A growth model for azobé, *Lophira alata*, in Gabon

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Photograph 1.
Young azobé trees , *Lophira alata*, growing in open space at Koungou falls (0º17'25"N, 12º34'21"E), northeastern Gabon.
Photograph N. L. Engone Obiang.

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RÉSUMÉ

UN MODÈLE DE CROISSANCE POUR L'AZOBÉ, *LOPHIRA ALATA*, AU GABON

L'azobé, *Lophira alata*, est un important bois d'œuvre d'Afrique centrale classé vulnérable dans la liste rouge de l'UICN. Bien que de nombreuses mesures de croissance aient été faites pour cette espèce, aucun modèle de croissance ne semble exister actuellement. L'objectif de ce travail était de faire la part, dans la croissance de l'azobé, entre l'effet de la taille de l'arbre et celui de la compétition locale. Un modèle de croissance a été ajusté pour l'azobé en utilisant les données de quatre sites de mesures au Gabon. Ce modèle de croissance a été conçu pour être utile à l'aménagement forestier, c'est-à-dire qu'il ne repose que sur des variables qui peuvent être calculées à partir des données d'inventaire forestier. Un modèle log-normal avec une réponse négative à la densité du peuplement et à sa surface terrière a été sélectionné. La relation entre la croissance et la taille de l'arbre était unimodale avec un maximum à 60 cm de diamètre à hauteur de poitrine. Un effet résiduel significatif du statut social de l'arbre a été trouvé (avec une croissance plus lente pour les arbres dominés) tandis qu'aucun effet résiduel du site n'a été trouvé.

Mots-clés : azobé, compétition, croissance, espèce héliophile, modèle non-linéaire, Gabon.

ABSTRACT

A GROWTH MODEL FOR AZOBÉ, *LOPHIRA ALATA*, IN GABON

Azobé, *Lophira alata*, is a major timber species in Central Africa classified as vulnerable into the IUCN red list. To date, despite numerous measures of increment, no growth model has been published for this species. This study aims to distinguish the effects between tree size and local competition on tree growth. A growth model was fitted for azobé, using data from four sites in Gabon. The growth model was designed to be useful for forest management that means it relied on variables that could be computed using forest inventory data. A lognormal growth model with a negative response to stand density and basal area has been selected. The relation between growth and size was unimodal with a maximum at 60 cm of diameter at breast height. A significant residual social status effect on growth has been found (with a slower growth for suppressed trees) while no residual site effect was found.

Keywords: azobé, competition, growth, heliophilous species, nonlinear model, Gabon.

RESUMEN

UN MODELO DE CRECIMIENTO PARA EL AZOBÉ, *LOPHIRA ALATA*, EN EL GABÓN

El azobé, *Lophira alata*, es una especie maderable importante de África central, clasificada vulnerable en la lista roja de la UICN. A pesar de muchos datos de crecimiento, resulta que actualmente no existe ningún modelo de crecimiento publicado para esta especie. Este estudio tiene como objetivo distinguir por un lado el factor tamaño del árbol y por otro lado los efectos de competencia entre árboles. Un modelo de crecimiento se ajustó para el azobé, utilizando datos de cuatro sitios en el Gabón. El modelo de crecimiento ha sido diseñado para ser de utilidad para el manejo forestal, lo que significa que se basó en variables que pueden ser calculadas a partir de datos del inventario forestal. Un modelo de crecimiento logarítmico normal con respuesta negativa en cuanto a la densidad y área basal ha sido seleccionado. La relación entre el crecimiento y el tamaño ha resultado unimodal, con un máximo de 60 cm de diámetro a altura del pecho. Un efecto residual significativo del estatus social del árbol ha sido detectado (con un crecimiento más lento de parte de los árboles dominados), mientras que no se constató ningún efecto residual del sitio.

Plabras clave: azobé, la competencia, el crecimiento, especies heliófilos, modelo no lineal, el Gabón.

