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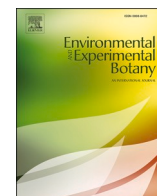**22** PUBLICATIONS   **454** CITATIONS

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Seedlings of shade-tolerant tree species are more vulnerable to chilling rain under a forest gap

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A R T I C L E   I N F O

A B S T R A C T

The manner in which tree species differ in their responses to chilling rain in warm and species-rich (sub-)tropical forests is not well understood. Understanding this variation between species is essential for linking the responses of individual plants to chilling rain with ecological consequences at the forest community and ecosystem levels. We hypothesized that chilling rain can induce detrimental effects on leaf photochemical processes, and the negative impacts are more evident for shade-tolerant species than light-demanding species. This trade-off between species' tolerance to shade and chilling rain may depend on the light environment to which plants are exposed. To test these hypotheses, we conducted two sequential experiments with five subtropical tree species, measuring their leaf photochemical processes during the phases of a chilling rain event and assessing their resistance and recovery. We determined species shade tolerance by integrating their functional traits associated with resource acquisition in a shade environment. Our results showed that F_v/F_m, a measure of maximum quantum yield of photosystem II, was co-determined by the plant's exposure to light and chilling rain. Seedlings exposed to a gap before the chilling rain generally had lower F_v/F_m than those exposed to shade before the rain treatment. Chilling rain, relative to ambient rain, significantly reduced F_v/F_m during the cold and sunny phase. However, the effects of chilling rain were only evident for shade-tolerant species with gap-exposure history. The reduction in F_v/F_m induced by chilling rain led to higher resistance of F_v/F_m to chilling rain for light-demanding species than shade-tolerant species, leading to a trade-off between species' tolerances to shade and chilling rain for plants with gap-exposure history, thus supporting the hypotheses. This trade-off was primarily due to variation in functional traits related to light-use strategy, such as specific leaf area, leaf area ratio, leaf thickness, relative volume growth rate, and root-shoot ratio. As light availability and species' tolerance to shade are critical abiotic and biotic factors determining forest community succession, respectively, these findings may improve the scalability of the physiological responses of individual plants to chilling rain to the dynamics of forest communities. Our results suggest that frequent chilling rain events and canopy disturbances may favor light-demanding species and alter the species composition of subtropical forests.

1. Introduction

Extreme cold waves are becoming more frequent in warm regions (IPCC, 2019; National Climate Center, 2008), which can cause severe damage to plant species in (sub-)tropical forests that are adapted to warm climate (Allen and Ort, 2001; Cunningham and Read, 2006). Extremely low temperatures and long rainy days induced by cold waves often inhibit and harm the photosystems of the leaves, thereby increasing the mortality risks of trees (Liu et al., 2020; Shao et al., 2011;

Song et al., 2018; Zhou et al., 2017). These negative impacts can restructure species composition and affect the community succession of forests if tree species vary in their responses to chilling events (Ge et al., 2015; Lusk et al., 2018; Ross et al., 2009; Song et al., 2018). However, a large knowledge gap remains on how species differ in their responses to chilling events in (sub-)tropical forests.

Extreme low temperatures usually cause severe physiological stress to leaves, which can be captured by the disruptions of photochemical processes in photosystems (Allen and Ort, 2001; Wise, 1995). The

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chloroplast, one organelle responsible for photosynthesis, is usually more susceptible to low temperatures than other organelles such as the mitochondria and nuclei in plant leaves (Kratsch and Wise, 2001). Within the chloroplast electron transport chain, photosystem II (PSII) is often more vulnerable to low temperatures than photosystem I (Huang et al., 2010). Low temperatures can disrupt many vital photochemical processes, such as photophosphorylation of the thylakoid membrane and thylakoid electron transport (Allen and Ort, 2001). These disruptions of photochemical processes can lead to photoinhibition or photodamage, as stressed leaves cannot effectively dissipate excess absorbed light energy, resulting in the accumulation of more reactive oxygen species (Wise, 1995). Photoinhibition and photoprotective processes induced by stress significantly limit plant photosynthetic efficiency and productivity (De Souza et al., 2022).

The responses to chilling rain may vary between light-demanding species and shade-tolerant species. Shade tolerance represents the degree of tolerance of a given plant to low light availability (Valladares and Niinemets, 2008). It is a fundamental and integrated trait determining tree species demographics and forest community succession (Chen et al., 2016; Comita et al., 2010; Reich, 2014). Shade tolerance can be explained by two, not mutually exclusive, hypotheses: the maximization of carbon gain (Givnish, 1988) and the use of assimilated carbon for defense and storage (Kitajima, 1994). Due to the fundamental role of photosynthesis in plants and economic constrains in resource allocation, shade tolerance often mediates plant resistance to other environmental stresses (Grubb, 2016; Puglielli et al., 2021; Valladares and Niinemets, 2008). For example, species that are tolerant to shade may be more vulnerable to low temperatures (Ge et al., 2015; Richardson et al., 2013; Ross et al., 2009), because shade-tolerant species may be more likely to be dehydrated (Valladares and Niinemets, 2008) when experiencing low temperature-induced photoinhibition (Allen and Ort, 2001).

Chilling rain events can substantially alter light availability in the forest understory, which can affect the responses of understory plants to chilling rain. Low temperatures often cause defoliation (Chen et al., 2017). Extreme chilling rain can even induce the mortality of canopy trees if large amounts of rain freeze on tree branches at one moment (Liu et al., 2020; Song et al., 2018). Canopy defoliation and tree mortality induced by chilling rain can increase light availability for understory plants originally occurring in a shade environment, thus exposing these understory plants to sudden, strong light when the rain stops. Sudden exposure to strong light after long, cold rainy days can severely stress the photosystems of the leaves (Allen and Ort, 2001). This photochemical stress induced by sudden strong light may vary between light-demanding species and shade-tolerant species, because light-demanding species are usually more adapted to a gap environment (Ge et al., 2015; Richardson et al., 2013), and shade-tolerant species usually have lower light saturation points and may accumulate more reactive oxygen species when receiving photon irradiance above saturation (Givnish, 2002).

The light-exposure histories of understory plants may further complicate plant responses to chilling rain (Feng and Cao, 2005; Roeber et al., 2021). Defoliation and mortality of canopy trees induced by either human or non-human disturbances can create canopy gaps and heterogeneous understory light availabilities (Liu et al., 2020; Martínez-Ramos et al., 2016; Song et al., 2018). Understory light availability is a fundamental determinant of the growth and survival of tree seedlings. Performance at the seedling stage will strongly influence the subsequent community composition and dynamics (Comita et al., 2010; Harms et al., 2000; Jia et al., 2020; Valladares and Niinemets, 2008). The heterogeneous landscape of understory light exposes understory seedlings to different light histories before chilling rain events, which may subsequently affect plant responses to chilling events. For example, shade-exposure history may prepare plants for responding to chilling rain by inducing cold acclimation via reducing reactive oxygen species in the leaves (Roeber et al., 2021). Light-exposure histories may also

modify plant functional traits that are associated with plant light-use strategies, which may further influence plant responses to low temperature. For example, leaf thickness may increase with irradiance (Niinemets and Kull, 1998), which can promote the tolerances of plants to low temperature and photodamage (Niinemets, 2016). How light-demanding species and shade-tolerant species with different light-exposure histories differ in their responses to chilling rain remains unknown, but this can have important implications for the co-impacts of canopy disturbance history and chilling rain on forest community dynamics.

