diameter.

Crown ratio model

The tree crown ratio models employed for this study are: Logistic function, Chapman-Richard and Exponential models since a crown ratio value ranges from 0 (i.e. no crown, dead or defoliated tree) to 1 (i.e. crown extends over the entire tree bole). The tree crown ratio model formulated to express crown ratio as a function of tree size (e.g. basal area, merchantable height). The original forms of the models are (eqs. 10-12):

$$CR = (1 - e^{-\beta X}) \quad (10)$$

$$CR = ((1 + e^{-\beta X})^{0.5})^{-1} \quad (11)$$

$$CR = b_o + e^{-\beta X} \quad (12)$$

where: CR, estimated crown ratio; βx, linear equation with parameter β and independent variable x (which includes individual tree characteristics such as merchantable height, diameter at breast height, crown length and total height); e, Naperian constant (2.72).

The multiple linear regression equation 13 for the independent variables is given as follows:

$$\beta_x = \beta_o + b_{x1} + c_{x2} + d_{x3} \quad (13)$$

where: $\beta_{x,}$ linear equation with parameter β and independent variable x; $\beta_{o,}$ the intercept; b, c, d are the parameters; x_1, x_2, x_3 are the independent variables (eq. 14).

$$CR = (1 - e^{-\beta_0 + bx_1 + cx_2 + dx_3})^{-1} \quad (14)$$

where: CR, crown ratio; e, Naperian constant (2.72); $\beta_{o,}$ the intercept; b, c, d are the parameters; x_1, x_2, x_3 are the independent variables.

Model evaluation

The models were evaluated with a view of selecting the best estimator for tree crown ratio. In this study, the evaluation was based on coefficient of determination (R^2) and standard error of estimate (SEE), computed in order to evaluate the fitted models. The significance of the parameter estimates was observed. In addition, residual values were plotted against the predicted crown ratio values to check constant error assumptions. The selected versions of the models are presented in Supplement 1.

The level of statistical significance was set at p-value > 0.05.

Results and discussion

A total of 1042 individual trees were identified and recorded from the sampling plot which covers an area of 2000 ha. In this sampling, 95 trees were recorded in the dominant canopy layer, covering about 9.1% of the total population of the forest plantation. 267 trees were recorded in the co-dominant layer and this accounted for about 25.6% while 403 trees were recorded for intermediate height layer with 38.7% of the total population. Meanwhile, the suppressed layer accounted for 26.6 % with 277 trees (Supplement 3).

This research revealed that the number of individual trees per hectare in the forest plantation was higher, compared to those reported by previous researchers for other tropical rainforests in Nigeria (Adekunle et al. 2004, Ojo 2004, Adekunle and Olagoke 2008). This is an indication that the protection of the Oluwa Forest reserve is very effective. Another scientific statement is that the mean basal area per hectare obtained for the forest plantation (92.65m^2/ha) was comparable with that reported in Onigambari Forest Reserve (Akinyemi et. al. 2002) and also higher than in Omo Forest reserve (Adekunle 2007).

It was also discovered that the values of the mean basal area were comparatively higher to those reported by Temesgen et al. (2005) who conducted a research on multispecies and multilayered stands of southeastern British Columbia. The mean values of stem volume values obtained for the forest plantation (7184.46m^2/ha) were as well far higher than those reported by Adekunle et al. (2004), Adekunle and Olagoke (2008) and Alder and Abayomi (1994) for tropical rainforest ecosystem in Nigeria.

Correlation among tree growth variables for individual dominant trees

The Pearson's correlation coefficients for the growth variables are presented (Tabs. 1-4). The correlation values obtained for individual dominant trees varied considerably between -0.01 and 0.68. Most of the tree growth variables have significant positive correlation with one another. The highest correlation was between merchantable height and total height (r = 0.68), followed by correlation between diameter breast height and total height (r = 0.62) and between diameter breast height and merchantable height (r = 0.53). Negative correlation was obtained between diameter breast height and crown length (r = -0.01), merchantable height and slender coefficient (r = -0.31), diameter breast height and crown ratio (r = -0.30), and total height and crown ratio (r = -0.26).

