Research article

Height growth and biomass partitioning during secondary succession differ among forest light strata and successional guilds in a tropical rainforest

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In closed-canopy systems globally, plants exhibit intense competition for light, prioritizing vertical growth to attain elevated positions within the canopy. Light competition is especially intense in tropical rainforests because of their dense shaded stands, and during forest succession because of concomitant changes in vertical light profiles. We evaluated how the height growth of individual tree differs among forest light strata (canopy, sub-canopy and understorey) and successional guilds (early, mid- and late successional species) during secondary succession in a Mexican rainforest. Fourteen secondary forest stands differing in time since agricultural abandonment (1–25 years) were monitored for seven consecutive years. For each stand and census year we estimated relative light intensity (RLI) for each height and categorized trees into forest light strata: understorey (RLI $\leqq$ 33.3%), sub-canopy (33.3% $\leqq$ RLI $\leqq$ 66.6%) and canopy (RLI $\geqq$ 66.6%), and into successional guilds based on the literature. We estimated two measures of height growth: absolute height growth (HG_{abs}, cm year^{-1}) calculated as the difference in tree height between two consecutive censuses, and biomass partitioning to height growth (HG_{bp}, in kg kg^{-1} × 100) calculated as the percentage of total aboveground biomass growth partitioned to height growth. Earlier in succession, trees for all strata had greater HG_{abs} and HG_{bp}, resulting in rapid vertical forest development. HG_{abs} was fastest for canopy trees, followed by sub-canopy and understorey trees. These differences in HG_{abs} among strata, combined with their interspecific variation and continuous recruitment of small individuals, lead to a rapid differentiation in tree sizes and increase stand structural heterogeneity. HG_{bp} was greater for understorey and sub-canopy trees than for canopy trees, reflecting ontogenetic changes in the light competition strategy from growth to persistence. With succession, both HG_{abs} and HG_{bp} decreased, most strongly for canopy trees, probably because of an increased exposure to drought stress. These successional changes stabilize stand size structure and reduce the rate of development.

Keywords: absolute height growth, biomass partitioning to height growth, forest light strata, light competition, secondary succession, tropical rainforest

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Introduction

In closed-canopy systems globally, plants exhibit intense competition for light, prioritizing vertical growth to attain elevated positions within the canopy, thereby enhancing their capabilities to intercept light (Hirose and Werger 1995, Falster and Westoby 2003). Light competition is especially strong in many tropical rainforests as they have a dense canopy, resulting in a marked decrease in irradiance from the canopy to the forest floor (Fauset et al. 2017). Light is therefore a limiting resource in the understorey of tropical rainforests, and juvenile trees prioritize height growth to compete for light. During secondary succession, vegetation growth results in rapid changes in the vertical light profiles (Matsuo et al. 2021, 2022). This alters the patterns in height growth across canopy layers, thereby driving the structural development of forests and promoting the transition from light-demanding to shade-tolerant species (Shipley et al. 2006, van Breugel et al. 2006, 2007). Yet, despite its importance, few studies have evaluated height growth patterns in successional tropical rainforests, where light competition is believed to play a major role in the development of forest

structure and composition (Matsuo et al. 2021). Here we analyse how height growth and biomass partitioning to height growth of trees vary among forest light strata and successional guilds, and during tropical forest succession.

