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Light effects on seedling growth in simulated forest canopy gaps vary across species from different successional stages

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Tropical forests continue to suffer from various kinds of disturbances in the Anthropocene. An immediate impact of disturbances on forest ecosystems is the creation of numerous large and small canopy gaps, which dramatically affect forest structure and function. Yet, we know little about the effect of canopy gaps on forest successional trajectory. More specifically, the responses of seedlings from different successional stages to increased light intensity under large and small canopy gaps in understory remain unclear. In this study, dominant tree seedlings from early-, mid-, and late-successional stages were selected, respectively from a tropical montane forest in Hainan Island, China to study their growth rate, biomass and traits. Our results showed that the light condition under small canopy gaps (SG, 10–15% of full sunlight) and large canopy gaps (LG, 40–50% of full sunlight) induced greater increment of relative growth rates for seedlings from early- and mid-successional stages relative to that in late-successional stage. Both SG and LG also significantly increased photosynthesis rate, leaf area (LA), light saturation point (LSP), root mass ratio (RMR) and root: shoot ratio, but decreased specific leaf area (SLA) of seedlings across successional stages. Tree seedlings from the early-successional stage displayed the greatest decrease in leaf mass ratio, increase in LA, LSP, and RMR, in comparison to those from mid- and late- successional stages. Light condition and SLA were the most important factors for seedlings' relative growth rate across successional stages. SLA connected the interaction between the light condition and successional stage on seedlings' growth, thereby jointly explaining the 93% variation of seedlings' growth, combining with area-based light saturated rate of CO_2 assimilation. Our study highlights the distinct effect of disturbance-induced canopy gaps on seedling regeneration in the understory in tropical forest due to the variation of light intensity. We suspect that the seedlings from late-successional stage will recover relatively slow after disturbances causing canopy losses, which can have detrimental impacts on structure feature and successional trajectory in tropical forest, as well as forest-based ecosystem services.

KEYWORDS

light condition, successional stage, seedling growth, photosynthetic properties, biomass allocation

Introduction

Tropical forests harbor over one half of global biodiversity on land, and play a crucial role in terrestrial carbon cycle (Malhi and Marthews, 2013; Behera et al., 2022). It is crucial to understand the sustainability of functions and services in tropical forest for ecosystem management in context of global change (Lohbeck et al., 2015). In the Anthropocene, deforestation and climate changes continue to exert tremendous stress on ecosystems (Broadbent et al., 2008; Thakur et al., 2022), inducing detrimental consequences for tropical forest diversity and associated ecosystem functions (Emanuel, 2005; Miller et al., 2011; Olivero-Lora et al., 2022). Several such disturbances, like drought, heat waves, disease outbreaks, and extreme weather events (e.g., typhoon) induce tree mortality and heavy defoliation, causing canopy senescence and resulting in numerous canopy gaps (Corona-Lozada et al., 2019; Thakur et al., 2022). As a double-edged sword, disturbance-induced formation of canopy gaps cause more opportunity for germination from the soil seed bank, as well as huge loss of tree biomass (Barlow and Peres, 2004). With the formation of canopy gaps, the environment at forest understory correspondingly shifts, e.g., the enhanced available light and nutrient release from decomposition of dead trees, affecting the seedlings' growth and the process of forest regeneration and succession after these disturbances are over (Prescott, 2002; Lin et al., 2003). Understanding the growth and survival of tree seedlings under canopy gaps at the understory is key for predicting forest resilience and also to help shed insights on the ongoing debate about the role of canopy gaps for maintaining forest's diversity and function (Muscolo et al., 2014; Wang and Lin, 2019; Xi et al., 2019).

In the understory, the nursery for young seedlings in tropical forests, the availability of light and nutrient determine seedlings' growth, survivorship and competition, driving forest regeneration and succession (Trauernicht et al., 2006; Mazzochini and Camargo, 2020). The formation of canopy gaps are generally considered to have positive effect on seedlings' growth, due to the alleviated limitation of light availability (Alvarez-Clare and Avalos, 2007; Westerband and Horvitz, 2015). However, what species of tree are recruited and be more stimulated by increased light, becomes a critical determinant for the forest recovery and subsequent trajectory of natural regeneration after disturbance, in the understory of tropical forest (Matsuo et al., 2021; Tourville et al., 2022; Wang et al., 2022).

For example, tree seedlings of species from different successional stages (e.g., early-, mid-, and late- stage) exhibit distinct survival, growth rates, and susceptibility to photoinhibition in understory habitats, due to their respective physiological and growth traits (Kitao et al., 2000; Martinez-Garza et al., 2005). In general, germination of early-successional tree species occur in tree-fall gaps, characterized by a high mortality rates and high inherent growth rates (Souza and Válio, 2003). Conversely, species germinated from the later successional stages (e.g., mid- and late-successional species) or shade-tolerant species germinated in relative deep shade, exhibit high survival and lower relative growth rates to adapt the potential nutrient limitation (Kneeshaw and Bergeron, 1998; Kitao et al., 2000). The distinct optimal illumination condition among species from different successional stages is one of the main factors that determines demography of the understory seedlings' community (Pollastrini et al., 2022). Thus, in facing with suddenly enhanced light intensity under canopy gaps after disturbance, seedlings of species from different successional stages might exhibit diverse response in growth (Hogan et al., 2022).

Besides of inherent difference in characteristics of germination and growth, species from different successional stages also represent differences in leaf traits (e.g., specific leaf area, SLA) and resource allocation strategies (e.g., pattern of biomass partitioning), which in turn regulate their ability to obtain above–(e.g., light and CO_2) and below-ground resources (e.g., nutrients and water) (Davidson et al., 2002; Toledo-Aceves and Swaine, 2008). Relative to the seedlings from the late-successional stage, that from early-successional stage generally have shorter leaf life-span, higher SLA, lesser investments to defense compounds and structures, and smaller root: shoot ratio (Reich et al., 1992; Antos and Halpern, 1997; Batuwatta and Singhakumara, 2014). These different traits among species from diverse successional stage control their growth rates in forest, regulating species' competitiveness and understory biodiversity together with forest succession (Hu et al., 2018; Tsai et al., 2018). Whether the seedlings from different successional stages, display diverse response in leaf-scale photosynthetic and/or individual morphological traits, to enhanced light intensity or not, become a crucial issue (Kitajima, 1994; Wang et al., 2022). Especially in the context of more frequent natural or anthropogenic disturbance in tropical forest, the formation of canopy gaps would affect future forest succession due to the distinct growth responses among different seedlings (Zong et al., 2018; Li et al., 2021).