Meanwhile the correlation values obtained for individual co-dominant trees varied between -0.72 and 0.78 (Tab. 2). Most of the tree growth variables have significant positive correlation with one another. The highest correlation was between merchantable height and total height (r = 0.78), followed by crown length and crown ratio (r = 0.78) and diameter breast height and merchantable height (r = 0.66). Negative correlation was obtained between merchantable height and crown length, total height and crown ratio (r = -0.09), diameter breast height and crown ratio (r = -0.15) and total height and slender coefficient (r = -0.22).

The correlation values recorded for individual trees in the intermediate layer varied between -0.34 and 0.92 (Tab. 3). Most of the tree growth variables have significant positive correlation with one another. The correlation was between crown length and crown ratio (r = 0.92), followed by diameter breast height and slender coefficient (r = 0.57), total height and slender coefficient (r = 0.52) and diameter breast height and merchantable height (r = 0.51). Negative correlation was obtained between diameter breast height and crown ratio (r = -0.34); total height and crown ratio (r = -0.61), crown ratio and slender coefficient and merchantable height and crown length (r = 0.28).

The values obtained for suppressed trees varied between -0.24 and 0.77 (Tab. 4). Most of the tree growth variables have significant positive correlation with one another. The highest correlation was between crown length and crown ratio (r = 0.77), followed by diameter breast height and slender coefficient (r = 0.54), merchantable height and slender coefficient (r = 0.40), and diameter breast height and crown length (r = 0.38). Negative correlation was obtained between total height and crown ratio, (r = -0.24), crown length and slender coefficient (r = -0.24), and crown ratio and slender coefficient (r = -0.26).

Generally, most of the tree growth variables were significantly and positively correlated with one another, which imply that an increase in one tends to be associated with an increase in the other variables. However, the correlation between the tree slenderness coefficient and the tree crown ratio, and the crown length and slenderness coefficients were low (r = 0.02 and 0.03 respectively). The result revealed negative correlations between crown ratio and diameter at breast height, crown length and diameter at breast height, crown ratio and total height. These negative correlation trends are expected and suggested that tall and slender tree with small diameter has lower crown ratio values. Similar pattern was observed by previous researchers (Chukwu et al. 2018)

Table 1: Correlation matrix for individual dominant tree growth variables.
Tabela 1: Matrika korelacij za rastne spremenljivke pri dominantih drevesih.

	DBH	MHT	THT	CL	SC	CR
DBH (m)	1.00					
MHT (m)	0.53**	1.00				
THT (m)	0.62**	0.68**	1.00			
CL (m)	-0.01	-0.56**	0.22**	1.00		
SC	-0.85**	-0.31**	-0.27**	0.10	1.00	
CR	-0.30**	-0.88**	-0.26**	0.88**	0.22**	1.00

Abbreviations: THT, total height; MHT, merchantable height; DBH, diameter at breast height; SC, slenderness coefficient; CL, crown length; CR, crown ratio; **, statistically significant correlation

Table 2: Correlation matrix for individual co-dominant tree growth variables.
Tabela 2: Matrika korelacij za rastne spremenljivke pri kodominantnih drevesih.

	DBH	MHT	THT	CL	SC	CR
DBH (m)	1.00					
MHT (m)	0.57**	1.00				
THT (m)	0.66**	0.78**	1.00			
CL (m)	0.28**	-0.09	0.54**	1.00		
SC	-0.72**	-0.27**	-0.21**	0.02	1.00	
CR	-0.15**	-0.66**	-0.09**	0.78**	0.21**	1.00

Abbreviations: THT, total height; MHT, merchantable height; DBH, diameter at breast height; SC, slenderness coefficient; CL, crown length; CR, crown ratio; **, statistically significant correlation.

Table 3: Correlation matrix for individual intermediate tree growth variables.
Tabela 3: Matrika korelacij za rastne spremenljivke pri srednjih drevesih.

	DBH	MHT	THT	CL	SC	CR
DBH (m)	1.00					
MHT (m)	0.51**	1.00				
THT (m)	0.28**	0.30**	1.00			
CL (m)	0.12**	0.03	0.18**	1.00		
SC	-0.57**	-0.17**	0.52**	0.03	1.00	
CR	-0.03	-0.30**	-0.06	0.92**	0.03	1.00

Abbreviations: THT, total height; MHT, merchantable height; DBH, diameter at breast height; SC, slenderness coefficient; CL, crown length; CR, crown ratio; **, statistically significant correlation.

Table 4: Correlation matrix for individual suppressed tree growth variables
Tabela 4: Matrika korelacij za rastne spremenljivke pri zavrtih drevesih.