In this study, we aimed to investigate (1) how species with different shade tolerances vary in their responses to chilling rain, and (2) how light-exposure histories (gap versus shade histories), associated with canopy disturbance, affect species responses to chilling rain. We assessed the responses to chilling rain by measuring the changes in the photochemical quantum yield of seedling leaves through chlorophyll fluorescence (Close and Beadle, 2003; Cunningham and Read, 2006; Feng and Cao, 2005; Huang et al., 2011). We exposed seedlings of five common subtropical tree species to two light levels (gap vs. shade). We then assigned seedlings of both light-exposure histories to ambient-rain versus chilling-rain treatments. We simulated the entire phase of a chilling-rain event to assess the dynamic responses of plants: (1) during the chilling rain phase characterized by both low temperature and low light availability; (2) when the rain stopped and light availability suddenly increased, but the temperature remained low; and (3) when both the temperature and light availability recovered to ambient levels. We hypothesized that (i) chilling rain has a detrimental effect on leaf photochemical processes, as low temperatures can harm the photosystems responsible for these processes; (ii) the negative effects of chilling rain are particularly evident during the phase of sudden exposure to strong light, which can cause severe stress to the photosystems after prolonged cold and rainy periods; (iii) shade-tolerant plant species are more susceptible to the negative effects of chilling rain than light-demanding species. This is because light-demanding species are typically more adapted to environments with high irradiance; and (iv) the differential impacts of chilling rain on shade-tolerant and light-demanding species are more evident for plants exposed to high irradiance before chilling rain. This is due to the cold acclimation of plants that have been exposed to shaded environments prior to the chilling rain.

2. Materials and methods

2.1. Study site

This study was conducted at the Heishiding Nature Reserve (111°53′ E, 23°27′ N, 150–930 m elevation), which is situated in Guangdong Province, southern China. The typical vegetation type is subtropical broad-leaved forest, dominated by plant species belonging to Fagaceae and Lauraceae. The climate of the study area is a subtropical moist monsoon climate with an annual mean temperature of ~19.6 °C and an annual mean precipitation of ~1744 mm. The monthly mean temperature ranges from 10.6 °C in January to 28.4 °C in July. However, abnormal chilling rain events (average temperature < 10 °C) occur occasionally in later winter or early spring and may last for weeks (Ding et al., 2008), which can cause severe damage and mortality to canopy trees and change light availabilities at the understory (Liu et al., 2020; Song et al., 2018).

2.2. Experimental design

We conducted two sequential experiments (Fig. 1) to assess how light-exposure histories (the first experiment) affect the photochemical responses of seedlings to a subsequent chilling rain event (the second experiment). We chose five subtropical tree species for the experiments: *Canarium album* (CAAL), *Cryptocarya concinna* (CRCO), *Castanopsis fissa*
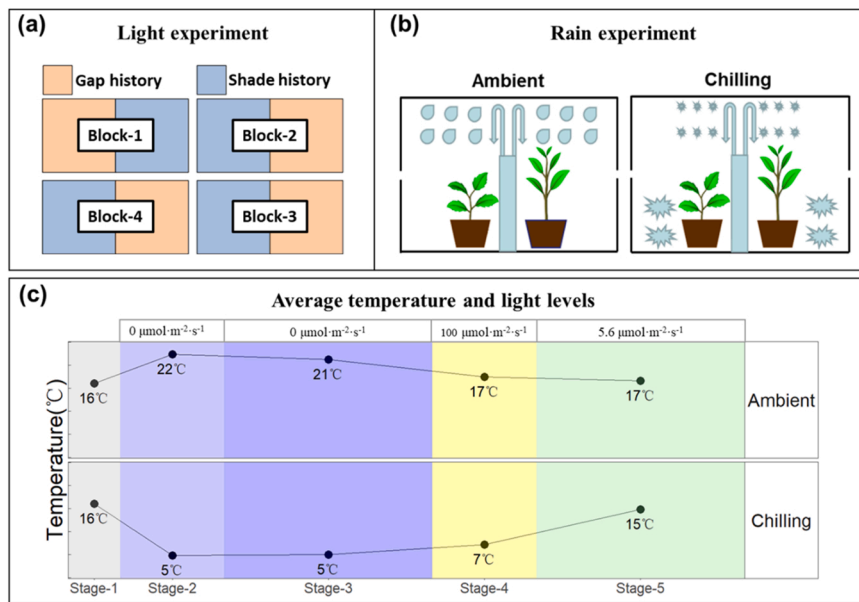
Fig. 1. Experimental design. (a) In the first experiment, we simulated two levels of light treatment (gap vs. shade), which were assembled into four blocks and lasted for 8 months. Seedlings of five species were randomly assigned to the two light treatments. (b) In the second experiment, one seedling per species per light level per block from the first experiment was randomly assigned to either ambient-rain or chilling-rain treatment. In each chamber, plants of different sizes represent different light-exposure histories before the rain treatment. (c) We simulated the entire phase of the chilling rain event: a 32-h chilling-rain phase (stages 2 and 3, in purple), an 8-h cold and sunny phase (stage 4, in yellow), and a 24-h recovery phase (stage 5, in green). We measured leaf chlorophyll fluorescence 5 times for each rain treatment, corresponding to the 5 stages of the second experiment. At stage 1, both treatments were under ambient temperature and without rain. After the first stage, we simulated the ambient rain vs. chilling rain for about 32 h. We measured chlorophyll fluorescence at the 12th hour (stage 2) and 32nd hour (stage 3) after the beginning of the rain treatments. This was followed by a sunny stage of 8 h (stage 4) with a simulated light level at the forest understory of a large forest gap and without rain. At stage 4, we maintained the original temperature treatments. In the final stage of about 24 h (stage 5), we allowed the temperature in the chilling-rain treatment to recover to ambient temperature under an ambient light environment on cloudy days. Black points show the mean temperature at each stage. Standard errors of mean temperature were not presented due to their small values. The width of each stage was proportional to its time span.

(CAFI), *Cyclobalanopsis hui* (CYHU), and *Cyclobalanopsis fleuryi* (CYFL) (Table S1). The species are common in the study site and were chosen based on the availability of seeds and seedlings after seed germination, as well as their differences in shade tolerance. All seeds were collected from the study site during the autumn and winter of 2017. The seeds were surface-sterilized (3 min distilled water, 1 min 70% ethanol, 3 min 2.625% NaOCl, 1 min 70% ethanol, 3 min distilled water) and kept in a refrigerator at 4 °C until late March 2018. We germinated the seeds in a shade house with 15% daylight. The seeds were placed in plastic boxes filled with moist and sterilized river sand.

2.2.1. Light experiment

In August of 2018, we began the light experiment with two levels of treatments: gap vs. shade. We manipulated the light levels by setting sunshade nets in the shade house and simulating the understory large-gap (35% transmittance at midday) or deep-shade (1% transmittance at midday) environment of the subtropical forest at the study site. We determined the light transmittance (%) as the ratio of light intensities within the corresponding nets of the shade house versus those above the shade house. The light intensities were measured on the same sunny day by using two calibrating LI-190 quantum sensors (LI-COR, Lincoln, NE, USA) attached to hand-held light meters (LI-250A, LI-COR). We transplanted the seedlings of the five species with similar sizes to pots (15 cm in diameter and 13 cm in height; one seedling per pot). The pots contained well-mixed soil from the edge of the forest from where the seeds were collected. Before the light treatments, we placed the pots in the shade house with 15% daylight for one week to ensure the success of transplantation. We used 24 or 48 pots per species based on the availability of seedlings. We randomly assigned the pots of each species to two light treatments and four blocks with equal numbers of pots (Fig. 1a) (N = 4 blocks × 2 light treatments × 5 species × 6 or 3 pots = 192 seedlings). The seedlings were watered every day with auto-watering systems. The air temperature and humidity were 21.81 ± 0.11 °C (mean ± standard error) and 91.62 ± 0.19%, respectively, in the gap treatment, and 21.52 ± 0.09 °C and 91.29 ± 0.17%, respectively, in the shade treatment during the experiment. We measured the basic diameter (3 cm from the ground) and height of the highest leaf buds of each seedling every two months. We randomized the positions of

the pots frequently. This light experiment lasted for eight months from August 2018 to March 2019.