In this study, we selected the dominant species from early-, mid-, and late-successional stages at the understory layer from a tropical forest in Hainan Island, which lies on the northern edge of Asian tropical rain forest as an important biodiversity hotspot in China (Li, 2002). The frequency and intensity of natural or anthropogenic disturbances, e.g., typhoon and selective logging, have increased tremendously in this district, resulting in a higher frequency of canopy gaps in tropical forest (Ding et al., 2017; Yang et al., 2017). The effects of canopy gap-induced increasing light intensity on seedlings' growth were hypothesized to be different among species from early-, mid-, and late-successional stages, consequently regulating the future recovery and successional trajectory for tropical forest after disturbances (Olivero-Lora et al., 2022). Thus, the relative growth rates of seedlings under manipulated three light conditions, i.e., light intensity in ambient understory of tropical forest (Control, 0–5% of full light), that in small (SG, 10–15% of full sunlight, to simulate the canopy opening caused by snapped branches and defoliation) and large canopy gap (LG, 40–50% of full sunlight, to simulate the canopy opening caused by tree fall and selective logging) (Valladares et al., 2000; Yang et al., 2017), were investigated together with their photosynthetic properties (e.g., light-saturated rate of CO_2 assimilation and apparent quantum efficiency) and resource allocation strategy (e.g., root: shoot ratio and leaf area ratio). Here, we seek to answer the following questions: (1) how does the increased light intensity due to canopy gaps, respectively affect relative growth rate of seedlings for tree species from early-, mid-, and late-successional stages of tropical forests; (2) what are the key properties of tree seedlings regulating their growth responses to enhanced light conditions?

Materials and methods

Experimental design

In order to probe the effects of light condition altered by canopy gaps on the growth of understory tree seedlings in tropical forest, six native tree species from early- [*Dolichandrone cauda-felina* (Hance) Benth. et Hook. F. and *Radermachera hainanensis* Merr.], mid- [*Syzygium cumini* (L.) Skeels and *Sterculia lanceolata* Cav.], and late- successional stages (*Dillenia turbinate* Finet et Gagnep. and *Cryptocarya chinensis* Hance) were selected from Jianfengling tropical montane rainforest (E 108°46′–109°45′, N 18°23′–18°50′, Hainan, China) (Li, 2002; Fang et al., 2004; Sheng et al., 2012). The seeds for each species were collected from the understory layer under five parent trees during seed dispersal stage in Jianfengling natural reserve and germinated in shallow trays filled with forest topsoil (Yang et al., 2011). The parent trees were selected in habitat without canopy opening to avoid the effect of disturbance on selected seeds. After growing in a nursery with 5% full sunlight, 1 month-old tree seedlings for each species with 20 replicates were removed to three shade-houses from June. The three shade–houses were covered with plastic shade nets of different thicknesses to achieve 0–5% (as control, i.e., the light condition in tropical forest understory without disturbance) (Capers and Chazdon, 2004), 10–15% (SG, as light condition under small canopy gaps caused by heavy defoliation or broken branches) and 40–50% of full sunlight (LG, as light condition under large canopy gaps caused by fallen tree) (Clark et al., 1996; Tobita et al., 2010; Yang et al., 2017), respectively. All the seedlings were received natural rainfall, and sprayed monthly with 100 ml solution of NPK (ammonium, phosphate, and potassium) compound fertilizer (2 g l^{-1}) and a fungicide solution (50% Carbendazim, Pesticide Technology Development Co., Ltd., Wuhan Scarlett, China) twice during the experiment in order to control fungal infections. In order to calculate the seedlings' relative growth rates for each species under Control, SG and LG treatments, the averaged initial biomass parameters (e.g., stem height, dry mass in leaves, stem and root) of each species were measured based ten additional replicates.

Measurements of photosynthetic, morphological properties, and relative growth rate

From July to October, the photosynthetic properties of five seedlings per species under three light treatments were measured from 09:00 to 11:30 a.m. under clear skies, by taking on five fully expanded leaves per plant. Light response curves were generated with a Li-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) using the "Light Curve" automatic program (Yang et al., 2008). Leaves were allowed 10 min to acclimate to light intensity changes before measurements at light levels of 2,000, 1,500, 1,000, 500, 200, 100, 50, 20, 10, and 0 μmol $m^{-2} \cdot s^{-1}$. Ambient temperature ranged from 24 to 28°C, and leaf chamber temperature was about 25°C. The leaf chamber environment was maintained at 370 mmol m^{-2} s^{-1} CO_2, 28 ± 2°C leaf temperature and 65 ± 5% relative air humidity in the measuring chamber, respectively. Light response curves (A/PAR) were fit using non-rectangular hyperbola least square curve fitting procedure (Equation 1, Eq. 1; Lambers et al., 1998):

$$Pn = \frac{AQE \times PAR + Pmax - \sqrt{(AQE \times PAR + Pmax) \times (AQE \times PAR + Pmax) - 4 \times AQE \times PAR \times k \times Pmax}}{2 \times k} \quad (1)$$

where AQE is the apparent quantum efficiency; PAR is photosynthetic available radiation; P_{max} (μmol CO_2 m^{-2} s^{-1}) is the light-saturated rate of CO_2 assimilation; R_d (μmol CO_2 m^{-2} s^{-1}) is the dark respiration rate; and *k* is the convexity or curvature factor. The light compensation point (LCP) was determined to be the light intensity on the light curve where the rate of photosynthesis exactly matches the rate of cellular respiration. The light saturation point (LSP) was calculated by the same equation, considering that LSP is the value when net photosynthetic rate (P_n) reaches 90% of P_{max} (Quero et al., 2006).