	DBH	MHT	THT	CL	SC	CR
DBH (m)	1.00					
MHT (m)	0.19**	1.00				
THT (m)	0.39**	-0.70**	1.00			
CL (m)	0.38**	0.54**	0.29**	1.00		
SC	0.64**	0.40**	0.16	-0.24**	1.00	
CR	0.35**	0.38**	-0.24**	0.77**	-0.26**	1.00

Abbreviations: THT, total height; MHT, merchantable height; DBH, diameter at breast height; SC, slenderness coefficient; CL, crown length; CR, crown ratio; **, statistically significant correlation.

Basal area and stem volume estimation

The forest had an average tree basal area of 92.65 m^2/ha while the average tree stem volume was 7184.46 m^2/ha. Information on tress basal area and stem volume per hectare for the forest plantation is presented in Supplement 2.

Height distribution of tree per plot in canopy layers in the study area

The distribution in height classes corresponding to each of the strata (canopy layers) in the study area is shown in Table 5. Four layers existed in the all the plots sampled in the plantation. Trees belonging to the dominant height class accounted for about 9.1% of the individuals sampled in the plantation. About 25.6% of the forest plantation belonged to the co-dominant layer while the intermediate layer accounted for about 38.7%. The suppressed layer accounted for about 26.6%. There was a major decrease in the number of trees reaching the heights above 25 m, compared to the significant increase in the number of trees reaching the heights of 14 m – 19.9 m. Also, there was lower number of individuals in the dominant canopy layer than in the suppressed and co-dominant height classes. The intermediate class recorded the highest number of trees in the overall canopy layer.

Crown ratio model

Three non-linear regression models (Logistics, Chapman-Richard, and Exponential) were used in the study. All the tree growth variables apart from the crown ratio (the dependent variable), were tested during model fitting processes. The selected version of the Logistics, Chapman-Richard and Exponential models, their parameters estimation and fit statistics for the canopy layers are represented in Table 6. Merchantable height and slenderness coefficient were found to consistently predict crown ratio in all the functions.

Table 5: Distribution of tree height per hectare in canopy layers in the study area.
Tabela 5: Razporeditev višine dreves v slojih krošenj na proučevanem območju.

Canopy layer	Height (m)	Number of trees / ha
Dominant	≥ 25	95
Co-dominant	20 - 24.9	267
Intermediate	14 – 19.9	403
Suppressed	≤ 13.9	277
Total		1042

The R^2 values for the three functions were fairly high for the dominant and co-dominant and intermediate layer with low values of standard errors of estimates (SEE). The suppressed layer which gave a lower fit to the data set in the functions gave significant result for the estimated parameters for all applied functions.

However, there were significant differences among growth variables under different canopy layers; hence the three models were fitted to the data set on the layer basis. The merchantable height and slenderness coefficient gave better fit to the data set and were found to be important in defining the tree crown ratio for *Tectona grandis* stand in Oluwa Forest reserve. The suitability of the other tree growth variable was investigated and failed to explain the tree crown ratio in the entire canopy layer, and were therefore not included in the model presentation result. The R^2 values for the three functions were consistently high under dominant, co-dominant, and intermediate layers with low SEE. The suppressed layers, which gave much lower fit to the data set in all the functions, however produced significant result for all the estimated parameters in all the functions. The R^2 value obtained in this study were generally higher in comparison with those reported previously for less diverse ecosystem (Temesgen et.al. 2005, Adesoye and Oluwadare 2008) with lower SEE value. This indicates better fit of the three functions to the data set than those fitted by previous researchers.

Table 6: Crown ratio models selected with parameter estimate and fit statistic for dominant, co-dominant, intermediate and suppressed layers in Oluwa Forest reserve using Logistic, Chapman-Richard and Exponential functions. Mean ± standard error is presented.

Tabela 6: Modeli razmerja krošenj, izbrani z oceno spremenljivk in statistiko primernosti za dominantne, kodominantne, srednje in zavrte plasti v gozdnem rezervatu Oluwa z uporabo logističnee, Chapman-Richard-ove in eksponentne funkcije. Predstavljena je srednja vrednost ± standardna napaka.

