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Nestor Engone Obiang, Alfred Ngomanda, Lee White, Kathryn Jeffery, Éric Chézeaux, et al.. Disentangling the effect of size and competition: a growth model for *Aucoumea klaineana* . *Annals of Forest Science*, Springer Verlag/EDP Sciences, 2013, 70 (3), pp.241-249. <10.1007/s13595-012-0255-7>. <hal-01201471>

HAL Id: hal-01201471

<https://hal.archives-ouvertes.fr/hal-01201471>

Submitted on 17 Sep 2015

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Disentangling the effect of size and competition: a growth model for *Aucoumea klaineana*

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Received: 11 June 2012 / Accepted: 15 November 2012 / Published online: 17 January 2013
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Abstract

• **Context** Okoume (*Aucoumea klaineana*) is the most important timber species in Gabon, while being classified as vulnerable in the IUCN red list. Thousands of growth measurements for this species have been performed since the 1950s but, because of a lack of integrated analysis, did not bring a consistent view on its growth pattern.
• **Aims** This study aims at disentangling the effects of tree size and local competition on tree growth.
• **Methods** A growth model was fitted for okoume, using data from seven sites in Gabon and Congo. The growth

model was designed to be useful for forest management, which means that it relied on variables that could be computed using forest inventory data.

• **Results** A lognormal growth model with a negative response to stand basal area was selected. A significant residual site effect on growth was found, with a slower growth in the sites near the border of the natural range of okoume than in the sites far from it.

• **Conclusion** Growth strongly responded to local stand attributes such as tree density and basal area. Growth decrease with stand age in monodominant okoume stands was correctly predicted, although tree age was not incorporated into the model.

Handling Editor: Jean Daniel Bontemps

Contribution of the co-authors N.L. Engone Obiang coordinated the research project and contributed to field work. A. Ngomanda supervised the work and contributed to field work. L.J.T. White, K.J. Jeffery and E. Chézeaux provided data. N. Picard contributed to field work, run the data analysis and wrote the paper.

Electronic supplementary material The online version of this article (doi:10.1007/s13595-012-0255-7) contains supplementary material, which is available to authorized users.

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Keywords Competition · Growth · Light-demanding species · Nonlinear model · Okoume · Tropical forest

1 Introduction

Aucoumea klaineana Pierre (Burseraceae), or *okoume* as it is commonly called in Gabon, is the most important timber species in Gabon. The volume of okoume entering mills was 931,473 m³ in 2007, which represented 82 % of the total

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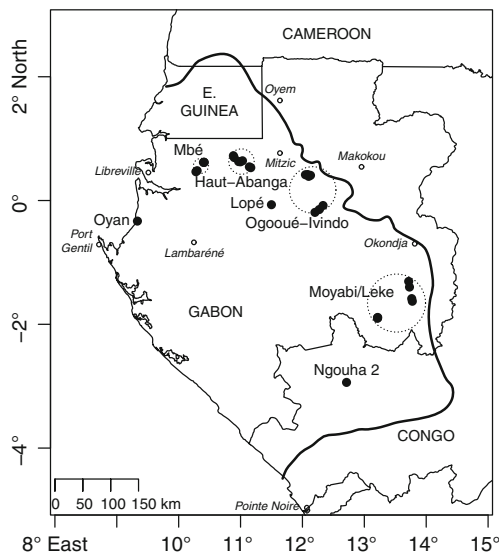


Fig. 1 Location of the seven study sites (dotted circles) and natural range of the okoume (thick solid line, as defined by Brunck et al. 1990). The black dots show the location of the permanent sample plots

timber production of Gabon (de Wasseige et al. 2009, Chapter 3). Although this species is abundant in Gabon, it has been classified as vulnerable in the IUCN red list because of logging and because it has a natural range that is restricted to western and central Gabon and areas of Equatorial Guinea, Republic of Congo and Cameroon (Fig. 1). Okoume is a strict light-demanding species that requires light to regenerate (Mapaga et al. 2002). As a pioneer species, it is able to colonise open spaces (Brunck and Grison 1990) and is also able to form monodominant stands (Peh et al. 2011). Like most light-demanding species, okoume is fast growing with a light wood (wood specific gravity of 378 kg m^{-3} on average; Zanne et al.).