After 12 months of experimental duration in shade houses to create canopy conditions caused by disturbances, 10 seedlings per species from three treatments of light conditions (i.e., Control, SG, and LG) were harvested for relative growth rate in mass (RGR_m, Eq. 2). Before being dried at 72°C in a forced air oven for 48 h for dry mass measurement, seedlings were separated into roots, stems and leaves, and washed for morphological characteristics determination, including specific leaf area (SLA, Eq. 3), leaf mass ratio (LMR, Eq. 4), stem mass ratio (SMR, Eq. 5), root mass ratio (RMR, Eq. 6), and leaf area ratio (LAR, Eq. 7).

$$\text{Relative growth rate in mass } (RGR_m, \text{mg g}^{-1}\text{d}^{-1}) = (\ln W_2 - \ln W_1)/(T_2 - T_1) \quad (2)$$

where W_2 and W_1 are the final and initial total dry weights per plant; and T_2–T_1 is the growth time interval (i.e., 12 months, Yang et al., 2011).

$$\text{Specific leaf area (SLA, cm}^2\text{ g}^{-1}) = \text{leaf area/leaf mass} \quad (3)$$

$$\text{Leaf mass ratio (LMR, g g}^{-1}) = \text{leaf mass/total plant mass} \quad (4)$$

$$\text{Stem mass ratio (SMR, g g}^{-1}) = \text{(stem + petiole mass)/total plant mass} \quad (5)$$

$$\text{Root mass ratio (RMR, gg}^{-1}) = \text{root mass/total plant mass} \quad (6)$$

$$\text{Leaf area ratio (LAR, cm}^2\text{ g}^{-1}) = \text{total leaf area/total plant mass} \quad (7)$$

where leaf total area of each seedling was measured using a Li-3000 leaf area meter (Li-Cor Inc., Lincoln, NE, USA, An et al., 2010).

Data analysis

The mean effect size of light condition changed by SG and LG on morphological and photosynthetic properties on tree seedlings from early-, mid-, and late-successional stages were calculated as Eq. 8–12 (Hedges et al., 1999):

$$\text{Mean effect size} = \frac{\sum_{i=1}^{2} W_i \times E_i}{\sum_{i=1}^{2} w_i} \tag{8}$$

$$E = ln\left(\frac{\overline{X_{SG\ or\ LG}}}{\overline{X_{CK}}}\right) = ln\left(\overline{X_{SG\ or\ LG}}\right) - ln(\overline{X_{CK}}) \tag{9}$$

$$w_i = \frac{1}{\mathbf{V}_i},\ v = \frac{S_{SG\ or\ LG}{}^2}{n_{SG\ or\ LG}\overline{X_{SG\ or\ LG}}^2} + \frac{S_{CK}{}^2}{n_{CK}\overline{X_{CK}}^2} \tag{10}$$

where, i is the number of species of tree seedlings from early-, mid-, and late-successional stages; $\overline{X_{SG\ or\ LG}}$ and $\overline{X_{CK}}$, $n_{SG\ or\ LG}$, and n_{CK}, $S_{SG\ or\ LG}$ and S_{CK} are the mean value, number of replication and standard deviation of morphological and photosynthetic properties for tree seedlings in SG or LG, and control treatment, respectively. A significant mean effect size of light condition changed by SG and LG on morphological and photosynthetic properties was considered only when the 95% confidence interval (CI) did not overlap with zero (Zhou et al., 2014).

The importance of morphological and photosynthetic properties on seedlings' RGR_m was expressed as %IncMSE (percent increase in mean squared error) using the package "RandomForest" (version 4.6-12, Liaw and Wiener, 2002) in R (R Core Team, 2015). The relationships among predictors with RGR_m were analyzed by Pearson correlation analysis. The effect of light conditions (Control, SG, and LG) and successional stage (early-, mid-, and late-) on the variables were examined by analysis of variance (ANOVA). The path analysis was performed using the "lavaan" package (version 0.6-12, Rosseel, 2010) in R to examine the effect of light conditions and successional stages on RGR_m through morphological and photosynthetic properties.

Results

Response of seedlings' relative growth rates to increased light intensity

In the control groups with ambient light intensity, seedlings from different successional stages exhibited significant differences in the relative growth rate (RGR_m, $p < 0.0001$), with the lowest values of –8.61 (± 0.41 standard error, s.e.) mg $g^{-1}d^{-1}$ at early-successional stage and the highest value of 5.61 (± 0.80 s.e.) mg $g^{-1}d^{-1}$ at late-successional stage (**Supplementary Table 1** and **Figures 1A–D**). Relative to control, both SG and LG induced significant increment of RGR_m for seedlings ($P < 0.05$, **Supplementary Table 1** and **Figure 1E**). Improved light condition caused greater enhancement of growth for seedlings from both early- and mid-successional stage than that from the late-one, that SG and LG increased RGR_m of seedlings from both early- and mid-successional stage significantly, but not always of the seedling RGR_m of late- successional tree species (**Figures 1A–C**). Canopy gaps could affect the structure of understory community due to these distinct positive effects of increased light intensity on relative growth rates among seedlings from different successional stages (**Figure 1**).

