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## Research paper

# Photosynthetic and biochemical responses of four subtropical tree seedlings to reduced dry season and increased wet season precipitation and variable N deposition

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**Interspecific variations in phenotypic plasticity of trees that are affected by climate change may alter the ecosystem function of forests. Seedlings of four common tree species (*Castanopsis fissa*, *Michelia macclurei*, *Dalbergia odorifera* and *Ormosia pinnata*) in subtropical plantations of southern China were grown in the field under rainout shelters and subjected to changing precipitation (48 L of water every 4 days in the dry season, 83 L of water every 1 day in the wet season; 4 g m<sup>-2</sup> year<sup>-1</sup> of nitrogen (N)), low N deposition (48 L of water every 2 days in the dry season, 71 L of water every 1 day in the wet season; 8 g m<sup>-2</sup> year<sup>-1</sup> N), high N deposition (48 L of water every 2 days in the dry season, 71 L of water every 1 day in the wet season; 10 g m<sup>-2</sup> year<sup>-1</sup> N) and their interactive effects. We found that the changes in seasonal precipitation reduced the light-saturated photosynthetic rate ( $A_{\text{sat}}$ ) for *C. fissa* due to declining area-based foliar N concentrations ( $N_a$ ). However, we also found that the interactive effects of changing precipitation and N deposition enhanced  $A_{\text{sat}}$  for *C. fissa* by increasing foliar  $N_a$  concentrations, suggesting that N deposition could alleviate N limitations associated with changing precipitation. Altered precipitation and high N deposition reduced  $A_{\text{sat}}$  for *D. odorifera* by decreasing the maximum electron transport rate for RuBP regeneration ( $J_{\text{max}}$ ) and maximum rate of carboxylation of Rubisco ( $V_{\text{cmax}}$ ). *Ormosia pinnata* under high N deposition exhibited increasing  $A_{\text{sat}}$  due to higher stomatal conductance and  $V_{\text{cmax}}$ . The growth of *D. odorifera* might be inhibited by changes in seasonal precipitation and N deposition, while *O. pinnata* may benefit from increasing N deposition in future climates. Our study provides an important insight into the selection of tree species with high capacity to tolerate changing precipitation and N deposition in subtropical plantations.**

**Keywords:** additional nitrogen deposition, biochemical traits, carbon reserves, phenotypic plasticity, photosynthetic traits, subtropical trees, variable dry and wet season precipitation.

## Introduction

Changes in seasonal precipitation pattern and atmospheric nitrogen (N) deposition have become two major factors in global environmental change (IPCC 2013), which affects the productivity and functioning of forest ecosystems (De Schrijver et al. 2008, Barros et al. 2019, Tang et al. 2020). Changes

in seasonal precipitation have resulted in subtropical forests becoming drier in the dry season but wetter in the wet season (Zhou et al. 2011), which may determine species-specific responses to climate change (Nicotra et al. 2010, N.P. He et al. 2020) and biome reorganization (G.Y. Zhou et al. 2014). Human activities and industrialization are predicted to increase

N deposition by 2.5-fold by the end of the century (Fowler et al. 2013). It has been shown that atmospheric N deposition may alleviate soil N limitation to plant growth and further increase forest productivity (Guerrieri et al. 2011, Zhang et al. 2020); however, excess N deposition may reduce plant growth and biodiversity (Bobbink et al. 2010, Borghetti et al. 2017). The main impacts of changing precipitation and N deposition on phenotypic plasticity, which is the ability of a genotype to exhibit different phenotypes in response to changes in the environmental conditions (Hoffmann and Sgro 2011, Drake et al. 2015), has been studied regarding physiological and biochemical traits, while few studies have investigated their interaction.

Most previous studies have investigated the effects of drought on subtropical trees in the growing season (wet season), but few have addressed seasonal changes in precipitation pattern (P. Li et al. 2018, Duan et al. 2022). During drought, plants close stomata to avoid embolism in response to impaired water transport capacity induced by declining water availability (Martorell et al. 2014), limiting CO<sub>2</sub> availability for photosynthesis (dos Santos et al. 2018). Additionally, lower organic matter decomposition rate induced by lower precipitation and higher nutrient leaching caused by higher precipitation could decrease soil nutrient availability, which would decrease foliar nutrient concentrations (Chen et al. 2019, Ge et al. 2022). In turn, this lowers the light-saturated photosynthetic rate ( $A_{\text{sat}}$ ) by decreasing photosynthetic capacity, consisting of the maximum electron transport rate for RuBP regeneration ( $J_{\text{max}}$ ) and maximum rate of carboxylation of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) ( $V_{\text{cmax}}$ ) (Limousin et al. 2010). Nonstructural carbohydrates (NSC, comprised of soluble sugars and starch) are sourced from photosynthesis, and are related to the balance of sources (photosynthesis) and sinks (growth and respiration) of carbon (Hartmann and Trumbore 2016); NSC helps plants osmoregulate to defend against stress and maintain physiological functioning (McDowell et al. 2022). Reduced foliar NSC concentrations due to lower photosynthesis may decrease the capacity of subtropical trees to adapt to changing precipitation (De Roo et al. 2020, Duan et al. 2022). Hence, tree resistance to changes in seasonal precipitation pattern is essential for maintaining growth and survival (Gessler et al. 2017, McGregor et al. 2021).

Nitrogen is a critical component of photosynthetic enzymes and chlorophyll that could directly regulate gas exchange (Tissue et al. 1993, Elser et al. 2007). In temperate forests with limiting N, low and high N depositions result in higher foliar N concentrations (Zhang et al. 2021a, 2021b), which further stimulates photosynthetic traits (Liang et al. 2020, Zhang et al. 2020). In contrast, several studies have demonstrated that low and high N depositions exert limited impacts on foliar N concentrations in N-rich forest ecosystems (Lu et al. 2018, Mao et al. 2021). Huang et al. (2021) found that low N deposition

has no impact on photosynthetic capacity for subtropical trees but reduces its growth so that it has higher NSC concentrations, which could help plants tolerate stress environments (Adams et al. 2017, Tang et al. 2020). However, soil acidification caused by high N deposition induces nutrient imbalance in subtropical forests with low P availability, which lowers foliar phosphorus (P) concentrations (Reed et al. 2011, Huang et al. 2016, Deng et al. 2017) and thereby decreases photosynthesis and NSC concentrations for subtropical trees (Liu et al. 2016, Shi et al. 2017, Mao et al. 2018).

Nitrogen deposition could alter the plasticity in photosynthetic and biochemical traits induced by changing precipitation, and the variations in magnitude and direction are related to the levels of N deposition (Barker et al. 2006, Zhang et al. 2021a). Low N deposition enhances hydraulic conductivity by increasing xylem conduit diameter (Hacke et al. 2010, Villar-Salvador et al. 2013), which exerts positive effects on stomatal conductance ( $g_s$ ) and photosynthesis under changing seasonal precipitation patterns (Xu et al. 2013, Zhang et al. 2014). Even low levels of natural N deposition could promote faster recovery of photosynthesis due to higher enzyme activity and chlorophyll concentrations (Patrick et al. 2009, Gessler et al. 2017). In contrast, excessive N deposition may strengthen the negative effects of changing precipitation on physiological traits, such as exacerbated nutrient imbalance (Liang et al. 2022), lower water supplies due to reduced root biomass (Dziedek et al. 2016) and higher vulnerability to xylem cavitation (Harvey and van den Driessche 1997).

Four common tree species (*Castanopsis fissa*, *Michelia macclurei*, *Dalbergia odorifera* and *Ormosia pinnata*) grown in subtropical plantations of southern China were chosen for this study, with *M. macclurei* exhibiting the highest capacity to tolerate drought (Wu et al. 2022). Previous studies demonstrated that extreme changing precipitation and high levels of N deposition occurring in southern China have seriously affected tree survival and species composition (G.Y. Zhou et al. 2014, Tian et al. 2018). Our goal was to determine which species exhibited the highest capacity to acclimate to changes in seasonal precipitation patterns, low and high N depositions, and their interactive effects. Here, we analyzed the responses of foliar physiological traits (photosynthetic rate and capacity) and biochemical traits (morphology, chemistry and carbon reserves) to the main and interactive effects of shifts in precipitation from the dry season to the wet season and additional N deposition. Specifically, we wanted to test the following hypotheses: (i) shifting precipitation from the dry to the wet season would decrease leaf nutrient concentrations and  $g_s$  for the four tree species, and subsequently result in lower photosynthetic traits; (ii) low N deposition would exert no effects on photosynthetic and biochemical traits for the four tree species, while high N deposition would decrease photosynthetic traits; and (iii) the interactive effects of changing precipitation and low N deposition would increase photosynthetic and biochemical traits, while the interactive

effects of changing precipitation and high N deposition would have a negative effect on photosynthetic and biochemical traits.

## Materials and methods

### Plant material and experimental design

In 2018, 18 plots were constructed in the South China Botanical Garden, CAS, Guangzhou, Guangdong province, China (N23°10'30.97", E113°21'9.81"). The mean annual temperature is approximately 21 °C, and the relative humidity averages 80% throughout the year. The mean annual precipitation is approximately 1900 mm; nearly 80% of the rainfall occurs during the wet season (April–September) and 20% during the dry season (October–March) (Wu et al. 2020). A plastic film, with a height of 7 m, extended above the tops of the trees was used to exclude natural rainfall from the plots. Each plot had an edge length of 3 m, with an edge height of 0.8 m. The wall of the plot was made of brick, cement and concrete, and the bottom of the plot was filled with local forest soil. *Castanopsis fissa*, *Michelia macclurei*, *Dalbergia odorifera* and *Ormosia pinnata* are dominant common species in native subtropical forests, and they are widely planted in plantations due to large biomass and economic value (Li et al. 2011, Yang et al. 2016, Wu et al. 2022). *C. fissa* is a sun-growing and late successional species, while the others are shade-growing and middle successional species (South China Botanical Garden, Chinese Academy of Sciences 2009). In May 2019, 1 year-old, similar-sized seedlings (height was ca 30 cm and stem basal diameter was ca 4 mm), grown outdoors in natural environmental conditions, were purchased from a nursery near the South China Botanical Garden. Five individuals per species were randomly transplanted into three plots for each treatment (4 species × 5 individual trees × 6 treatments × 3 plots = 360 trees). Each individual tree was transplanted in a randomized block design, and spacing between individual trees was ~50 cm in each plot.

