



Vertical stratification reduces competition for light in dense tropical forests



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ABSTRACT

Differential growth response to light level is widely accepted as a potential mechanism for maintaining tree species richness in tropical forests. The position of tree species in the hierarchy of the canopy is considered an important indicator of species light capture and growth strategy. Paradoxically, the relative importance of species identity and competition for light in determining individual tree growth is poorly documented at the adult stage. In this study, we used a hierarchical Bayesian model to quantify the overall importance of species identity, light and belowground competition as determinants of tree growth in French Guiana tropical forest. Light competitive status is assessed by a crown exposure score and below ground competition is estimated from local crowding. We examined species sensitivity to both types of competition in relation to adult stature.

Our results are based on annual diameter increments of more than 13,510 stems from 282 species monitored over 10 years. Mean annual growth rate was 0.11 cm y^{-1} with species identity explaining 35% of the individual variation in growth rate. Crown exposure and local crowding explained 3.5% and 2.4% of the variation in growth rate, respectively. Predicted changes in growth rate as crown exposure (resp. local crowding) index changed from lower to upper interquartile level was 0.03 cm y^{-1} (resp. 0.02 cm y^{-1}). Species sensitivity to crown exposure and to local crowding were positively correlated (i) with predicted growth rate at high-light standardized conditions and (ii) with adult stature.

This vertical niche partitioning is invoked to explain the limited contribution made by level of light competition for predicting individual tropical tree growth as the community-level response is dominated by the abundance of small-statured species with low sensitivity to light level.

Light appears to drive the stem growth rate of tropical trees through species differentiation more than through individual tree growth limitation. This vertical stratification complements the previously reported regeneration niche and together these provide evidence for light niche partitioning in the three-dimensional space of tropical forests.

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1. Introduction

Growth and survival response to changing light levels is a fundamental component of the life-history strategy of trees in tropical forests (Poorter and Arets, 2003) and has been proposed as a potential mechanism for the maintenance of species richness (Brokaw and Busing, 2000). At the adult stage, the position of the species in the hierarchy of the canopy is considered an important indicator of species light capture and growth strategy, even if the small-large paradigm for adults has received considerably less

attention than the gap-shade paradigm for juveniles. Previous studies (Thomas and Bazzaz, 1999; Gourlet-Fleury and Houllier, 2000; Rüger et al., 2012) have shown that tall-statured species tend to be characterized by light wood, high growth rate and high growth sensitivity to competition for light. Paradoxically, although the differentiation of species in term of light requirement and the effect of light on tree growth are widely acknowledged (Oldeman and van Dijk, 1991), the quantification of their contribution to individual tree growth relative to other determinants has been poorly documented, particularly at the adult stage. (Rüger et al., 2011) found that size and light explained on average 12% of growth rate variations in a tropical forest community in Panama, and that size was slightly less determinant than light. This contrasted with a

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large body of literature assuming that light availability shapes tree growth (Valladares, 2003). Regarding species importance, the increasing number of studies predicting species effect on individual tree growth from functional traits implicitly lends support to the central importance of species identity but these studies provide no quantification of species identity importance. Competition for water and nutrients, estimated by diameter-based competition indices (e.g. local density), has been considered in a few studies (Gourlet-Fleury, 1998; Moravie et al., 1999; Uriarte et al., 2004) but, to the best of our knowledge, its importance has seldom been examined in combination with competition for light. Recently, (van Breugel et al., 2012) found that, despite low soil fertilities, competition for light was more important than belowground competition for nutrients in limiting the growth of two pioneer species during early succession. Competition for belowground resources is often seen as size-symmetric, based on the assumption that nutrient uptake is proportional to plant size. In contrast, competition for light is assumed to be size-asymmetric as taller individuals preempt resources by casting shade on their shorter neighbors and depriving them of light disproportionately to their size (Schwinning and Weiner, 1998; Freckleton and Watkinson, 2001). The inherent asymmetry of light competition and symmetry of below-ground competition suggests that it may be possible to disentangle their effects (by accounting for all neighboring trees or only those taller than the focal tree in competition indices) and compare their importance in shaping forest dynamics.

The study described herein aimed to quantify the overall importance of species identity and resource competition in determining tropical tree growth. We also examined to what extent species differentiation in term of growth strategy is related to adult stature as a proxy of species light requirement. This study area was carried out in French Guiana, in the Guiana shield region characterized by Precambrian granitic and metamorphic formation. Guiana shield is the end of a gradient in tree composition and function across Amazonia revealed by the study of (ter Steege et al., 2006). This gradient of genus-level community composition parallels a major gradient in soil fertility, in community wood density and in seed mass. In the Guiana shield region, soils are poorer, tree wood is denser and seed mass is larger than in southwestern Amazonia. As these functional traits are known to be related to species response to the canopy disturbance level, the study of (ter Steege et al., 2006) suggests that long-term disturbances regimes might be lower in the Guiana shield region than in western Amazonia and that the dominance of Caesalpiniaceae in the Guiana shield may result from their high seed mass as an adaptation to poor soils (ter Steege et al., 2006) but also to shade conditions produced by low rates of disturbance.

We specifically addressed the following questions: (i) what is the structure of the competitive environment and the structure of the community in term of adult stature and growth rate? (ii) what is the absolute importance of crown position and local crowding as growth limiting factors? (iii) is there a significant correlation between species potential growth rate, sensitivity to competition and adult stature, (iv) what proportion of growth variation is due to species identity, crown position and local crowding at the community scale?