2.2.2. Rain experiment

In the early spring of 2019, after the light experiment, we began the rain experiment with two levels (ambient rain vs. chilling rain). The chilling rain treatment simulated an extreme event of chilling rain, while the ambient rain treatment simulated rainy weather with ambient temperature. Southern China often has cloudy and rainy days during early spring. However, extreme cold waves can sharply reduce the temperature and extend the rainy days. This experiment simulated such an extreme chilling rain event that is predicted to occur more frequently in southern China due to climate change (Ding et al., 2008; Duan et al., 2012). We randomly assigned one individual per species per light-exposure history per block to each rain treatment, which resulted in a total of 80 pots (N = 4 blocks × 2 light histories × 5 species × 2 rain treatments). However, two species (CAAL and CYHU) did not have enough seedlings due to rare mortality events during the light-history experiment, which resulted in a final number of 76 pots (Table S1). For each rain treatment of each block, we randomly assigned the pots into two bubble chambers (Fig. 1b). We simulated the rain using a humidifier in each chamber. For the chilling-rain treatment, we provided ice-water mixtures for the humidifiers and added ice packs within the chambers; for the ambient-rain treatment, we provided ambient-temperature water for the humidifiers (Fig. 1b). The chilling rain experiment included three phases (Fig. 1c). (1) A 32-h chilling-rain phase. In this first phase, seedlings were under cloudy, ambient, or chilling rain, with low photosynthetic photon flux density (PPFD, ~0 $\mu mol \cdot m^{-2} \cdot s^{-1}$). (2) An 8-h cold and sunny phase, where we simulated a cold and sunny day following the rainy days. Therefore, we stopped the rain simulation, suddenly increased the light availability, but maintained the original temperature treatments. We set the light availability to about 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (continuous instantaneous PPFD for 8 h), which represents the light level in the forest understory of large forest gaps on a sunny day in (sub-)tropical forests (Chazdon, 1986). This cold and sunny phase simulated the scenario whereby the chilling rain caused defoliation and suddenly increased the light availability for the original shade environment but had negligible impacts on the original

gap environment. We simulated the light with a full-spectrum imitation sunlight lamp (50 W) in a shade house. (3) A final 24-h recovery phase. Temperature in the chilling-rain treatment naturally recovered to ambient temperature under the ambient light level of a cloudy day ($\sim$5.6 μmol·m^{-2}·s^{-1} at midday) (Fig. 1c). To assess the dynamic responses of plants to the chilling rain event, we measured leaf chlorophyll fluorescence five times for each rain treatment (Fig. 1c): once before the chilling-rain treatment (stage 1), twice during the chilling-rain phase (stages 2 and 3), once during the cold and sunny phase (stage 4), and once during the recovery phase (stage 5). We randomized the positions of the pots every 4 h during daytime. We recorded the temperature and air humidity in each chamber every 30 min with a temperature and humidity sensor (Anymetre-TH20E, China). We conducted all the measurements in a blockwise manner.

2.2.3. Chlorophyll fluorescence

To evaluate the photochemical responses of plants to the chilling rain event, we measured the leaf chlorophyll fluorescence parameters of dark-adapted seedlings across the five stages (Fig. 1c) using a portable fluorometer (PAM-2500, Heinz Walz GmbH, Effeltrich, Germany). The dark adaptation periods were 0.5 h at least. We tagged one healthy and mature leaf for each seedling so that we could measure the same leaves across the stages. The tagged leaves were exposed to a low measuring light to obtain the minimal fluorescence (F_0). The maximum fluorescence (F_m) in the dark-adapted state was measured after a saturation pulse ($\sim$10000 μmol·m^{-2}·s^{-1}, 0.8 s). After that, actinic irradiance was switched on until the fluorescence yield became stable to obtain steady-state fluorescence yield (F_s). The light-adapted state maximum fluorescence yield (F_m') was determined by applying repetitive saturation pulses. The following chlorophyll fluorescence parameters were calculated: $F_v/F_m = (F_m-F_0)/F_m$; $Y(II) = (F_m'-F_s)/F_m'$ (Baker, 2008; Murchie and Lawson, 2013). The ratio F_v/F_m is the maximum quantum yield of PSII after dark adaptation when all the PSII reaction centers are open. This index is often used as an indicator of plant stress such as photoinhibition and chilling injury (Feng and Cao, 2005; Huang et al., 2010; Mai et al., 2010). $Y(II)$ is the effective quantum yield of PSII photochemistry after light adaption.

2.2.4. Functional traits

We measured six traits that are closely related to plant light-use strategies, namely leaf thickness (Thickness), specific leaf area (SLA), leaf area ratio (LAR), root-shoot ratio (RSR), leaf mass fraction (LMF), and relative growth rate (RGR) (Valladares and Niinemets, 2008) (Table S2). We harvested all the seedlings involved and not involved in the rain treatments for the measurement of leaf morphology traits and whole-plant traits (Table S2). For leaf morphology traits, we selected 1–4 healthy and fully expanded leaves per seedling. We measured leaf thickness using a micrometer. We measured leaf area by scanning the leaves in a scanner (EPSON V370, China) and deriving the area with ImageJ software (version 1.43 u, USA). SLA was calculated as the ratio between leaf area and dry mass. We also measured whole-plant traits associated with biomass allocation and growth. We obtained the biomass of the leaves, stems, and roots separately. We calculated the LAR as the ratio between the total leaf area and overall biomass of an individual, the RSR as the dry mass ratio between the root and shoot (including the stem and leaves), and the LMF as the dry mass ratio between the leaves and the whole plant. We obtained the dry mass by drying the plant materials to constant weight in an oven at 60 °C for 72 h. We calculated the monthly RGR of an individual between census intervals as $RGR = (\ln V_{t2} - \ln V_{t1})/\Delta t$ (Kothari et al., 2021), where V is the plant volume (calculated as $\pi \cdot r^2 \cdot h$, in which h is the height and r is the basal radius) and Δt is the time interval. We averaged the RGRs of three census intervals. We did not find a significant difference between traits involved and not involved in the rain experiment (Table S3). Therefore, we merged all these traits for the subsequent analyses.

2.3. Statistical analysis

2.3.1. Effects of light treatment on traits

To assess the trait responses of each plant species to light-exposure treatment, we conducted ANOVAs by sequentially setting block, light treatment, species, and the interaction between light treatment and species as independent variables. To test the overall effects of light treatment on traits across species, we used the above general linear models and tested the significance of the light treatment using its interaction with species as an error term. This procedure allows for generalization across all species in this study, which is an alternative to mixed-effects models that set the interaction between species and light treatment as a random-effects term (Chen et al., 2022; Schmid et al., 2017). We did not test the overall effects of light treatment with mixed-effects models, because these models cannot converge. We conducted the above analyses for each trait separately. We log-transformed SLA, RSR, and LAR to improve the normality of the residuals.

2.3.2. Shade tolerance

To measure the shade tolerance of species, we conducted principal component analysis (PCA) with species-specific mean trait values of seedlings from the shade treatment (Fig. S1). We only used the traits from the shade treatment because they often better represent plant abilities to maximize resource acquisition in the shade than the trait values under the gap environment (Valladares and Niinemets, 2008).