### Treatments

The natural distribution ratio of precipitation between the dry and wet seasons is 1:3 (Chen and Zhang 2021), and in the past five decades, the average precipitation in the dry season was reduced but that in the wet season was increased (Zhou et al. 2011, G.Y. Zhou et al. 2014). At the same time, in the past three decades, this area experienced high rates of atmospheric nitrogen (N) deposition (34–50 kg N ha<sup>-1</sup> year<sup>-1</sup>) (Lu et al. 2013, Zheng et al. 2018). Since each plot had an edge length of 3 m, using the average precipitation for the past five decades, the average volume of water per day in the control was 24 and 71 L in the dry and wet seasons, respectively; and the N deposition rate in the control was 4 g N m<sup>-2</sup> year<sup>-1</sup> (Huang et al. 2015, Zheng et al. 2020). We used these values as the baseline

for our six treatments: (i) control: normal precipitation (48 L of water every 2 days in the dry season, 71 L of water every 1 day in the wet season) + background N deposition (4 g m<sup>-2</sup> year<sup>-1</sup>); (ii) changing precipitation (P): dry-season precipitation was reduced 50% (48 L of water every 4 days) and the reduced dry-season precipitation was added during wet-season (83 L of water every 1 day in the wet season) + background N deposition (4 g m<sup>-2</sup> year<sup>-1</sup>); (iii) low N deposition (LN): normal precipitation (48 L of water every 2 days in the dry season, 71 L of water every 1 day in the wet season) + 2 times background N deposition (8 g m<sup>-2</sup> year<sup>-1</sup>); (iv) high N deposition (HN): normal precipitation (48 L of water every 2 days in the dry season, 71 L of water every 1 day in the wet season) + 2.5 times background N deposition (10 g m<sup>-2</sup> year<sup>-1</sup>); (v) the interaction of changing precipitation and low N deposition (PLN): dry-season precipitation was reduced 50% (48 L of water every 4 days in the dry season) and the reduced dry-season precipitation was added during wet-season (83 L of water every 1 day in the wet season) + 2 times background N deposition (8 g m<sup>-2</sup> year<sup>-1</sup>); (vi) the interaction of changing precipitation and high N deposition (PHN): dry-season precipitation was reduced 50% (48 L of water every 4 days in the dry season) and the reduced dry-season precipitation was added during wet-season (83 L of water every 1 day in the wet season) + 2.5 times background N deposition (10 g m<sup>-2</sup> year<sup>-1</sup>) (Figure 1). The amount and frequency of watering were controlled by an automatic irrigation system, which was located on the soil surface. Watering occurred at night over four intervals per night to reduce potential run-off. We artificially added wet N deposition by spraying NH<sub>4</sub>NO<sub>3</sub> solution since roots can directly uptake ammonium and nitrate. All trees were maintained in control precipitation and N conditions for 15 months after planting. The treatment of changing precipitation was initiated in August 2020, and NH<sub>4</sub>NO<sub>3</sub> solution (N deposition) was also added in August 2020 and then every 2 months thereafter. All treatments were maintained for 12 months until measurements were taken in August 2021. Each plot was distributed randomly with three replicates per water treatment.

Air temperature ( $T_{\text{air}}$ , °C) and humidity (RH, %) for all treatments were monitored and recorded together, using a HMP155A temperature probe. Soil temperature ( $T_{\text{soil}}$ ) at 5-cm depth was automatically recorded in each plot using Campbell 109 constantan-copper thermocouples (Campbell Scientific, Logan, UT, USA). Soil volumetric water content (SVWC, m<sup>3</sup> m<sup>-3</sup>) at 5-cm depth in each plot was measured at the same depth using time domain reflectometer probes (CS616). All environmental measurements were taken for the duration of the experiment.

### Leaf morphological and chemical traits

In August 2021, three leaves of each species from randomly selected individuals per plot were measured for the

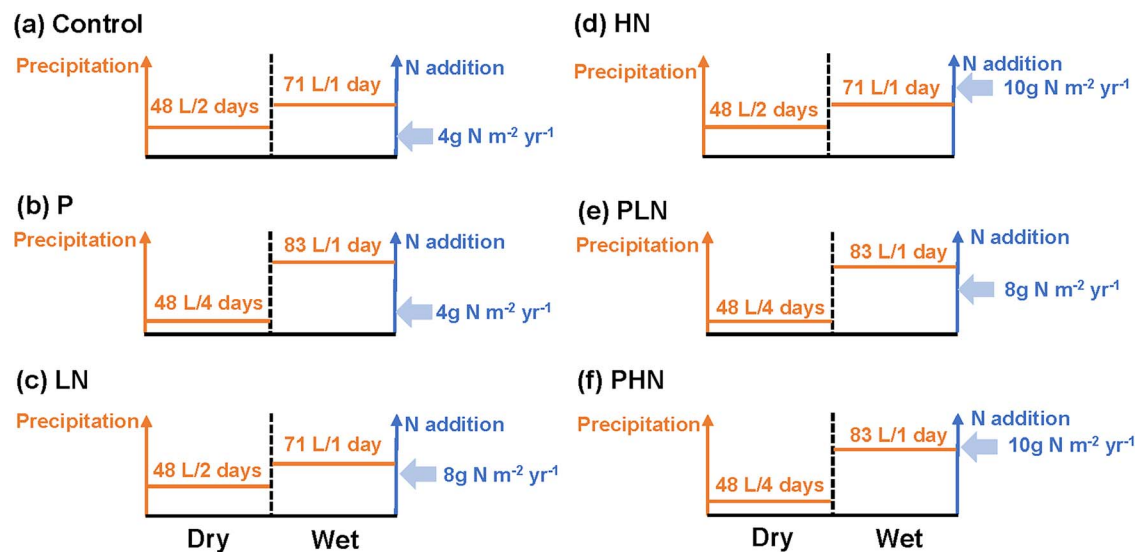


Figure 1. Representation of the design of (a) control, (b) changing precipitation (P), (c) low nitrogen (N) deposition (LN), (d) high N deposition (HN), (e) the interaction between changing precipitation and low N deposition (PLN), and (f) the interaction between changing precipitation and high N deposition (PHN).

cross-sectional thickness of leaf (LT,  $\mu\text{m}$ ), using an image analysis software (OPTPro 2012 4.0, Optec XTS20, Chongqing Optec Instrument). Ten mature leaves per species per treatment (10 leaves  $\times$  4 species  $\times$  6 treatments = 240 leaves) were selected to measure leaf fresh weight (LFW, g) and leaf area (LA,  $\text{cm}^2$ ) with a leaf area meter (LI-3100, Li-Cor Biosciences, Lincoln, NE, USA). Leaves were then dried in a drying oven for 72 h at 65 °C until complete drying, before measuring leaf dry mass (LDW, g). Leaf dry matter content (LDMC, %) was calculated as  $100\% * (\text{LDW}/\text{LFW})$ . Leaf mass per area (LMA,  $\text{g cm}^{-2}$ ) was calculated as  $\text{LDW}/\text{LA}$  (Bartlett et al. 2012).

Five leaves were harvested to analyze the chlorophyll concentration (Chl,  $\mu\text{g cm}^{-2}$ ). Five leaf disks (6 mm diameter) from one individual per treatment per chamber were cut and dipped into 5 mL of 80% acetone; see Arnon (1949). Mature foliar samples were randomly collected from the four tree species in plots. Oven-dried foliar samples were ground to fine powder in a ball mill. Mass-based foliar N concentrations ( $N_m$ ,  $\text{mg g}^{-1}$ ) were measured using the Kjeldahl method (Bremner and Mulvaney 1982). Mass-based foliar P concentrations ( $P_m$ ,  $\text{mg g}^{-1}$ ) were measured photometrically after samples were digested with  $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$  (Anderson and Ingram 1989). Area-based foliar N concentrations ( $N_a$ ,  $\text{g m}^{-2}$ ) were calculated as  $N_m \times \text{LMA}$ , and area-based foliar P concentrations ( $P_a$ ,  $\text{g m}^{-2}$ ) were calculated as  $P_m \times \text{LMA}$  (He et al. 2019).

### Photosynthetic traits

The net assimilation vs intercellular  $\text{CO}_2$  concentration ( $A-C_i$ ) curves were measured on fully expanded leaves from three or four seedlings per plot per species ( $n = 3-4$ ) between 09:00 and 14:00 h on clear days in August 2021, using a portable open path gas exchange system (Licor-6800, Li-Cor, Lincoln,

NE, USA) equipped with a leaf chamber fluorometer (6800-40). The  $A-C_i$  curves were measured at saturating PAR of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , leaf temperature (25 °C) and ambient relative humidity inside the leaf chamber ( $\sim 60\%$ ). The  $A-C_i$  curves were generated using leaf chamber  $\text{CO}_2$  values of (in order): 400, 300, 200, 100, 50, 400, 600, 800, 1000 and  $1200 \mu\text{mol mol}^{-1}$ . Leaf light-saturated photosynthetic rate ( $A_{\text{sat}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and stomatal conductance ( $g_s$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ) were selected, at  $\text{CO}_2$  of  $400 \mu\text{mol mol}^{-1}$ . The maximum rate of photosynthetic ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylation ( $V_{\text{cmax}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and apparent maximum rate of photosynthetic electron transport ( $J_{\text{max}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) were estimated from  $A-C_i$  curves, using the 'fitaci' function in R package 'plantecophys' (Duursma 2015).

### Nonstructural carbohydrates concentrations

Samples were collected in August 2021 to determine the concentrations of NSC. Ground samples (50 mg) were weighed and then extracted with 4 mL of 80% aqueous ethanol (v/v) in a polyethylene tube. The mixture was boiled in a water bath at 80 °C for 30 min, and then centrifuged at 3000 r.p.m. for 5 min. The supernatant was collected and the pellet reextracted once with 4 mL of 80% aqueous ethanol (v/v) and once with 4 mL of distilled water; this was repeated twice. The concentrations of soluble sugars were determined on the supernatants colorimetrically at 620 nm, using the anthrone-sulfuric acid method (Ebell 1969). The concentrations of starch were determined on the pellets remaining after perchloric acid extraction (35% v/v) and also assayed colorimetrically at 620 nm, following the modified anthrone method (Hansen and Moller 1975). Nonstructural carbohydrates concentrations were defined as the

sum concentrations of starch and soluble sugars (Duan et al. 2019).

### Soil properties

In June 2021, after 10 months of treatment, we collected soils (0–10 cm) from each plot of each treatment to determine soil available N concentrations ( $\text{mg kg}^{-1}$ ) and available P concentrations ( $\text{mg kg}^{-1}$ ). After soil was extracted with 1 M KCl solution, available N concentrations were determined colorimetrically (Liu et al. 2017). Available P concentrations were extracted with 0.03 M  $\text{NH}_4\text{F}$  and 0.025 M HCl and measured by inductively coupled plasma optical emission spectrometer (ICP-OES) (Optima 2000 DV, Perkin Elmer, USA) (Bray and Kurtz 1945).

### Growth measurements

The stem diameter (mm) and height (cm) of all seedlings per species in each plot were measured in September 2021 (13 months treatment).

### Statistical analysis

Data were assessed using the Kolmogorov–Smirnov test for normality and Levene's test for homogeneity of variance prior to statistical analysis. When the data did not conform to the assumption of normality and homogeneity of variances, they were logarithmically transformed. A one-way ANOVA was used to evaluate the effects of P, LN, HN, PLN and PHN on environmental variables ( $T_{\text{soil}}$  and SVWC), soil properties (available N and P concentrations), foliar anatomical traits (LT, LDMC and LMA), foliar chemical traits (Chl,  $N_a$  and  $P_a$ ), photosynthetic traits ( $A_{\text{sat}}$ ,  $g_s$ ,  $V_{\text{cmax}}$  and  $J_{\text{max}}$ ), carbon reserves (soluble sugar, starch and NSC concentrations) and tree growth (stem diameter and height), followed by Tukey's multiple comparison test. A three-way ANOVA was used to assess the effects of changing precipitation, N deposition, species, and their interactions on photosynthetic and biochemical traits. Differences were statistically significant at  $P < 0.05$ . Data were analyzed using SPSS 24.0 (SPSS Inc., Chicago, IL, USA).