2. Material and methods

2.1. Inventory data

The study was carried out at the lowland tropical forest of Paracou experimental site in French Guiana (Gourlet-Fleury et al., 2004). Mean annual rainfall was 2875 ± 510 mm over the 1986–2005 period with a 3-month dry season from mid-August to

mid-November (Wagner et al., 2011). The study site is characterized by a patchwork of hills (100–300 m in diameter and 20–50 m high) separated by streams. Its tree community shows the high species diversity typical of tropical rainforest and a very high proportion of rare species: in our dataset 75% of species account for 10% of the total tree population (>10 cm diameter at breast height (DBH)). The total number of stems and total basal area are respectively c. 600 ha⁻¹ and c. 30 m² ha.

Each tree >10 cm DBH in six 6.25 ha plots of unlogged forest was mapped, identified and its circumference at 1.30 m (or above buttresses in present) measured every one or 2 years from 2003 to 2011 to the nearest half cm. In order to reduce the effects of year-to-year measurement inaccuracy and errors, annual diameter growth rate (cm y⁻¹) in 2007 was calculated as a weighted mean (weights were inter-annual census periods in days) of growth rates over the 2003–2011 census period. Mean annual growth rate was log-transformed to homogenize the variance of the residuals. As a few trees had negative growth rates over the period, a constant value of +0.2 cm y⁻¹ (an offset superior to the minimum negative growth rate value of -0.19 cm y⁻¹) was added to the observed growth rates (hereafter referred as G , cm y⁻¹) to obtain strictly positive values prior to log-transformation. To avoid edge effects when calculating competition indices, all individuals within 15 m of plot boundaries (4198 trees) were excluded from the growth analysis.

2.2. Resource competition indices

The scarcity of studies quantifying light as a growth driver is partly a consequence of the difficulties encountered when attempting to estimate individual light availability over large sampling areas. The size asymmetric index used here corresponded to the crown exposure or position (CP) of each individual tree in the six plots and was measured at the Paracou experimental site in 2007 (22,917 trees). Crown position indices are used to standardize visual assessments of the relative position of individual tree crowns in the forest canopy and of the direction of incident light. Trees were classified according (Synnot, 1979) into crown position classes as follows:

- (1) Lower understorey trees, entirely shaded vertically and laterally by others crowns.
- (2) Upper understorey trees entirely shaded vertically but with some direct side light.
- (3) Lower canopy trees, partly exposed and partly shaded vertically by others crowns.
- (4) Upper canopy trees, exposed in entire vertical plan but with other crowns laterally.
- (5) Emergent, entirely exposed, free from competition for light, at least within the 90 inverted cone in which the crown lies.

As CP values of 5 were rare (<2%) we decided to pool these with CP values of 4 in our growth models. This decision was motivated by the fact that preliminary tests with models using CP as a categorical predictor suggested that the response was linear up to CPscore = 4 but tended to saturate beyond. CP was considered as a quantitative variable (measurement variable sensu (Sokal and Rohlf, 2010)) in the subsequent analysis. CP is negatively correlated with tree competition pressure whereas LBA increases with level of competition. All species were treated as equivalent for competition pressure (species identity was not considered). Competition for light will hereinafter be referred to as 'crown position effect'.

Competition for belowground resources was taken into account through a size-symmetric index based on local crowding. Local basal area (LBA) was calculated as the sum of the basal area of

the neighboring trees (>10 cm DBH) in a circular plot. Preliminary tests were conducted on a subset of fairly abundant species ($N > 30$, 74 species) to determine the optimal neighborhood for the evaluation of local crowding (LBA). We applied successively the following linear model with LBA indices based on a neighborhood radius of 10, 15 and 20 m:

$$\begin{aligned} \log(G + 0.2) \sim & \text{DBH} + \log(\text{DBH}) + \log(\text{CP}) + \log(\text{LBA}) \\ & + \text{species} \times (\text{DBH} + \log(\text{DBH}) + \log(\text{CP}) \\ & + \log(\text{LBA})) \end{aligned} \quad (1)$$

The model minimizing AIC used LBA indices based on a neighborhood radius equal to 15 m.

This is a distance-independent index in that it does not take into account the distance between the focal tree and its competitors within the prescribed plot area.

Belowground competition will hereinafter be referred to as 'crowding effect'.

2.3. Growth model

Palm species (*Arecaceae*) that have no secondary growth were excluded from the analysis (388 trees). Similarly, trees whose taxonomic resolution was not achieved to species level and trees for which height of DBH measurement had been changed over the census period were also excluded from the growth analysis (3870 trees). In all, 13,510 individuals representing 282 species (all non-excluded species with two or more individuals) were included in the growth analysis.

We used a hierarchical Bayesian model, which included a species random effect, to quantify growth response to DBH, CP and LBA. This approach was selected as it can include rare species and provide robust estimates despite their low abundance (Dietze et al., 2008; Rüger et al., 2011). Relationships among predictors are shown as Supplementary material (Fig. S2). To evaluate how much redundancy occurred between LBA, DBH and CP indices we used linear discriminant analysis to predict CP from either LBA or DBH. We then computed Cohen's kappa coefficient κ , which accounts for the agreement occurring by chance. κ ranges between 0 (no agreement) and 1 (complete agreement). κ was equal to 0.05 when LBA was used as predictor of CP and 0.29 when DBH was used. This indicated that redundancy between predictors was limited and that CP was more closely related to tree size than to local crowding. Therefore, we included LBA, CP and DBH as predictors. We compared different candidate models consisting of (i) a logarithmic transformation of CP and LBA, and (ii) a log-transformed DBH term (allowing a humped-shape response form) in addition to DBH. We used the deviance information criterion (DIC) to select the best model.

