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Vertical stratification reduces competition for light in dense tropical forests

Marilyne Laurans [a,*], Bruno Hérault [b], Ghislain Vieilledent [c], Grégoire Vincent [d]

[a] CIRAD, UMR AMAP, TA A-51/PS1, Bd de la Lironde, 34398 Montpellier Cedex 5, France
[b] CIRAD, UMR ECOFOG, BP 709, 97379 Kourou Cedex, French Guiana
[c] CIRAD, UPR BSEF, 34398 Montpellier Cedex 5, France
[d] IRD, UMR AMAP, TA A-51/PS1, Bd de la Lironde, 34398 Montpellier Cedex 5, France

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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.

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

* Corresponding author. Tel.: +33 467616586.
E-mail address: laurans@cirad.fr (M. Laurans).

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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 m^2 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