2.3.3. Dependence of photochemical responses to chilling rain on light-exposure history

To test how light-exposure histories (gap vs. shade treatments) affected the photochemical responses of each species to the chilling rain event, we conducted ANOVAs separately for each species and each chlorophyll fluorescence parameter (F_v/F_m and $Y(II)$) per treatment stage. We set block, light treatment, rain treatment, and the interaction between light treatment and rain treatment as independent variables.

To assess the overall interactive effects of light-exposure history and rain treatment on leaf chlorophyll fluorescence parameters across species, we conducted ANOVAs by sequentially including block, species, light treatment, rain treatment, and light treatment × rain treatment, species × light treatment, species × rain treatment, and species × light treatment × rain treatment as independent variables. We tested the significance of light treatment, rain treatment, and light treatment × rain treatment by using species × light treatment, species × rain treatment, and species × light treatment × rain treatment as the error terms, respectively. This procedure allows for the testing of generalization across species.

2.3.4. Temporal dynamics of F_v/F_m and $Y(II)$

To evaluate the temporal dynamics of plant photochemical responses to the rain treatments, we calculated three sets of stability indices: the resistance, recovery, and resilience of F_v/F_m or $Y(II)$ (Eqs. 1–3):

$$Resistance = ln\left(\frac{CF \quad in \quad stage4}{CF \quad in \quad stage1}\right), \tag{1}$$

$$Recovery = ln\left(\frac{CF \quad in \quad stage5}{CF \quad in \quad stage4}\right), \tag{2}$$

$$Resilience = ln\left(\frac{CF \quad in \quad stage5}{CF \quad in \quad stage1}\right), \tag{3}$$

where CF represents the chlorophyll fluorescence parameter. Plants may experience the most intense stress when seedlings that experienced long chilling temperatures are suddenly exposed to strong light (Allen and Ort, 2001), which corresponds to the cold and sunny phase (stage 4) of the rain experiment. Thus, we calculated the resistance by comparing the differences in F_v/F_m and $Y(II)$ between stage 4 and the stage before

the rain treatment (stage 1). To assess the overall interactive effects of light-exposure history and chilling rain on the stabilities of chlorophyll parameters across species, we conducted ANOVAs by sequentially including block, species, light treatment, rain treatment, light treatment × rain treatment, species × light treatment, species × rain treatment, and species × light treatment × rain treatment as independent variables. We tested the significance of the light treatment and rain treatment by using species × light treatment and species × rain treatment as the error term, respectively. We tested the significance of light treatment × rain treatment by using species × light treatment × rain treatment as the error term.

To further explore the effects of light treatment on the stabilities of chlorophyll parameters, we conducted ANOVAs separately for seedlings from the ambient-rain and chilling-rain treatments. To further explore the effects of rain treatment on the stabilities of the chlorophyll parameters, we conducted ANOVAs separately for seedlings from the shade and gap treatments. For these ANOVAs with subsets of the data, we sequentially included block, species, the corresponding experimental treatment, and the interaction between species and the treatment as the independent variables. To assess the overall corresponding treatment effects across species, we tested the significance of the corresponding treatment by using species × treatment as the error term. We performed all these analyses separately for resistance, recovery, and resilience.

2.3.5. Relationship between species shade tolerances and the temporal dynamics of F_v/F_m and $Y(II)$

To test whether species variation in their responses to chilling rain was associated with species light-use strategies, we calculated the relative difference in stabilities as the difference in log-transformed stability indices between the chilling-rain treatment and the ambient-rain treatment, and we performed linear regressions (i) between species shade tolerance and relative difference in stabilities; and (ii) between each single trait and relative difference in stabilities. We standardized the values of each trait to mean zero and unit standard deviation before the regressions. We conducted the linear regressions separately for seedlings with shade- and gap-exposure histories. We have included the results of the F_v/F_m stabilities in the Appendix A and have published the results of $Y(II)$ stabilities on an open data repository (Appendix B).

The PCA was performed using the "*FactoMineR*" package (Lê et al., 2008). We conducted *F*-tests using non-standard residual terms with the "*aov.ftest*" function in the "*Pascal*" package (Niklaus, 2019). We performed multiple comparisons between treatments for each species based on the two-way interactions in the corresponding ANOVAs using the "*emmeans*" package with Tukey's adjustment method (Lenth, 2021). All analyses were conducted in R 4.1.0 (R Development Core Team, 2019).
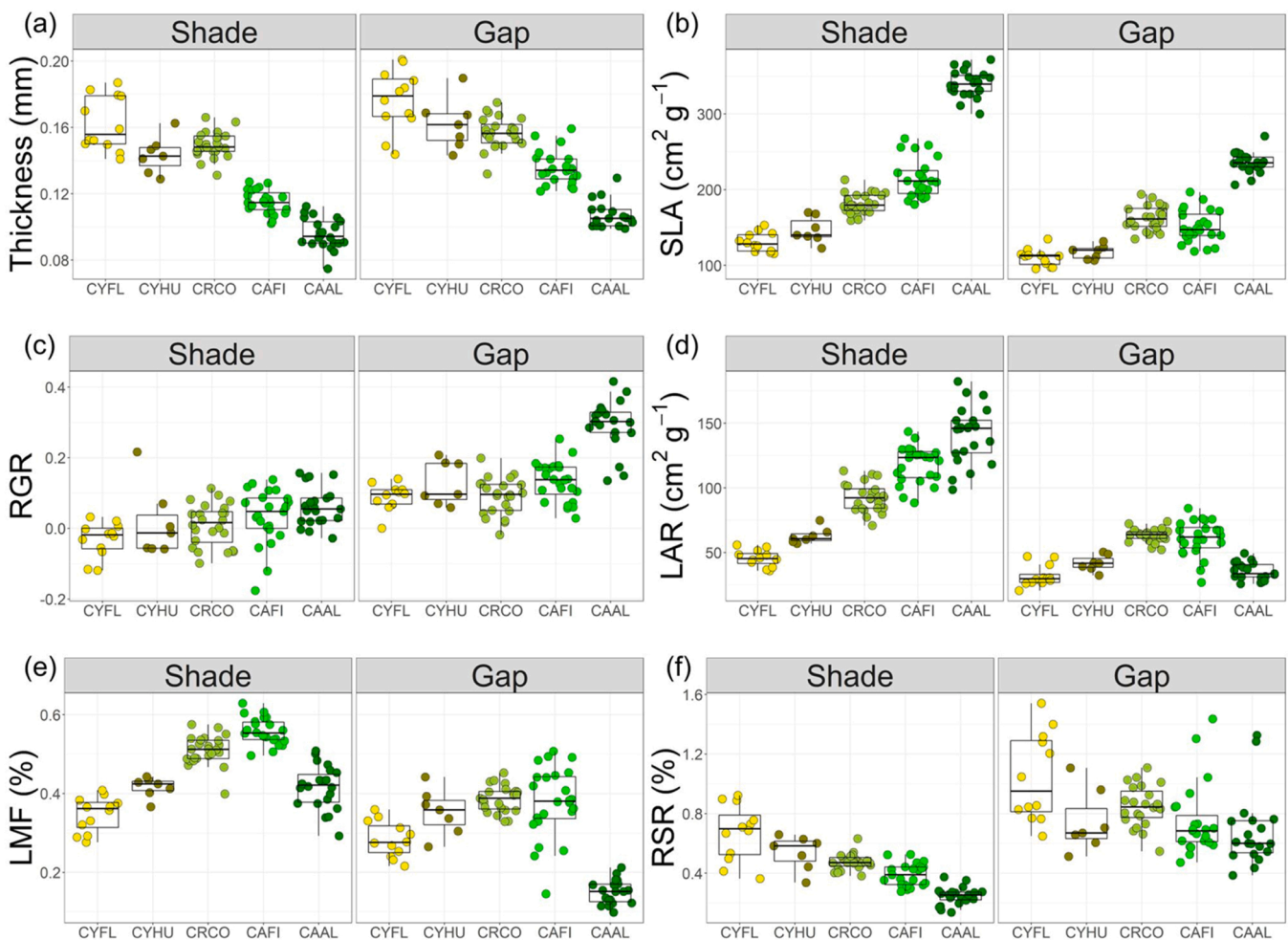