Response of seedlings' photosynthetic and morphological properties to increased light intensity

Improved light intensity (i.e., in SG and LG) caused higher photosynthesis rates (P_n) relative to that in control, inducing 24.6–212.1, 35.0–107.8, and 17.8–50.2% increase of mass- and area-based light-saturated rate of CO_2 assimilation (A_{mass} and A_{area}) for species at early-, mid-, and late-successional stage, respectively ($P < 0.05$, **Figures 2A–F**). Leaf area (LA) and light saturation point (LSP) in both SG and LG were greater than that in control ($P < 0.05$, **Supplementary Tables 1**, **2**), while the pattern of specific leaf area (SLA) was contrary (**Figures 2G–I** and **Supplementary Table 2**). Increased light intensity induced larger positive effects on both LA and LSP for seedlings from early-successional stage than that from mid- and late-ones (**Figure 2**). Relative to SG, LG induced greater effect on seedlings' photosynthetic properties, especially for species from early-successional stage (**Figure 2** and **Supplementary Table 1**). Both dark respiration (R_d) and light compensation point (LCP) displayed positive response to LG ($P < 0.05$) but not to SG ($P > 0.05$, **Figures 2G–I**, and **Supplementary Table 2**).

Both SG and LG caused positive effect on root: shoot ratio (R/S) and root mass ratio (RMR) for seedlings from all three successional stages, while only LG significantly decreased seedlings' leaf area ratio (LAR) due to the dependence on both light condition and successional stages ($P < 0.05$, **Figures 2D–F** and **Supplementary Tables 1**, **3**). Species at early-successional stage displayed the greatest decrease of leaf mass ratio (LMR) and increase of RMR in comparison with that at mid- and late-successional stage, especially for those at late- stage, seedlings displayed no significant decrease of LMR under both SG and LG ($P < 0.05$, **Figure 2F** and **Supplementary Figure 1**). Seedlings from early-stage displayed greater positive responses of both photosynthetic and morphological properties to enhanced light intensity, suggesting a larger advantage in growth in early-stage tree species over mid- and late-successional tree species (**Figures 2**, **3**).

Regulation of successional stage on RGR_m's response to increased light condition

Among the predictor variables, we confirmed that light condition was the most important factor for seedlings' RGR_m, followed by SLA, LA, LAR, successional stage, and LSP (**Figure 1F**). Light condition increased LA, RMR, R/S, R_d, LCP, LSP and A_{area}, but decreased SLA (**Figures 2**, **3**, **5**), and displayed significant interactions with successional stage on SLA, R_d, LCP and A_{area} (P = 0.021, 0.014, 0.012 and 0.048, **Supplementary Table 1**). RGR_m displayed positive correlations with A_{area}, LA, LSP and R/S (R^2 = 0.51, 0.39, 0.46, and 0.24, respectively, $P < 0.05$, **Figures 4A–C, F**), while exhibited negative relationship with SLA and LAR (R^2 = 0.52 and 0.45, $P < 0.01$, **Figures 4D, E**). The positive effects of improved light condition on RGR_m included direct and indirect pathways (through SLA and A_{area}, **Figure 5**). The regulation of species' successional stage on RGR_m was through the path of SLA. Light condition, A_{area} and SLA all had direct path to affect RGR_m, and jointly explained 93% of seedlings' RGR_m in total (P = 0.319, **Figure 5**). As one of crucial traits of plants, SLA represented the important regulation of successional

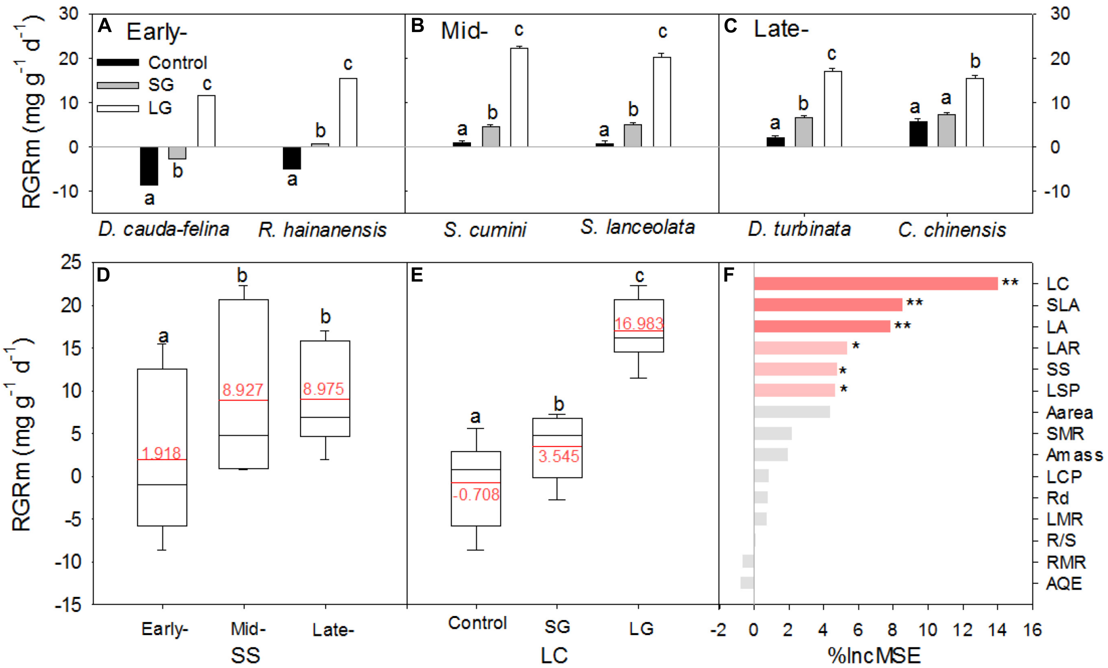

FIGURE 1
Relative mass growth rate [RGR_m, **(A–D)**] for tree seedlings at early– **(A,D)**, mid- **(B,D)** and late-successional stage **(C,D)**, and in light conditions of Control, SG and LG **(E)**, and the importance of predictor variables for RGR_m in random forest modelling **(F)**. Control, 0–5% of full sunlight; SG: small canopy gaps, 10–15% of full sunlight; LG: large canopy gaps, 40–50% of full sunlight. The red lines and figures in plots **(D,E)** are the mean value of RGR_m in each group. LC, SLA, LA, LAR, SS, LSP, LCP, A_{area}, A_{mass}, SMR, R_d, LMR, R/S, RMR, and AQE in panel **(F)** were abbreviations of light condition, specific leaf area, leaf area, leaf area ratio, successional stage, light saturation and compensation point, area- and mass- based light saturated rate of CO_2 assimilation, stem mass ratio, dark respiration, leaf mass ratio, root: shoot ratio, root mass ratio, and apparent quantum efficiency, respectively. In random forest modeling, "1," "2," and "3" were assigned to treatments of Control, SG and LG; and species at early-, mid-, and late-successional stage, respectively. %IncMSE is the per cent increase in mean squared error. Error bars and the different letters in plots **(A–E)** are standard error (n = 25) and significant difference at $P < 0.05$, respectively. Symbols ** and * in plot **(F)** indicates statistical significance at $P < 0.01$ and 0.05, respectively.

stages on seedlings' RGR_m in responding to enhanced light intensity after disturbance-induced canopy gaps (**Figures 1F**, **5**).