The length and shape of the vertical light gradient vary within and among forest stands, reflecting the vertical distribution of foliage (Fauset et al. 2017, Matsuo et al. 2021). Light extinction from the upper canopy to the forest floor can be modelled using a logistic sigmoid curve that relates relative light intensity (RLI, in %) to height in the stand, and ranges from a few % at the forest floor to 100% of full light above the canopy (Matsuo et al. 2021, 2022). With a logistic sigmoid curve, the steepest part of the light gradient is the height of the inflection point (HIP, Matsuo et al. 2021), which indicates where 50% of the irradiance is attained and where any small increase in height results in the largest net increase in light. Based on the HIP of the stand, trees can be classified into three forest light strata reflecting the position along the light gradient: understorey (trees with a height below the HIP: RLI $\leq$ 33.3%), sub-canopy (trees with a height closest to the HIP: 33.3% $\leq$ RLI $\leq$ 66.6%) and canopy (trees with a height above the HIP: RLI $\geq$ 66.6%) (Fig. 1a).
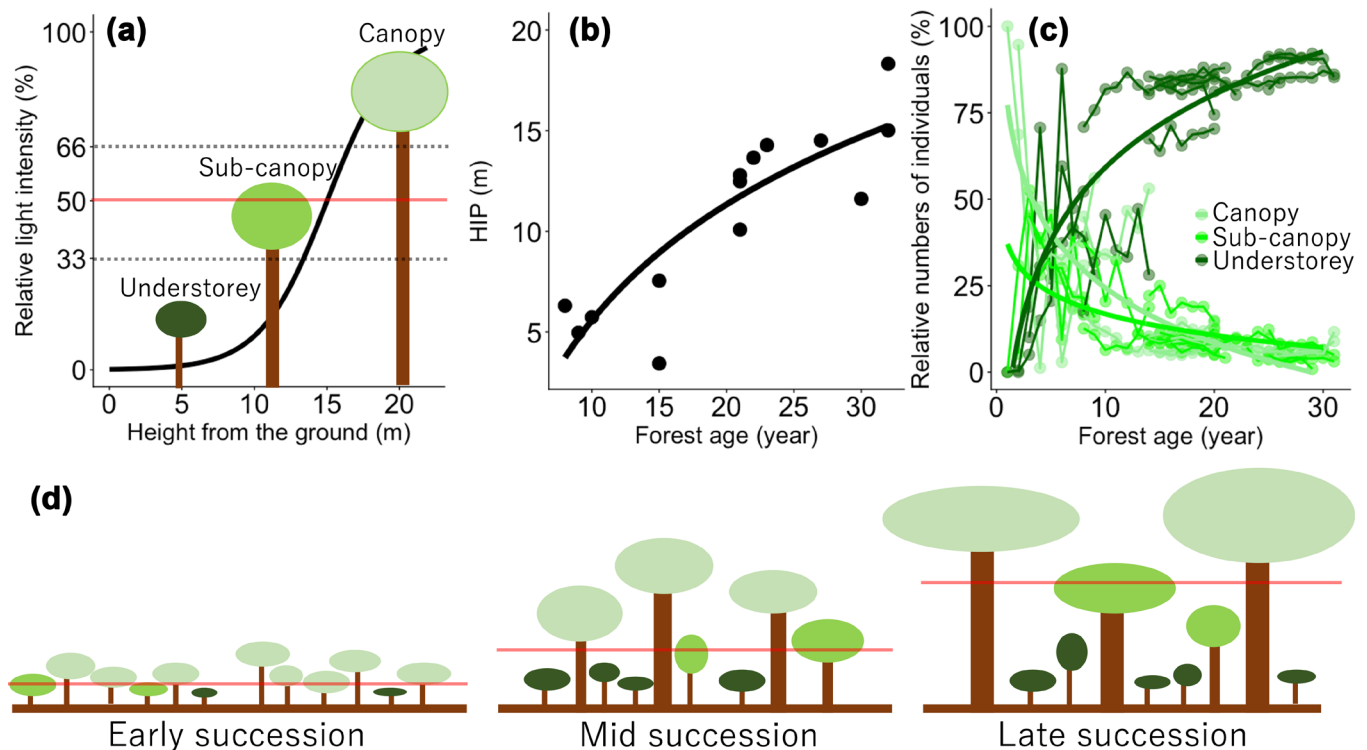

Figure 1. Conceptual diagram of the changes in forest light strata (i.e. the position of trees within the forest's vertical light gradient) during secondary succession. (a) Height of the inflection point (HIP) and relative light intensity (RLI, in%) along the vertical forest profile (i.e. the height in the stand where RLI is 50%; HIP, in m) and forest light strata. The vertical light gradient is closely approximated by a sigmoid curve with the HIP of the stand indicated by the red line. Trees are classified into three forest light strata; understorey (trees with a height below the HIP: RLI $\leq$ 33.3%), sub-canopy (trees with a height closest to the HIP: 33.3% $\leq$ RLI $\leq$ 66.6%) and canopy trees (trees with a height above the HIP: RLI $\geq$ 66.6%). Black dotted lines indicate the classification of forest light strata. (b) Changes in the HIP during succession (modified from Matsuo et al. 2021). Black dots represent the HIP per plot, and the black line represents the regression line. (c) Changes in relative abundance of trees by stratum during succession. Each dot represents the relative abundance of each stratum for each census year and forest stand, and each thin line connects the dots for a given forest stand. (d) A summarized illustration of HIP and forest light strata during succession based on (a–c).

Trees in different forest light strata are expected to follow different optimal height growth strategies. First, for understorey trees, an increase in height leads to a modest increase in light. Hence, they may follow a 'pessimistic' strategy (sensu Kohyama 1987) and expand crowns horizontally to maximize current light capture (Chazdon and Pearcy 1991, King 1996) and persist under shaded conditions until canopy gap is formed. Alternatively, they may follow an 'optimistic' strategy and invest more biomass in height growth to improve future light conditions (King 1996, Poorter et al. 2005). Second, for sub-canopy trees there is a premium on height growth, as a small increase in tree height results in the largest increase in light availability because the HIP indicates the steepest part of the light gradient (Matsuo et al. 2021). Third, canopy trees may have diminishing returns on height growth and thus invest more in diameter growth to improve stability against wind (Sterck and Bongers 1998) and water supply against drought stress (Jackson et al. 2021), or in horizontal crown growth to increase light interception (King 1996).

Tree species differ in their light competition strategies because of different ecological and functional traits (e.g. light demand, maximum stature, and leaf and seed traits, Kitajima and Poorter 2008). Notably, trees belonging to different successional guilds (i.e. early, mid- and late successional) are known to differ in their optimal height growth strategies for light competition. Most early successional species are light demanding and tend to follow an 'optimistic' strategy favouring biomass partitioning towards height growth. In contrast, most mid- and late successional species are shade tolerant, and favour a more 'pessimistic' strategy by investing relatively more in horizontal crown growth (Iida et al. 2012).

During secondary succession, vegetation development increases the HIP and decreases the light attenuation per metre height from the forest canopy to the floor concomitantly (de Almeida et al. 2020, Matsuo et al. 2021), which may have a strong influence on tree height growth strategies. Early in succession, there is a strong competitive advantage in allocating more biomass to height growth, due to a lower position of the HIP and a steeper light attenuation rate (Fig. 1). Therefore, trees might have faster height growth and a greater biomass partitioning to height growth, which fuels fast forest stand development and tree size differentiation (Poorter et al. 2021). With succession, an increased HIP and more gradual light attenuation rate lead to lower height growth rate and the relatively less biomass partitioning to height growth, which might stabilize stand size structure and reduce the rate of development.