The selected model minimizing DIC took the following form:

$$\begin{aligned} \log(G_{ik} + 0.2) = & \beta_0 + b_{0,k} + (\beta_1 + b_{1,k}) \log(\text{DBH}_i) + (\beta_2 + b_{2,k}) \\ & \times \log(\text{CP}_i) + (\beta_3 + b_{3,k}) \text{DBH}_i + (\beta_4 + b_{4,k}) \\ & \times \log(\text{LBA}_i) + \varepsilon_i \end{aligned} \quad (2)$$

with n_k observations for each species k . G_{ik} represents the DBH increment (cm y^{-1}) of tree i of species k . 0.2 is the constant required by the occurrence of negative increments.

The process error ε_i was modeled as a normal distribution:

$$\varepsilon_i \sim N(0, \sigma^2) \quad (3)$$

The model used a multivariate normal prior for the fixed effect parameters $\beta_0, \beta_1, \beta_2, \beta_3$ and also for the random effect parameters b_0, b_1, b_2, b_3 :

$$[\beta_0, \beta_1, \beta_2, \beta_3] \sim N_4(\mu_\beta, V_\beta) \quad (4)$$

$$[b_{0k}, b_{1k}, b_{2k}, b_{3k}] \sim N_4(0, V_b)$$

The variance-covariance matrix V_b followed an Inverse-Wishart prior distribution:

$$V_b \sim \text{Inverse} - \text{Wishart}(r, R) \quad (5)$$

The residual error variance σ^2 followed an Inverse-Gamma distribution:

$$\sigma^2 \sim \text{Inverse} - \text{Gamma}(v, 1/\delta) \quad (6)$$

A Bayesian inference of model parameters was performed using Algorithm 2 of (Chib and Carlin, 1999). Bayesian analyses were carried out with the R statistical software (R Development Core and Team, 2011) and the twoe R package which aims at modeling tropical forest dynamics in a Bayesian framework (<http://twoe.org/>). To test if a species grew in a significantly different manner compared to mean species behavior, we computed the 95% credibility intervals of the species random effects from the posterior marginal distributions. The inclusion of zero in the interval was taken as an indication that the random species effect was not significantly different from zero and that the species did not grow in a significantly different manner from the average species. We also present the results obtained after the application of the Dunn-Sidak multiple comparison correction (Šidák, 1967).

2.4. Adult stature and sensitivity to resource competition

Adult stature was estimated by the 95th percentile of DBH of a subset of trees with $\text{DBH} > 0.1 \times \text{maximum DBH}$ (hereinafter referred to as D95). This index has been shown (King et al., 2006a) to be little affected by sample size.

Species growth sensitivity to resource competition was characterized by the posterior mean of CP effect and LBA effect model parameter distribution (b_2 and b_4 respectively). We used Pearson's correlation analysis to test for relationships between species sensitivity to resource competition, predicted growth rate under standardized conditions and adult stature. We also tested the effect of rare species on the strength of these relationships by applying an abundance filter (from 5 to 500 individuals per species) to the dataset before computing correlation coefficients.

2.5. Absolute importance of crown position and local crowding

The terminology used to quantify the effects of competition has been examined by (Welden and Slauson, 1986) and has been the subject of long-running debate (Brooker et al., 2005; Freckleton et al., 2009; Damgaard and Fayolle, 2010; Kikvidze et al., 2011; Rees et al., 2012). We followed (Craine, 2009) and used *absolute* importance of competition to refer to the variation in DBH increment caused by competition (considering either competition as a whole or one of its components), and *relative* importance to refer to the variation in DBH increment caused by competition (or one of its components) relative to all other factors driving DBH increment. We quantified the absolute importance of crown position effect ($\text{CP}_{\text{imp}_{\text{abs}}}$) and local crowding effect ($\text{LBA}_{\text{imp}_{\text{abs}}}$) for each species as the difference between the maximum and minimum predicted growth rate value for the whole-community interquartile range of CP (from 25th to 75th percentile point, i.e. from $\text{CP} = 1.7$ to $\text{CP} = 3$, we applied a linear interpolation within each class of CP) and LBA distributions (from 25th to 75th percentile point, i.e. from $\text{LBA} = 1.7$ to $\text{LBA} = 2.3 \text{ m}^2$). Interquartile range CP and LBA represents intermediate conditions experienced by the majority of species.

The fixed values of DBH, CP or LBA required for these predictions were computed as the median values across the community.

Predicted DBH increment (pred_{log}) of tree i of species k was back-transformed to the arithmetic scale (pred_{ari}) as follows:

$$\text{pred}_{i,\text{ari}} = e(\text{pred}_{i,\text{log}} + \sigma^2/2) \quad (7)$$

We used the median of $\text{CP_imp}_{\text{abs}}$ and $\text{LBA_imp}_{\text{abs}}$ across species to compare the absolute importance of CP and LBA in unit growth rate for a standardized and non-specific range of crown exposure index (CP) or local basal area (LBA).

2.6. Relative importance of crown position and local crowding

Explained variance (r^2) of DBH increment (G) was calculated for the whole community as follows:

$$r^2 = (1 - \text{var}(\varepsilon))/\text{var}(G) \quad (8)$$

We evaluated the relative importance of each predictor as the difference between the r^2 value of the full model and the r^2 value of the model excluding the given predictor. The predictive ability of species identity was the r^2 of a linear model that included species as the single predictor.

For lack of suitable data the model did not include an explicit error term affecting CP. CP as any scoring technique is however prone to a measurement error and to an additional rounding error resulting from discretization. Through blind repeated measurements (Vincent et al., 2002) found an error rate of ~26% between

two independent estimates, thereby confirming previous results from (Clark and Clark, 1992). We investigated by numerical simulations the impact of the rounding error coupled with an error rate of 26% and estimated that the CP estimation error might account for about 2% of the total unexplained variance in DBH increment. In addition, it is likely that taller trees within a CP class tend to receive more light than smaller trees within the same CP class; this slight bias is however considered negligible in comparison with the CP measurement error.