We estimated the phenotypic plasticity of variables by calculating the response ratio (RR) with changing precipitation, N deposition and their interactive effect (the mean values measured in P, LN, HN, PLN and PHN divided by the mean value measured in control). Spearman correlation analysis was used to analyze the correlation between RR of variables for the four tree species. Differences were statistically significant at  $P < 0.05$ . Data were analyzed using R (version 4.2.0; R Foundation for Statistical Computing).

## Results

### Environmental and soil variables

There were limited treatment effects on  $T_{\text{air}}$ , RH and  $T_{\text{soil}}$  (Figure 2a–d). Altering precipitation, and the interactive effect

of changing precipitation and low N deposition reduced SVWC compared with low N deposition in the dry season (Figure 2e and f,  $P < 0.05$ ). The available N concentrations in high N deposition were significantly higher than low N deposition, and the interactive effect of changing precipitation and low N deposition (Figure S1a available as Supplementary data at *Tree Physiology Online*,  $P < 0.05$ ). In addition, the interactive effect of changing precipitation and low N deposition decreased the available P concentrations compared with control and low N deposition (Figure S1b available as Supplementary data at *Tree Physiology Online*,  $P < 0.05$ ).

### Leaf morphological and biochemical traits

Overall, changing precipitation and species had significant effects on LT and LDMC, and LMA was affected by species (Table 1,  $P < 0.05$ ). *D. odorifera* exposed to low N deposition had higher leaf thickness (LT) and LMA than control (Figure S2c and k available as Supplementary data at *Tree Physiology Online*,  $P < 0.05$ ). *O. pinnata* under high N deposition displayed increasing LDMC compared with control (Figure S2h available as Supplementary data at *Tree Physiology Online*,  $P < 0.05$ ). When measurements were made at altering precipitation, N deposition and their interactive effects, *O. pinnata* had the lowest LT and LMA among the four tree species (Figure S2a–l available as Supplementary data at *Tree Physiology Online*).

Overall, Chl changed with species, and the concentrations of  $N_a$  and  $P_a$  were influenced by N deposition and species (Table 1,  $P < 0.05$ ). High N deposition induced lower Chl concentrations for *M. macclurei* (Figure 3b,  $P < 0.05$ ). *C. fissa* under changing precipitation exhibited lower foliar  $N_a$  concentrations than control (Figure 3e,  $P < 0.05$ ). Compared with control, low N deposition enhanced foliar  $N_a$  concentrations for *D. odorifera* and foliar  $P_a$  concentrations for *M. macclurei* (Figure 3g and j,  $P < 0.05$ ). *M. macclurei* exposed to changing precipitation and N deposition exhibited lowest Chl concentrations, while *D. odorifera* under low N deposition had highest foliar  $N_a$  concentrations (Figure 3a–l).

### Photosynthetic traits

In general, changing precipitation and species both affected  $A_{\text{sat}}$  (Table 1,  $P < 0.05$ ). Altering precipitation reduced  $A_{\text{sat}}$  for *C. fissa*, while the interactive effects of changing precipitation and N deposition enhanced  $A_{\text{sat}}$  for *C. fissa* compared with altering precipitation (Figure 4a,  $P < 0.05$ ). Altering precipitation and high N deposition induced lower  $A_{\text{sat}}$  for *D. odorifera* (Figure 4c,  $P < 0.05$ ). High N deposition increased  $A_{\text{sat}}$  for *O. pinnata* (Figure 4d,  $P < 0.05$ ).

$g_s$  was influenced by species (Table 1,  $P < 0.05$ ). Low N deposition significantly enhanced  $g_s$  for *M. macclurei* compared with control (Figure 4f,  $P < 0.01$ ). Higher  $g_s$  for *O. pinnata*

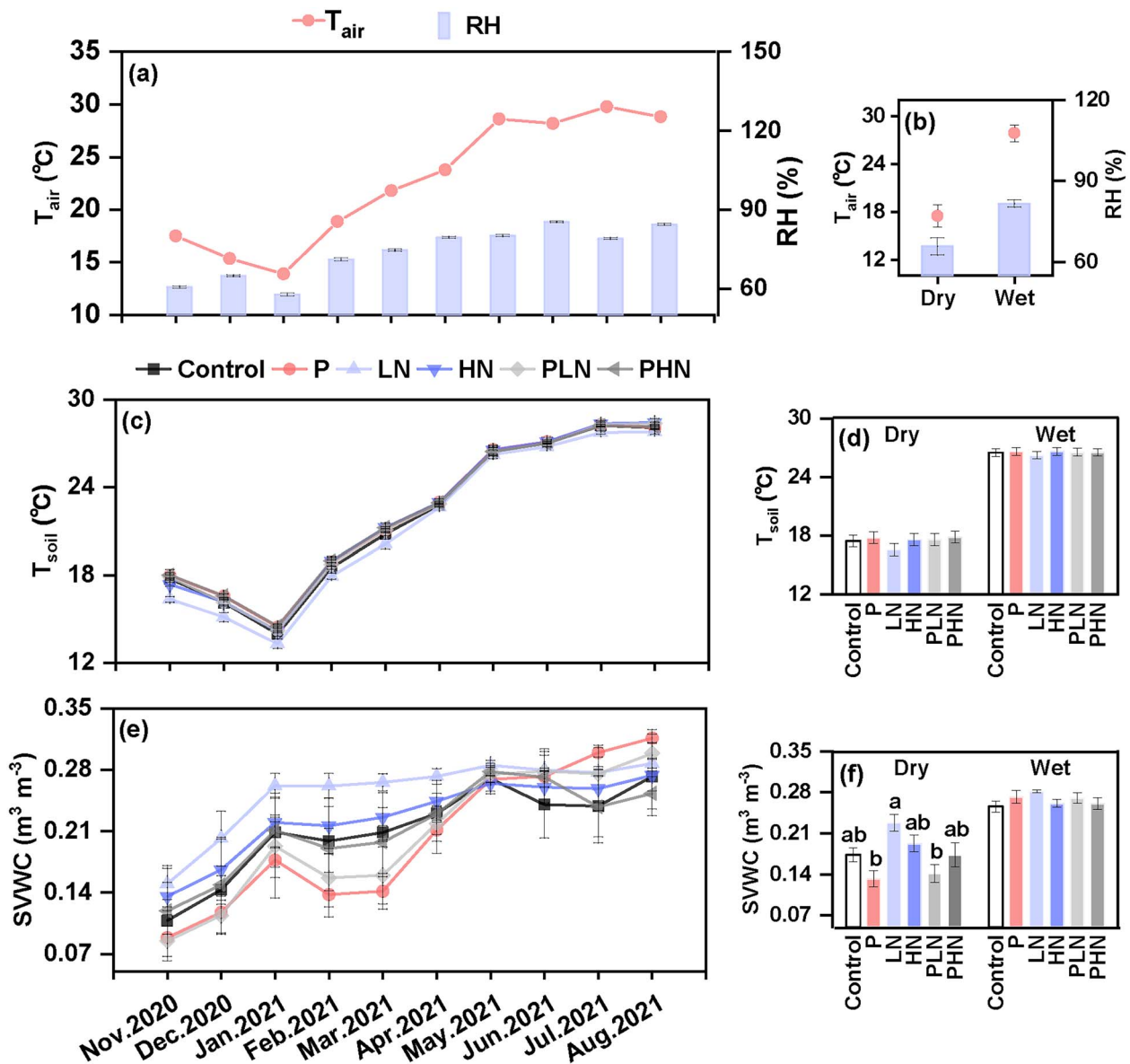


Figure 2. (a) Monthly average air temperature ( $T_{air}$ , °C,  $n = 3$ ) and humidity (RH, %,  $n = 3$ ) from November 2020 to August 2021; (b) the annual average  $T_{air}$  (°C,  $n = 30$ ) and RH (%) ( $n = 30$ ); (c) monthly average soil temperature ( $T_{soil}$ , °C,  $n = 3$ ) from November 2020 to August 2021 subjected to control, changing precipitation (P), low nitrogen (N) deposition (LN), high N deposition (HN), the interaction between changing precipitation and low N deposition (PLN), and the interaction between changing precipitation and high N deposition (PHN); (d) the annual average  $T_{soil}$  (°C,  $n = 15$ ) subjected to control, P, LN, HN, PLN and PHN in the dry and wet seasons, respectively; (e) monthly average SVWC ( $m^3 m^{-3}$ ,  $n = 3$ ) from November 2020 to August 2021 subjected to control, P, LN, HN, PLN and PHN; (f) the annual average SVWC ( $m^3 m^{-3}$ ,  $n = 15$ ) subjected to control, P, LN, HN, PLN and PHN in the dry and wet seasons, respectively. Different letters indicate significant differences ( $P < 0.05$ ) between means based on Tukey's multiple comparison test.

was observed in high N deposition than control (Figure 4h,  $P < 0.05$ ).

Changing precipitation and species both affected  $J_{max}$ , and  $V_{cmax}$  was obviously influenced by changes in precipitation (Table 1,  $P < 0.05$ ). *M. macclurei* under high N deposition exhibited lower  $J_{max}$  than low N deposition (Figure 4j,  $P < 0.01$ ). Altering precipitation led to declining  $J_{max}$  and  $V_{cmax}$  for *D. odorifera* compared with control (Figure 4k and o,  $P < 0.05$ ). *O. pinnata* exposed to high N deposition had higher

$V_{cmax}$  than control (Figure 4p,  $P < 0.05$ ). Among these four tree species, *O. pinnata* subjected to high N deposition had highest  $A_{sat}$ ,  $g_s$ ,  $J_{max}$  and  $V_{cmax}$  (Figure 4).

#### Nonstructural carbohydrates

Overall, changing precipitation and species both affected sugar concentrations, and starch and NSC concentrations were influenced by species (Table 1,  $P < 0.05$ ). Compared with altering precipitation, the interactive effect of changing precipitation and

Table 1. Effects of changing precipitation (P), additional nitrogen depositions (N), species (S) and their interactions on LT ( $\mu\text{m}$ ,  $n = 3$ ), leaf water content (LDMC, %,  $n = 3$ ), leaf mass per area (LMA,  $\text{g cm}^{-2}$ ,  $n = 3$ ), the total concentrations of chlorophyll a and chlorophyll b (Chl,  $\mu\text{g cm}^{-2}$ ,  $n = 3$ ), nitrogen concentrations per unit area ( $N_a$ ,  $\text{g m}^{-2}$ ,  $n = 3$ ), phosphorus concentrations per unit area ( $P_a$ ,  $\text{g m}^{-2}$ ,  $n = 3$ ), the light-saturated photosynthetic rate ( $A_{\text{sat}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ), stomatal conductance ( $g_s$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ), the area-based maximum rate of photosynthetic electron transport ( $J_{\text{max}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ), the area-based maximum rate photosynthetic Rubisco carboxylation ( $V_{\text{cmax}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ), the concentrations of soluble sugars (sugars,  $\text{mg g}^{-1}$ ,  $n = 3$ ), starch ( $\text{mg g}^{-1}$ ,  $n = 3$ ) and NSC ( $\text{mg g}^{-1}$ ,  $n = 3$ ), stem diameter (mm,  $n = 15$ ) and height (cm,  $n = 15$ ).