This study evaluates how the height growth of an individual tree differs among forest light strata and successional guilds during succession. To do so, we used two measures of height growth: absolute height growth (HG$_{abs}$, cm year^{-1}) and biomass partitioning to height growth (HG$_{bp}$, in kg kg^{-1} × 100) calculated as the percentage of total aboveground biomass (AGB) growth partitioned to height growth of trees. We chose these two measures because HG$_{abs}$ is linked to forest structural development and HG$_{bp}$ is related to the trees' strategy to compete for light. We addressed three questions:

1) how do HG$_{abs}$ and HG$_{bp}$ of trees differ among forest light strata? We hypothesize that 1) throughout succession, HG$_{abs}$ is greatest for canopy trees followed by sub-canopy and understorey trees, reflecting the vertical light gradients; ii) throughout succession, HG$_{bp}$ is greatest for sub-canopy trees because they experience the largest gains in light conditions for a given height growth, intermediate for understorey trees because they are strongly light limited and lowest for canopy trees because they are least light limited. 2) How do HG$_{abs}$ and HG$_{bp}$ of trees differ among successional guilds? We hypothesize that HG$_{abs}$ and HG$_{bp}$ should increase with light demand because of their adaptation to well-lit conditions, and thus be the largest for early successional species, intermediate for mid-successional species and lowest for late successional species. 3) How do HG$_{abs}$ and HG$_{bp}$ change during succession? We hypothesi that both HG$_{abs}$ and HG$_{bp}$ of trees for all strata and guilds decrease during succession because the increased HIP and more gradual light attenuation rate diminish returns on investment in height growth. We also hypothesize that such a successional decrease in height growth rate is fastest for canopy trees because of increasing wind and drought stress.

Material and methods

Study site

Research was conducted in the La Selva Lacandona region, near Loma Bonita (16°04′N, 90°55′W), southeast Mexico. The climate is warm and humid with a mean annual temperature of 24°C, and mean annual precipitation of approximately 3000 mm (Martínez-Ramos et al. 2009). The dominant vegetation comprises lowland tropical rainforests and semi-deciduous forests (Ibarra-Manríquez and Martínez-Ramos 2002).

Secondary forest plots were selected on abandoned maizefields ('milpas') in areas with undulating hills, between 115 and 300 m a.s.l., with acidic soil (pH 4–5) derived from sedimentary rocks (sandy and clay) (Siebe et al. 1995, van Breugel et al. 2007). Land-use history was determined based on information from landowners and other residents. The maizefields had been established after clear-cutting the original old-growth forest, used for maize cultivation for one year, and subsequently abandoned. All plots were bordered by remaining old-growth forests or well connected to them by secondary forest and possess similar geomorphology and land-use history.

Field survey

We combined a chronosequence and longitudinal approach (Martínez-Ramos et al. 2021). We selected 14 secondary forest stands differing in time since agricultural abandonment. Fallow age ranged from 1 to 25 years at the start of the census in 2012 (van Breugel et al. 2006, Martínez-Ramos et al. 2021). Each plot located in each stand was 40 × 10 m and subdivided into four 10 × 10 m (sub-plots). Every individual with a stem diameter at breast height (DBH; diameter

at 1.3 m height) more than 1 cm was mapped, identified to species and its DBH and height were measured every year for seven consecutive annual censuses.

Estimation of light conditions for each tree individual and forest light strata

To assign an individual tree to different forest light strata, we estimated the RLI for each tree in each census year. In each of the 14 forest stands the vertical light profile was measured in February 2019 under overcast sky conditions with a photosynthetic photon flux density (PPFD) sensor attached to a 20 m telescopic carbon rod (Onoda et al. 2014). Irradiance was measured at 1 m height intervals from 1 m up to 22 m height (20 m + 2 m height of the person holding the equipment). This was done for four points per sub-plot, yielding up to 88 light environments per sub-plot depending on the canopy height. At each height, PPFD was measured for five seconds and averaged. RLI (in %) was then calculated as the irradiance at that point of measurement divided by the irradiance simultaneously measured above the canopy or in a nearby open area, multiplied by 100.

For each subplot we related the RLI to height from the ground using a logistic curve, and estimated two parameters: the height of inflection point of vertical light profile (HIP_{light}, in m) and the light attenuation rate per metre (unitless) at this inflection point (Matsuo et al. 2021, 2022).

$$RLI = 100 / [1 + exp\{(-\text{Light attenuation rate} \times (\text{height} - HIP_{light})\}] \quad (1)$$