Introduction

Lophira alata Banks ex C.F.Gaertn. (Ochnaceae), or azobé as it is commonly called in Gabon, is the second most important timber species in Gabon after okoume (*Aucoumea klaineana*). The volume entering mills was 37,700 m³ for azobé in 2007, which represented 3% of the total 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. Azobé is in Gabon at the southern limit of its natural range that extends till Casamance in Senegal. Azobé is a non-pioneer light-demanding species whose seedlings can settle under the forest cover and need light only at a given development stage (PALLA *et al.*, 2002; DOUCET, 2003; BIWOLÉ *et al.*, 2012). Yet, azobé seedlings and saplings can also be found in open spaces in full light (photograph 1). Azobé is sometimes found as a companion species of okoume in forest regrowth on savannah (WHITE *et al.*, 2000). It is classified in the group 5 of OLDEMAN, VAN DIJK (1991), in the "forest-gap" type of ALEXANDRE (1982), in the group of long cicatricial species of MANGENOT (1958), or in the group of late secondary species of BUDOWSKI (1965). Azobé is a monoecious deciduous wind-dispersed species, with a loss of leaves during one or two weeks in December (photographs 2 and 3). Paradoxically, it is a fast growing species with a heavy wood (wood specific gravity of 0.897 g/cm³ on average; ZANNE *et al.*, 2009).

The growth of azobé has mainly been studied in plantations (PALLA *et al.*, 2002; BIWOLÉ *et al.*, 2012). In natural forests, its growth is reported to be in the range 0.2–1 cm/yr depending on the light availability (see PICARD, GOURLET-FLEURY, 2011 for a synthesis). Large individuals that reach the canopy (photograph 4) have a faster growth (PALLA *et al.*, 2002). Despite the many data on the growth of azobé, there is little of published growth model for this species. Yet, modelling would be required to combine all the scattered data on growth, and to disentangle the factors that influence it. The present study aims at defining a management-oriented growth model for azobé, using data from permanent sample plots at four sites in Gabon. 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.

Material and methods

Study sites

Data were collected in four sites across Gabon (figure 1). The Mbé site is located in the southern part of the Monts de Cristal National Park (0°28'N, 10°17'E). It consists of five 1-ha permanent sample plots that were established in 2004 and remeasured in 2009 (SUNDERLAND *et al.*, 2004). The Haut-Abanga site is located at the eastern piedmont of the Monts de Cristal mountain range, in a forest concession (0°32'-0°44'N, 10°53'-11°10'E). It consists of seven 1-ha permanent sample plots that were established in 2000 and remeasured in 2003 and 2006. The Lopé site is located in the northern part of the Lopé National Park (0°04'S, 11°30'E) (WHITE *et al.*, 1995). It consists of five 0.5-ha permanent sample plots along a transect that were established in 1989 and remeasured in 1994 and 2001. The Ogooué-Ivindo site is located at the West of the Ivindo National Park, in a forest concession (0°11'S-0°25'N, 12°03'-12°20'E). It consists of four 1-ha permanent sample plots that were established in 2001-2002 and remeasured four years later.

Photograph 2.
Azobé tree, *Lophira alata*, with its red new leaves in the canopy, right after the defoliation period, along the Ivindo river bank near Koungou falls (0°30'42"N, 12°48'9"E), northeastern Gabon.
Photograph N. L. Engone Obiang.
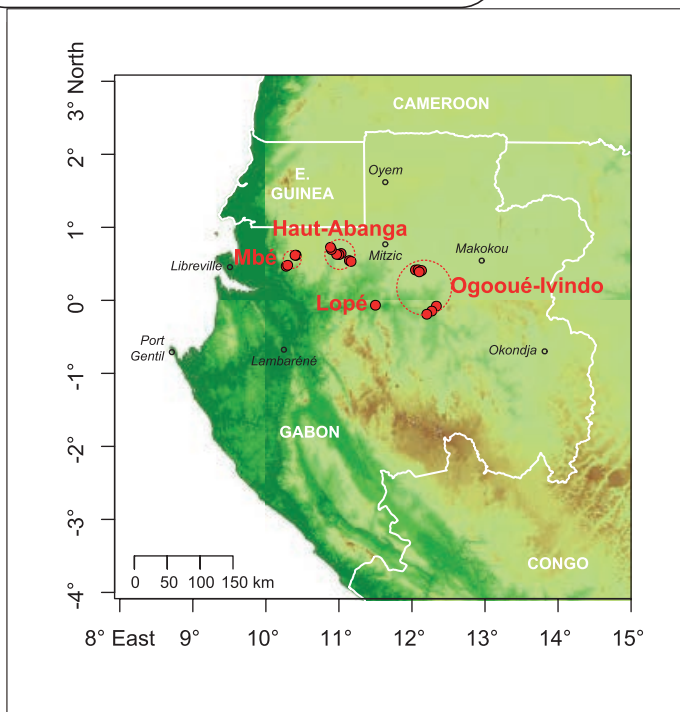
Figure 1.
Location of the four study sites (dotted circles) and of the permanent sample plots within each site (dots).