3. Results

3.1. Structure of the competitive environment and structure of the community

Coefficients of variation for CP and LBA were 0.48 and 0.25, respectively, indicating that light access was more variable than local crowding.

In all, 70% of the 13,510 individuals were located in shaded conditions ($\text{CP} = 1$ or $\text{CP} = 2$) and had a $\text{DBH} < 25$ cm (Fig. 1a). At the species level, 75% of the 282 species had a median CP value of 2 or less, and a median DBH of 22 cm or less (Fig. 1b). D95 varied from 11 to 92 cm, but 75% of the species did not exceed 41 cm (Fig. 1b). Predicted growth rate in standardized conditions varied from 0.01 cm y^{-1} to 0.87 cm y^{-1} with a median equal to

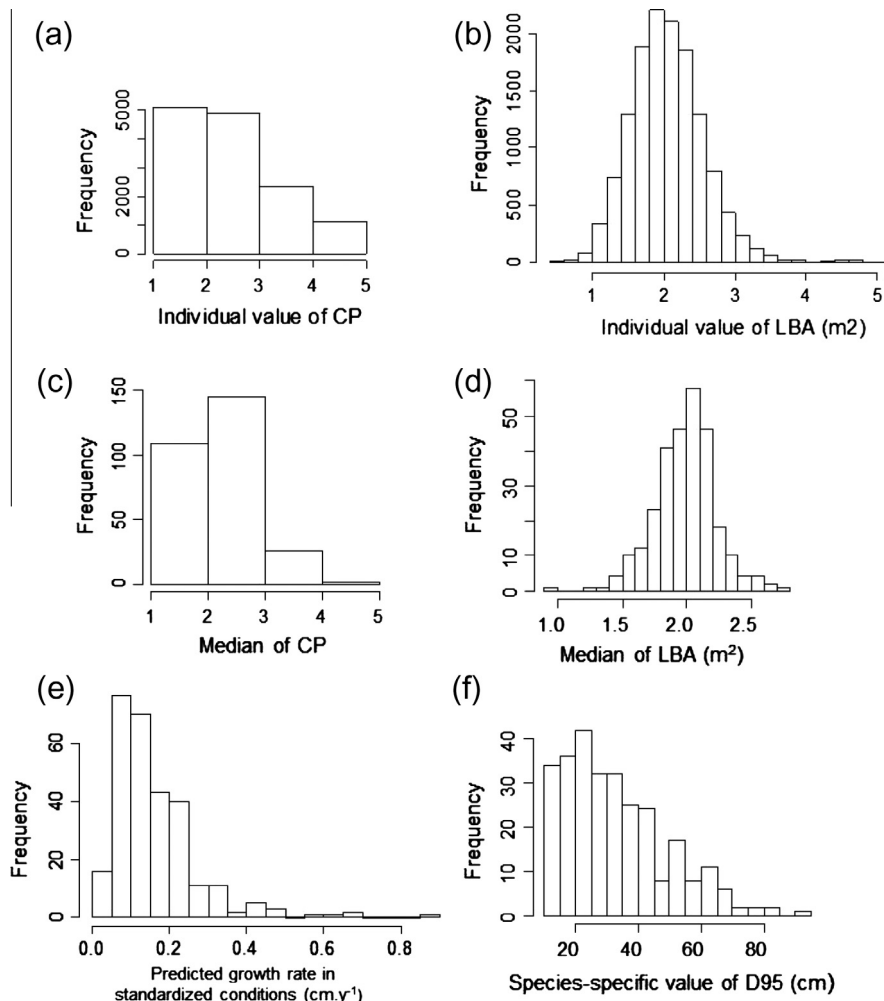


Fig. 1. Distribution of individual values for CP (a), LBA (m^2) (b) and species median values for CP (c), LBA (m^2) (d), predicted growth rate in standardized conditions (cm y^{-1}) (e) and adult stature (D95 in cm) (f) at the Paracou experimental site.

0.14 cm y⁻¹ (Fig. 1b). CP median and standard deviation values across species correlated with D95 (Fig. 2). A simple regression between CP and species showed that species identity explained 17% of CP variation but only 5% of LBA variation. A Kruskal-Wallis test confirmed that CP values varied significantly across species ($P < 0.0001$).

3.2. Community pattern of growth sensitivity to resource competition and DBH

All but one species (*Pradosia cochlearia* (Lecomte) T.D.Penn.) grew faster at high light levels and 98% grew faster at low local density (see sign of $\alpha_2 g$ and $\alpha_4 g$ model parameters on Table S1).

The most abundant species were moderately responsive to resource competition (Table S3), and the rare species showed the entire range of growth responsiveness to resource competition. For 12 (3 species with the Dunn-Sidak multiple comparison correction (Šidák, 1967)) of the 282 species (4.2%) and 4138 of the 13,510 trees (30.6%), the CP model parameter was significantly (significance level = 5%) different (4 more, 8 less) from the species mean (Table S1). For 16 (2 species with the Dunn-Sidak multiple comparison correction) of the 282 species (5.6%) and 4254 of the 13,510 trees (31.5%), the LBA model parameter was significantly (significance level = 5%) different (7 more, 9 less) from the species mean (Table S1). For 28 (10 species with the Dunn-Sidak multiple comparison correction) of the 282 species (10%) and 5409 of the 13,510 trees (40%), the DBH or log DBH model parameter was significantly (significance level = 5%) different from the species mean (Table S1). Uncertainty over model parameters was exponentially and negatively related to species abundance. Consequently, the analysis of absolute and relative importance of CP and LBA, as described in the next section, was restricted to species represented by more than 20 individuals (101 of the 282 species).