Function	Parameter	Dominant layer	Co-dominant layer	Intermediate layer	Suppressed layer
Logistic	a_o	1.21±0.14	0.27±0.09	0.25±0.03	-1.27±0.09
	a_1	-0.11±0.01	-0.11±0.01	0.03±0.00	0.02±0.01
	a_2	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Chapman	a_o	0.09±0.22	0.59±0.02	-0.61±0.06	-0.56±0.07
-Richard	a_1	0.17±0.01	0.27±0.03	0.17±0.07	14.16±1.49
	a_2	-0.00±0.00	0.02±0.00	-0.02±0.00	0.00±141.22
Exponential	a_o	0.19±0.05	-0.40±0.03	-0.07±0.07	-0.47±0.02
	a_1	-0.13±0.03	0.03±0.00	-0.05±0.01	-32.28±6.87
	a_2	0.00±0.00	0.00±0.00	-5.74±3.82	0.23±49387.19

Logistic: R^2 (Dominant layer) = 0.657; R^2 (Co-dominant layer) = 0.643, R^2 (Intermediate layer) = 0.647; SEE (for all) = 0.2.

Chapman-Richard: R^2 (Dominant layer) = 0.704; R^2 (Co-dominant layer) = 0.763; R^2 (Intermediate layer) = 0.747; R^2 (Suppressed layer) = 0.430, SEE (for all) = 0.2.

Exponential: R^2 (Dominant layer) = 0.711; R^2 (Co-dominant layer) = 0.738; R^2 (Intermediate layer) = 0.720; R^2 (Suppressed layer) = 0.427, SEE (for all) = 0.2.

Table 7: Growth variables for dominant, co-dominant, intermediate and suppressed layers in Oluwa Forest reserve. Mean ± standard deviation and minimum to maximum range are presented.
Tabela 7: Spremenljivke rasti za prevladujoče, kodominantne, srednje in zavrte plasti v gozdnem rezervatu Oluwa. Predstavljene so srednje vrednosti ± standardni odklon in razpon vrednosti.

Statistical value	Canopy layer	Growth variable				
		BA	DBH	MHT	SC	CR
Mean ± SD	Dominant	0.06±0.04	27.19±0.73	14.43±3.32	97.58±31.42	0.41±0.10
	Co-dominant	0.05±0.03	23.68±0.01	12.60±3.09	94.06±33.45	0.38±0.00
	Intermediate	0.06±0.06	19.08±8.00	9.75±2.48	92.62±39.98	0.36±0.01
	Suppressed	0.16±0.67	10.48±0.01	4.88±0.21	90.40±36.38	0.37±0.01
Minimum – maximum	Dominant	0.01–0.18	9.55–47.43	6.60– 1.20	209.42-533.48	0.17–0.72
	Co-dominant	0.00–0.20	4.45–56.93	4.50–19.80	49.09–330.34	0.42–0.70
	Intermediate	0.00–0.52	4.46– 2.20	3.80–17.40	29.69–583.88	0.04–0.82
	Suppressed	0.00–0.16	0.03–0.92	1.70–14.90	6.28–202.80	0.78–0.98

Abbreviations: BA, basal area; MHT, merchantable height; DBH, diameter at breast height; SC, slenderness coefficient; CR, crown ratio; SD, standard deviation.

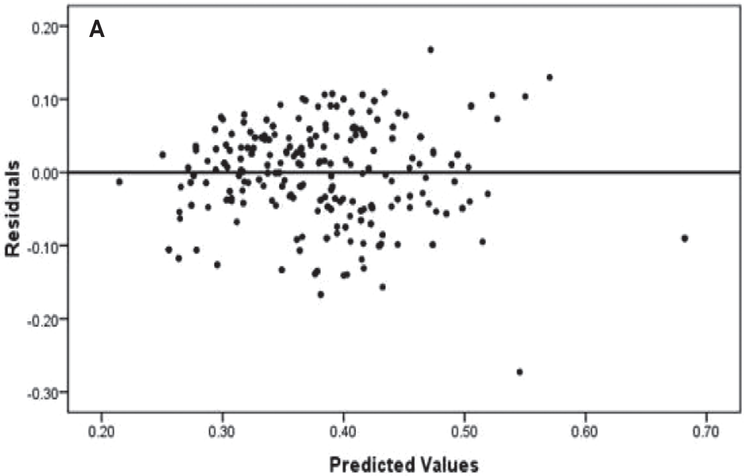
Mean comparison of the growth variables for the canopy layers

The mean slenderness coefficient decreases with decreasing crown ratio at different stages of the canopy layer (Tab. 7). Dominant class had the highest value and suppressed individual class recorded the lowest value. This indicates that trees that are tall and slender had lower crown ratio values. However, the average diameter at breast height followed the same trend as the dominant class recorded the highest value (27.19 m) and the suppressed class had the lowest (10.48 m).