Thousands of growth measurements for okoume have been performed since the 1950s in its whole natural range (Brunck and Grison 1990; FAO 1981; Fuhr 1999; Rocek 1981) but, as average growth values have most of the time been reported in the literature, it has been difficult to take advantage of the available information. Moreover, growth measurements have been made using different techniques (ring analysis, diameter monitoring), which may bring different estimates of growth (Détienne et al. 1998). As okoume is a pioneer species that requires canopy gaps to settle, it is often naturally found in cohorts of individuals with the same age. It thus makes sense to use stand age as a predictor variable of tree growth. Durrieu de Madron et al. (2000) reported for okoumes growing in mixed stands a growth pattern that increases with diameter until 30 cm diameter at breast height (dbh) and then decreases with diameter for $\text{dbh} \geq 40 \text{ cm}$. Conversely, Nasi (1997) reported for okoumes growing in even-aged cohorts a growth pattern that constantly increases with diameter. These results may

seem paradoxical unless the effect of age-dependent stand structure and competition on growth is disentangled from the effect of tree size.

The effect of environmental conditions on the growth of okoume has also been highlighted. It is generally admitted that the growth of okoume is maximal on the coastal part of its natural range and decreases as one moves deep inland (Brunck and Grison 1990; Durrieu de Madron et al. 2000), but no difference between the coastal part and inland (Croisé and Fabbri 1991) and even the reverse signal (Doucet 2003, p. 234) has been reported. These contrasted results can be understood given the light-demanding behaviour of okoume and its ability to enhance growth when the canopy is opened. Local stand structure variation may thus hinder wider scale site-related signals of growth. Understanding the growth of okoume would require disentangling the effect of site conditions and the effect of disturbances.

Despite the many data on the growth of okoume, almost no growth model has been published for this species. Yet, modelling would be required to combine all the scattered data on growth and to disentangle the factors that influence it. One growth model has been defined for okoume (Louppe et al. 2000; Mapaga et al. 2002) but had several apparent statistical shortcomings that limited its usefulness. The present study aims at defining a management-oriented growth model for okoume, using data from permanent sample plots at seven sites in Gabon and Congo. To our knowledge, this is the first model using data at a national scale and thus including contrasted environmental conditions in terms of climate and stand attributes. Structural characteristics of the forest stand were included as predictors in the model to account for disturbances (e.g. logging), and between-site growth differences were tested. Only those predictors that comply with the information collected in forest inventories were used, so that the model can be used to refine management plans.

2 Material and methods

2.1 Study sites and data set

Seven sites (six in Gabon and one in Congo) covering the natural range of okoume were used for this study (Fig. 1). The main site characteristics are given in Table 1 and details are reported in the [Supplementary material](#). These sites covered the whole range of mixing and ageing for okoume populations, from young monodominant okoume populations (Oyan, Ngouha 2) to old declining okoume populations (Mbé, Haut-Abanga, Ogooué-Ivindo), and intermediate situations (Lopé, Moyabi/Leke). In total, these sites represented 76 permanent sample plots and 61.5 ha of full inventory.

Table 1 Characteristics of study sites

Site	<i>D</i>	<i>R</i>	<i>p</i>	<i>S</i>	<i>m</i>	Density (ha ⁻¹)			Basal area (m ² ha ⁻¹)			<i>n</i>	<i>N</i>
						Min.	Max.	Mean	Min.	Max.	Mean		
Oyan	85.3	1,745	34	22	6–10 ^a	263	2,552	512	2.8	50.7	28.8	51,367	7,466
Ngouha 2	56.0	1,645	13	13	1–3 ^a	370	735	543	16.6	41.4	27.8	5,602	2,522
Moyabi/Leke	27.6	1,800–2,000	7	7	1	432	545	469	29.8	38.6	35.3	182	182
Lopé	24.1	1,474	5	2.5	3	233	341	297	22.4	30.8	26.3	237	137
Haut-Abanga	13.8	1,800–2,000	7	7	2	270	512	394	22.9	44.4	32.5	153	99
Ogooué-Ivindo	11.8	1,400–1,900	5	5	1	268	443	350	28.5	39.7	35.5	36	36
Mbé	7.5	2,000–3,500	5	5	1	547	590	562	28.8	44.9	39.5	37	37