3.3. Absolute importance of crown position and local crowding

Species-specific CP and LBA absolute importance values ($CP_{imp_{abs}}$ and $LBA_{imp_{abs}}$) were evaluated under standardized conditions (DBH = 18 cm, CP = 2.3, LBA = 2 m²) and a standardized range of variation (from 25th to 75th percentile: 1.7–3 for CP and 1.7–2.3 m² for LBA). Median values for $CP_{imp_{abs}}$ and $LBA_{imp_{abs}}$ corresponded to 0.03 cm y⁻¹ and 0.02 cm y⁻¹, respectively (Fig. 5). The median value for species-specific predicted growth

rate under standardized conditions was found to be 0.15 cm y⁻¹. CP absolute importance varied from 0.002 cm y⁻¹ to 0.17 cm y⁻¹ and LBA absolute importance from 0 cm y⁻¹ to 0.11 cm y⁻¹ across species (Fig. 5 and Table S1).

3.4. Is there a significant correlation between species potential growth rate, sensitivity to competition and adult stature?

Species sensitivity to CP (CP effect model parameter b_2) and species sensitivity to LBA (LBA effect model parameter b_4) were significantly correlated with both adult stature and predicted growth rate under high-light standardized conditions (CP = 3, DBH = 19 cm, LBA = 1.9 m²) (Table S3 and Fig. 3). Small-statured species showed slower growth rates and lower sensitivity to competition than tall-statured species (Table S3 and Fig. 4). Species sensitivity to CP was significantly correlated with species sensitivity to LBA (Table S3 and Fig. S3).

3.5. Relative importance of species, crown position and local crowding

At the community level, about 54% of the variation in growth rate was accounted for by the hierarchical growth model. Species effect explained 35% of the variation in growth rate. CP competition index and LBA competition index explained 3.5% and 2.4% of the variation in growth rate, respectively. Tree size explained 6.3% of the variation in growth rate.

The sum of each predictor contribution does not sum up to r^2 because we do not conduct a variance decomposition but rather estimate type III sum of square for LBA, CP and tree size (see Section 2).

4. Discussion

4.1. Absolute importance of resource competition as growth limiting factors

In the study described herein, most of the trees were located in shaded conditions, and all but one species responded positively to an increase in CP. These observations confirm the pervasive competition for light taking place between neighboring trees which limits their growth. As expected, we found that the crown position effect on DBH increment was biologically very significant. Indeed the median change in growth rate (0.03 cm y⁻¹) associated with the CP interquartile range ($CP_{imp_{abs}}$) was 20% of the median of

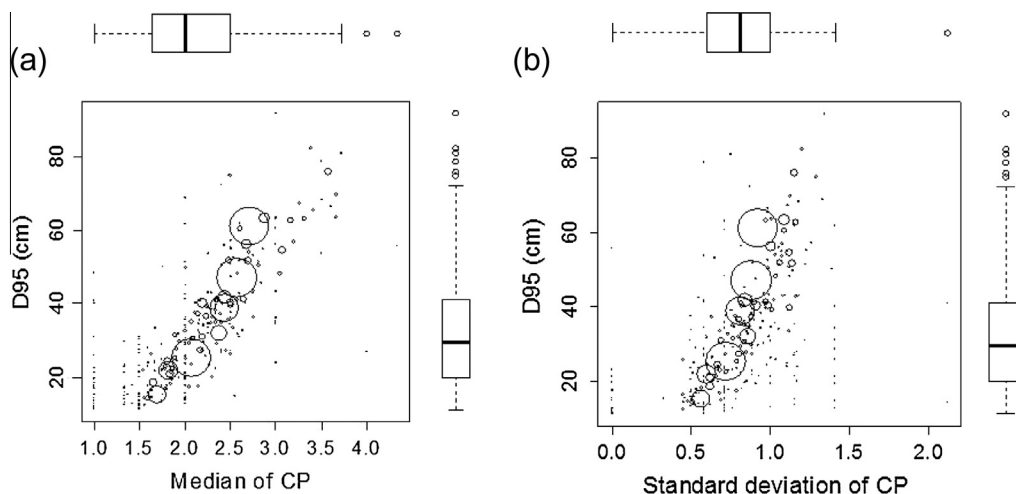


Fig. 2. Relationship between species median and standard deviation values for CP (a) and adult stature (D95 in cm) (b) at the Paracou experimental site. Symbol size is function to species abundance.