Fig. 2. Functional traits between the shade and gap treatments of the five species. Points represent individual trait values. Boxes display the data distribution, with the lower, median, and upper hinges corresponding to the 25th, 50th, and 75th percentiles, respectively. Species are ranked by their index of shade tolerance—species that are more tolerant to shade are at the right side of the horizontal axes. Note: CYFL, CYHU, CRCO, CAFI and CAAL represent *Cyclobalanopsis fleuryi*, *Cyclobalanopsis hui*, *Cryptocarya concinna*, *Castanopsis fissa* and *Canarium album*, respectively; Thickness, SLA, RGR, LAR, LMF and RSR represent leaf thickness, specific leaf area, relative growth rate, leaf area ratio, leaf mass fraction and root-shoot ratio, respectively.

3. Results

3.1. Species variation in responses to light

Species showed large differences in their traits under the shade environment (Fig. 2), reflecting differentiation in shade tolerance among species. For example, the LAR and SLA of CAAL were about 3.1 and 2.6 times higher than those of CYFY, respectively. The first principal axis (shade tolerance PC1, ST.PC1) of the PCA accounted for 81.7% of the variance of the six traits under the shade environment (Fig. S1). Species with a larger value of ST.PC1 showed a higher LAR, a larger SLA, a faster RGR, a lower RSR, and a thinner leaf thickness (Table S4; Fig. S1). Based on the expected associations between traits and shade tolerance (Table S2), we used ST.PC1 as the index of shade tolerance: species with a larger value of ST.PC1 were more tolerant of shade.

All species showed consistent responses of their traits to gap versus shade treatments (Table S5; Fig. S2; Appendix B. SI1). Species in the gap environment grew faster than those in the shade environment. Species in the shade environment developed higher LAR, larger SLA, higher LMF, and lower RSR, suggesting higher resource investments into light-harvesting processes for plants under light limitation.

3.2. Effects of light and rain treatments on leaf photochemical quantum yield

Light-exposure history significantly changed both maximum (F_v/F_m) and effective ($Y(II)$) photochemical quantum yield across species (Fig. 3, S3; Table S6). Seedlings exposed to a gap before the rain treatments generally had a lower F_v/F_m and $Y(II)$ than those exposed to shade before the rain treatments. These differences in photochemical responses to light-exposure histories varied widely among species (Fig. 3a, S3a; Appendix B. SI2 and SI3). Large differences occurred before the initiation of both the ambient-rain and chilling-rain treatments for species CRCO and CAFI, and no significant difference was observed across most stages of the ambient-rain or the chilling-rain events for CYFL and CYHU.

Seedlings with different light-exposure histories showed different patterns in their responses of F_v/F_m to the ambient- vs. chilling-rain treatments. Seedlings previously exposed to shade generally reduced their F_v/F_m under chilling rain relative to ambient rain when the rain treatments lasted for a long time (after 32 h of rain initiation, from stage 3), yielding a significant difference between the rain treatments across species (Fig. 3b; Table S7), although the difference for each single species was not significant (Fig. 3a; Appendix B. SI2).

Seedlings exposed to a gap prior to the rain treatments showed wide between-species variation in their responses to the rain treatments (Fig. 3a). The chilling-rain treatment, relative to the ambient rain treatment, significantly reduced F_v/F_m when the rain stopped and the seedlings were subsequently exposed to light (stage 4, Fig. 3a; Appendix B. SI2). However, these effects were only evident for shade-tolerant species (CAFI and CAAL) with a gap-exposure history, which led to a nonsignificant difference in F_v/F_m between the rain treatments across species (Fig. 3b; Table S7). Effects of chilling rain on $Y(II)$ were nonsignificant (Table S7; Fig. S3).

3.3. Temporal stabilities in responses to the rain treatment

Light exposure subsequent to the rain events (stage 4) reduced the F_v/F_m of the seedlings relative to the values before the rain events (stage 1; Fig. 3), leading to the negative resistance of F_v/F_m (Fig. 4a, b). The negative resistance of F_v/F_m was prevalent across species for seedlings with both gap and shade histories and under both the ambient-rain and chilling-rain treatments (Fig. 4a, b), suggesting that sudden light exposure after rainy days could cause photochemical stresses for seedlings, irrespective of light-exposure history and rain temperature.

However, the variation in the resistance of F_v/F_m was interactively affected by light-exposure histories and rain temperatures (Table 1). Chilling rain, relative to ambient rain, significantly reduced the resistance of F_v/F_m for seedlings with both the shade and gap histories (Fig. 4a; Table S8; Appendix B. SI4). This reduction in resistance under chilling rain, relative to ambient rain, was more evident for the shade-tolerant species (CAFI and CAAL) previously exposed to a gap. This was consistent with the observation of large reductions in F_v/F_m under chilling rain for these two species when their seedlings with gap-exposure history were exposed to sudden light after a long rain duration (i.e., at stage 4; Fig. 3a). Seedlings exposed to shade before the chilling rain treatment were more resistant in their F_v/F_m than those exposed to a gap before the chilling rain treatment (Fig. 4b; Table S9; Appendix B. SI4). However, these were only evident when seedlings experienced chilling rain rather than ambient rain.

The recovery of F_v/F_m also co-depended on light-exposure history and rain temperature (Table 1) but in a different way to the resistance of F_v/F_m (Fig. 4c, d). The F_v/F_m of seedlings from the chilling-rain treatment tended to recover faster than that of seedlings from the ambient-rain treatment, which was only statistically significant for seedlings
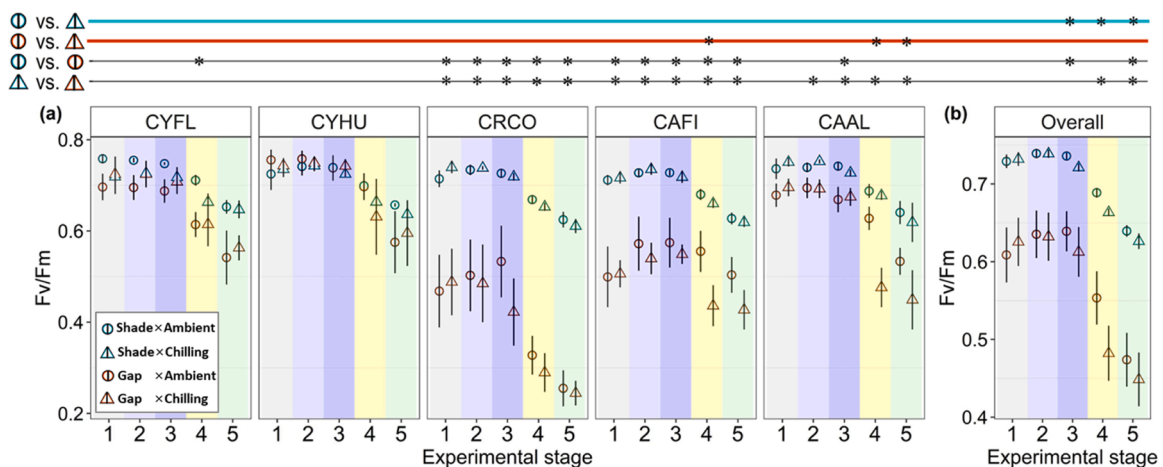