Variables	P	N	S	N × P	N × S	P × S	N × P × S
Foliar morphology							
LT	<b>6.46*</b>	1.17	<b>164.29***</b>	0.81	<b>3.87**</b>	<b>6.47***</b>	<b>6.10***</b>
LDMC	<b>5.44*</b>	2.17	<b>19.39***</b>	0.55	2.17	9.80	1.18
LMA	0.71	1.57	<b>38.98***</b>	0.08	1.32	2.30	<b>3.44**</b>
Chl	1.78	0.70	<b>19.34***</b>	0.29	1.43	0.67	1.08
Foliar chemistry							
$N_a$	3.63	<b>4.78*</b>	<b>73.62***</b>	0.47	1.61	1.81	<b>6.64***</b>
$P_a$	3.55	<b>3.55*</b>	<b>12.76***</b>	0.30	2.01	0.59	1.49
Photosynthesis							
$A_{\text{sat}}$	<b>15.47***</b>	1.05	<b>10.93***</b>	2.67	<b>6.72***</b>	<b>8.55***</b>	<b>6.30***</b>
$g_s$	2.96	3.02	<b>4.37**</b>	2.10	<b>2.55*</b>	2.71	<b>4.37**</b>
$J_{\text{max}}$	<b>5.59*</b>	0.53	<b>4.90**</b>	0.64	<b>3.26**</b>	2.54	<b>2.84*</b>
$V_{\text{cmax}}$	<b>8.59**</b>	0.91	2.01	0.71	<b>3.20*</b>	<b>3.92*</b>	<b>2.71*</b>
Carbon reserves							
Sugar	<b>12.40***</b>	0.58	<b>174.86***</b>	<b>6.14**</b>	<b>3.76**</b>	0.75	0.82
Starch	0.20	0.21	<b>56.35***</b>	1.66	0.31	0.41	0.83
NSC	2.48	0.02	<b>93.02***</b>	<b>3.44*</b>	1.04	0.25	0.87
Tree growth							
Stem diameter	2.52	2.14	<b>80.56***</b>	0.89	1.12	1.54	1.48
Height	2.32	2.78	<b>95.33***</b>	1.89	<b>3.32*</b>	2.31	<b>5.44**</b>

Numbers are *F*-values and asterisks indicate the level of significance (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). Bold indicates that significance is below 0.05.

high N deposition increased soluble sugar concentrations for *C. fissa* (Figure 5a,  $P < 0.05$ ). Low and high N depositions resulted in lower soluble sugar concentrations for *D. odorifera* than control, and the interactive effect of changing precipitation and high N deposition also decreased its soluble sugar concentrations compared with altering precipitation (Figure 5c,  $P < 0.05$ ). Low N deposition decreased starch and NSC concentrations for *O. pinnata* (Figure 5h and i,  $P < 0.05$ ). High N deposition, and the interactive effect of changing precipitation and high N deposition induced decreasing NSC concentrations for *D. odorifera* (Figure 5k,  $P < 0.05$ ). Lowest soluble sugar, starch and NSC concentrations were observed in *D. odorifera* subjected to all treatments (Figure 5).

### Tree growth

Overall, species had significant effects on stem diameter and height (Table 1,  $P < 0.05$ ). There was no significant change in stem diameter and height for the four tree species exposed to all treatments (Figure S3a–h available as Supplementary data at *Tree Physiology* Online).

### Relationships among response ratios of studied traits for the four tree species

The relationship among RR of studied traits was analyzed by Spearman correlation analysis. The RR of LMA was positively

correlated with RR of LT ( $R^2 = 0.46$ ,  $P < 0.001$ ). The RR of  $J_{\text{max}}$  was positively influenced by RR of Chl ( $R^2 = 0.16$ ,  $P < 0.001$ ). RR of  $V_{\text{cmax}}$  was positively related to RR of  $P_a$  ( $R^2 = 0.13$ ,  $P = 0.003$ ). RR of  $A_{\text{sat}}$  was positively affected by The RR of  $g_s$  ( $R^2 = 0.64$ ,  $P < 0.001$ ), The RR of  $J_{\text{max}}$  ( $R^2 = 0.30$ ,  $P < 0.001$ ) and RR of  $V_{\text{cmax}}$  ( $R^2 = 0.47$ ,  $P < 0.001$ ) (Figure 6).

### Phenotypic plasticity to main and interactive effects of changing precipitation and N deposition

The capacity of trees to alter photosynthetic and biochemical traits varied with species and treatments. *C. fissa* exhibited low phenotypic plasticity to altering precipitation but high to the interactive effects of changing precipitation and N deposition according to their RRs (Figure S4a available as Supplementary data at *Tree Physiology* Online). Phenotypic plasticity for *M. macclurei* was not affected by all treatments (Figure S4b available as Supplementary data at *Tree Physiology* Online). *D. odorifera* under all treatments had low plasticity (Figure S4c available as Supplementary data at *Tree Physiology* Online). *O. pinnata* exhibited highest plasticity to high N deposition (Figure S4d available as Supplementary data at *Tree Physiology* Online). Overall, *D. odorifera* was the most negatively influenced by all treatments due to lowest plasticity, while *O. pinnata* may be supported by high N deposition due to its highest plasticity

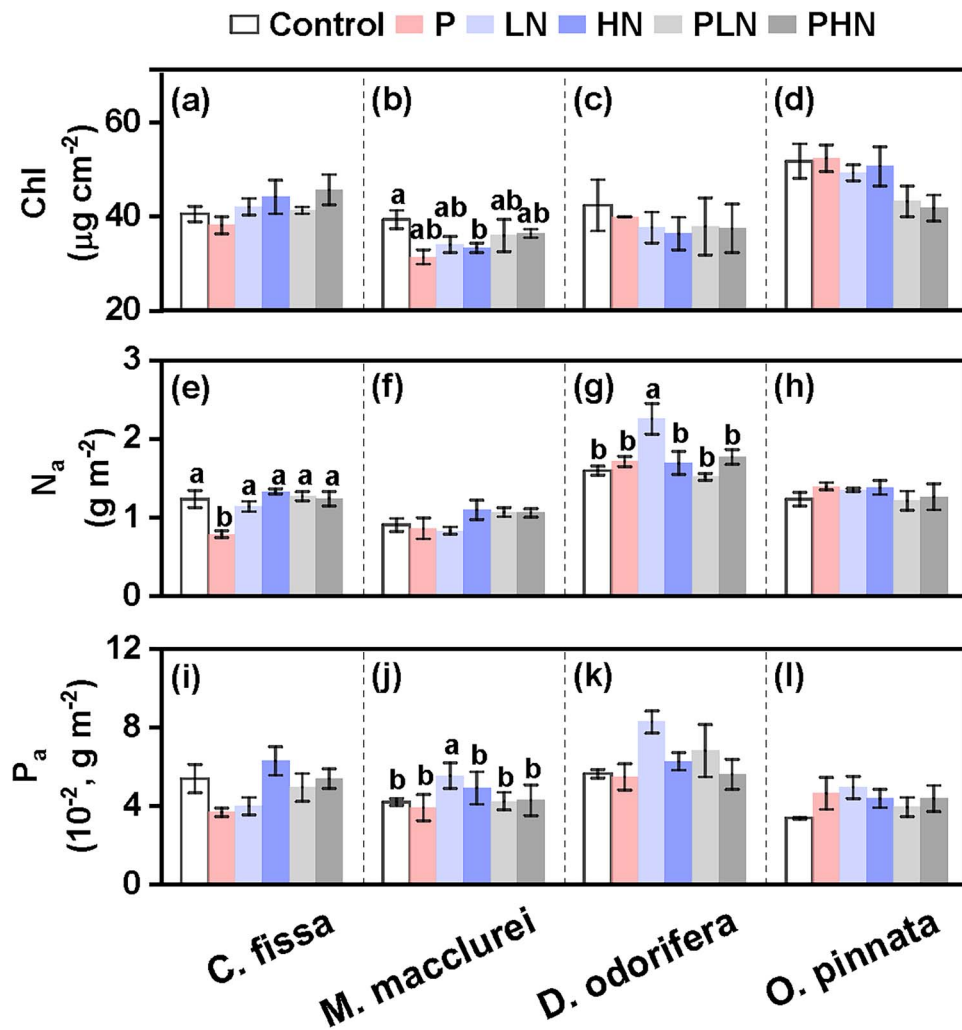


Figure 3. (a–d) The total concentrations of chlorophyll a and chlorophyll b (Chl,  $\mu\text{g cm}^{-2}$ ,  $n = 3$ ), (e–h) nitrogen concentrations per unit area ( $N_a$ ,  $\text{g m}^{-2}$ ,  $n = 3$ ) and (i–l) phosphorus concentrations per unit area ( $P_a$ ,  $\text{g m}^{-2}$ ,  $n = 3$ ) for *C. fissa*, *M. macclurei*, *D. odorifera* and *O. pinnata* in August 2021 subjected to control, changing precipitation (P), low nitrogen (N) deposition (LN), high N deposition (HN), the interaction between changing precipitation and low N deposition (PLN), and the interaction between changing precipitation and high N deposition (PHN). Values are means  $\pm$  standard errors. Different lowercase letters above the error bars indicate significant differences ( $P < 0.05$ ) in Chl,  $N_a$  and  $P_a$  among treatments for the four tree species based on Tukey's multiple comparison test.

(Figure S4 available as Supplementary data at *Tree Physiology* Online).

## Discussion

In this experiment, we found that (i) changing precipitation decreased  $A_{\text{sat}}$  for *C. fissa* and *D. odorifera* due to declining foliar  $N_a$  concentrations and photosynthetic capacity, respectively. (ii) Low N deposition had no significant impacts on photosynthetic traits for the four tree species. High N deposition reduced  $A_{\text{sat}}$  for *D. odorifera* due to declining  $J_{\text{max}}$ , leading to reduced soluble sugar and NSC concentrations. However, *O. pinnata* under high N deposition had higher  $A_{\text{sat}}$  related to increasing  $g_s$  and  $V_{\text{cmax}}$ , which enhanced starch and NSC concentrations. (iii) The interactions of changing precipitation and two levels of

N depositions both enhanced  $A_{\text{sat}}$  for *C. fissa* due to higher foliar  $N_a$  concentrations.