To estimate the RLI for each tree in each census year we used a three-step approach: 1) we developed an allometric equation relating the plot average value of two parameters (HIP_{light} and light attenuation rate) of the logistic light curve to the vertical forest structure of that plot (see the Supporting information for the flow chart of the calculation). To describe vertical structure we used the vertical cumulative basal area (BA), as this is closely related to vertical light profile (Matsuo et al. 2021). We calculated the basal area of single-stemmed trees as $\pi \times (DBH/2)^2$. For multi-stemmed trees, we calculated the basal area of each stem and then summed these. Then, we analysed the height distribution of tree basal area in each sub-plot, by plotting the cumulative value of tree basal area against the corresponding height (i.e. by ranking individuals in increasing order of tree height). For multi-stemmed trees, we used the height of the tallest stem as the vertical position of the tree. To summarize these vertical basal area profiles, we again used a logistic sigmoid model (Eq. 1) to relate cumulative basal area to height and obtained the height of the inflection point of cumulative basal area (HIP_{BA}, the height at which the changes in tree basal area are maximized), and the slope at the HIP_{BA} ($slope_{BA}$, the change in basal area per unit of height at HIP_{BA}) for each census year and sub-plot. We then regressed HIP_{light} against HIP_{BA}, and light

attenuation rate against $slope_{BA}$, using a simple linear regression model with the average value of each variable for each plot (Supporting information):

$$HIP_{light} = 1.10362 \times HIP_{BA} - 1.69365 \quad (r = 0.96) \quad (2)$$

Light attenuation rate at HIP
$$= 0.42974 \times Slope_{BA} + 0.726547 \quad (r = 0.86) \quad (3)$$

2) We then used these equations to estimate the two parameters of the vertical light profile based on the vertical cumulative BA for each subplot and census year (Supporting information). 3) Finally, we inserted these parameters in Eq. 1 to estimate a RLI value of each tree in each year (Supporting information).

To assess the height growth of an individual tree across forest light strata, we classified trees into three forest light strata; understorey (RLI $\leq$ 33.3%), sub-canopy (33.3% $\leq$ RLI $\leq$ 66.6%) and canopy (RLI $\geq$ 66.6%; Fig. 1a). The number of trees per light stratum varies among different plots due to forest structure (Fig. 1c). These ordinal light strata allow us to test our hypothesis that trees with height close to the HIP (sub-canopy trees) partition relatively more biomass to height growth than do either understorey or canopy trees.

Successional guilds

To assess height growth among successional guilds, we allocated species into three pre-defined successional guilds (early, mid- and late successional species, Arasa-Gisbert et al. 2021) based on different existing studies and literature in the Neotropics (Guevara et al. 1986, Renner 1986, Greig 1993, Martínez-Garza and González-Montagut 1999, Hooper et al. 2004, Elevitch and Francis 2006, Sorenson 2006, van Breugel et al. 2007, Schönbeck et al. 2015, Santos-Heredia et al. 2016, Velázquez and Wiegand 2020, Arasa-Gisbert et al. 2021, Martínez-Ramos et al. 2021) and unpublished long-term monitoring data from this study site. These successional guilds are defined by the time that they appear, how long they persist during succession and by their light requirement for growth and survival (Supporting information). Early successional species are mostly light demanding, and recruit early in succession (< 5 year; Uhl 1987, Peña-Claros 2003) and dominate the first 10–20 years of succession. Mid-successional species grow and survive under the canopy of early successional species, and dominate from 20 to 100 years of succession (sensu Finegan 1996). Late successional species are shade-tolerant, recruit continuously throughout succession and dominate the canopy after 100 years of succession until major disturbances occur (Swaine and Hall 1983, Finegan 1996). The classification was done for 163 out of 168 species, representing 99.7% of all the individuals in our study (Supporting information). The species for which we could not find any information about the successional guild were excluded from our analyses.

Absolute height growth and biomass partitioning to height growth

To assess the height growth strategies, we calculated two different measures of the height growth: absolute height growth (HG_{abs}, cm year^{-1}) as the difference in tree height between two consecutive censuses and biomass partitioning to height growth (HG_{bp}, in kg kg^{-1} × 100, i.e. as a %) calculated as the vertical biomass growth rate (kg year^{-1}) divided by the total AGB growth rate (kg year^{-1}) multiplied by 100, indicating the percentage of total AGB growth partitioned to height growth (see Supporting information for the flow chart of the calculation). To calculate this, we estimated both total AGB growth and vertical biomass growth using allometric equations based on DBH, height and wood density. We first estimated the vertical biomass growth rate. For this, we estimated the diameter at the top height (D_{top}, cm) based on a simple equation for stem taper (Eq. 4, Metcalf et al. 2009):

$$D_{top} = DBH \times e^{-a \times (h-1.3)} \tag{4}$$

where a is the taper parameter, and h is tree height (m). We assumed $a = 0.039$ obtained for Panamanian rainforest trees (Cushman et al. 2014). Then, we estimated the vertical biomass growth rate (Eq. 5, Chave et al. 2005):

Vertical biomass growth rate

$$= F \times \rho \times \left(\pi D_{top}^{2} / 4 \right) \times HG_{abs} \tag{5}$$

where F is a mean form factor (0.06 for broadleaved trees, Cannell 1984), ρ is mean species-specific wood density (g cm^{-3}) and D_{top} is the diameter at the top height (cm). Wood density data for species in this study site were obtained from a previous study (Lohbeck et al. 2012) and, when data for some species were unavailable, we used data from the same genus or family level or average wood density in this study site. For each tree, AGB was estimated using the following allometric equation for tropical forest trees (Eq. 6, Chave et al. 2014):

$$AGB_{total} = 0.0673 \times (\rho \times DBH^2 \times H)^{0.976} \tag{6}$$

Total AGB growth rate was then calculated as the difference in the AGB_{total} between two consecutive censuses. Finally, we estimated HG_{bp} as the ratio between our estimated vertical biomass growth rate and total AGB growth rate, multiplied by 100.