Discussion

Changes in the canopy structure and resource availability due to various anthropogenic activities continue to alter forest regeneration and ecosystem functioning. Here, we tested whether the increased light availability (and intensity) due to various size of canopy gaps created from anthropogenic activities differentially affect the growth rates of tree seedlings from different successional stages, which are crucial for predicting future forest recovery and successional trajectory. The results agreed with our hypothesis that the light condition under small canopy gaps (SG, 10–15% of full sunlight) and large canopy gaps (LG, 40–50% of full sunlight) induced greater increment of relative growth rates for seedlings from early- and mid-successional stages relative to that in late- successional stage.

Effect of light condition under canopy gap on growth of seedlings at different successional stages

Canopy opening readily alleviate the light limitation for understory plants in a forest (Lin et al., 2003; Lee et al., 2017). In our study, seedlings grown with light intensity to mimic small (SG) and large canopy gap (LG) displayed significantly higher RGR_m than that with ambient light intensity (Control, $P < 0.05$, **Figure 1** and **Supplementary Table 1**). Moreover, we found that the development of leaf area (LA, **Figures 2**, **4**) was one of the most important mechanisms to improve photosynthetic assimilation for plant individuals at enhanced light availability (Evans and Poorter, 2001; Tang et al., 2021). The formation of canopy gaps was verified to be beneficial for the understory regeneration in Jianfengling tropical montane rainforest (Feldmann et al., 2020), without considering the impacts on the direction of forest succession.

Exposed to increased light intensity, seedlings at early successional stage with a negative RGR_m in ambient light condition, exhibited the greatest improvement in their RGR_m (**Figure 1**), altering the survival rate, competition and dynamics of seedling community in the tropical forest understory subsequently (Valladares et al., 2000). In contrast, relative to seedlings from early- and mid- successional stage, those from the late-successional stage displayed a lower increment in RGR_m at increased light intensity (**Figure 1**), potentially confirming to the narrow niche breadth of species from the late-successional stage (Parrish and Bazzaz, 1982; Carscadden et al., 2020). Therefore, the canopy gaps due to defoliation (with the equivalent light intensity in SG) and tree fall (with the equivalent light intensity in LG) would trigger the changes of understory productivity, biodiversity and successional trajectory in disturbed patches, altering the structural heterogeneity in tropical forest (Takafumi et al., 2010; Lee et al., 2017).