Relationship between residual and estimated Crown ratio

The evaluation of the residual plots (Figs. 3-5) and its error analysis revealed that error variance is constant across the predicted crown ratio. Logistics, Chapman-Richard and Exponential functions were observed to have constant error variances.

In the graphical relationship between the residuals and estimated crown ratio obtained with the three functions, all the residual values are in the positive and negative region which implied that crown ratio values were consistently predicted. Exponential and Chapman-Richard functions judging from their error analyses appeared well in the three functions owing to the fact that constant error variances distributed well both in the positive and negative region of the x-axis (i.e. the estimated crown ratio values). This is desirable for a good model. This trend was similar to the findings of Soares and Tome (2001) and Adesoye and Oluwadare (2008). Therefore, based on the evaluation of the error analyses, Chapman-Richard and Exponential functions are recommended for predicting crown ratio in the stand because they were more precise in their predictive abilities.



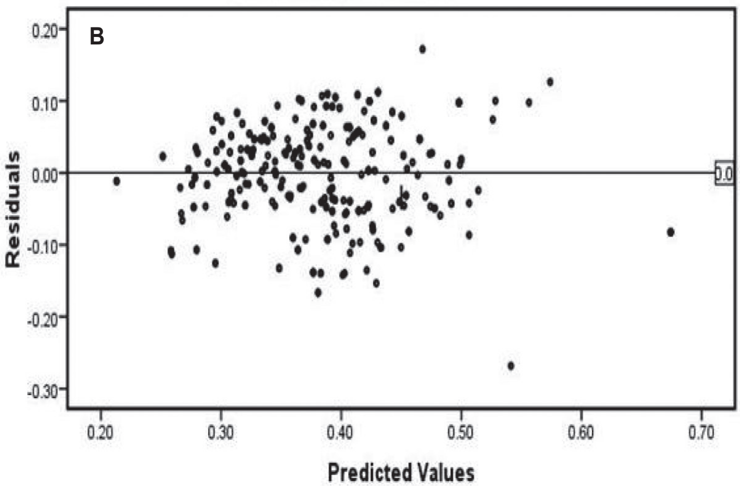


Figure 3: Relationship between residual and predicted values using **A** - Logistic and **B** - Exponential models in dominant layer.

Slika 3: Razmerje med rezidualno in predvideno vrednostjo pri **A** - logističnem in **B** - eksponentnem modelu za dominantni sloj.