D dominance of okoume (in percent of stand basal area), *R* annual rainfall (in millimetre), *p* number of plots, *S* cumulated area of plots (in hectare), *m* number of remeasurement times (the first inventory is not counted) = maximum number of longitudinal observations for the same tree (shorter longitudinal sequences can be obtained if the tree dies), *n* number of observations for okoume (including remeasurements of the same tree), *N* number of distinct okoume trees

^aDepending on the plot

An observation was defined as a couple (D_1, D_2) of diameters for the same tree at two different times $t_1 < t_2$, from which the growth rate was computed as $A = (D_2 - D_1)/(t_2 - t_1)$. Covariables for each observation were the tree density and the basal area at time t_1 of the plot to which the tree belonged, and the social status of the tree. In total, there were 57,614 observations and 10,479 distinct trees. The site of Oyan alone represented 89 % of the observations and 71 % of the trees (Table 1). Because some trees were remeasured, data included longitudinal sequences of growth, with an average sequence length of 5.5 observations per tree. The longest sequences were found at Oyan (Table 1). The social status of the tree described its vertical location in the canopy. At Oyan and Ngouha 2, it was noted as dominant, codominant or suppressed. In the other sites, a distinction between dominant and suppressed was made only. A preliminary study showed that there was actually no significant difference between the growth of suppressed and codominant trees, so that no distinction was finally made between codominant and suppressed trees. The social status was missing information for 6.5 % of the observations.

2.2 Growth modelling

The growth model was designed as a tool for forest management. It had to remain simple enough so that it can be used with the data available from forest inventories, while being able to account for the main determinants of growth. A trade-off between detailed, location-specific prediction and general, less precise prediction of growth thus had to be solved. As okoume is a light-demanding species whose growth strongly responds to light availability, a description of the environment had to be incorporated in the model to explain differences in growth between trees of the same

size. We chose a potential \times reducer model type, which is a classical approach to growth modelling (Botkin et al. 1972). In this approach, growth is modelled as a function of intrinsic tree and site potentialities, modified by the effect of tree local environment (e.g. stand density, tree-to-tree competition for resources). The ‘potential’ expresses the growth of a tree that does not experience any constraint from its environment (but including the ontogeny-related growth decline). Classical growth curves for the potential were reviewed by Zeide (1993). The ‘reducer’ expresses the reduction of growth due to environmental constraints and is usually computed from competition indices that describe the resource partitioning between trees. Classical competition indices were reviewed by Biging and Dobbertin (1992, 1995).

After preliminary selection, three types of growth curves were retained for the potential component, all of which were particular cases of the general expression:

$$A_{\text{pot}} = \exp\{a + b \ln(D) + c[\ln(D)]^2 + d \ln[e - \ln(D)]\} \quad (1)$$

where a, b, c, d and e are the parameters to estimate and D is the tree dbh (in centimetre). The power growth model has two parameters α and β :

$$A_{\text{pot}} = \alpha D^\beta \quad (2)$$

and follows from (1) by setting $a = \ln(\alpha)$, $b = \beta$ and $c = d = 0$. This model is the one predicted by the metabolic scaling theory of plant growth (Coomes and Allen 2009; Enquist et al. 1999).

The lognormal growth model (Uriarte et al. 2004a) has three parameters G, K and Y :

$$A_{\text{pot}} = G \exp\left\{-\left[\frac{1}{Y} \ln\left(\frac{K}{D}\right)\right]^2\right\} \quad (3)$$

and follows from (1) by setting $a = \ln(G) - [\ln(K)/Y]^2$, $b = 2 \ln(K)/Y^2$, $c = -1/Y^2$ (which implies $c < 0$) and $d = 0$. Parameter $G = \exp[a - b^2/(4c)]$ (in centimetres per year) is the maximum growth rate, $K = \exp[-b/(2c)]$ (in centimetre) is the diameter where growth reaches its maximum and $Y = 1/\sqrt{-c}$ (no unit) is a shape parameter that determines the breadth of the growth function. The terminology ‘lognormal’ here follows from the fact that (3) corresponds to the density of the lognormal distribution with parameters $\ln K$ and $Y/\sqrt{2}$ and does not imply any lognormal distribution for A_{pot} . This growth function is flexible and can model increasing, decreasing or unimodal diameter–growth relationships. When compared to other classical growth functions like the Gompertz or the Korf equation, it has the advantage that it decreases to zero as diameter increases to infinity.