Fig. 3. Effects of light and rain treatments on maximum photochemical quantum yield of PSII (F_v/F_m) at different stages of the rain experiment for each species (a) and across species (b). Species are ordered by the index of shade tolerance—species that are more tolerant to shade occur at the right of panel a. Circles and triangles represent mean values at the ambient-rain and chilling-rain treatments, respectively. Blue and red shapes represent mean values at the shade and gap treatments, respectively. Error bars indicate standard errors. Background colors correspond to different experimental stages illustrated in Fig. 1. " * " represents significant difference in F_v/F_m between corresponding treatments ($P < 0.05$; Tables S6, S7; Appendix B. SI2).
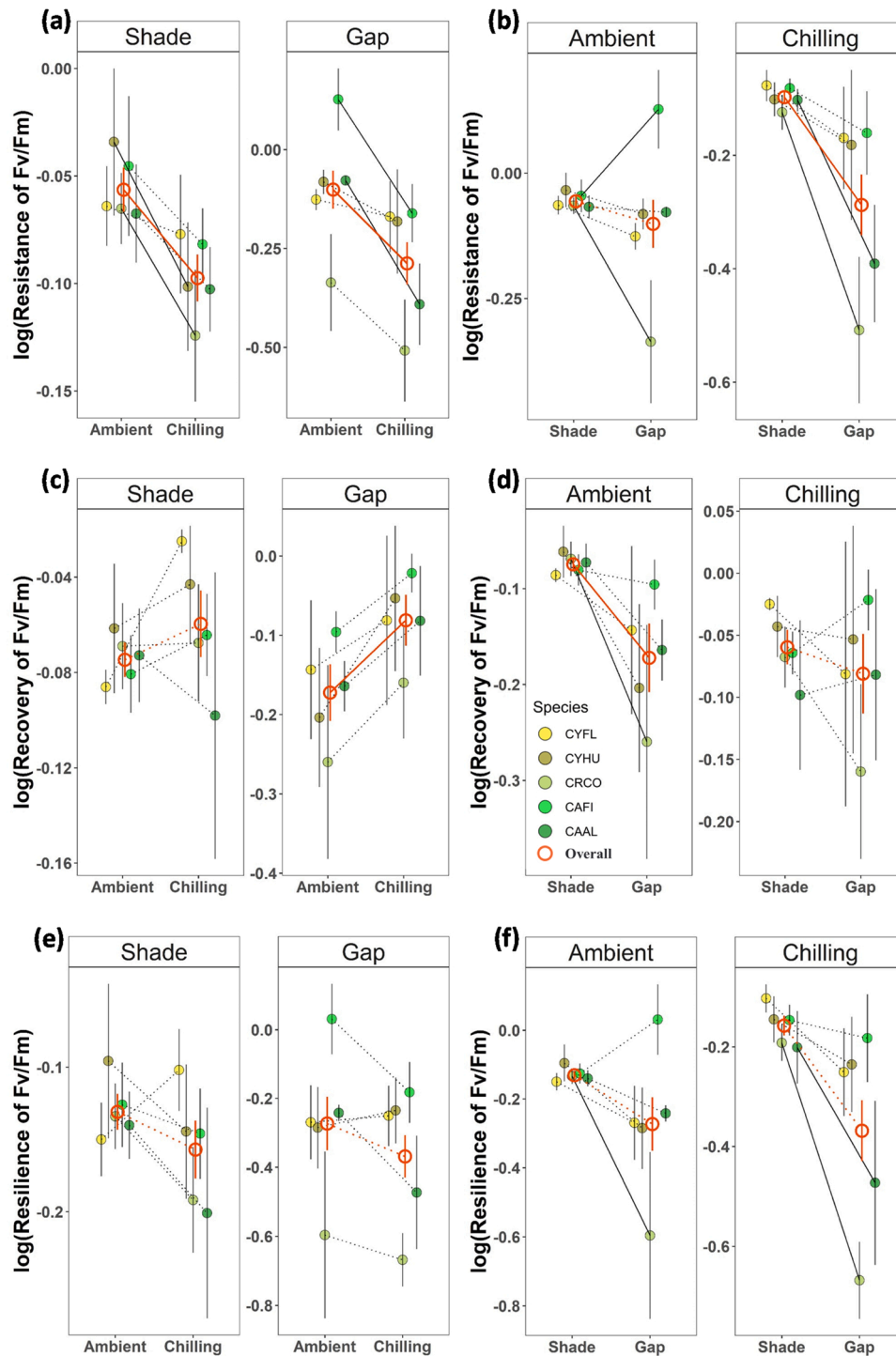
Fig. 4. Differences in the resistance (a, b), recovery (c, d), and resilience (e, f) of F_v/F_m for seedlings between the ambient- vs. chilling-rain treatments, with the shade- vs. gap-exposure histories. Red empty circles represent mean values across species; filled circles represent species-specific mean values. Error bars indicate standard errors. Solid lines represent significant differences between corresponding treatments ($P < 0.05$; Tables S8, S9, Appendix B. SI4).

with gap-exposure history (Fig. 4c; Table S8). The different trends in resistance vs. recovery yielded nonsignificant differences in the resilience of F_v/F_m between the ambient- vs. chilling-rain treatments (Fig. 4a, c, e; Table S8). Seedlings exposed to shade before the rain recovered faster than those previously exposed to a gap. However, this was only evident for seedlings under the ambient-rain treatment (Fig. 4d; Table S9). Neither the light treatment nor the rain treatment had significant effects on the resilience of F_v/F_m across species (Fig. 4e, f; Tables 1, S8, S9).

Neither the light-exposure history nor the rain treatment had consistent or interactive effects on the stabilities of *Y(II)* across species (Fig. S4; Appendix B. SI5). The rain treatments did not significantly change the temporal stabilities of *Y(II)* for most species (Fig. S4; Appendix B. SI6 and SI7). Seedlings with shade-exposure history recovered faster in their *Y(II)* than those exposed to a gap before the chilling-rain treatment (Fig. S4d; Appendix B. SI6 and SI8).

Table 1

ANOVA table for the overall effects of light and rain treatments on the stabilities of F_v/F_m across species.

Stability index	Effect	F ratio (DF, DDF)	*P* value
Resistance			
	Light treatment	3.64 (1, 4)	0.130
	Rain treatment	**17.96 (1, 4)**	**0.014**
	Light treatment × Rain treatment	**7.92 (1, 4)**	**0.049**
Recovery			
	Light treatment	4.52 (1, 4)	0.101
	Rain treatment	**31.67 (1, 4)**	**0.005**
	Light treatment × Rain treatment	**10.44 (1, 4)**	**0.032**
Resilience			
	Light treatment	4.07 (1, 4)	0.114
	Rain treatment	3.38 (1, 4)	0.140
	Light treatment × Rain treatment	1.45 (1, 4)	0.296

Note: Results are from ANOVAs by sequentially setting block, species, light treatment, rain treatment, light treatment × rain treatment, species × light treatment, species × rain treatment, and species × light treatment × rain treatment as independent variables. We tested the significance of a treatment using its interaction with species as an error term. DF, numerator degrees of freedom; DDF, denominator degrees of freedom, which are residual degrees of freedom among the stabilities of F_v/F_m of the five species to the corresponding treatments. Significant values ($P < 0.05$) are shown in bold.