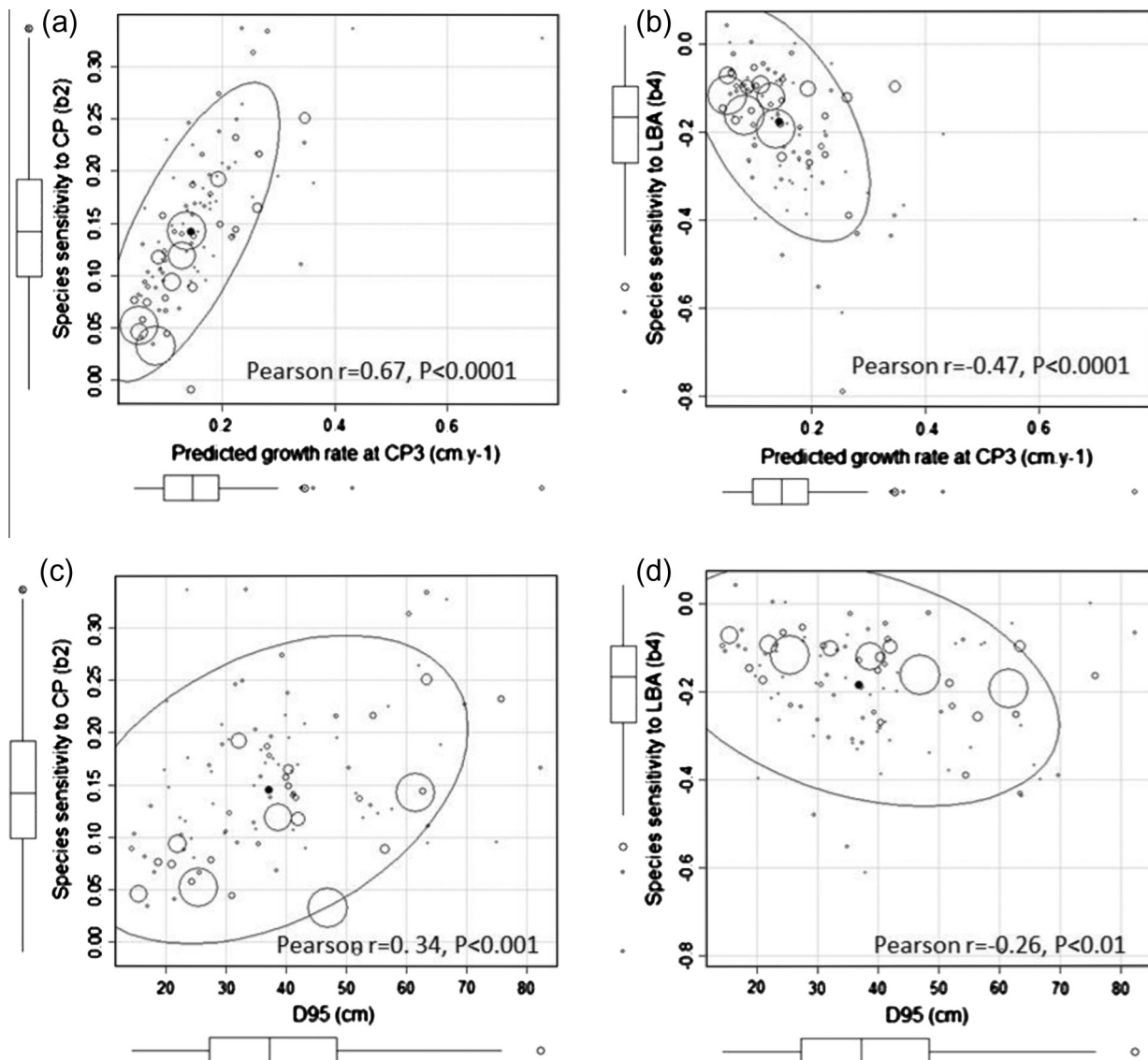


Fig. 3. Relationship between species sensitivity to CP (a, c) or LBA (b, d) with predicted growth rate under high-light conditions (CP = 3, DBH = 18 cm and LBA = 2 m²) and adult stature (D95 in cm) for the 101 species with $N > 20$ individuals. Pearson's correlation coefficient and the P -value are given and data concentration ellipse is plotted. Symbol size is function to species abundance.

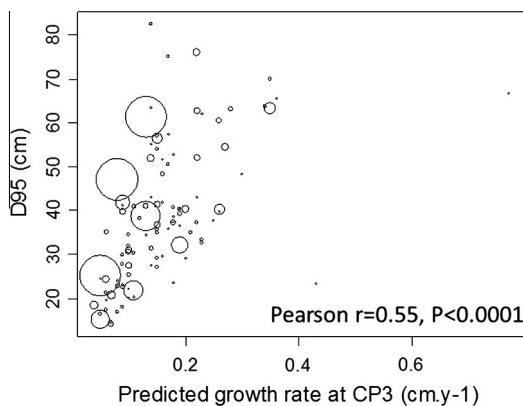


Fig. 4. Relationship between predicted growth rate at CP3 (cm.y⁻¹) and adult stature (D95 in cm) for the 101 species with $N > 20$ individuals at the Paracou experimental site. Symbol size is function to species abundance.

predicted mean DBH increment (0.14 cm y⁻¹). This result is consistent with the widely recognized importance of light as a key limiting factor of growth in tropical forest. Our results further suggest that crown position effect is more important both in relative and absolute terms than local crowding effect in Paracou tropical forest. This finding confirms and extends the results of (King et al., 2005) and (van Breugel et al., 2012) who focused juveniles of 21 large-statured species and two pioneer species, respectively.

4.2. Light indirectly drives individual tree growth through species vertical niche and functional differentiation

We observed a significant positive correlation between species adult stature, potential growth rate and sensitivity to light competition (Figs. 3 and 4). Previous studies (Falster and Westoby, 2005, Poorter et al., 2008) have shown that slow growth rate and low sensitivity of growth to light were associated with high survivorship in deep shade and formed part of a general strategy of resource conservation: high LMA (Leaf Mass per Area), low