We excluded one individual that yielded HG_{bp} exceeding 100%, as this must range between 0 and 100%. In 21% of our observations, trees showed negative diameter growth rate due to stem breakage caused by falling debris; stem or bark dieback or shrinkage due to pathogens, drought, shade or other stresses; some dead stems for multi-stemmed trees; or measurement errors (Sheil 2003, Sheil et al. 2017). In 11%

of our observations trees yielded negative height growth rate due to bending or breakage of the trunk/crown, or measurement errors (Clark and Clark 2001). In 6% of all observations, trees showed both negative diameter growth and height growth. These negative patterns in diameter or height growth rate are common in tropical wet forests (Clark and Clark 1991, 2001, Sheil et al. 2017), especially in early successional stages because 1) trees often have softer wood than those in old-growth forests, and thus are more vulnerable to abiotic and biotic disturbance agents (e.g. windthrown, fallen branches, liana load and pathogens), leading to negative diameter and/or height growth rate (Van Gelder et al. 2006, Chave et al. 2009), 2) trees exhibit greater slenderness (height/DBH ratio) and hence are more prone to bend or break (Jaouen et al. 2007, Chen et al. 2017) and 3) many trees on abandoned agricultural land regenerate through resprouting. As a result, these are often multi-stemmed trees, and breakage or death of some stems lead to negative overall diameter growth rate of an individual as the remaining stem is smaller. Because this study aims to understand how height growth patterns are determined by light conditions, we excluded all the negative growth data from the analysis to minimize the effects of biophysical hazards, and other stresses and disturbances, on the underlying height growth patterns. Individuals with only one entry in census data were excluded from the analysis. Over the seven consecutive annual censuses, approximately 9% of individuals died.

Statistical analysis

All statistical analyses were conducted using R software ver. 4.2.1 (www.r-project.org). To evaluate how HG_{abs} and HG_{bp} vary across forest light strata and successional guilds during succession, we employed linear mixed models using the 'lme4', 'performance' and 'lmerTest' packages in R (Bates 2007, Kuznetsova et al. 2017, Lüdecke et al. 2021). HG_{abs} and HG_{bp} were response variables, while forest age (year), forest light strata, successional guilds and the interaction between forest age and forest light strata were included as fixed variables. As random variables, we included forest stands to account for the fact that trees were nested within stands; tree individuals to account for the repeated measures of the same individuals; and species to understand how species differ in their height growth strategies. HG_{abs} and HG_{bp} were log$_{10}$ transformed prior to the analysis. To assess the overall differences in HG_{abs} and HG_{bp} among forest light strata, estimated marginal means of the forest strata were estimated based on the linear mixed models at mean stand age and mid-successional species as a reference using the *emmeans* function in the 'emmeans' package (Lenth et al. 2019). Similarly, estimated marginal means of successional guilds were estimated at mean stand age and sub-canopy as a reference, using the same function. Additionally, we employed the linear mixed model with HG_{abs} including individuals with negative growth rate as a response variable, using the same fixed and random variables to evaluate whether inclusion of negative growth rate influenced our results.

Results

On average, absolute height growth was 58.7 cm per year and trees partitioned 17.4% of their AGB growth to height growth. Based on the estimated marginal means from the linear mixed models, HG_{abs} was fastest for canopy trees (48.0 ± 0.06 SE cm $year^{-1}$), followed by sub-canopy trees (42.7 ± 0.06 cm $year^{-1}$) and understorey trees (31.4 ± 0.06 cm $year^{-1}$ $p < 0.001$; Fig. 2a). In contrast, HG_{bp} was greater for understorey and sub-canopy trees (understorey: 12.5 ± 0.05%, sub-canopy: 11.9 ± 0.05%) than for canopy trees (10.0 ± 0.05% $p < 0.001$; Fig. 2d). HG_{abs} did not differ significantly among successional guilds (Fig. 2b). In contrast, early successional species partitioned significantly more of their biomass growth to height growth (12.5 ± 0.05%) than

mid- (11.3 ± 0.05%) and late successional species (10.7 ± 0.06%; $p < 0.01$; Fig. 2e).