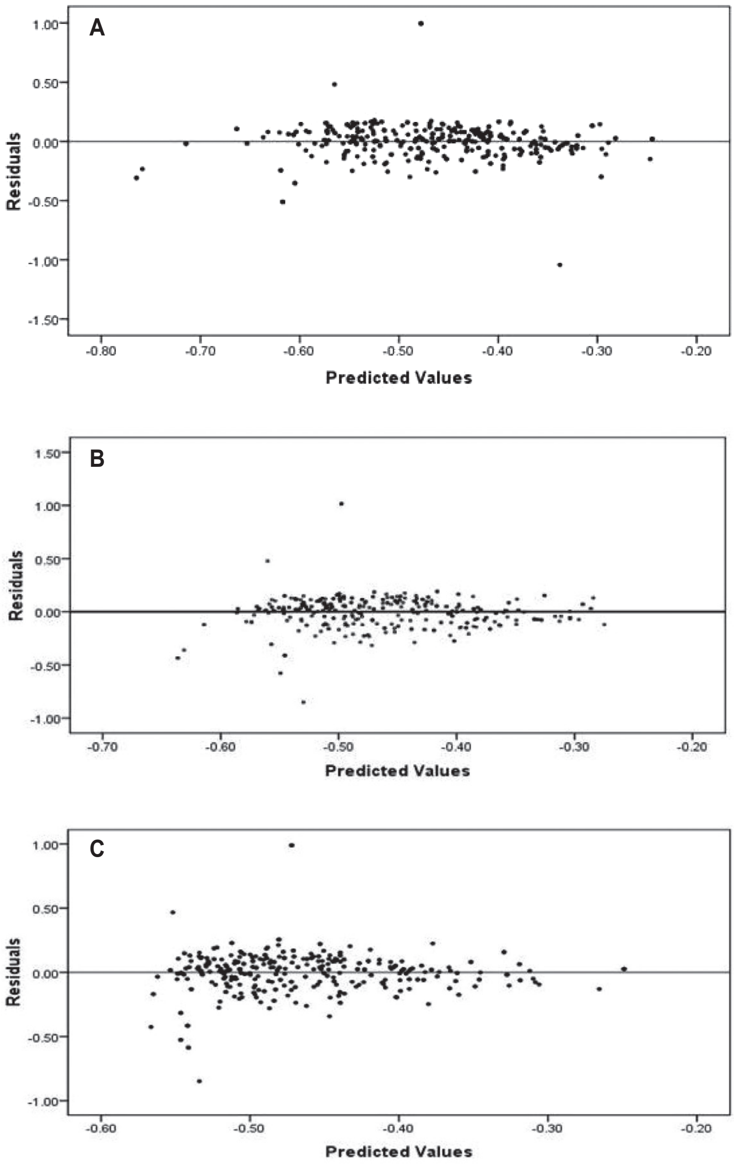


Figure 4: Relationship between residual and predicted values using **A** - Logistic, **B** - Exponential and **C** - Chapman-Richard model in intermediate layer.

Slika 4: Razmerje med rezidualno in predvideno vrednostjo pri **A** - logističnem, **B** - eksponentnem in **C** - Chapman-Richardovem modelu za srednji sloj.

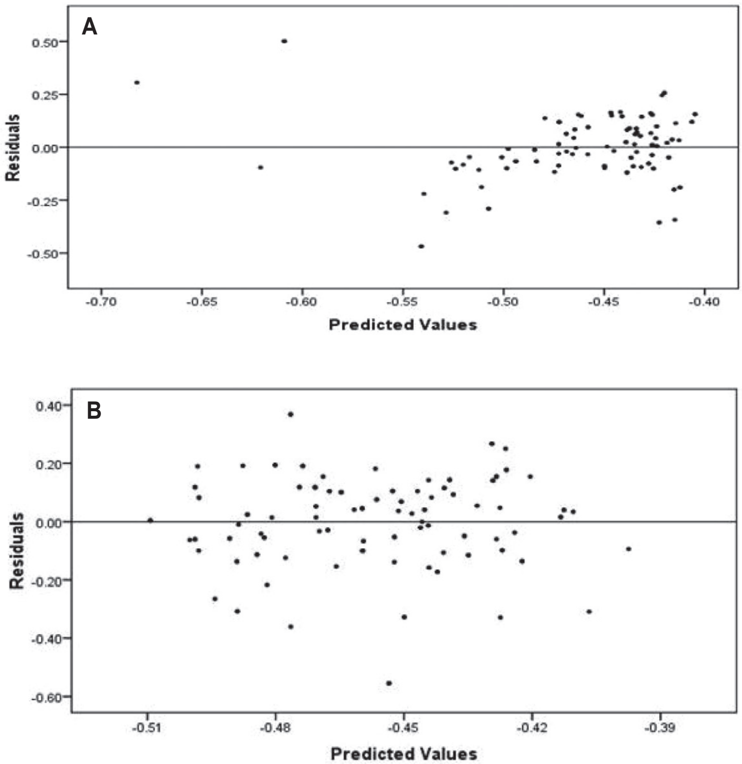


Figure 5: Relationship between residual and predicted values using **A** - Logistic and **B** - Chapman-Richard model in suppressed layer.

Slika 5: Razmerje med rezidualno in predvideno vrednostjo pri **A** - logističnem in **A** - Chapman-Richardovem modelu za zavrti sloj.

Model fitting and evaluation

Model fitting and evaluation are important parts of model building. Fitting of crown ratio models was based on the total data set. A number of different models were examined for predicting crown ratio using Logistic, Chapman-Richard and Exponential functions and the selected versions of the models are presented in Supplement 1.

One unique independent variable that features in all the models was tree slenderness coefficient. This proves that tree slenderness coefficient is one of the factors contributing to the size of tree crown ratio. Similar pattern was observed in the studies conducted by Hanus et al. (2000), Hasenauer and Monserud (1996) and Hann (1997). Merchantable height was another important variable used in modeling. Adesoye and Oluwadare (2008) and Marshall et al. (2003) also found merchantable height as an important variable for modeling crown.