The Korf model has three parameters G , P and Y :

$$A_{\text{pot}} = G \frac{D}{P} \left[\ln \left(\frac{P}{D} \right) \right]^{1+Y} \exp\{(1+Y)[1 - \ln(1+Y)]\} \quad (4)$$

and follows from (1) by setting $a = \ln(G/P) + (1+Y)[1 - \ln(1+Y)]$, $b = 1$, $c = 0$, $d = Y + 1$ and $e = \ln(P)$. Parameter $G = P \exp[a - d(1 - \ln d)]$ (in centimetres per year) is the maximum growth rate, $Y = d - 1$ (no unit) is a shape parameter that determines the breadth of the growth function and $P = \exp(e)$ (in centimetre) is the maximum asymptotic dbh. This growth function has an asymmetrical modal shape. When $Y = 0$, it simplifies to the Gompertz model. A limitation of this model is that diameter cannot overcome P .

Whereas expressions (2), (3) and (4) rely on parameters that have a direct interpretation, expression (1) is generally more convenient for model fitting. In particular, expression (1) shows that the power growth model is a first-order polynomial on log-transformed variables, whereas the lognormal model is a second-order polynomial on log-transformed variables.

Because the exponential is the only link function that maps any negative value onto the unit interval while transforming an additional competitor into a multiplicative decrease on growth, the reducer was defined as $\exp(-\alpha C)$, where C is a competition index and α is a positive coefficient (Biging and Dobbertin 1995; Caplat et al. 2008; Gourlet-Fleury and Houllier 2000). In tropical rain forest, and especially for light-demanding species, the main competition is for light. This competition is asymmetric, since small trees are shadowed by large trees but not the converse. Then, the competition index C also has to be asymmetric. Commonly used indices are the number of trees greater than the subject tree at a distance less than R from it or the basal area of trees greater than the subject tree at a

distance less than R from it (Gourlet-Fleury and Houllier 2000). These indices are distance dependent (sensu Biging and Dobbertin 1992) and require to know the local neighbourhood of each tree. This is already too detailed to be of practical use for forest management. However, if R is large enough, they can be approximated by $N[1 - F(D)]$ and $B[1 - F(D)]$, respectively, where N is the tree density, B is the basal area and F is the distribution function of the diameter distribution (Verzelen et al. 2006; Supplementary material). Most natural tropical rain forests have a reverse-J diameter distribution that can be modelled by an exponential distribution. The diameter distribution in our study sites conformed to this pattern (Supplementary material). Then, $F(D) = 1 - \exp(-\mu D)$, and a good surrogate for the reducer function is

$$\text{red}(D, N, B) = \exp[-(\alpha N + \beta B + \gamma N B) \exp(-\mu D)] \quad (5)$$

where α , β , γ and μ are the parameters to estimate, D is the diameter of the subject tree and N and B are the stand-level variables that characterise the biotic environment. The growth function is finally defined as

$$A(D, N, B) = A_{\text{pot}}(D) \times \text{red}(D, N, B) \quad (6)$$

where A is the growth rate (in centimetres per year) of a tree with diameter D growing in a forest stand with density N and basal area B and A_{pot} is defined by (2), (3) or (4).

2.3 Statistical analysis

Longitudinal sequences of growth on the same individual tree resulted in autocorrelation among observations, thus violating the assumption of independent errors that is required for ordinary least squares fitting. Autocorrelation may result from several processes. First, because of genetic differences, different trees in the same growing conditions may have different growth performances. Mixing different growth curves brings positive autocorrelation with respect to the average growth curve. Individual differences in growth can be accounted by adding a random effect on the model parameters. Second, growth in trees often presents temporal autocorrelation: a tree that has grown faster than expected at a given year will tend to grow faster than expected at the subsequent year too. This autocorrelation can be accounted by specifying a correlation structure on the residuals of the same longitudinal sequence. The growth models were thus fitted using the framework of non-linear mixed-effects model with an intra-individual correlation structure on residuals.