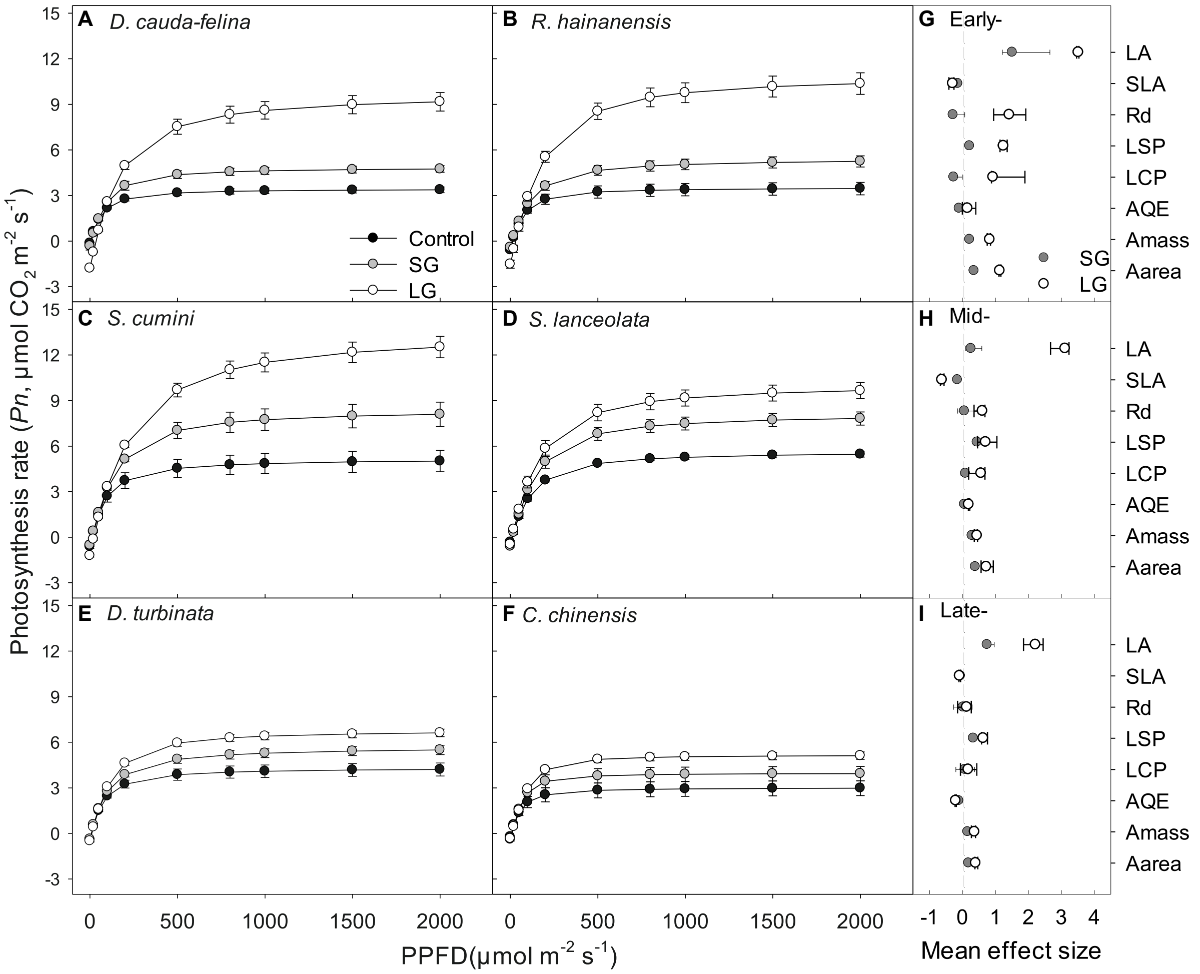

FIGURE 2
Photosynthetic light response curves **(A–F)** for seedlings grown in light conditions under Control, SG and LG, and the mean effect size **(G–I)** of SG and LG on leaf area (LA), specific leaf area (SLA), dark respiration (R_d), light saturation point (LSP), light compensation point (LCP), apparent quantum efficiency (AQE), mass-, and area- based light saturated rate of CO_2 assimilation (A_{mass} and A_{area}) for seedlings at early- **(G)**, mid- **(H)** and late-successional stage **(I)**. Control: 0–5% of full sunlight; SG: small canopy gaps, 10–15% of full sunlight; LG: large canopy gaps, 40–50% of full sunlight. Light curves were fitted by non-linear regression using non-rectangular hyperbola least square curve fitting procedure (Lambers et al., 1998). Data points in plots **(A–F)** and **(G–I)** represent mean ± s.e. [standard error, n = 25 (5 plants × 5 leaves)] and mean ± CI (the 95% confidence interval), respectively. If the CI in plots **(G–I)** did not overlap with zero (the gray dotted line), a significant mean effect of SG and/or LG was considered (P < 0.05).

Effect of light condition under canopy gap on photosynthetic properties of seedling at different successional stages

The different response of RGR_m among seedlings from three successional stages could be firstly reflected by corresponding changes in leaf-scale photosynthetic properties (**Figures 1**, **2**, **4**), which is the foundation for regulating plant carbon assimilation to take the advantage from enhanced light due to temporary canopy gaps (Kneeshaw and Bergeron, 1998; Yao et al., 2015). Especially for the greatest improvement of RGR_m for seedlings at early successional stage could be ascribed to their changes in photosynthetic properties, e.g., a significant enhancement of light saturated point (LSP, **Figures 2**, **4**). We suspect that greater LSP may have benefited the seedlings to achieve a higher saturated photosynthetic rate, such as the light–demanding species from the early stage of succession (Ackerly, 1996; Qi et al., 2004). Especially for light condition in LG, seedlings from early-successional stage displayed the largest improvement in both mass- and area-based light-saturated rate of CO_2 assimilation (A_{mass} and A_{area}, **Figure 2**), thus the more light penetrated into forest understory the more advantage would be found for seedlings from early-successional stage (Baul et al., 2022). Beside changes in LSP, light compensation point (LCP) and dark respiration (R_d) in seedlings from early successional stages may also have enhanced due to increased growth respiration driven by accelerated development of leaf and total biomass (**Figures 1**, **2**; Marcelis et al., 1998; Inoue et al., 2022). Furthermore, seedlings from early- and mid-successional stages declined their specific leaf area (SLA, **Figure 2**) as a response to improved light conditions, especially in LG treatment, while that from the late- with an original successional stage lower SLA had no significant changes in SLA (**Figure 2** and **Supplementary Table 3**), displaying the evolutionary conservatism in this functional trait among these plant species (Schweizer et al., 2013; Letcher et al., 2015). The intensity and range of disturbance would be crucial for species composition and successional process in understory patches in tropical forest, the larger canopy gap might brought

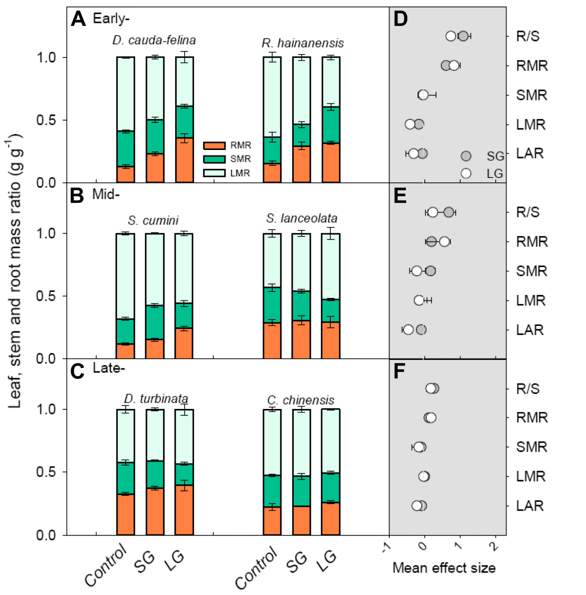

FIGURE 3
Leaf, stem and root mass ratio [LMR, SMR, and RMR, **(A–C)**] of seedlings in Control, SG, and LG, and the mean effect size **(D–F)** of SG and LG on root: shoot ratio (R/S), root, stem, and leaf mass ratio (RMR, SMR, and LMR), and leaf area ratio (LAR) for tree seedlings at early- **(D)**, mid- **(E)**, late-successional stage **(F)**. Control, 0–5% of full sunlight; SG: small canopy gaps, 10–15% of full sunlight; LG: large canopy gaps, 40–50% of full sunlight. The bars in plots **(A–C)** and **(D–F)** represent standard error (n = 5 plants) and 95% confidence interval (CI), respectively. If the CI in plots **(D–F)** did not overlap with zero (the gray dotted line), a significant mean effect of SG and/or LG was considered (P < 0.05).

more advantage for seedlings from early- and mid-successional stages (Yamashita et al., 2000; Liu B. et al., 2012).