An observation was defined as a couple (D_1, D_2) of diameters at breast height (dbh) 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. Because some trees were remeasured twice, data included longitudinal sequences of growth, with a maximum sequence length of two observations. In total, there were 248 observations and 139 distinct trees (table I). The social status classified the trees as dominant or suppressed. However, the social status was rarely collected in the permanent sample plots and was missing information for 68% of the observations. Given the small number of available observations, the whole data set was used for model fitting and no validation was performed.

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. A potential x reducer model type was chosen, which is a classical approach to growth modelling (BOTKIN *et al.*, 1972). After preliminary selection, three types of growth curves were retained for the 'potential' component, all of which were particular cases of the general expression (equation 1):

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

where *a*, *b*, *c*, *d*, *e* are parameters to estimate and *D* is tree dbh (in cm).

The power growth model has two parameters α and β (equation 2):

$$A_{pot} = \alpha D^\beta$$

and follows from (equation 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, ALLEN, 2009). The lognormal growth model (URIARTE *et al.*, 2004) has three parameters *G*, *K*, *Y* (equation 3):

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

and follows from (equation 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 cm yr$^{−1}$) is the maximum growth rate, $K = \exp[−b/(2c)]$ (in cm) 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 Korf model has three parameters *G*, *P*, *Y* (equation 4):

$$A_{pot} = R\ D\ \left[\ln\left(\frac{P}{D}\right)\right]^{1+Y}$$

Table I.
Characteristics of study sites: *R* is annual rainfall (mm), *p* is the number of plots, *S* is the cumulated area of plots (ha), *m* is the number of remeasurement times (the first inventory is not counted) = maximum number of longitudinal observations for the same tree, *n* is the number of observations for azobé (including remeasurements of the same tree), and *N* is the number of distinct azobé trees.

Site	R	p	S	m	Density (ha⁻¹)			Basal area (m²/ha)			n	N
					Min.	Max.	Mean	Min.	Max.	Mean		
Lopé	1 474	5	2.5	2	233	341	285	22.4	30.8	25.6	146	80
Haut-Abanga	1 800-2 000	7	7	2	270	441	363	22.9	44.4	25.2	91	48
Mbé	2 000-3 500	5	5	1	547	569	556	39.3	44.5	41.6	7	7
Ogooué-Ivindo	1 400-1 900	4	4	1	268	443	328	28.5	36.3	32.2	4	4

and follows from (1) by setting $a = \ln(R)$, $b = 1$, $c = 0$, $d = Y + 1$ and $e = \ln(P)$. Parameter $R = \exp(a)$ (in yr^{-1}) is related to the maximum growth rate (that equals $RP \exp\{(1 + Y)[\ln(1 + Y) - 1]\}$), $Y = d - 1$ (no unit) is a shape parameter that determines the breadth of the growth function, and $P = \exp(e)$ (in cm) is the maximum diameter that a tree can asymptotically attain. When $Y = 0$, it simplifies to the Gompertz model.

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

Following BIGING, DOBBERTIN (1995), the 'reducer' was defined as: $\exp(-\alpha C)$, where C is a competition index and α a positive coefficient. After preliminary selection, two competition indices were retained: $N \exp(-\mu D)$ where N is stand density, and $B \exp(-\mu D)$ where B is stand basal area. The size-dependent exponential term modeled the asymmetry of competition that declines as trees get larger, since small trees are shadowed by large trees but not the converse. Adding the interaction between stand density and basal area, the reducer was thus modeled as (equation 5):

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

where α, β, γ, μ are parameters to estimate.
The growth function was finally defined as (equation 6):

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

where A is the growth rate (in cm/yr) of a tree with diameter D growing in a forest stand with density N and basal area B, and A_{pot} is defined by equation (2), (3) or (4). Reducer equation (5) can equivalently be written as:

$$\text{red}(D, N, B) = \exp\{-[\gamma(N - N_0)(B - B_0) - \alpha\beta/\gamma] \exp(-\mu D)\}$$

where $N_0 = -\beta/\gamma$ and $B_0 = -\alpha/\gamma$. This shows that, in the particular case when $\mu = 0$, the scaling parameter of the potential A_{pot} is confused with $\exp(\alpha\beta/\gamma)$, which brings numerical instability. To solve this numerical instability, we used (N_0, B_0, γ) as the set of parameters to estimate rather than (α, β, γ), and replaced the reducer with a pseudo reducer: $\exp[-\gamma(N - N_0)(B - B_0)]$ that can be greater than one. The density-independent term $\exp(\alpha\beta/\gamma)$ was included into the potential (that was consequently lower than with the reducer). Parameterization (α, β, γ) or (N_0, B_0, γ) was used depending on whether μ was significantly different from zero or not.