The three growth models were fitted using the parameterisation defined by (1). An individual tree random effect with normal distribution was added on the a parameter. Several intra-individual correlation structures were tested, and

a continuous autoregressive process of order 1 was retained: $Cor(\epsilon_t, \epsilon_s) = \phi^{|s-t|}$, where ϵ_t and ϵ_s are the residuals of the growth observations collected at year t and s from the same tree and ϕ is the correlation between two observations 1 year apart. Models were fitted by maximising the log-likelihood. All computations were performed using the R software (R Development Core Team 2012) and the nlme package. The fitted Korf, power and lognormal models were compared on the basis of the regression R^2 and of the Akaike information criterion (AIC).

Analyses of variance of the model residuals with respect to site and social status were achieved to test for a residual site or social status effect. These two factors were not directly included in the model to keep it as a management tool. When a significant effect was detected, the analysis of variance was complemented with a Tukey’s multiple comparisons test.

3 Results

3.1 Plot characteristics

The plots used to fit the growth model for okoume had diverse characteristics in terms of tree density and basal area (Table 1), with a non-linear negative correlation between these two variables (Fig. 2). The youngest plots that corresponded to recent forest regrowth over savannah had a very high density (up to $2,500 \text{ ha}^{-1}$) with a low basal area. As

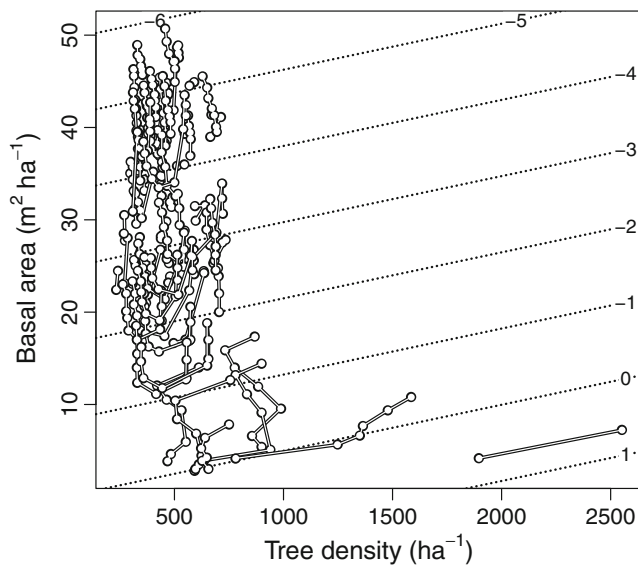


Fig. 2 Characteristics of the plots used to fit the growth model for okoume (white dots), and contour lines (dotted lines) of the logarithm of the ‘reducer’ component of the fitted growth model as a function of tree density and basal area. White lines connect the same plot along its temporal sequence. The reducer was computed for a null diameter (so that $\exp(-\mu D) = 1$)

Table 2 Number of parameters associated to the predictors (p), regression R^2 , and Akaike information criterion (AIC) for the three growth models for okoume (*A. klaineana*) fitted at seven study sites in Gabon and Congo

Model	p	R^2	AIC
Lognormal	6	0.709	70,273
Korf	7	0.707	70,458
Power	6	0.703	71,019

trees got older, their density decreased (first quickly, then more slowly) while their basal area increased (first slowly, then more quickly). Hence, the sample of plots included a non-linear gradient from young dense plots to mature plots with a low density and a high basal area. The young plots with the highest densities and the mature plots with the largest basal areas were both found at Oyan (Table 1).

3.2 Growth model

The model with the lowest AIC was the lognormal model, then the Korf model and finally the power model (Table 2). The γ parameter associated with the interaction between stand density and basal area in the reducer was not significantly different from zero for the lognormal model, whereas all model parameters were significantly different from zero for the Korf and the power models. The following growth model was thus selected for okoume (Table 3):