### Photosynthetic and biochemical responses to changing precipitation

Significant reductions in foliar  $N_a$  concentrations for *C. fissa* under changing precipitation may be due to limited capacity to acquire and transport N (De Long et al. 2019). Lower foliar  $N_a$  concentrations for *C. fissa* led to its declining  $A_{\text{sat}}$  (Ouyang et al. 2021), which may be due to lower Rubisco activity (Gao et al. 2018).  $g_s$  for *D. odorifera* may recover from changing precipitation according to the finding of X.M. Li et al. (2021). We found that reduced  $A_{\text{sat}}$  for *D. odorifera* was related to lower  $J_{\text{max}}$  and  $V_{\text{cmax}}$ , suggesting that declining photosynthesis for *D. odorifera* caused by altering precipitation was due to



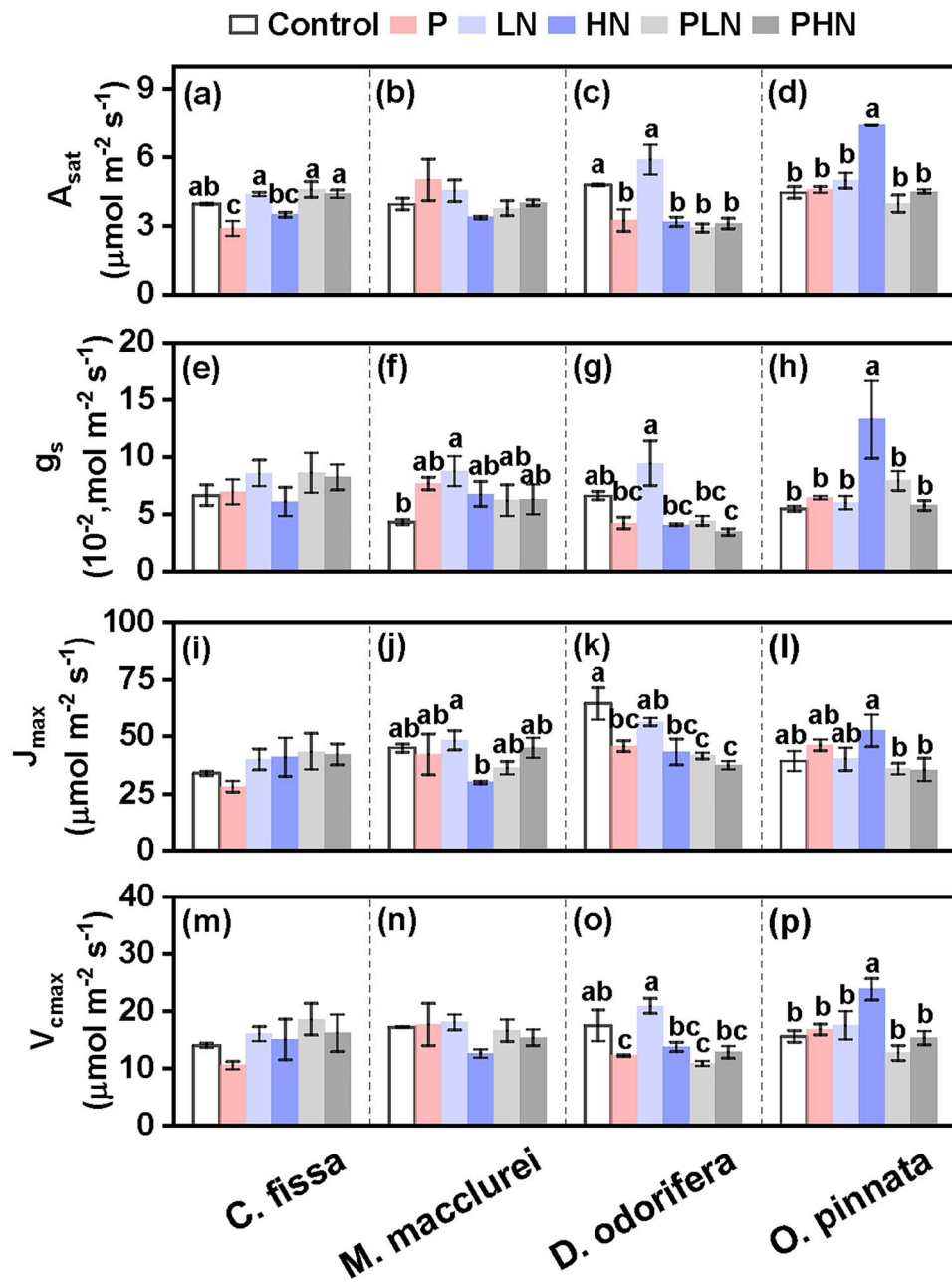


Figure 4. (a–d) The light-saturated photosynthetic rate ( $A_{sat}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ), (e–h) stomatal conductance ( $g_s$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ), (i–l) the area-based maximum rate of photosynthetic electron transport ( $J_{max}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ) and (m–p) the area-based maximum rate photosynthetic Rubisco carboxylation ( $V_{cmax}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 3$ ) for *C. fissa*, *M. macclurei*, *D. odorifera* and *O. pinnata* in August 2021 subjected to control, changing precipitation (P), low nitrogen (N) deposition (LN), high N deposition (HN), the interaction between changing precipitation and low N deposition (PLN), and the interaction between changing precipitation and high N deposition (PHN). Values are means  $\pm$  standard errors. Different lowercase letters above the error bars indicate significant differences ( $P < 0.05$ ) in  $A_{sat}$ ,  $g_s$ ,  $J_{max}$  and  $V_{cmax}$  among treatments for the four tree species based on Tukey's multiple comparison test.

biochemical traits rather than stomata (S.X. Zhou et al. 2014, Duan et al. 2019). Contrary to our findings, Drake et al. (2017) demonstrated that stomatal and biochemical limitations to photosynthesis simultaneously occurred during drying and wetting events through models. Photosynthesis for *C. fissa* and *D. odorifera* was reduced by changing precipitation, which may

inhibit their growth and survival, similar to findings by Bauman et al. (2022). In contrast, photosynthetic traits for *M. macclurei* and *O. pinnata* were not affected by changing precipitation, which may be driven by higher resistance to drought in the dry season (Limousin et al. 2013) or resilience to increasing precipitation in the wet season (X.M. Li et al. 2021).

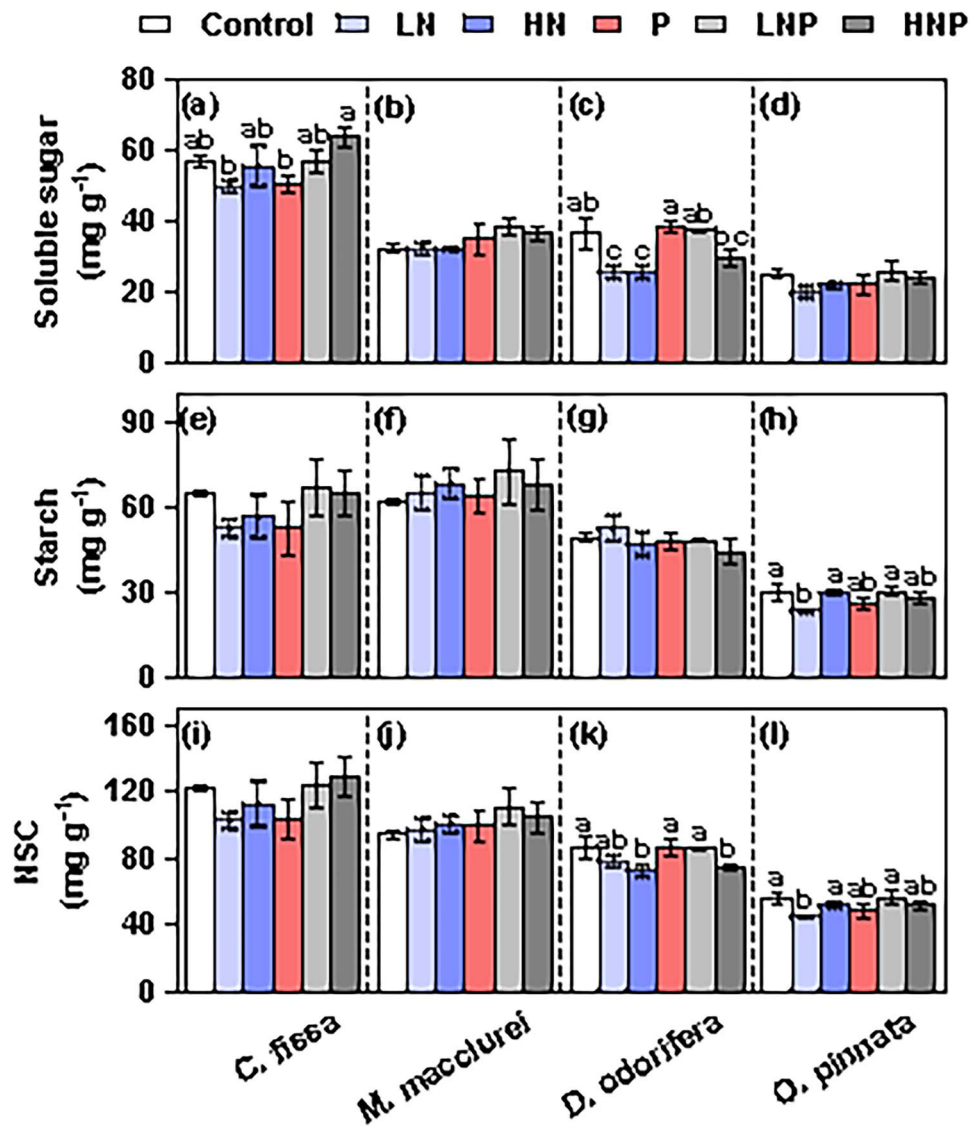


Figure 5. (a–d) The concentrations of soluble sugars (soluble sugars, mg g<sup>-1</sup>,  $n = 3$ ), (e–h) the concentrations of starch (starch, mg g<sup>-1</sup>,  $n = 3$ ) and (i–l) the concentrations of total nonstructural carbohydrates (NSC, mg g<sup>-1</sup>,  $n = 3$ ) for *C. fissa*, *M. macclurei*, *D. odorifera* and *O. pinnata* in August 2021 subjected to control, changing precipitation (P), low nitrogen (N) deposition (LN), high N deposition (HN), the interaction between changing precipitation and low N deposition (PLN), and the interaction between changing precipitation and high N deposition (PHN). Values are means  $\pm$  standard errors. Different lowercase letters above the error bars indicate significant differences ( $P < 0.05$ ) in soluble sugars, starch and NSC among treatments for the four tree species based on Tukey's multiple comparison test.

### Photosynthetic and biochemical responses to additional N deposition

Enhanced P uptake due to higher root phosphatase activity may lead to increasing foliar P<sub>a</sub> concentrations for *M. macclurei* under low additional N deposition (Zhang et al. 2019). Increased LT for *D. odorifera* caused by low N deposition led to higher LMA (Gorsuch et al. 2010). Although low N deposition had no significant effect on available N concentrations, higher foliar N<sub>a</sub> concentrations for *D. odorifera* under low additional N deposition might be attributable to increasing N uptake and resorption efficiency (Chen et al. 2015, Wang et al. 2021).

Higher foliar N<sub>a</sub> concentrations for *D. odorifera* induced by low additional N deposition may increase respiration, contributing to its lower soluble sugar concentrations (Du et al. 2020). Similarly, reduced starch and NSC concentrations caused by low additional N deposition were observed in *O. pinnata*, which might be due to increasing consumption of carbohydrates for maintaining higher respiration and growth (W.B. Li et al. 2018).