Photograph 3.
Fruit of azobé, *Lophira alata*, at Ipassa (0°30'42"N, 12°48'9"E), near the city of Makokou, northeastern Gabon.
Photograph N. L. Engone Obiang.

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 can be addressed by adding a random effect in the model to account for individual tree variability in growth performance, and/or by adding a correlation structure on the residuals of the same longitudinal sequence. Because longitudinal sequences were short (two observations at most), the latter option was here retained. The autocorrelation was modeled as: $\text{Cor}(\varepsilon_t, \varepsilon_s) = \phi^{|s - t|}$, 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 one year apart. Models were fitted by maximizing 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.

Table II.
Number of parameters associated to the predictors (p), regression R^2, and Akaike information criterion (AIC) for the three growth models for azobé, *Lophira alata*, fitted at four study sites in Gabon.

Model	p	R^2	AIC
lognormal	6	0.350	77.49
power	6	0.350	77.60
Korf	6	0.318	84.78

Table III.
Parameter values for the lognormal growth model for azobé, *Lophira alata*: *a*, *b*, *c* are the coefficients of the second-order polynomial on log-transformed variables for potential growth, N_0 is the parameter for the stand density effect on growth, B_0 is the parameter for the stand basal area effect on growth, and γ is the parameter for the interaction effect of density and basal area on growth.

Parameter	Estimate	Unit	Std. Error	t value	Pr(› t)
a	-10.285	[-]	1.64	-6.3	‹ 0.001
b	4.865	[-]	0.91	5.4	‹ 0.001
c	-0.595	[-]	0.12	-4.8	‹ 0.001
N_0	287.4	ha^{-1}	11.4	25.1	‹ 0.001
B_0	24.7	m^2/ha	0.8	31.6	‹ 0.001
γ	$1.37 \cdot 10^{-3}$	m^{-2}/ha^{-2}	$5.0 \cdot 10^{-4}$	2.7	0.007

Results

The model with the lowest AIC was the lognormal model, but the power model provided a similar quality of fit (table II). The only model for which μ was significantly different from zero was the power model. Hence, with the exception of the power model, the second parameterization of the reducer based on (N_0, B_0, γ) was used. The following growth model was thus selected for azobé (table III):

$$A = 0.72 \exp \left\{ -\left[\frac{1}{1.30} \ln\left(\frac{59.8}{D}\right) \right]^2 - 1.37 \times 10^{-3} \left(N - 287.4 \right)\left(B - 24.7 \right) \right\}$$