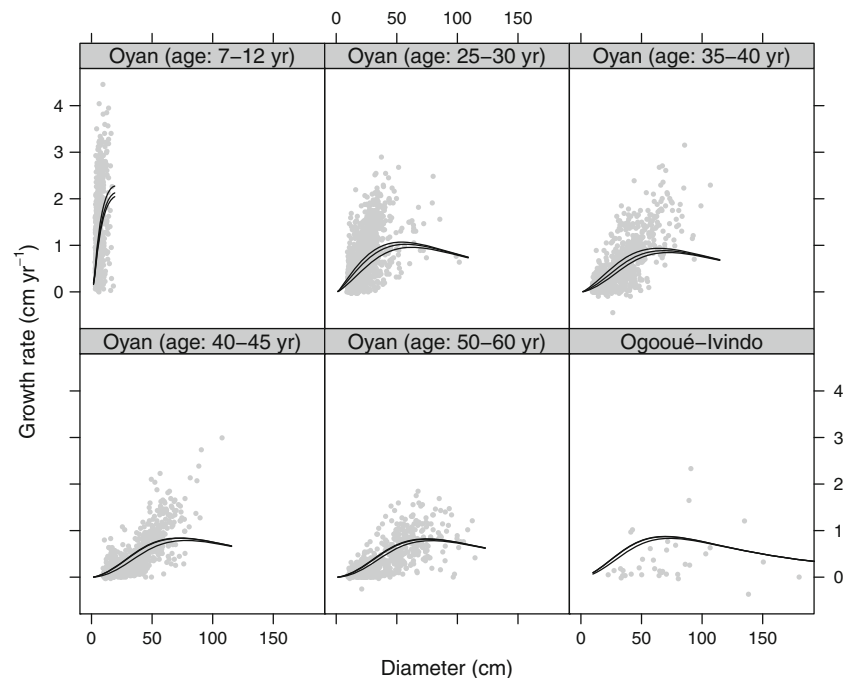
$$A = 2.26 \exp \left\{ - \left[\frac{1}{1.61} \ln \left(\frac{21.0}{D} \right) \right]^2 - (0.121B - 6.038 \cdot 10^{-4}N) \times \exp(-3.350 \cdot 10^{-2}D) \right\}$$

Table 3 Parameter values for the lognormal growth model for okoume (*A. klaineana*)

Parameter	Estimate	Unit	Std. error	t value	$Pr(> t)$
a	-2.750	[-]	$1.6 \cdot 10^{-1}$	-17.5	<0.001
b	2.343	[-]	$9.5 \cdot 10^{-2}$	24.8	<0.001
c	-0.385	[-]	$1.4 \cdot 10^{-2}$	-26.9	<0.001
α	$-6.038 \cdot 10^{-4}$	ha	$5.1 \cdot 10^{-5}$	-12.0	<0.001
β	0.121	$\text{m}^{-2} \text{ha}$	$2.3 \cdot 10^{-3}$	52.2	<0.001
μ	$3.350 \cdot 10^{-2}$	cm^{-1}	$7.7 \cdot 10^{-4}$	43.4	<0.001

a, b, c coefficients of the second-order polynomial on log-transformed variables for potential growth, α parameter for the stand density effect on growth, β parameter for the stand basal area effect on growth, μ parameter for the tree size effect on competition

Fig. 3 Observed (grey dots) and predicted (black lines) growth rates versus diameter for okoumes (*A. klaineana*) in seven permanent sample plots at Ogooué-Ivindo, Gabon and in 19 permanent sample plots with different ages ranging from 7 to 60 years at Oyan, Gabon



where D is in centimetre, N in per hectare, B in square metres per hectare, and A in centimetres per year. The standard deviation of the random effect on a was 0.518, whereas the residual standard deviation was 0.403 cm year^{-1} . The intra-individual correlation parameter was $\phi = 0.15$. The potential growth rate culminated at 2.26 cm year^{-1} at a diameter of 21.0 cm in an empty plot. The μ parameter of the reducer component corresponded to an exponential distribution with a mean diameter of $\mu^{-1} = 29.9$ cm. All other things being equal, the growth reducer was half that of a tree of diameter 10 cm for a tree of diameter $\ln(2)/\mu + 10 = 30.7$ cm. The shape of the reducer for a fixed diameter is shown in Fig. 2. Growth decreased as basal area increased. Tree density had a correcting effect on basal area: given two plots with the same basal area, the plot with the largest average tree size (hence the lower density) had a smaller growth than the plot with the smallest average tree size (hence the greater density).