3.4. Relationship between species shade tolerance and their responses to chilling rain

Light-demanding species were more resistant in F_v/F_m to chilling rain relative to ambient rain than shade-tolerant species (Fig. 5). However, this negative relationship between species shade tolerance and the relative difference in the resistance of F_v/F_m was only evident for seedlings with gap-exposure history but not for those with shade-exposure history (Fig. 5**b**). The trade-off between species tolerance to shade and chilling rain was primarily the result of traits related to resource allocation, such as SLA, LAR, leaf thickness, RGR, and RSR (Fig. 6). We did not find significant relationships between species shade tolerance and the relative difference in recovery or resilience of F_v/F_m for seedlings exposed to a gap or shade environment beforehand (Fig. 5).

We did not find a significant relationship between species shade tolerance and the relative difference in the stabilities of *Y(II)* (resistance, recovery, and resilience) for seedlings with either light-exposure history (Fig. S5). Species with thicker leaves tended to show higher resistance and resilience in *Y(II)* than species with the opposite trait; however, these effects were only significant when the seedlings were exposed to a gap beforehand (Fig. S6).

4. Discussion

Understanding species variation in their responses to chilling rain in warm and species-rich (sub-)tropical forests can help improve forecasts about the impacts of cold waves on forest community composition. In this study, we investigated how species with different shade tolerances varied in their responses to an extreme chilling rain event. We assessed seedling responses to chilling rain by measuring leaf photochemical quantum yield (e.g., F_v/F_m), which is fundamental to plant photosynthesis and productivity (Baker, 2008; Murchie and Lawson, 2013). We found a trade-off between species tolerance to shade and chilling rain if seedlings of these species were exposed to a forest-gap environment before chilling rain. These results imply that more frequent chilling rain events, together with more frequent canopy disturbances, may offer relative advantages to light-demanding species than shade-tolerant species and alter species compositions in (sub-)tropical forests.

To derive fair and strict assessments of the impacts of chilling rain on plants, we simulated an ambient rain event as a control and monitored plant responses in the complete phases (a chilling-rain phase, a cold and sunny phase, and a recovery phase) of rain events in the chilling rain experiment, that is, we did not assess plant responses to chilling rain solely based on the difference between plant performance before vs. after the initiation of a temperature treatment, as has been conducted in most previous studies (Cavender-Bares et al., 1999; Cunningham and Read, 2006; Feng and Cao, 2005; Huang et al., 2010; Richardson et al., 2013; Robakowski, 2005; Yan et al., 2021). Relying solely on the before-and-after evaluation of plant responses to an extreme climatic event may result in biased inference, as plant behavior may exhibit significant temporal variation both during extreme events and under ambient conditions. This happened in our experiment: light exposure subsequent to the rain events reduced the F_v/F_m of seedlings relative to the values before the rain events in both the ambient- and chilling-rain treatments. Therefore, we may infer that the chilling rain had very strong impacts on all the species based on the temporal changes in the chilling treatment only, but the inference should change if we compare the temporal differences between the chilling vs. ambient treatments. This implies that conclusions from previous studies that lack ambient events as true controls and that are solely based on temporal differences in plant responses to extreme climatic events should be approached with caution. It also reveals the complexity of a chilling rain event when the entire phase is considered. Variation in temperature and light availabilities during the entire phase can jointly affect the responses of plants to chilling rain. As chlorophyll fluorescence is highly dependent on PPFD in the plant growth environment, a proper control with the same PPFD values as the treatment is necessary to reveal the true impacts of chilling rain. We found that light plays important roles in regulating plant responses to chilling rain. (1) The most substantial changes in leaf F_v/F_m occurred in the phase when plants were suddenly exposed to light after experiencing long ambient or chilling rain. The reduction of F_v/F_m during this sunny phase (stage 4) was more evident under chilling rain than under ambient rain. (2) Shade-tolerant species were more vulnerable to chilling rain with regard to their F_v/F_m responses than light-demanding species. (3) However, the above reduction of F_v/F_m in the chilling rain treatment and the trade-off between species tolerances to shade and chilling rain were more evident for plants exposed to a forest gap, but not shade, before the rain treatment. These results suggest that sudden exposure to light can harm the photosystems of plants exposed to prolonged rainy days (with low light availability), which confirms the findings of previous studies (Ishibashi and Terashima, 1995). This stress to photosystems can be more severe if the rain is chilling (Allen and Ort, 2001; Huang et al., 2011) and for plant species adapted to a shade environment, as revealed by this study. The trade-off between species tolerance to shade and chilling rain under a forest gap implies that more frequent chilling rain events may increase the relative advantages to light-demanding species than shade-tolerant species, thus altering the community composition of (sub-)tropical forests. The relative advantages to light-demanding species brought by chilling events may be more evident if forests are subjected to large disturbances or during early successional stages, which expose understory plants to more forest gaps (Houter and Pons, 2005; Jin et al., 2018; Lovelock et al., 1994; Ross et al., 2009; Song et al., 2018). Why light-exposure history alters plant responses to chilling rain remains largely unknown. One possibility is that light exposure is a signal for daily or seasonal changes to plants, thereby regulating the genes involved in cold acclimation (Roeber et al., 2021).