where D is in cm, N in ha^{-1}, B in m^2/ha, and A in cm/yr. The residual standard deviation for this model was 0.285 cm/yr (figure 2) and the intra-individual correlation parameter was ϕ = 0.76. Predicted growth for azobé culminated at a diameter of 59.8 cm. For the observed plots, predicted maximum
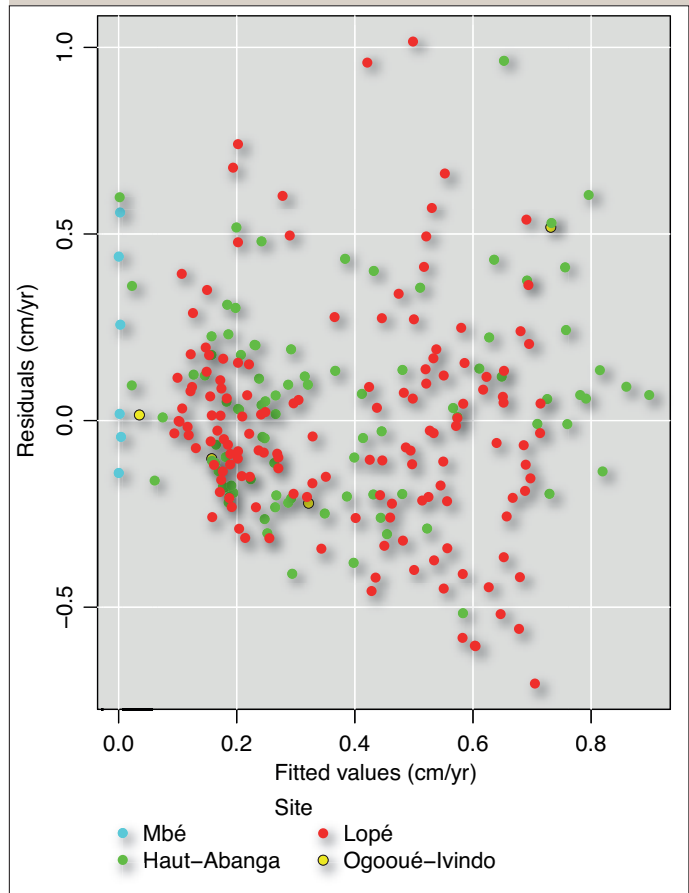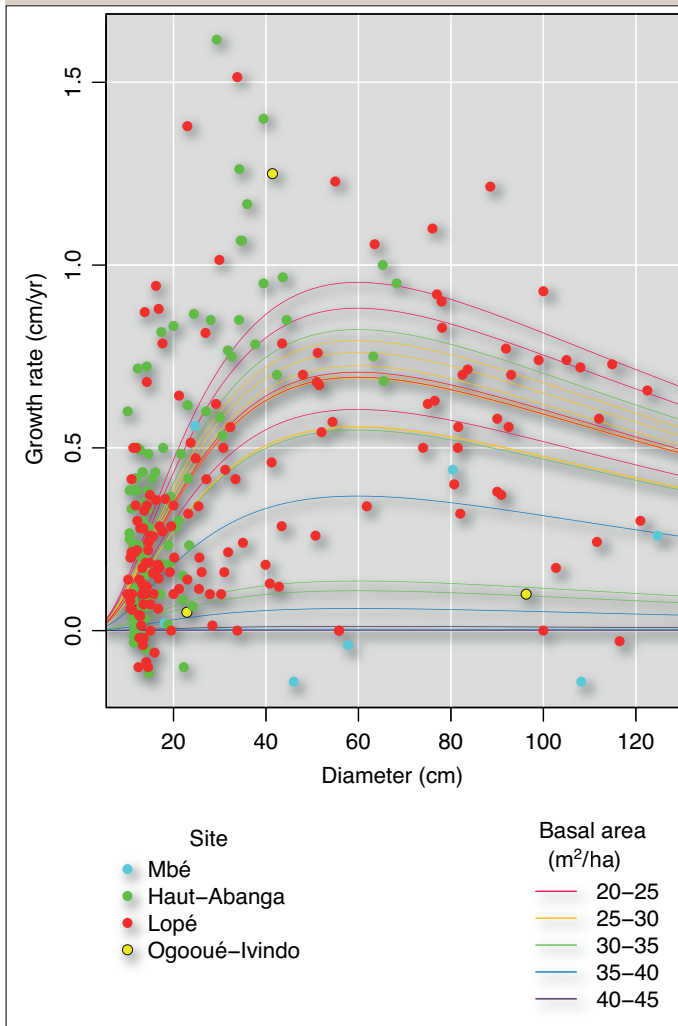

Figure 2.
Residuals versus fitted values for the lognormal growth model of azobé, *Lophira alata,* at four sites in Gabon (indicated by different colors).

growth rate decreased from 0.95 cm/yr for a tree density of 402 ha^{-1} and a basal area of 22.9 m^2/ha at Haut-Abanga, to almost nil for a tree density of 569 ha^{-1} and a basal area of 44.5 m^2/ha at Mbé (Figure 3).