To show how the predicted growth for okoume compares with observations, we selected a few plots with contrasted characteristics in terms of density and basal area (showing all data for okoume would result in illegible plots). Observations were taken from Oyan, where the most contrasted plots were found, and from Ogooué-Ivindo, that is representative of old-growth okoume populations in mixed stands. As the age of plots (i.e. the time since forest has colonised savannah) was known at Oyan, this further enabled us to check that the age effect was correctly accounted by the model using density and basal area. At Oyan, in 19 plots classified into five age classes, the pattern of growth was similar to that found in plantations, where the growth rate was an

increasing function of diameter over most of the diameter range, with a maximum growth rate that decreased with age (Fig. 3). Although age was not included as an explanatory variable in the model, the fitted growth model for okoume was able to predict this pattern. At Ogooué-Ivindo, the modal shape of the growth curve was more apparent (Fig. 3).

3.3 Residual effect of site and social status

A significant residual site effect on the growth of okoume was found ($F_{6, 57,607} = 27.7$, p value < 0.001), with the highest growth at Mbé and Oyan and the lowest growth at Moyabi/Leke and Ogooué-Ivindo (Table 4). A significant positive correlation was found between the mean plot-level residual and the distance from the plot to the limit of the

Table 4 Mean site-level residual of the lognormal growth model for okoume (*A. klaineana*), with the groups of sites as defined by Tukey's post hoc test

Group	Site	Mean residual (cm year^{-1})
a	Mbé	0.064
ab	Oyan	-0.029
abc	Lopé	-0.071
abc	Ngouha 2	-0.084
bcd	Haut-Abanga	-0.123
cd	Moyabi/Leke	-0.191
d	Ogooué-Ivindo	-0.265

natural range of okoume (Pearson correlation coefficient = 0.45, p value = 0.02).

A significant residual social status effect on the growth of okoume was also found ($F_{1, 53,728} = 489.2$, p value < 0.001): the growth of dominant okoumes (mean residual, 0.02 cm year⁻¹) was greater than that of suppressed okoumes (mean residual, -0.05 cm year⁻¹). Moreover, as the proportion of dominant okoumes significantly varied across sites (χ^2 test, $\chi^2 = 524.3$ with 4 degrees of freedom, p value < 0.001) with a smaller proportion of dominant okoumes in those sites where residual growth was greater (e.g. 47 % dominant okoumes at Oyan versus 83 % dominant okoumes at Ogooué-Ivindo), the site effect and the status effect could not be confused.

4 Discussion

4.1 Understanding growth variability

In agreement with its light-demanding behaviour, the growth of okoume strongly responded to stand attributes such as density or basal area, with increased growth as basal area decreased (Ouédraogo 2011). This may explain why so variable growth rates have been reported for this species (see [Supplementary material](#) for a compilation of reported growth values in the literature). The growth of okoume is highly variable because okoume trees are able to react to local changes in light availability (canopy gap, thinning), even for old individuals (Bedel 1969). Thinning strongly enhances the growth of suppressed and small dominant trees, but not much that of large dominant trees (Fuhr et al. 1998a, b, 2001; Fuhr 1999). Hence, because of local disturbances that once favoured their growth, some individuals can present elevated growth rates even when the neighbouring stand does not grow that fast (Doucet 2003). Thus, understanding and predicting the growth of okoume requires, at least, to disentangle the effects of tree size and of stand attributes.

Okoume had a predicted growth curve with a unimodal shape with respect to diameter. The maximum of the predicted growth rate for okoume varied with the stand density and basal area (Fig. 3). A unimodal growth curve had already been observed for okoume in mixed stands, but with different modes: Clément et al. (1979) found, at Sindara, a maximum growth rate for okoumes between 30 and 50 cm in diameter, while Geiser (1972) found a maximum for okoumes between 10 and 30 cm in diameter. Hence, the present model provides an explanation for such a variability in the location of the mode.

Going deeper into the understanding of the growth of okoume may be achieved by using a finer description of the

local neighbourhood of each tree, or by addressing additional descriptors such as the site, the climate or the geology. Because okoume can be found both in monodominant and mixed stands, the identity of neighbouring species and the prevalence of intra- or inter-specific competition may matter (Uriarte et al. 2004b). A distance-dependent competition index could also be used to get a local description of growth conditions (Biging and Dobbertin 1992; Caplat et al. 2008; Gourlet-Fleury and Houllier 2000). The social status of the tree, which could be refined using Dawkins codes (Synnott 1979), also gives information on its local neighbourhood, even if it is partly redundant with size since most suppressed trees have a small diameter and most dominant trees have a large diameter. The present study showed that the social status had a significant effect on the growth of okoume.