The other variables failed to adequately explain crown ratio variation and were therefore not included in the models. The SEE differences were small since crown ratio is constrained to the interval of 0 and 1. This was also noticed in the work carried out by Temesgen et al. (2005) and Adesoye and Oluwadare (2008). Generally, the models consistently gave good fit to the *Tectona grandis* plantation data in Oluwa Forest reserve.

The evaluation of the residual plots (Figs. 3-5) revealed that error variance was constant across the predicted crown ratio. In the graphical relationship between the residuals and estimated crown ratio obtained with the logistic function, all the residual values were in both negative and positive regions but were farther from one another which implied that crown ratio values were slightly consistent. Exponential and Chapman-Richard functions judging from their error analysis appeared 'constant' error variance distributed both in the positive and negative regions of the x-axis (i.e. the estimated crown ratio values), which is highly desirable. Similar trend was observed by Soares and Tome (2001) and Adesoye and Oluwadare (2008). Based on the evaluation of the error analysis, Chapman-Richard and exponential functions are highly recommended for predicting crown ratio in the stand. Although the R^2 values for suppressed canopy layer were lower compared to other layers. They were more precise in their predictive abilities.

Conclusions

Based on the examined result in the study, the basal area and tree stem volume per hectare in forest plantation were higher than the values suggested for a well-stocked tropical rainforest in Nigeria. There were fewer tree species in the class with higher diameter and height than in the classes with smaller diameter and lower height. These trees of higher diameter classes formed the dominant layer which could be the result of their early and fast growth as there were more trees in the co-dominant and intermediate layer than in the dominant and suppressed layer. Meanwhile, the lack of emergence reflected the past disturbance of the ecosystem. The higher mean basal area, stem volume, and tree height per hectare recorded in this study compared to other tropical rainforest in other part of Nigeria are also very significant. Most of the tree growth variables were significantly different in different canopy layers of the study area.

The forest canopy was very diverse and the tree growth variables related considerably well with each other. It is recommended on this note that strict measure should be put in place to prevent any illegal action that may disrupt the delicate equilibrium of the ecosystem. The mean basal area obtained was greater than $90m^2$ that is suggested for a well-stocked forest plantation and a robust tropical forest plantation in Nigeria. It is comparable with data obtained in other parts of West Africa in similar ecosystems. It is highly recommended that such structure should be sustained in the region and by extension, encouraged in other parts of the World. However, based on the evaluation models, the three functions investigated in this study for crown ratio modeling (Chapman-Richard, Logistic and Exponential functions) gave constant and accurate result for all the canopy layers. Chapman-Richard and Exponential functions are recommended as crown ratio models for *Tectona grandis* plantation in Oluwa Forest reserve.

Povzetek

Raziskave drevesnih krošenj prispevajo k poznavanju več ključnih atributov gozdnih ekosistemov: biotske raznovrstnosti, produktivnosti, gospodarjenja z gozdovi, gozdnega okolja in prisotnosti prostoživečih živali. Spremenljivka razmerje krošenj se uporablja za oceno rasti in umrljivosti posameznih dreves in za oceno primernosti habitatov. Velikost drevesne krošnje je v povezavi z rastjo drevesa in njegovih različnih delov. Raziskava preizkuša tri različne nelinearne modele (logistični, Chapman-Richardov in eksponentni) za nasad vrste *Tectona grandis* v gozdnem rezervatu Oluwa (država Ondo, Nigerija). Modeli so pokazali, da so parametri bazalna površina, prostornina debel in povprečna višina drevesa na hektar zelo pomembni. Ker noben model ni uporaben za vse namene, je pri testiranju pomembno upoštevati različne plasti krošenj. Namen te študije je bil z uporabo empiričnih podatkov izboljšati razumevanje strukture krošenj v različnih plasteh gozdnih sestojev različne starosti ter določili indekse gostote sestojev.