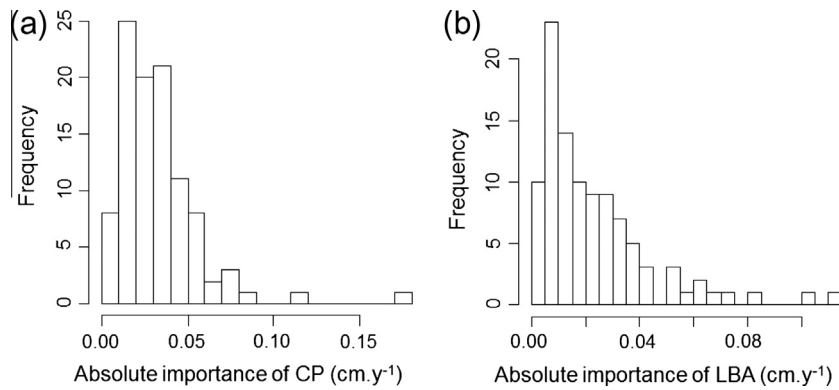


Fig. 5. Distribution of species-specific absolute importance of CP (a) and LBA (b) for 101 species ($N > 20$) at the Paracou experimental site.

photosynthetic capacity, and slow turnover of organs, confer tolerance to shade (Veneklaas and Poorter, 1998, Poorter and Werger, 1999, Westoby et al., 2002) by increasing nutrients residence time. These traits generate slow growth rates and prevent a flexible response to the spatial patchiness of light and soil resources (Chapin et al., 1993, Westoby et al., 2002). It is likely – in small-statured species – that full sunlight does not correspond to the most favorable growth conditions: the cost of thermal stress and evapotranspiration in high-light conditions might outweigh the benefits of increased light availability for photosynthesis (Givnish, 1988, Vincent, 2001, Semchenko et al., 2012). However our results contrast with previous studies exploring the impact of logging on tropical tree growth (Delcamp et al., 2008, Herault et al., 2010). The latter studies found that relative increment in fast growing species were not systematically greater than slower growing species. This discrepancy may be explained by the fact that these studies did not consider actual individual tree access to light. Overall, our findings provide support to the idea that light is a key determinant of species differentiation in term of vertical niche and growth strategy in tropical tree community.

Furthermore, we found that species effect explained 35% of the variation in growth rate at the community level. The strength of the species effect has previously been reported (Gourlet-Fleury, 1998) and is implicit in at least one other study conducted at the same site (Herault et al., 2011). However, this result may not have been clearly recognized or sufficiently highlighted. Taken together, our findings suggest that the strength of the species effect in our model may reflect species adaptation to the vertical light gradient. In other words, light indirectly drives individual tree growth variation through species niche and functional differentiation. This interpretation is in accordance with the results of a recent study conducted by (Rüger et al., 2012) in a Panamanian tropical forest community. These authors showed that adult stature (but also wood density considered as another proxy of shade-tolerance) was a significant predictor of species-level parameters (intrinsic growth rate and light response) of their growth model.

4.3. Why is the predictive power of light competition so limited?

In contrast of its absolute importance, crown position explained only 3.5% of the total growth rate variation. Thus, light significantly limits DBH increment but is only one of the many factors determining this increment. Regarding the prediction of individual growth rate for the entire community, crown position was strikingly less predictive than species identity. Below, we review the likely reasons why crown position has such a limited predictive power for DBH increment. First, Dawkins index is based on a coarse, empirical and indirect quantification of the light resource

(Moravie et al., 1999). Crown position error is likely responsible for only c. 2% point of unexplained variance which, given the observed predictive power of crown position (3.5%), is far from negligible. We consider that the noise affecting crown position scores downplayed the relative importance of crown position effect but cannot explain much more than 2% of the unexplained variance.

Second, the highly skewed distribution of species median crown position (Fig. 1) reflects the distribution of adult stature which illustrates the species-specificity of stratum occupation in tropical forests. This result is consistent with the study of (King et al., 2006b) pointing to the greater proportion of small-statured than high-statured tree species in tropical forests. As a consequence of the abundance of understory species and of the scarcity of gaps, many species experience a limited range of light conditions (Fig. 1), and this limits the predictive power of crown position. The segregation of species along the vertical light gradient was associated with the high abundance of small-statured species ($D_{95} < 45$ cm for 80% of species). Small-statured species were shown to be growing slower (Fig. 4) and to be less sensitive to competition than high-statured species that experience a major ontogenetic change in light availability (Fig. 3). According to literature these functional attributes indicate a specialization to low-light understory. This pattern of community structure is consistent with the presumably low disturbance rates of Guiana shield forests. We therefore contend that the minor importance of competition for light in determining individual tree growth results from the abundance of small-statured species which are mostly specialized in low-light conditions (Fig. 6). In summary, light vertical gradient probably does strongly control tropical trees growth rate at the community scale, but more so through its effect on species vertical niche differentiation than through the sub-optimal access to light of individual trees.

4.4. Sources of unexplained inter-individual variation in growth rate

The 54% growth rate variation explained by our model is in line with a number of previous studies conducted in tropical tree communities (Gourlet-Fleury, 1998, Rüger et al., 2011) that failed to explain much more than 50% of the growth variability observed. Three interdependent factors: size, species and crown position, typically explain about half of the average annual diameter growth variation in tropical forests. DBH measurement errors most likely contributed little to the growth rate residual variance since they were largely averaged out by considering DBH increment over a period of 8 years. Higher predictive ability values for tropical tree species were reported in at least two studies, but these focused on selected trees at the juvenile stage (size class 8–20 cm DBH)

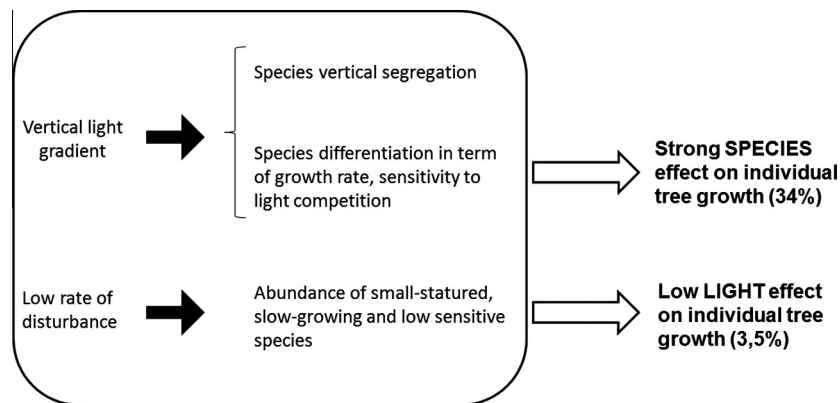


Fig. 6. Interpretation of the strong species effect and the low light effect on individual tree growth in French Guiana tropical forest.