A linear mixed model showed that HG_{abs} was greater for canopy trees followed by sub-canopy and understorey trees (Fig. 2a) and decreased with succession for all strata (Fig. 2b, Table 1a). The regression lines for each forest stratum indicates that for 1-year-old forests, HG_{abs} was fastest for canopy trees (71.6 cm $year^{-1}$) followed by sub-canopy (54.9 cm $year^{-1}$) and understorey trees (45.5 cm $year^{-1}$) (Fig. 2c). During succession, HG_{abs} declined most rapidly for canopy trees followed by understorey and sub-canopy trees. For 30-year-old forests (the oldest forest in this study), HG_{abs} among forest light strata had nearly converged (canopy: 33.5 cm $year^{-1}$, sub-canopy: 34.1 cm $year^{-1}$, understorey: 22.6 cm $year^{-1}$) (Fig. 2c).
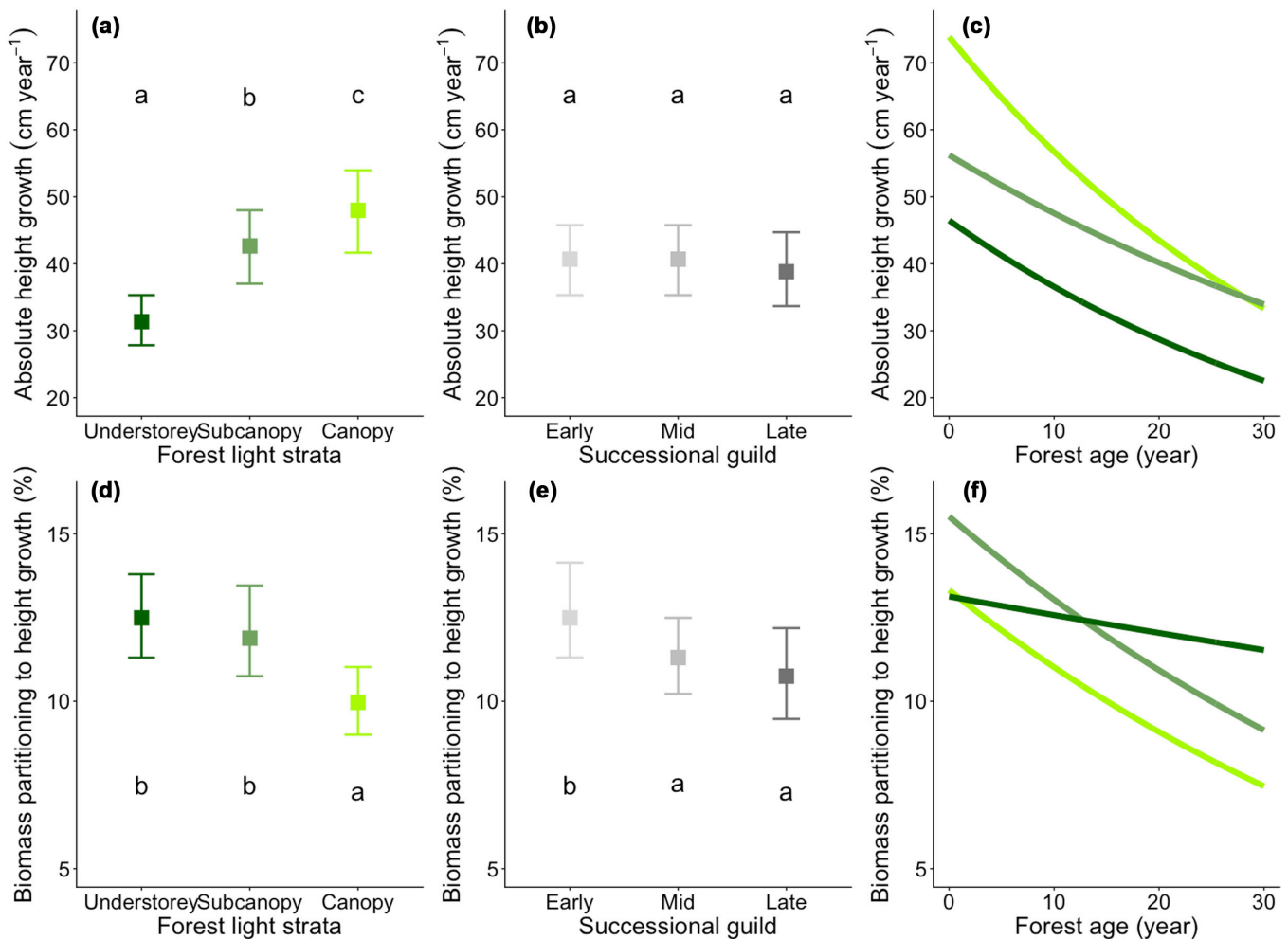

Figure 2. Absolute height growth (cm $year^{-1}$, top row) and biomass partitioning to height growth (the partitioning of total aboveground biomass growth to height growth, in kg kg^{-1} × 100, i.e. as a %, bottom row) for trees across (a) and (d) forest light strata; and (b) and (e) successional guilds during succession. Estimated marginal means and their 95% confidential intervals are shown. Different letters indicate significant differences in estimated marginal means at mean stand age and sub-canopy or mid-successional species as a reference using the *emmeans* function. Successional patterns in (c) absolute height growth and (f) biomass partitioning to height growth. Regression lines are drawn for each stratum based on the linear mixed models at mean stand age and mid-successional species as a reference (Table 1). In the linear mixed models, both measures of height growth were log_{10}-transformed. Values are back transformed for better visualization.

Table 1. Results of a linear mixed model with a) absolute height growth (cm year^{-1}) and b) biomass partitioning to height growth (the partitioning of total aboveground biomass growth to height growth, in kg kg^{-1} × 100, i.e. as a %) as response variables, and the age of forest stand (Age), forest light strata (understorey, sub-canopy and canopy trees), successional guild (early, mid- and late successional species) and an interaction between forest age and forest light strata as fixed variables; and forest stands, tree individual and species as random variables. In a) the Conditional R^2 was 0.19 and Marginal R^2 was 0.12, and in b) the Conditional R^2 was 0.09 and Marginal R^2 was 0.02. Both measures of height growth were $\log_{10}$ transformed.