Rezultati so pokazali, da je bila bazalna površina in obseg drevesnega debla na hektar v gozdnih nasadih višja od vrednosti, izmerjenih v visoko produktivnem tropskem deževnem gozdu v Nigeriji. V razredu z višjim premerom in višino je bilo manj drevesnih vrst kot v razredih z manjšim premerom in manjšo višino. Drevesa višjih razredov premera so tvorila prevladujočo plast, kar bi lahko bil rezultat njihove zgodnje hitre rasti, saj je bilo v kodominantni in srednji plasti plasti več dreves kot v dominantni in zavrti plasti. Omejeno

pojavljanje mladih rastlin odraža pretekle motnje ekosistema. V tej študiji smo zabeležili tudi višjo povprečno osnovno površino, prostornino stebla in višino dreves na hektar v primerjavi z drugimi tropskimi deževnimi gozdovi v Nigeriji. Večina spremenljivk rasti dreves se je v različnih krošnjah na območju proučevanja bistveno razlikovala.

Plast krošenj je bila zelo raznolika in spremenljivke rasti dreves so se med seboj precej dobro povezovale. Zato priporočamo sprejetje strogih ukrepov za preprečevanje kakršnihkoli nezakonitih ukrepov, ki bi lahko porušili občutljivo ravnovesje ekosistema. Povprečna bazalna površina je bila večja od 90 m^2, kar je značilno za produktiven gozdni nasad oziroma za vitalne tropske gozdove v Nigeriji. Ta podatek je primerljiv tudi s podatki, pridobljenimi v drugih delih Zahodne Afrike v podobnih ekosistemih. Zelo priporočljivo je, da se takšna struktura ohranja v regiji in spodbuja tudi v drugih delih sveta. Vse tri funkcije, uporabljene v tej študiji za modeliranje razmerja krošenj (Chapman-Richardova, logistična in eksponentna), so dale zanesljive rezultate za vse plasti krošenj. Uporabo Chapman-Richardove in eksponentne funkcije pa priporočamo za modeliranje razmerja krošnje za nasad *Tectona grandis* v gozdnem rezervatu Oluwa.

Acknowledgements

The authors wish to acknowledge Professor P. O. Adesoye, currently in the University of Venda, South Africa, for the assistance regarding experimental design and methodology. We also acknowledge Mr. Afolabi Gbenga and Mr. Olugade Tayo both in the Department of Forest Resources Management, University of Ibadan, for their technical assistance. We gratefully appreciate the cooperation of The Ondo State Ministry of Land and Housing, Alagbaka, Akure for the administrative map supplied. Anonymous reviewers are also greatly appreciated for their constructive comments on the manuscript.

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List of supplements

Supplement 1: Fitting of experimental data with selected tree crown ratio models for dominant, co-dominant, intermediate and suppressed layers.
Dodatek 1: Ujemanje podatkov z izbranimi modeli krošnje za dominantni, kodominantni, srednji in zavrti sloj.

Function	Dominant layer	Co-dominant layer	Intermediate layer	Suppressed layer
Logistic	0.66±0.20	0.64±0.20	0.65±0.16	0.41±0.15
Chapman-Richard	0.70±0.17	0.76±0.20	0.75±0.17	0.43±0.16
Exponential	0.71±0.17	0.74±0.20	0.72±0.16	0.43±0.16

Values are expressed as R^2 ± SEE

Supplement 2: Tree basal area and stem volume per plot in forest reserve.
Dodatek 2: Površina drevesne baze in prostornina debla na vzorčnem mestu v gozdnem rezervatu.

Plot	Basal area (m^2)	Stem volume (m^3)
1	43.29	3, 716.89
2	49.56	4, 204.16
3	53.02	4, 816.72
4	53.26	4, 941.89
5	38.77	3, 476.27
6	133.91	10, 259.63
7	160.17	10, 477.57
8	101.55	3, 064.33
9	106.03	7, 892.71
10	151.61	11, 081.72
11	132.94	9, 215.09
12	136.93	9, 368.11
13	78.87	5, 544.59
14	112.22	8, 478.86
15	147.01	9, 598.89
16	82.61	7, 182.57
17	103.26	8, 616.16
18	64.33	6, 460.89
19	76.53	7, 214.86
20	87.09	8, 077.26
Total	1, 912.96	143, 686.17
Mean	95.65	7, 184.31

Supplement 3: Tree canopy and percentage of individual layer.
Dodatek 3: Delež dreves po slojih drevesnih krošenj.

Canopy layer	Number of trees	Percentage (%)
Dominant	95	9.12
Co-dominant	267	25.62
Intermediate	403	38.68
Suppressed	277	26.58
Total	1042	100.00