(King et al., 2005) or on a single, highly-responsive fast growing species (Moravie et al., 1999). Even though choosing appropriate growth predictors is contingent on the precise aims of a given modeling project, our findings suggest that even fairly crude models may provide useful insights into forest dynamics. If the primary goal is predicting growth patterns at community level then correct species identification should be a priority. Conversely it might not always be worthwhile considering individual tree competitive status.

Stepping beyond the methodological limitations inherent to light exposure estimates and model specification, ecological considerations might also explain why such a large part of the intra-specific variance remains unexplained. First, growth allocation between diameter and height is likely to shift during tree life in response to changing environmental conditions (Collinet, 1997, Henry and Aarssen, 1999) and between the stem and other tree parts (Poorter and Nagel, 2000). Second, tree growth depends on individual genetics, age, stage of development (Clark et al., 2003, Barthélémy and Caraglio, 2007) and historical factors (e.g. herbivore or past physical damage, local physiological constraints) that determine tree vigour. In their study in Malaysia (Pasoh and Lambir LTP), (King et al., 2005) evaluated that 16% of all trees measured (865 trees, 21 species), had suffered severe crown damage. (Rutishauser et al., 2011) performed a crown assessment in French Guiana at the same study site (3752 individual trees > 40 cm DBH) and also provided evidence of marked crown structure variability within species. These authors showed that crown fragmentation explained 14% to 31% of growth rate variation in six out of eight abundant species. (Vincent et al., 2002) came to a similar conclusion in Dipterocarp agroforests in Sumatra (Indonesia), using the crown form index proposed by (Dawkins, 1958): at the time he proposed the CP index accounting for crown form (CF) to the growth model increased the variance explained by 7.8–25.6% points depending on the experimental plot. A similar result was found in rubber agroforest (Vincent et al., 2011a). Remarkably, CF was a better predictor of growth than CP in both studies. Thus, major alterations in crown shape are likely to concern a significant part of the tree community and thus constitute an important driver of individual tree growth. Unfortunately, DBH is still the standard and only tree dimension recorded extensively in permanent sample plots of tropical forests because of the difficulties inherent to measuring canopy structure variables. Third, the spatial heterogeneity of soil resources is a potential driver of tree growth (Davies, 2001, Baker et al., 2003). But, when studying the effect of soil drainage quality on the structure and dynamics of the forest at our site, (Morneau, 2007) found that soil type (drainage and topography) had hardly any measurable effect on individual tree growth in the few species spanning a large range of soil conditions, and

this occurred in spite of a marked species segregation along drainage gradients. Therefore, the edaphic constraint mostly affected tree growth through environmental filtering.

5. Conclusion

The study described herein sheds new light on the determinants of tropical tree growth and species differentiation in terms of sensitivity to light competition with respect to their adult stature.

Modeling of forest dynamics plays an important role in predicting carbon storage and the effect of natural (under the influence of global change factors) or anthropic-induced disturbances on the structure and functioning of tropical forests (Chave et al., 2008, Baraloto et al., 2012). By explicitly considering resource competition, tree size and species, our Bayesian growth model left about 45% of DBH increment variation unexplained. Part of this unexplained variance stems from errors in variable measurements and in model specification, and the rest from a number of additional effects – not considered here – that are either difficult to measure (genetic variability), difficult to predict (crown form) or of low intensity with extremely local relevance (fertility pulse following past disturbance).

Our results critically point to competition for light making an unexpectedly low contribution to individual tree growth variations, contrasting with a major effect of species identity. We showed that this pattern of variation is likely to result from a vertical niche partitioning of species and an abundance of small-statured species. These species are moderately responsive to light competition stemming from their adaptation to understorey conditions resulting from the low rates of disturbance of Guiana shield forests. Our findings suggest that light predominantly drives the stem growth rate of tropical trees through species differentiation rather than through individual tree growth limitation. This hypothesis could be tested by carrying out a similar study in western Amazonia forests where the rate of disturbance is likely to be higher and where community are not dominated by shade-tolerant dense-wooded and large-seeded species.

Vertical stratification complements the previously reported regeneration niche which together provide evidence for light niche partitioning in the three-dimensional space of tropical forests. It is striking that spatial segregation in relation to the local drainage regime, much like vertical segregation into preferred canopy stratum described here, contributes to community forest spatial organization by environmental filtering or niche differentiation (Sabatier et al., 1997, John, 2007, Kraft et al., 2008, Vincent et al., 2011b). Taken together these observations suggest that pervasive albeit subtle ecological specialization may largely drive local community spatial organization and dynamics in tropical rainforest.

The role previously ascribed to randomness in local species assemblage may have been overemphasized for lack of suitable data to assess the role of intricate multiple deterministic processes across highly diverse communities. As larger datasets from long term monitoring plots become available we may gradually be able to distinguish between essentially stochastic processes (e.g. propagule dispersal) and inconspicuous environmental filtering.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.05.059>.

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