High N deposition significantly lowered photosynthetic traits for *D. odorifera*, but increased that for *O. pinnata*. Similar to Zhang et al. (2016), reduced Chl concentrations for *M. macclurei* under high N deposition may be due to lower

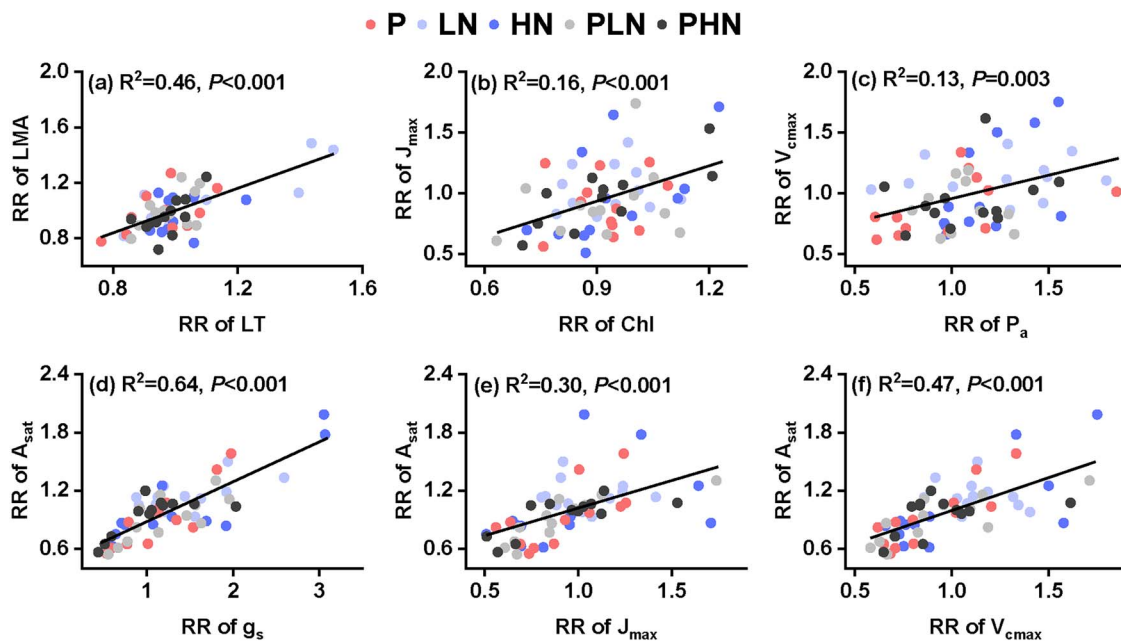


Figure 6. (a) Correlation analysis between the RR of LT ( $n = 15$ ) and RR of leaf mass per area (LMA,  $n = 15$ ); (b) correlation analysis between RR of the total concentrations of chlorophyll (Chl,  $n = 15$ ) and RR of the area-based maximum rate of photosynthetic electron transport ( $J_{\max}$ ,  $n = 15$ ); (c) correlation analysis between RR of phosphorus concentrations per unit area ( $P_a$ ,  $n = 15$ ) and RR of the area-based maximum rate photosynthetic Rubisco carboxylation ( $V_{\max}$ ,  $n = 15$ ); (d) correlation analysis between RR of stomatal conductance ( $g_s$ ,  $n = 15$ ) and RR of the light-saturated photosynthetic rate ( $A_{\text{sat}}$ ,  $n = 15$ ); (e) correlation analysis between RR of  $J_{\max}$  and RR of  $A_{\text{sat}}$ ; (f) correlation analysis between RR of  $V_{\max}$  and RR of  $A_{\text{sat}}$ .

macro-nutrient concentrations induced by soil acidification (Teglia et al. 2022). Root biomass allocation may be lowered by soil acidification achieved by high N deposition (Zhao et al. 2022), which may limit the capacity of N and P uptake and result in declining foliar  $P_a$  concentrations for *M. macclurei* and  $N_a$  concentrations for *D. odorifera* when compared with low N deposition (Wright et al. 2011, X.W. Li et al. 2021). Thus, lower foliar Chl and  $P_a$  concentrations for *M. macclurei* would contribute to its declining  $J_{\max}$  (Croft et al. 2017, Harmens et al. 2017). Similarly, reduced foliar  $N_a$  concentrations for *D. odorifera* were observed in high N deposition, which resulted in lower  $J_{\max}$  and further decreased  $A_{\text{sat}}$  (Feng and Dietze 2013, Fleischer et al. 2013). Additionally, high N deposition may reduce hydraulic conductance for *D. odorifera* (Domec et al. 2009, Wang et al. 2016), which decreased  $g_s$  and finally limited  $A_{\text{sat}}$  (Viet et al. 2012). Reduced soluble sugar and NSC concentrations for *D. odorifera* were attributed to its declining  $A_{\text{sat}}$  (Li et al. 2020, Zhang et al. 2021b). In contrast, high N deposition enhanced  $g_s$  for *O. pinnata* by increasing hydraulic conductance, ultimately resulting in higher  $A_{\text{sat}}$  (Zhang et al. 2021a). In addition, the enhancements in Rubisco activity and N allocation to Rubisco caused by increasing N availability may contribute to higher  $V_{\max}$  and  $A_{\text{sat}}$  for *O. pinnata* (Wang et al. 2017). High N deposition may exceed the N threshold of *D. odorifera* due to negative impacts on its photosynthetic traits, but not for *O. pinnata* (Fleischer et al. 2013, Wang et al. 2017).

#### Photosynthetic and biochemical responses to interactive effects of changing precipitation and N deposition

Higher foliar  $N_a$  concentrations were found in the interactive treatment of changing precipitation and low N deposition compared with altering precipitation, which could facilitate  $A_{\text{sat}}$  for *C. fissa* by enhancing Rubisco activity and content (Yamori et al. 2011, Gao et al. 2018). This result suggested that low N deposition could relieve N limitation for *C. fissa* induced by changing precipitation (Rivero-Villar et al. 2021). While the interactive effect of changing precipitation and low N deposition exerted no significant effect on photosynthetic traits for *D. odorifera* compared with changing precipitation, indicating that low N deposition cannot alleviate the negative impacts of changing precipitation on photosynthesis for *D. odorifera*.

*C. fissa* under the interactive effect of changing precipitation and high N deposition displayed higher  $A_{\text{sat}}$  correlated with higher foliar  $N_a$  concentrations than altering precipitation, which led to higher soluble sugar concentrations (Zhang et al. 2021a, 2021b) and helped it regulate osmotic pressure to better acclimate to environment (Hartmann and Trumbore 2016). The interactive effect of changing precipitation and high N deposition had no obvious effect on photosynthesis for *D. odorifera*. Lower soluble sugar and NSC concentrations for *D. odorifera* were observed in the interactive effect of changing precipitation and high N deposition compared with altering precipitation, which may be due to carbon allocation prioritizing respiration

and growth over storage (Zhang et al. 2021a) and further hinder physiological function and recovery (Adams et al. 2017, Kannenberg and Phillips 2020). These results showed that high N deposition did not exert negative impacts on subtropical trees subjected to changing precipitation.

### Implications for changing precipitation, N deposition and their interaction on fates of trees

Changes in photosynthetic and biochemical traits achieved by climate change may affect plant resistance and survival (Liu et al. 2017, Schulte-Uebbing and de Vries 2018), and substantial intraspecific differences may induce changes in ecosystem function (Aspinwall et al. 2015, Ramirez-Valiente and Cavender-Bares 2017, Baez and Homeier 2018, Cooper et al. 2019, Manu et al. 2022). Changes in precipitation, without changing total precipitation, may inhibit the growth of *C. fissa* and even increase its mortality risk due to reduced  $A_{\text{sat}}$  in future (Brando et al. 2010, Liu et al. 2017). Higher foliar  $N_a$  concentrations and  $A_{\text{sat}}$  for *C. fissa* were more evident in the interactive effects of changing precipitation and N deposition than the main effect of changing precipitation, indicating that N deposition could alleviate N limitation on photosynthesis for *C. fissa* caused by changing precipitation (Zhang et al. 2021a). Additionally, N deposition could facilitate water acquisition for *C. fissa* during altered seasonal precipitation, which was driven by increasing soluble sugar concentrations under the interaction of changing precipitation and N depositions (W.Q. He et al. 2020). Thus, adding N could relieve the negative impacts of changing precipitation on physiology and growth for *C. fissa*. The growth and survival for *D. odorifera* in future might be decreased by changing precipitation and N deposition, which was related to declining photosynthetic rate and capacity (Li et al. 2022). Additionally, *D. odorifera* may show low resistance to stress related to reduced soluble sugar and NSC concentrations (Hartmann and Trumbore 2016, Wiley et al. 2016). In contrast, high N deposition exerted positive impacts on photosynthetic traits for *O. pinnata*, indicating that the growth and survival of *O. pinnata* in subtropical plantations may benefit from increasing N deposition (Limpens et al. 2003, Sefcik et al. 2007). Overall, altering seasonal precipitation exerted the most negative effects on plant traits; among these four tree species, *D. odorifera* was most negatively affected by all treatments, while *M. macclurei* was least affected. Generally, mature trees exhibit greater resistance to environmental stress than seedlings (Niinemets 2010), while knowing the adaptation strategy of seedlings to climate change may help us predict species distribution of trees during forest regeneration in tropical plantations (Pozner et al. 2021).

### Authors' contributions

T.W. analyzed the data and wrote the manuscript. D.T. and J.X.L. revised the manuscript. Y.T.S., W.S., H.Y.L., X.L., S.M.Y. and X.J.L. contributed to data collection. J.H.Y., J.H. and J.X.L. designed the

experiment. All authors have read and agreed to the published version of the manuscript.

### Data availability statement

Data will be made available on request.

### Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

### Conflict of interest

The authors declare no conflict of interest in the preparation of this research paper.

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### References

- Adams HD, Zeppel MJB, Anderegg WRL et al. (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat Ecol Evol* 1:1285–1291.
- Anderson JM, Ingram J (1989) *Tropical soil biology and fertility*. CAB International, Wallingford.
- Arnon DI (1949) Copper enzymes in isolated chloroplasts—polyphenoloxidase in *Beta vulgaris*. *Plant Physiol* 24:1–15.
- Aspinwall MJ, Loik ME, de Dios VR, Tjoelker MG, Payton PR, Tissue DT (2015) Utilizing intraspecific variation in phenotypic plasticity to bolster agricultural and forest productivity under climate change. *Plant Cell Environ* 38:1752–1764.
- Baez S, Homeier J (2018) Functional traits determine tree growth and ecosystem productivity of a tropical montane forest: insights from a long-term nutrient manipulation experiment. *Glob Chang Biol* 24:399–409.
- Barker DH, Vanier C, Naumburg E, Charlet TN, Nielsen KM, Newingham BA, Smith SD (2006) Enhanced monsoon precipitation and nitrogen deposition affect leaf traits and photosynthesis differently in spring and summer in the desert shrub *Larrea tridentata*. *New Phytol* 169:799–808.
- Barros FO, Bittencourt PRL, Brum M et al. (2019) Hydraulic traits explain differential responses of Amazonian forests to the 2015 El Niño-induced drought. *New Phytol* 223:1253–1266.
- Bartlett MK, Scoffoni C, Ardy R, Zhang Y, Sun S, Cao K, Sack L (2012) Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods Ecol Evol* 3:880–888.
- Bauman D, Fortunel C, Cernusak LA et al. (2022) Tropical tree growth sensitivity to climate is driven by species intrinsic growth rate and leaf traits. *Glob Chang Biol* 28:1414–1432.