The trade-off between species tolerances to shade and chilling rain was primarily the result of traits related to resource allocation, such as leaf thickness, SLA, and RSR. Species with thicker leaves, smaller SLA, and larger RSR tended to be more resistant in F_v/F_m under chilling rain than species with the opposite traits. Leaves with greater cell wall thickness and rigidity are found to experience less photodamage from cold (Niinemets, 2016). Plants with larger leaf surface area per unit dry mass (i.e., smaller SLA) often have stronger evapotranspiration, which may cool leaves to even lower temperatures under chilling rain (Lusk et al., 2018). Furthermore, low biomass investment in roots (i.e., small
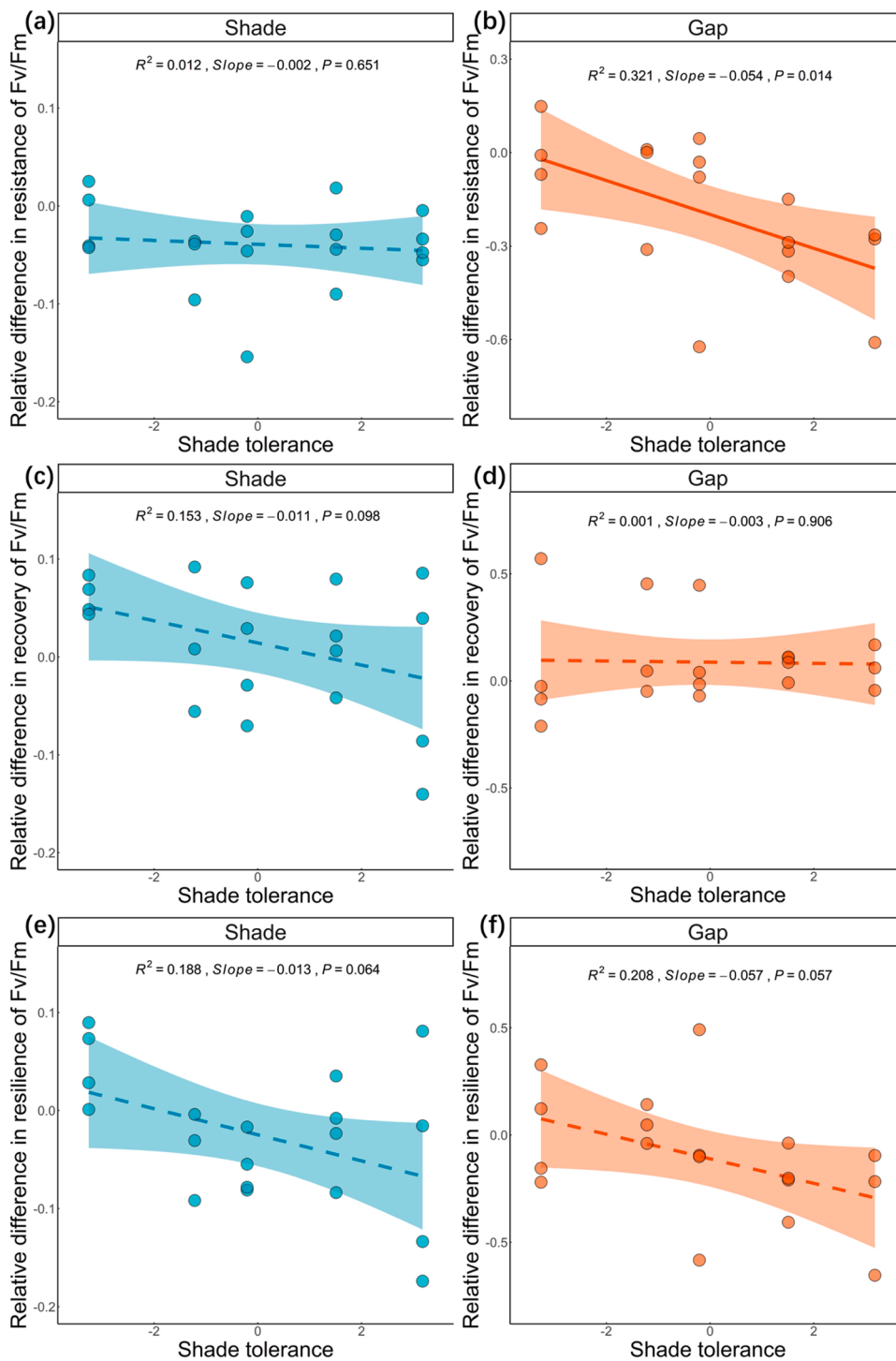
Fig. 5. Relationships between species-specific shade tolerance and relative differences in stabilities (resistance, recovery, and resilience) of F_v/F_m in the chilling-rain vs. ambient-rain treatments for seedlings with shade- (a, c, e) or gap-exposure history (b, d, f). Circles represent species-specific mean values per block. Solid lines indicate significant results ($P < 0.05$). Shaded areas represent the 95% CIs (confidence intervals). Relative differences in stabilities were calculated as the difference in log-transformed stability indices in the chilling-rain vs. ambient-rain treatments.

RSR) may be inconducive to water uptake (Niinemets and Valladares, 2006) and may intensify chill-induced water loss.

It is difficult to spot substantial changes in growth or survival during chilling rain, except for very extreme events (Shao et al., 2011), because a chilling rain event often lasts for short time, usually from 5 to 10 days (Zhang and Qian, 2011). However, the instantaneous damages to photosystems during this short term can produce long-term impacts. Firstly, photodamage caused by chilling rain typically requires a considerable amount of time to recover. This is evident from the negative values observed in the photochemical parameters during a 24-hour recovery phase in our experiment. The full-recovery time from photoinhibition

can last for days for some species due to the blockage of linear electron flow from PSII to PSI or the production of reactive oxygen species (Feng and Cao, 2005; Huang et al., 2010; Mai et al., 2010). Second, relatively short-term photodamage may affect plant performance in the long term, because the photodamage may cause carbon starvation and reduce resistance to natural enemies (McDowell et al., 2008), especially for seedlings. However, we should also note that the recovery rate of photodamage after chilling rain may depend on the levels of irradiance and other environmental factors, especially if we measure the recovery by chlorophyll fluorescence parameters. Future studies can provide more insights by monitoring the long-term impacts of chilling rain on plants in
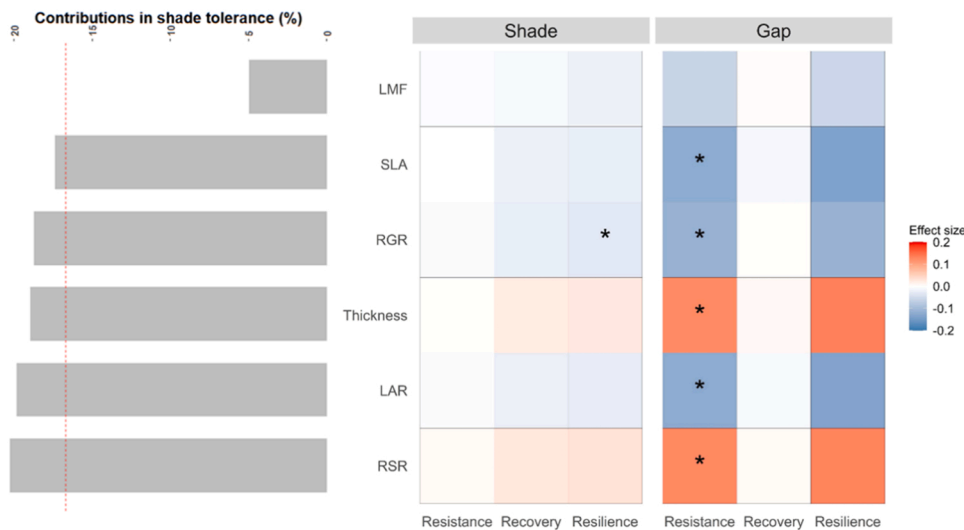
Fig. 6. Relationships between species-specific traits and relative difference in stabilities (resistance, recovery, and resilience) of *Fv/Fm* in the chilling-rain vs. ambient-rain treatments for seedlings with shade- or gap-exposure history. Colors show the relative sizes and directions of the standardized effects estimated from simple linear regressions between the stability index and traits. Red and blue colors represent positive and negative effects, respectively. The asterisk indicates that the CIs of slope coefficients did not include zero, representing significant results. Relative differences in stabilities were calculated as the differences in log-transformed stability indices in the chilling-rain vs. ambient-rain treatments.

different environmental contexts and focusing on parameters other than photochemical processes.

We focused on the impacts of chilling rain on tree seedlings, which represents a regeneration stage that is critical to future forest community composition and dynamics (Comita et al., 2010; Harms et al., 2000; Jia et al., 2020). The findings from this study may not be directly translated to other stages (e.g., adult trees). Extreme chilling rain can cause mortality to canopy trees if large amounts of rain freeze on tree branches at one moment (Liu et al., 2020; Song et al., 2018). However, how species vary in their mortality rates during such chilling rain events remains largely unknown. The mechanisms driving species variation should be very different between seedlings and adult trees and between moderate chilling rain and extreme chilling rain.

5. Conclusions

In this study, we revealed that light availability and plant light-use strategy were critical in regulating the responses of subtropical tree seedlings to chilling rain. Shade-tolerant species exposed to a forest gap before chilling rain were more vulnerable to chilling rain than light-demanding species. These findings imply that more frequent chilling rain events, together with forest canopy disturbances, may increase the regeneration advantage for light-demanding species than for shade-tolerant species.

CRediT authorship contribution statement

Shixiao Yu, Wenbin Li and Yuxin Chen designed and planned the research; Wenbin Li, Yuxin Chen, Yandan Lu and Yong Shen performed the experiments; Wenbin Li and Yuxin Chen analyzed and interpreted the data; Wenbin Li and Yuxin Chen wrote the manuscript with help from every author.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The raw data of the experiment and Appendix B are available on figshare: https://figshare.com/s/627889d5ac789a5bf226 (DOI: 10.6084/m9.figshare.22723159).

Author statement

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2023.105420.

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