Different from other photosynthetic properties with positive or negative responses, the apparent quantum yields (AQE) didn't change even for the seedlings from the early-successional stage (**Figure 2** and **Supplementary Table 1**), which agreed with the correlated results in comparing AQE between shade-tolerant species (i.e., from the late-successional stage) and pioneer species (i.e., from the early-successional stage) previous studies (e.g., Ramos and Grace, 1990; Marenco et al., 2001; Tsvuura et al., 2010).

Effect of light condition under canopy gap on morphological properties in seedlings at different successional stages

Apart from the regulation in leaf-scale photosynthesis properties, seedlings would also alter allocation strategy of photosynthates to the organs acquiring the resource that strongly limits seedling growth (McCarthy and Enquist, 2007; Zhou et al., 2020). In this study, the sensitivity of root mass ratio was greater than that of leaf and stem mass ratio under improved light intensity (**Figure 3**; Poorter and Nagel, 2000). The adequate root development was considered to be crucial for improving seedlings' survival in forest understory, since more belowground sources, e.g., nutrients and water, could support seedlings with an accelerated growth and a greater competitiveness in understory community (Landhausser and Lieffers, 2001; Myers and Kitajima, 2007). Correspondingly, the vertical biomass allocations between below- and above- ground biomass, reflected in root: shoot ratio (R/S) in these seedlings were altered by improved light availability (**Figure 3**; Poorter and Nagel, 2000). However, the significant positive response of R/S to both SG and LG exhibiting an increasing trend from late- to early-successional stage (**Figure 3**), that the seedlings from early- and mid- successional stages displayed a greater morphological plasticity than that from late- stage (Yan et al., 2006). The greater increment of R/S for seedlings from early- and mid- successional stages would be more beneficial for root nutrient absorption, particularly for phosphorus capture, in tropical montane forests, such as our study site (Liu et al., 2010, Liu F. et al., 2012). Thus, seedlings from early- and mid- could successional stages take advantage of the transitory opportunity of improved light condition caused by anthropogenic disturbances, regulating seedlings' niche-partitioning and successional process in the understory of tropical forest (Dupuy and Chazdon, 2006; Yang et al., 2011).

In contrast to the positive correlation between R/S and RGR_m, leaf area ratio (LAR) exhibited a negative relationship with RGR_m (**Figure 4**). Under higher light intensity, per unit leaf area or shoot mass could provide greater productivity for plant individual than ambient light condition in understory (Kong et al., 2016), that seedlings with lower LAR and higher R/S potentially had a sufficient functions of above-ground organs, e.g., adequate photosynthetic capacity under increased light intensity (Shafiq et al., 2021). Therefore, canopy gap-induced greater light intensity could drive the trade-off between above- and below-ground biomass allocation, regulating morphological properties of seedlings for better resource acquisition and growing (Freschet et al., 2013; Baez and Homeier, 2018).

The dependence of seedlings' RGR_m on successional stage in responding to increased light condition under canopy gap

Our results show that the seedlings in the understory from different successional stages are characterized by diverse strategies in responding to improved light condition caused by canopy gap after disturbance (**Figures 1–3**). In ambient light condition of understory, seedlings from the late-successional stage had a higher RGR_m, ensuring a greater competitiveness relative to seedlings from early- and mid-successional stages in the understory tree community (**Figure 2**; Gao et al., 2016). However, greater light availability due to canopy gaps provided a potential opportunity for the seedlings from early- or mid- successional stages to offset the competitive advantage of late-successional plants (Abbas et al., 2020).

Seedlings' RGR_m in the understory of tropical forest performed a dependence on the light condition, while the successional stage of species displayed a significant regulation on changes of RGR_m through effects on A_{mass}, LAR and SLA (**Figure 5**). Thereinto, SLA was a critical traits connected the effects of light condition and successional stage on seedlings' growth, and playing the most important role for RGR_m after light condition (**Figures 1F**, **5**; Baez and Homeier, 2018). For different seedlings, interspecific functional trait differentiation had been indicated to mainly associate with SLA, that at early-successional stage are generally characterized by a higher SLA relative to that at mid- and late- stages (**Supplementary Table 3**; Wang et al., 2012). Light condition and successional stage