- Bobbink R, Hicks K, Galloway J et al. (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol Appl* 20:30–59.
- Borghetti M, Gentilesca T, Leonardi S, van Noije T, Rita A, Mencuccini M (2017) Long-term temporal relationships between environmental conditions and xylem functional traits: a meta-analysis across a range of woody species along climatic and nitrogen deposition gradients. *Tree Physiol* 37:4–17.
- Brando PM, Goetz SJ, Baccini A, Nepstad DC, Beck PSA, Christman MC (2010) Seasonal and interannual variability of climate and vegetation indices across the Amazon. *Proc Natl Acad Sci USA* 107:14685–14690.
- Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. *Soil Sci* 59:39–46.
- Bremner J, Mulvaney C (1982) Nitrogen-total methods of soil analysis, part 2, chemical and microbiological properties, 2nd edn. American Society of Agronomy, Inc., Madison.
- Chen FS, Niklas K, Liu Y, Fang XM, Wan SZ, Wang HM (2015) Nitrogen and phosphorus additions alter nutrient dynamics but not resorption efficiencies of Chinese fir leaves and twigs differing in age. *Tree Physiol* 35:1106–1117.
- Chen LC, Wang LJ, Martin CE, Lin TC (2019) Mediation of stemflow water and nutrient availabilities by epiphytes growing above other epiphytes in a subtropical forest. *Ecohydrology* 12:7. <https://doi.org/10.1002/eco.2140>.
- Chen SG, Zhang Y (2021) Water saving potential and economic viability assessment of rainwater harvesting system for four different climatic regions in China. *Water Supply* 21:386–400.
- Cooper HF, Grady KC, Cowan JA, Best RJ, Allan GJ, Whitham TG (2019) Genotypic variation in phenological plasticity: reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost. *Glob Chang Biol* 25:187–200.
- Croft H, Chen JM, Luo XZ, Bartlett P, Chen B, Staebler RM (2017) Leaf chlorophyll content as a proxy for leaf photosynthetic capacity. *Glob Chang Biol* 23:3513–3524.
- De Long JR, Semchenko M, Pritchard WJ et al. (2019) Drought soil legacy overrides maternal effects on plant growth. *Funct Ecol* 33:1400–1410.
- De Roo L, Salomon RL, Oleksyn J, Steppe K (2020) Woody tissue photosynthesis delays drought stress in *Populus tremula* trees and maintains starch reserves in branch xylem tissues. *New Phytol* 228:70–81.
- De Schrijver A, Verheyen K, Mertens J, Staelens J, Wuyts K, Muys B (2008) Nitrogen saturation and net ecosystem production. *Nature* 451:E1. <https://doi.org/10.1038/nature06578>.
- Deng Q, Hui DF, Dennis S, Reddy KC, Xu X (2017) Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: a meta-analysis. *Glob Ecol Biogeogr* 26:713–728.
- Domec JC, Palmroth S, Ward E, Maier CA, Therezien M, Oren R (2009) Acclimation of leaf hydraulic conductance and stomatal conductance of *Pinus taeda* (loblolly pine) to long-term growth in elevated CO<sub>2</sub> (free-air CO<sub>2</sub> enrichment) and N-fertilization. *Plant Cell Environ* 32:1500–1512.
- dos Santos VAHF, Ferreira MJ, Rodrigues JVFC, Garcia MN, Ceron JVB, Nelson BW, Saleska SR (2018) Causes of reduced leaf-level photosynthesis during strong El Niño drought in a Central Amazon forest. *Glob Chang Biol* 24:4266–4279.
- Drake JE, Aspinwall MJ, Pfautsch S et al. (2015) The capacity to cope with climate warming declines from temperate to tropical latitudes in two widely distributed *Eucalyptus* species. *Glob Chang Biol* 21:459–472.
- Drake JE, Power SA, Duursma RA et al. (2017) Stomatal and non-stomatal limitations of photosynthesis for four tree species under drought: a comparison of model formulations. *Agric For Meteorol* 247:454–466.
- Du Y, Lu RL, Xia JY (2020) Impacts of global environmental change drivers on non-structural carbohydrates in terrestrial plants. *Funct Ecol* 34:1525–1536.
- Duan HL, Li YY, Xu Y, Zhou SX, Liu J, Tissue DT, Liu JX (2019) Contrasting drought sensitivity and post-drought resilience among three co-occurring tree species in subtropical China. *Agric For Meteorol* 272-273:55–68.
- Duan HL, de Dios VR, Wang DF et al. (2022) Testing the limits of plant drought stress and subsequent recovery in four provenances of a widely distributed subtropical tree species. *Plant Cell Environ* 45:1187–1203.
- Duursma RA (2015) Plantecophys-an R package for analysing and modelling leaf gas exchange data. *PLoS One* 10:e0143346. <https://doi.org/10.1371/journal.pone.0143346>.
- Dziedek C, von Oheimb G, Calvo L, Fichtner A, Kriebitzsch WU, Marcos E, Pitz WT, Hardtle W (2016) Does excess nitrogen supply increase the drought sensitivity of (*Fagus sylvatica* L.) seedlings? *Plant Ecol* 217:393–405.
- Ebell LF (1969) Variation in total soluble sugars of conifer tissues with method of analysis. *Phytochemistry* 8:227–233.
- Elser JJ, Bracken MES, Cleland EE et al. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10:1135–1142.
- Feng XH, Dietze M (2013) Scale dependence in the effects of leaf ecophysiological traits on photosynthesis: Bayesian parameterization of photosynthesis models. *New Phytol* 200:1132–1144.
- Fleischer K, Rebel KT, van der Molen MK et al. (2013) The contribution of nitrogen deposition to the photosynthetic capacity of forests. *Global Biogeochem Cycles* 27:187–199.
- Fowler D, Pyle JA, Raven JA, Sutton MA (2013) The global nitrogen cycle in the twenty-first century: introduction. *Philos Trans R Soc B Biol Sci* 368:20130165. <https://doi.org/10.1098/rstb.2013.0165>.
- Gao JW, Wang F, Sun JY et al. (2018) Enhanced rubisco activation associated with maintenance of electron transport alleviates inhibition of photosynthesis under low nitrogen conditions in winter wheat seedlings. *J Exp Bot* 69:5477–5488.
- Ge XG, Wang CG, Wang LL, Zhou BZ, Cao YH, Xiao WF, Li MH (2022) Drought changes litter quantity and quality, and soil microbial activities to affect soil nutrients in moso bamboo forest. *Sci Total Environ* 838:156351. <https://doi.org/10.1016/j.scitotenv.2022.156351>.
- Gessler A, Schaub M, McDowell NG (2017) The role of nutrients in drought-induced tree mortality and recovery. *New Phytol* 214:513–520.
- Gorsuch PA, Pandey S, Atkin OK (2010) Temporal heterogeneity of cold acclimation phenotypes in *Arabidopsis* leaves. *Plant Cell Environ* 33:244–258.
- Guerrieri R, Mencuccini M, Sheppard LJ, Saurer M, Perks MP, Levy P, Sutton MA, Borghetti M, Grace J (2011) The legacy of enhanced N and S deposition as revealed by the combined analysis of  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$  and  $\delta^{15}\text{N}$  in tree rings. *Glob Chang Biol* 17:1946–1962.
- Hacke UG, Plavcova L, Almeida-Rodriguez A, King-Jones S, Zhou WC, Cooke JEK (2010) Influence of nitrogen fertilization on xylem traits and aquaporin expression in stems of hybrid poplar. *Tree Physiol* 30:1016–1025.
- Hansen J, Moller I (1975) Percolation of starch and soluble carbohydrates from plant-tissue for quantitative-determination with anthrone. *Anal Biochem* 68:87–94.
- Harmens H, Hayes F, Sharps K, Mills G, Calatayud V (2017) Leaf traits and photosynthetic responses of *Betula pendula* saplings to a range