Predictor variable	a) Estimate	a) SE	a) t-value	a) p-value	b) Estimate	b) SE	b) t-value	b) p-value
Intercept (sub-canopy/mid-successional)	1.76	0.05	39.4	< 0.001	1.22	0.04	32.8	< 0.001
Age (sub-canopy trees/mid-successional)	−0.007	0.002	−3.1	0.002	−0.0071	0.02	−3.6	< 0.001
Understorey trees	−0.081	0.03	−2.7	0.007	−0.068	0.03	−2.5	0.011
Canopy trees	0.12	0.03	4.4	< 0.001	−0.062	0.02	−2.6	0.009
Age × understorey trees	−0.003	0.002	−1.7	0.095	0.0053	0.002	3.3	< 0.001
Age × canopy trees	−0.0042	0.002	−2.3	0.02	−0.001	0.002	−0.34	0.73
Early successional	−0.001	0.02	−0.044	0.97	0.047	0.02	2.7	0.008
Late successional	−0.015	0.02	−0.63	0.53	−0.020	0.02	−0.99	0.33

HG_{bp} was larger for understorey and sub-canopy trees than for canopy trees (Fig. 2d); it was also larger for early successional species than for mid- and late successional species (Fig. 2e) and decreased with succession for canopy and sub-canopy trees (Table 1b). For 1-year-old forests, HG_{bp} was greatest for sub-canopy trees (15.3%) compared to canopy (13.2%) and understorey trees (13.1%) (Fig. 2f). During succession, HG_{bp} declined most rapidly for canopy trees followed by sub-canopy and understorey trees, and hence diverged with succession (Fig. 2f). For 30-year-old forests, understorey trees partitioned most biomass growth to height growth (11.5%) followed by sub-canopy (9.1%) and canopy trees (7.5%). Similar patterns arose for relative tree height instead of using forest light strata, indicating that relative tree height is also a good indicator of the vertical position of trees (Supporting information). When including the negative growth rate for the analysis of absolute height growth, slightly different patterns resulted with larger differences in absolute height growth among forest light strata and with lower absolute height growth for early successional species than for mid- and late successional species (Supporting information).

Discussion

We evaluated how absolute height growth and biomass partitioning to height growth vary with forest light strata, successional guilds and during succession. HG_{abs} was greatest for canopy trees followed by sub-canopy and understorey trees whereas HG_{bp} was lowest for canopy trees. HG_{abs} did not differ significantly among successional guilds while HG_{bp} was greatest for early successional species. Both HG_{abs} and HG_{bp} decreased with succession, especially for canopy trees.

Absolute height growth and biomass partitioning to height growth among forest strata

HG_{abs} was fastest for canopy trees throughout succession followed by sub-canopy and understorey trees (Fig. 2a). This is expected because light availability increases from the understorey to the canopy, which determines the photosynthetic activity and overall tree growth (Boardman 1977).

In contrast, throughout succession HG_{bp} was larger for sub-canopy and understorey trees than canopy trees (Fig. 2d, f, Table 1b). This means that understorey trees tend to follow an 'optimistic' strategy by investing a greater proportion of biomass towards height growth (Fig. 2d, King 1996, Poorter et al. 2006). Most understorey trees are therefore regenerating individuals of canopy tree species that have a high demand for light and maximum stature (Thomas and Bazzaz 1999, Sheil et al. 2006). Additionally, understorey trees are sheltered by taller trees from strong winds, allowing them to partition more biomass to height growth than to diameter growth (Anten et al. 2005). Sub-canopy trees were hypothesized to invest most biomass in height growth because light attenuation rate is steepest in the sub-canopy layer (Fig. 1a). In line with our hypothesis, we found that HG_{bp} was next to understorey trees, indeed largest for sub-canopy trees (Fig. 2d). This indicates that trees that are light limited or that occur at the steepest part of the light gradient obtain the largest returns from investment in height growth. HG_{bp} was smallest for canopy trees as they are not light-limited and thus shift their biomass partitioning from height to diameter growth for mechanical stability (Onoda and Anten 2011, Prado-Junior et al. 2016) and for water transport capacity (Grote et al. 2016), or to reproduction (Thomas 2011). Although biomass partitioning to height growth was smallest for canopy trees, they have the fastest absolute height growth, reflecting their greatest biomass growth rate. The great growth rate of canopy trees throughout succession therefore contributes to stand structural development (van Breugel et al. 2006, Lebrija-Trejos et al. 2008) and biomass accumulation during tropical forest succession.

Absolute height growth and biomass partitioning among successional guilds and species

Against our expectation, absolute height growth did not significantly differ among successional guilds (Fig. 2b, Table 1a), because within guilds species differ in absolute height growth. Some early successional species such as *Cecropia peltata* showed rapid absolute height growth for light competition, whereas others such as *Piper aduncum* and *P. auritum* grew less rapidly. Instead of fast growth, these species invest in

reproduction by producing many tiny seeds (seed volume < 0.2 mm³, Lohbeck et al. 2013), maximizing opportunities to reach a suitable area for their germination and increase abundance (van Steenis 1958, Poorter et al. 2023). Other early successional species, such as *P. hipsidum* and *Solanum umbelatum*, had slower absolute height growth because they have a very short adult stature (< 5 m, Martínez-Ramos unpubl.) which constrains height growth.