The pseudoreducer component had a saddle shape with an inflection point that corresponded to a stand density of 287 ha^{-1} and a basal area of 25 m^2. However, not all combinations of tree density and basal area were realistic. The plots used to fit the growth model for azobé ranged from mature to old-growth forest, with a significant correlation between tree density and basal area (Pearson's correlation coefficient: 0.75, T = 5.05, *p-value* ‹ 0.001; figure 4). This correlation between predictors implies that the effects of stand density and basal area on growth cannot be separated and must be jointly interpreted. Hence, in the range of sampled plots, the reducer (and thus growth) decreased as stand basal area increased or as stand density increased (figure 4).
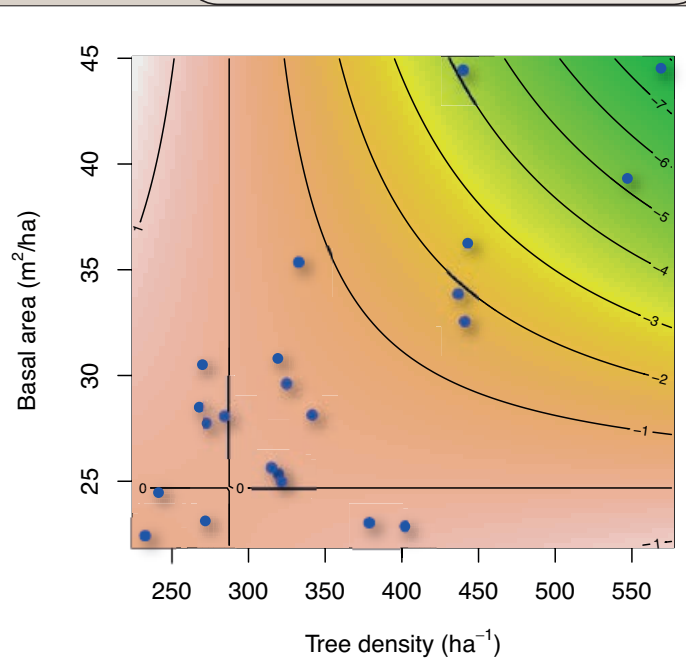
No significant residual site effect on growth was found ($F_{3,244}$ = 1.36, *p*-value = 0.25). There was a significant residual social status effect ($F_{1,78}$ = 7.15, *p*-value = 0.009), with a slower growth for suppressed azobés (mean residual: 0.00 cm/yr) than for dominant azobés (mean residual: 0.19 cm/yr).

Figure 3.
Observed (dots) and predicted (lines) growth rate of azobé, *Lophira alata*, as a function of diameter, at four sites in Gabon. The different lines correspond to different combinations of stand density and basal area (with different colors that correspond to different ranges of basal area); the same combinations were used as those found in the calibration data set, *i.e.* those that correspond to the permanent sample plots where data were collected.

Figure 4.
Logarithm of the pseudo-reducer of the fitted growth model as a function of tree density in ha[1] and basal area in m²/ha (image and contour lines), and characteristics of the plots used to fit the growth model for azobé, *Lophira alata* (blue dots). The higher the surface is, the greater the predicted growth is. The pseudo-reducer is the reducer times a normalizing constant; it can be greater than one (but the reducer is always less than one).

Discussion

In agreement with its light-demanding behaviour, the growth of azobé strongly responded to stand attributes such as density or basal area, with increased growth as basal area or density decreased. This may explain why so variable growth rates have been reported for this species (PICARD, GOURLET-FLEURY, 2011; BIWOLÉ *et al.*, 2012). The residual standard deviation of growth is still high, showing that the model only captured part of the individual variability in growth (figures 2 and 3). Nevertheless, this is quite common in natural tropical rain forests (OUÉDRAOGO, 2011), and the residual standard deviation obtained here is actually of the same order as those obtained in other studies (e.g. 0.345 cm/yr in French Guiana, GOURLET-FLEURY, HOULLIER, 2000; or 0.403 cm/yr for *Aucoumea klaineana* in central Africa, ENGONE et al., 2013).

The negative growth response of azobé to both stand density and basal area makes a difference with strict pioneer species that generally have a negative growth response to basal area but a positive correcting effect of stand density, thus allowing for fast growth in young open stands without over-topping trees (OUÉDRAOGO, 2011). Azobé had a predicted growth curve with a unimodal shape with respect to diameter. Its maximum potential growth rate was reached at a relatively high diameter (≈ 60 cm). ROLLET (1974, p. 72) reported a similar pattern of growth for azobé in Nigeria. This pattern is consistent with the non-pioneer light-demanding behaviour of azobé: azobé can bear shading in its early stage and requires light at a more advanced stage of development (PALLA *et al.*, 2002; DOUCET, 2003). The power model provided a quality of fit similar to that of the lognormal model. The exponent β of the power model (2) was estimated to 2.02 (95% confidence interval: 1.17-2.87), and was thus significantly different from the theoretical value of 1/3 according to the metabolic scaling theory (COOMES, ALLEN, 2009). No site effect on azobé growth was detected, but this may result from the limited number of available observations.

In management plans, forest managers predict the growth of azobé 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.

Photograph 4.
Large azobé tree, *Lophira alata*, in the Mondah forest near Libreville (0°34'25"N, 9°20'03"E), northwestern Gabon. Photograph N. L. Engone Obiang.

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