4.2 Growth and ecological behaviour

Okoume reached its maximum potential growth rate at a small diameter (approximately 20 cm), which is consistent with its pioneer behaviour: okoume needs light at its earliest stage to survive and grow. Because stand density and basal area are correlated predictors, their effect cannot be analysed separately. Nevertheless, basal area was the main predictor of competition whereas stand density acted as a corrective factor. Conditionally on basal area, stand density had a positive effect of growth. This may seem paradoxical but is typical of pioneer species that grow very fast in dense stands with very low basal area, i.e. open stands full of recruits without overtopping trees (Ouédraogo 2011).

The modal diameter–growth curve is common in natural forests (Gourlet-Fleury and Houllier 2000; Monserud and Sterba 1996; Zeide 1989). It contrasts with the power relationship predicted by the metabolic scaling theory of plant growth (Coomes et al. 2011; Enquist et al. 1999). Although a modal growth curve could result from the combined action of a size-dependent competition reducer and of a monotonous increasing potential growth, the fit of the power model to the okoume data did not support this view, with an estimated exponent $\beta = -0.43$ (95 % confidence interval -0.48, -0.37) for (2) that was significantly different from the theoretical value of 1/3 according to the metabolic scaling theory (Coomes and Allen 2009; Coomes et al. 2011).

A specificity of okoume is its natural range that is limited to a small region as compared to other tropical species, with a sharp transition from local abundance to absence (Groulez 1963; Leroy Deval 1973). Several non-exclusive explanations have been put forward to explain it, given that okoume grows on all types of soil except swampy soils (Mapaga et al. 2002). First, the natural range of okoume could be delimited by the climate (de Saint Aubin 1963).

Second, the present range could result from an extension from a restricted refuge area during the last ice age (Born 2007; Muloko 2001; White et al. 2000). The present study showed that there was a significant site effect on the growth of okoume, with a slower growth in the sites near the border of its natural range than in the sites far from it. This is consistent with previous studies that found a greater growth for okoume in the coastal range than inland (Durrieu de Madron et al. 2000; Geiser 1972), and advocates for a climatic dependence of the natural range of okoume, since if the border of the natural range was a (re)colonising front, no slower growth near it would be expected.

4.3 Implications for forest management

Because most observations came from Oyan and because the most contrasted conditions were encountered in Oyan, the model obtained was essentially an Oyan one. Mean site-level residuals could be used as a site correction for growth (Table 4) but these differences, even though statistically significant, were actually quite low as compared to average okoume growth.

In management plans, forest managers used to predict the growth of okoume as a simple average growth rate. The present model provides a more detailed description of growth, while remaining simple enough since diameter, density and basal area are generally available from forest inventory data in central Africa. Using distance-dependent competition indices to refine the prediction of growth, although commonly used in forest dynamics models, is presently inconsistent with forest management practices in the natural tropical rain forests of central Africa.

As okoume is able to form monodominant stands (Peh et al. 2011) with cohorts of trees of the same age, it has often been considered that the growth of okoume in these almost pure stands should be considered separately from its growth in mixed stands (Détienne et al. 1998; Durrieu de Madron et al. 2000). The growth of okoumes in monodominant stands would be similar to that of trees in even-aged plantations, with age as a required predictor of growth (Nasi 1997). However, the present study showed that stand basal area and density could adequately predict the growth of okoumes in monodominant stands, without using age as a predictor. This has important implication for the management of these monodominant stands, since their age is generally unknown to the forest manager.

Acknowledgments Data for the Haut-Abanga, Ogooué-Ivindo and Moyabi/Leke sites were kindly provided by the private forestry company Rougier-Gabon. Data for the Oyan and Ngouha 2 sites were provided by CIRAD. The authors would like to thank the Government of Gabon for permission to work in the Lopé National Park and CIRMF and the Gabon Wildlife Department for the logistical support

during fieldwork. Joachim Dibakou, Jean Thoussaint Dikangadissi, Edmond Dimoto, Benoit Nziengui, Aimé Batsielili and Ludovic Momont provided exceptional field assistance during the project.

Funding This study was supported by the AIRD contract AIRES-Sud no. 7148. Data for Lope were collected with financial support from the Leverhulme Trust, ECOFAC (EU DG VIII) and the Wildlife Conservation Society.

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