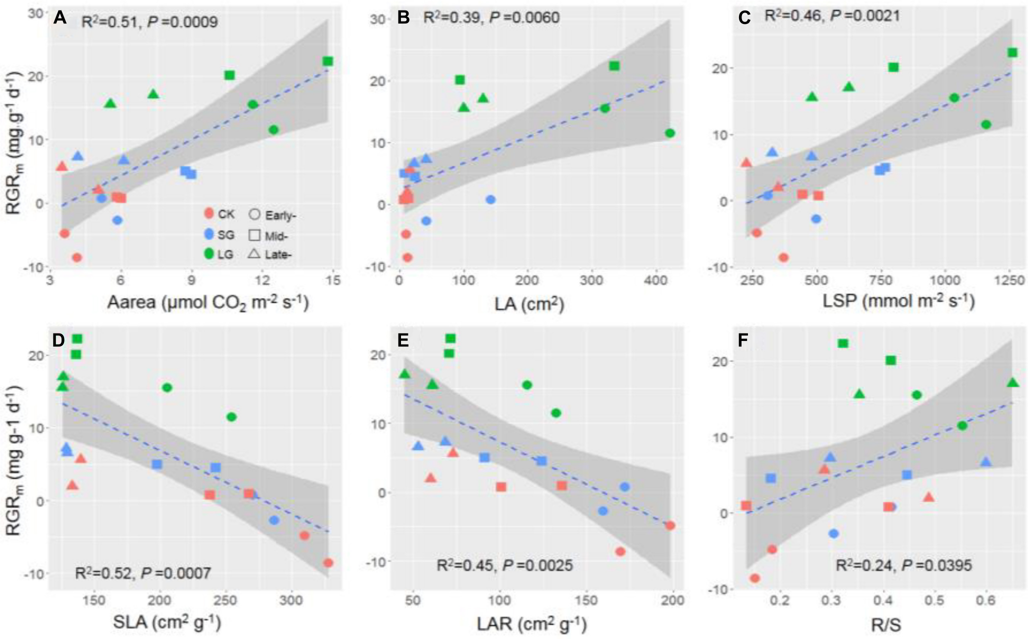

FIGURE 4
The relationship between relative mass growth rate (RGR_m) with area- based light saturated rate of CO_2 assimilation [A_{area}, **(A)**], leaf area [LA, **(B)**], light saturation point [LSP, **(C)**], specific leaf area [SLA, **(D)**], leaf area ratio [LAR, **(E)**], and root: shoot ratio [R/S, **(F)**]. The gray shadow represents the 95% confidence interval for the estimates.

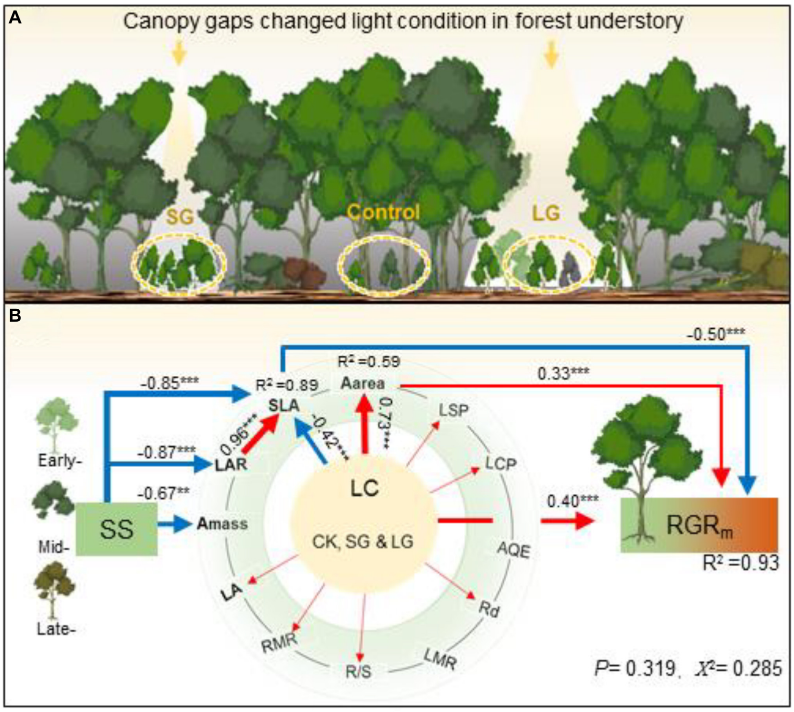

FIGURE 5
Illustration of disturbance-caused canopy gaps' impact on light condition (LC, i.e., Control, SG, and LG) in forest understory **(A)**, and their effects on seedlings' relative mass growth rate [RGR_m, **(B)**] for tree species at different successional stage (SS, i.e., early-, mid-, and late- successional stage) based on the path analysis. Control, 0–5% of full sunlight; SG: small canopy gaps, 10–15% of full sunlight; LG: large canopy gaps, 40–50% of full sunlight. In path analysis, "1," "2", and "3" were assigned to treatments of Control, SG and LG; and species at early-, mid-, and late-successional stage, respectively. The red and blue arrows indicate significantly positive and negative effects of light condition (LC), successional stage (SS), leaf area (LA), specific leaf area (SLA), dark respiration (R_d), light saturation point (LSP), light compensation point (LCP), apparent quantum efficiency (AQE), mass-, and area- based light saturated rate of CO_2 assimilation (A_{mass} and A_{area}), leaf mass ratio (LMR), root mass ratio (RMR) and root: shoot ratio (R/S) on RGR_m ($P < 0.05$), respectively. Symbols **, *** indicate statistical significance at $P < 0.01$ and 0.001. In Chi-square test for the path model, the P-value (0.319, >0.05) calculated from one-tailed test indicated that model fit had been established.

displayed a significant interaction on seedlings' SLA, jointly affected seedlings' RGR_m in the understory of tropical forest (**Supplementary Table 1** and **Figure 5**; Kitao et al., 2000). Under the more frequency and intensity disturbances, the advantage of seedlings from late-successional stage would be weaken much more than that from early- and mid-successional stages, slowing down the process of forest forward succession.

Conclusion

Natural and anthropogenic disturbance induced canopy gaps affecting the forest structure and function. Increased light intensity under canopy gaps were verified to accelerate the relative growth rate (RGR_m) of seedlings, improving the understory productivity in Jianfengling tropical rainforest. Relative to the seedlings from late- successional stages, early- and mid-successional stage seedlings displayed stronger positive response of RGR_m due to the higher improvement of leaf area, light saturation point, mass- or area-based light saturated rates of CO_2 assimilation, root mass ratio and root: shoot ratio, as well as the decrement of specific leaf area and leaf area ratio. Light condition and SLA were the most important factors for seedlings' relative growth rate across successional stages. The formation of canopy gaps would open up opportunities for the seedlings of tree species from the early- and mid-successional stages, being beneficial for species diversity and habitat heterogeneity, while go against the forward successional process due to the depressed advantage of species from late-successional stage in tropical forest. Especially, in the context of global climate change, facing higher frequency and intensity of natural disturbance (i.e., typhoon and forest fire), whether the succession of tropical forest would be redirected by too many big scale canopy gaps should depend on both disturbance *per se* and forest stability.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding authors.

Author contributions

LZ completed the experiment and analyzed the data with substantial contributions from MT, WY, and SA. LZ, WY, and SA conceived, designed, and oversaw the study. LZ wrote the manuscript with substantial contribution from MT. ZJ and YH did the statistical analysis with suggestions from LZ. MT, SA, and XZ commented on the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.1088291/full#supplementary-material

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