Early successional species partitioned the greatest portion of biomass growth to height growth (Fig. 2e, Table 1b); they produce slender stems and a shallow crown at the top of the tree (Poorter and Werger 1999, Chen et al. 2017), thus prioritizing vertical growth (Sterck et al. 2001, Kitajima et al. 2005). Later successional species partitioned relatively less biomass to height growth; they are more shade-tolerant and prioritize horizontal stem and crown growth to maximize current light interception (Kohyama 1987, Sterck et al. 2001, Iida et al. 2012).

The large variations in height growth within each stratum and successional guild suggest large inter-specific variation in ecological strategies. Therefore, a functional trait approach may further advance our understanding of height growth in relation to light competition in hyper-diverse tropical rainforests.

Successional changes in absolute height growth and biomass partitioning

In early succession, absolute height growth was fastest for canopy trees followed by sub-canopy and understorey trees (Fig. 2c, Table 1a). Hence, the strong race for the canopy should lead to rapid forest development (van Breugel et al. 2006). Different absolute height growth among forest light strata, combined with large inter-specific variation, and continuous recruitment of small individuals in the understorey lead to a rapid size differentiation (Poorter et al. 2021). During succession, absolute height growth declined in all strata, and largest for canopy trees, probably because of increasing drought stress induced by longer hydraulic path lengths (Koch et al. 2004, Sharma et al. 2020) and risk of breakage due to wind (Onoda and Anten 2011). As a result, forest development may slow down, and size structure becomes more consistent in later succession.

When including trees with negative growth, most results were relatively similar, though as noted there were some differences (Supporting information). First, differences in absolute height growth among forest light strata increased (Supporting information); understorey individuals in particular had reduced absolute height growth, likely reflecting the contribution of stem bending or breakage (Clark and Clark 2001). Indeed, the percentage of trees with negative absolute height growth increased from the canopy to the understorey (canopy: 12.6%, sub-canopy: 13.5% and understorey: 20.0%). Second, early successional species had the lowest absolute height growth rate than later successional species (Supporting information). Early successional rainforest species generally have 1) softer wood and thus are more vulnerable to damage (Van Gelder et al. 2006, Chave et al. 2009) and 2) possess slender stems closer to the structural limit than later successional species and hence are prone to bend or break (Jaouen et al. 2007, Chen et al. 2017), resulting in more frequent height loss. Different frequencies and extents of height loss from damage will influence tree growth trajectories and survival (Clark and Clark 1991, 2001), and result in forest development during succession. Because height loss is common during forest succession (Putz et al. 1983, Clark and Clark 2001), future studies should investigate the causes for better understanding of individual height growth patterns.

In early succession, biomass partitioning was largest for sub-canopy trees (Fig. 2f). Because light attenuation rate is steeper in earlier succession and is maximized in the sub-canopy layer around the HIP (Fig. 1a), sub-canopy trees partition most biomass to height growth, because any small increase in height leads to a disproportional increase in captured light. In all forest light strata, biomass partitioning decreased with forest age, and this decrease was weakest for understorey trees, leading to the greatest biomass partitioning of understorey trees in later succession (Fig. 2f). A reduced investment in height growth for canopy and sub-canopy trees during succession might be caused by successional decrease in light attenuation rate (Matsuo et al. 2021, 2022). The steepest light attenuation rate at the HIP occurs in early succession (Supporting information), which might enhance more biomass partitioning to height growth. Later in succession, leaves are more gradually distributed along the forest's vertical profile, and light attenuation rate is more gradual (de Almeida et al. 2020), reducing light attenuation rate at the HIP. This results in the diminishing returns on height growth in later-successional stages and hence more biomass partitioning to diameter growth. The shift in biomass partitioning from vertical to horizontal growth indicates successional changes in strategy from rapid growth to increased persistence.

Conclusions

Absolute tree height growth and biomass partitioning to height growth vary among forest light strata, successional guilds and successional stages. Trees for all strata have the fastest absolute height growth and biomass partitioning to height growth in early succession, reflecting a steep light attenuation rate in the forest canopy. This fast absolute height growth of (canopy) trees leads to rapid vertical development in early succession. In addition, marked differences in absolute height growth among forest light strata and species and continuous recruitment lead to increasing differentiation in tree sizes and structural heterogeneity. During succession, absolute height growth declined in all strata, being exceptionally marked for canopy trees, which slows down the rate of stand development and stabilizes the stand size structure. Biomass partitioning to height growth declined with succession in all strata, reflecting the diminishing returns on height growth.

Over succession, biomass partitioning shifts from vertical to horizontal growth, reflecting a shift in ontogenetic strategy from one favouring growth to another favouring persistence.

Author contributions

Tomonari Matsuo: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Methodology (lead); Validation (equal); Visualization (lead); Writing – original draft (lead). **Frans Bongers**: Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Miguel Martínez-Ramos**: Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Masha T. van der Sande**: Conceptualization (equal); Funding acquisition (supporting); Methodology (equal); Supervision (equal); Visualization (equal); Writing – review and editing (equal). **Lourens Poorter**: Conceptualization (equal); Funding acquisition (equal); Formal analysis (equal); Methodology (equal); Supervision (equal); Visualization (equal); Writing – review and editing (equal).

Data availability statement

Data are available from DANS (Data Archiving and Networked Services) upon reasonable request: https://doi.org/10.17026/LS/5N8RZT (Matsuo et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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