- of ground-level ozone concentrations at a range of nitrogen loads. *J Plant Physiol* 211:42–52.
- Hartmann H, Trumbore S (2016) Understanding the roles of nonstructural carbohydrates in forest trees—from what we can measure to what we want to know. *New Phytol* 211:386–403.
- Harvey HP, van den Driessche R (1997) Nutrition, xylem cavitation and drought resistance in hybrid poplar. *Tree Physiol* 17:647–654.
- He NP, Li Y, Liu CC et al. (2020) Plant trait networks: improved resolution of the dimensionality of adaptation. *Trends Ecol Evol* 35:908–918.
- He PC, Wright IJ, Zhu SD et al. (2019) Leaf mechanical strength and photosynthetic capacity vary independently across 57 subtropical forest species with contrasting light requirements. *New Phytol* 223:607–618.
- He WQ, Liu HY, Qi Y, Liu F, Zhu XR (2020) Patterns in nonstructural carbohydrate contents at the tree organ level in response to drought duration. *Glob Chang Biol* 26:3627–3638.
- Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. *Nature* 470:479–485.
- Huang J, Zhang W, Zhu XM, Gilliam FS, Chen H, Lu XK, Mo JM (2015) Urbanization in China changes the composition and main sources of wet inorganic nitrogen deposition. *Environ Sci Pollut Res* 22:6526–6534.
- Huang J, Wang XM, Zheng MH, Mo JM (2021) 13-year nitrogen addition increases nonstructural carbon pools in subtropical forest trees in southern China. *For Ecol Manage* 481:118748. <https://doi.org/10.1016/j.foreco.2020.118748>.
- Huang ZQ, Liu B, Davis M, Sardans J, Penuelas J, Billings S (2016) Long-term nitrogen deposition linked to reduced water use efficiency in forests with low phosphorus availability. *New Phytol* 210:431–442.
- IPCC (2013) Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York, NY.
- Kannenberg SA, Phillips RP (2020) Non-structural carbohydrate pools not linked to hydraulic strategies or carbon supply in tree saplings during severe drought and subsequent recovery. *Tree Physiol* 40:259–271.
- Li G, Zhou GY, Wang X, Wu ZM, Qiu ZJ, Zhao HB, Liang RY (2011) Aboveground biomass of natural *Castanopsis fissa* community at the Xiaokeng of NanLing Mountain, Southern China. *Acta Ecol Sin* 31:3650–3658.
- Li P, Zhang L, Yu GR et al. (2018) Interactive effects of seasonal drought and nitrogen deposition on carbon fluxes in a subtropical evergreen coniferous forest in the East Asian monsoon region. *Agric For Meteorol* 263:90–99.
- Li RS, Yu D, Zhang YK et al. (2022) Investment of needle nitrogen to photosynthesis controls the nonlinear productivity response of young Chinese fir trees to nitrogen deposition. *Sci Total Environ* 840:156537. <https://doi.org/10.1016/j.scitotenv.2022.156537>.
- Li WB, Hartmann H, Adams HD et al. (2018) The sweet side of global change-dynamic responses of non-structural carbohydrates to drought, elevated CO<sub>2</sub> and nitrogen fertilization in tree species. *Tree Physiol* 38:1706–1723.
- Li WB, Zhang HX, Huang GZ, Liu RX, Wu HJ, Zhao CY, McDowell NG (2020) Effects of nitrogen enrichment on tree carbon allocation: a global synthesis. *Glob Ecol Biogeogr* 29:573–589.
- Li XM, Bao JT, Wang J, Blackman C, Tissue D (2021) Antecedent drought condition affects responses of plant physiology and growth to drought and post-drought recovery. *Front For Glob Change* 4. <https://doi.org/10.3389/ffgc.2021.704470>.
- Li XW, Zhang CL, Zhang BB et al. (2021) Canopy and understory nitrogen addition have different effects on fine root dynamics in a temperate forest: implications for soil carbon storage. *New Phytol* 231:1377–1386.
- Liang XS, Ma W, Hu JX, Zhang BC, Wang ZW, Lu XT (2022) Extreme drought exacerbates plant nitrogen-phosphorus imbalance in nitrogen enriched grassland. *Sci Total Environ* 849:157916. <https://doi.org/10.1016/j.scitotenv.2022.157916>.
- Liang XY, Zhang T, Lu XK et al. (2020) Global response patterns of plant photosynthesis to nitrogen addition: a meta-analysis. *Glob Chang Biol* 26:3585–3600.
- Limousin JM, Misson L, Lavoire AV, Martin NK, Rambal S (2010) Do photosynthetic limitations of evergreen *Quercus ilex* leaves change with long-term increased drought severity? *Plant Cell Environ* 33:863–875.
- Limousin JM, Bickford CP, Dickman LT et al. (2013) Regulation and acclimation of leaf gas exchange in a pinon-juniper woodland exposed to three different precipitation regimes. *Plant Cell Environ* 36:1812–1825.
- Limpens J, Berendse F, Klees H (2003) N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. *New Phytol* 157:339–347.
- Liu J, Wu NN, Wang H, Sun JF, Peng B, Jiang P, Bai E (2016) Nitrogen addition affects chemical compositions of plant tissues, litter and soil organic matter. *Ecology* 97:1796–1806.
- Liu YL, Parolari AJ, Kumar M, Huang CW, Katul GG, Porporato A (2017) Increasing atmospheric humidity and CO<sub>2</sub> concentration alleviate forest mortality risk. *Proc Natl Acad Sci USA* 114:9918–9923.
- Lu X, Gilliam FS, Yu G, Li L, Mao Q, Chen H, Mo J (2013) Long-term nitrogen addition decreases carbon leaching in a nitrogen-rich forest ecosystem. *Biogeosciences* 10:3931–3941.
- Lu XK, Vitousek PM, Mao QG et al. (2018) Plant acclimation to long-term high nitrogen deposition in an N-rich tropical forest. *Proc Natl Acad Sci USA* 115:5187–5192.
- Manu R, Corre MD, Aleeje A, Mwanjalolo MJG, Babweteera F, Veldkamp E, van Straaten O (2022) Responses of tree growth and biomass production to nutrient addition in a semi-deciduous tropical forest in Africa. *Ecology* 103:e3659. <https://doi.org/10.1002/ecy.3659>.
- Mao QG, Lu XK, Mo H, Gundersen P, Mo JM (2018) Effects of simulated N deposition on foliar nutrient status, N metabolism and photosynthetic capacity of three dominant understory plant species in a mature tropical forest. *Sci Total Environ* 610-611:555–562.
- Mao QG, Chen H, Wang C, Pang ZQ, Mo JM, Lu XK (2021) Effect of long-term nitrogen and phosphorus additions on understory plant nutrients in a primary tropical forest. *Forests* 12. <https://doi.org/10.3390/f12060803>.
- Martorell S, Diaz-Espejo A, Medrano H, Ball MC, Choat B (2014) Rapid hydraulic recovery in *Eucalyptus pauciflora* after drought: linkages between stem hydraulics and leaf gas exchange. *Plant Cell Environ* 37:617–626.
- McDowell NG, Sapes G, Pivovarov A et al. (2022) Mechanisms of woody-plant mortality under rising drought, CO<sub>2</sub> and vapour pressure deficit. *Nat Rev Earth Environ* 3:294–308.
- McGregor IR, Helcoski R, Kunert N et al. (2021) Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest. *New Phytol* 231:601–616.
- Nicotra AB, Atkin OK, Bonser SP et al. (2010) Plant phenotypic plasticity in a changing climate. *Trends Plant Sci* 15:684–692.
- Niinemets U (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For Ecol Manage* 260:1623–1639.
- Ouyang SN, Gessler A, Saurer M et al. (2021) Root carbon and nutrient homeostasis determines downy oak sapling survival and recovery from drought. *Tree Physiol* 41:1400–1412.

- Patrick LD, Ogle K, Bell CW, Zak J, Tissue D (2009) Physiological responses of two contrasting desert plant species to precipitation variability are differentially regulated by soil moisture and nitrogen dynamics. *Glob Chang Biol* 15:1214–1229.
- Pozner E, Bar-On P, Livne-Luzon S et al. (2021) A hidden mechanism of forest loss under climate change: the role of drought in eliminating forest regeneration at the edge of its distribution. *For Ecol Manage* 506:119966. <https://doi.org/10.1016/j.foreco.2021.119966>.
- Ramirez-Valiente JA, Cavender-Bares J (2017) Evolutionary trade-offs between drought resistance mechanisms across a precipitation gradient in a seasonally dry tropical oak (*Quercus oleoides*). *Tree Physiol* 37:889–901.
- Reed SC, Cleveland CC, Townsend AR (2011) Functional ecology of free-living nitrogen fixation: a contemporary perspective. *Annu Rev Ecol Evol Syst* 42:489–512.
- Rivero-Villar A, Ruiz-Suarez G, Templer PH, Souza V, Campo J (2021) Nitrogen cycling in tropical dry forests is sensitive to changes in rainfall regime and nitrogen deposition. *Biogeochemistry* 153:283–302.
- Schulte-Uebbing L, de Vries W (2018) Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate, and boreal forests: a meta-analysis. *Glob Chang Biol* 24:e416–e431.
- Sefcik LT, Zak DR, Ellsworth DS (2007) Seedling survival in a northern temperate forest understory is increased by elevated atmospheric carbon dioxide and atmospheric nitrogen deposition. *Glob Chang Biol* 13:132–146.
- Shi XM, Song L, Liu WY et al. (2017) Epiphytic bryophytes as bio-indicators of atmospheric nitrogen deposition in a subtropical montane cloud forest: response patterns, mechanism, and critical load. *Environ Pollut* 229:932–941.
- South China Botanical Garden, Chinese Academy of Sciences (2009) *Flora of Guangdong*. Guangdong Science and Technology Press, Guangzhou.
- Tang SB, Zhang LL, Lambers H, Ren WD, Lu XF, Hou EQ, Fu SL, Kuang YW (2020) Addition of nitrogen to canopy versus understory has different effects on leaf traits of understory plants in a subtropical evergreen broad-leaved forest. *J Ecol* 109:692–702.
- Teglia A, Di Baccio D, Matteucci G et al. (2022) Effects of simulated nitrogen deposition on the nutritional and physiological status of beech forests at two climatic contrasting sites in Italy. *Sci Total Environ* 834:155362. <https://doi.org/10.1016/j.scitotenv.2022.155362>.
- Tian D, Du EZ, Jiang L et al. (2018) Responses of forest ecosystems to increasing N deposition in China: a critical review. *Environ Pollut* 243:75–86.
- Tissue DT, Thomas RB, Strain BR (1993) Long-term effects of elevated CO<sub>2</sub> and nutrients on photosynthesis and rubisco in loblolly-pine seedlings. *Plant Cell Environ* 16:859–865.
- Viet HD, Kwak JH, Lee KS, Lim SS, Matsushima M, Chang SX, Lee KH, Choi WJ (2012) Foliar chemistry and tree ring  $\delta^{13}\text{C}$  of *Pinus densiflora* in relation to tree growth along a soil pH gradient. *Plant Soil* 363:101–112.
- Villar-Salvador P, Penuelas JL, Jacobs DF (2013) Nitrogen nutrition and drought hardening exert opposite effects on the stress tolerance of *Pinus pinea* L. seedlings. *Tree Physiol* 33:221–232.
- Wang AY, Wang M, Yang D, Song J, Zhang WW, Han SJ, Hao GY (2016) Responses of hydraulics at the whole-plant level to simulated nitrogen deposition of different levels in *Fraxinus mandshurica*. *Tree Physiol* 36:1045–1055.
- Wang M, Zhang WW, Li N, Liu YY, Zheng XB, Hao GY (2017) Photosynthesis and growth responses of *Fraxinus mandshurica* Rupr. seedlings to a gradient of simulated nitrogen deposition. *Ann For Sci* 75.
- Wang X, Wang B, Wang CZ et al. (2021) Canopy processing of N deposition increases short-term leaf N uptake and photosynthesis, but not long-term N retention for aspen seedlings. *New Phytol* 229:2601–2610.
- Wiley E, Rogers BJ, Hodgkinson R, Landhausser SM (2016) Nonstructural carbohydrate dynamics of lodgepole pine dying from mountain pine beetle attack. *New Phytol* 209:550–562.
- Wright SJ, Yavitt JB, Wurzburger N et al. (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* 92:1616–1625.
- Wu T, Tissue DT, Li X et al. (2020) Long-term effects of 7-year warming experiment in the field on leaf hydraulic and economic traits of subtropical tree species. *Glob Chang Biol* 26:7144–7157.
- Wu T, Tan ND, Tissue DT et al. (2022) Physiological traits and response strategies of four subtropical tree species exposed to drought. *Environ Exp Bot* 203:105046. <https://doi.org/10.1016/j.envexpbot.2022.105046>.
- Xu WZ, Deng XP, Xu BC (2013) Effects of water stress and fertilization on leaf gas exchange and photosynthetic light-response curves of *Bothriochloa ischaemum* L. *Photosynthetica* 51:603–612.
- Yamori W, Nagai T, Makino A (2011) The rate-limiting step for CO<sub>2</sub> assimilation at different temperatures is influenced by the leaf nitrogen content in several C<sub>3</sub> crop species. *Plant Cell Environ* 34:764–777.
- Yang Q, Liu JA, Wu Y, He YH, Dong WT, Su SS, Zhou GY (2016) *Dalbergia odorifera* forest associated species adaptability evaluation. *J Cent South Univ For Technol* 36:33–38.
- Zhang DY, Peng YF, Li F, Yang GB, Wang J, Yu JC, Zhou GY, Yang YH (2019) Trait identity and functional diversity co-drive response of ecosystem productivity to nitrogen enrichment. *J Ecol* 107:2402–2414.
- Zhang HX, McDowell NG, Adams HD et al. (2020) Divergences in hydraulic conductance and anatomical traits of stems and leaves in three temperate tree species coping with drought, N addition and their interactions. *Tree Physiol* 40:230–244.
- Zhang HX, Li XR, Guan DX, Wang AZ, Yuan FH, Wu JB (2021a) Nitrogen nutrition addition mitigated drought stress by improving carbon exchange and reserves among two temperate trees. *Agric For Meteorol* 311:108693. <https://doi.org/10.1016/j.agrfor.2021.108693>.
- Zhang HX, Yuan FH, Wu JB et al. (2021b) Responses of functional traits to seven-year nitrogen addition in two tree species: coordination of hydraulics, gas exchange and carbon reserves. *Tree Physiol* 41:190–205.
- Zhang YM, Zhou XB, Yin BF, Downing A (2016) Sensitivity of the xerophytic moss *Syntrichia caninervis* to prolonged simulated nitrogen deposition. *Ann Bot* 117:1153–1161.
- Zhang ZL, Liu GD, Zhang FC, Zheng CX, Ni FQ, Kang YH, Zeng Y (2014) Effects of nitrogen content on growth and hydraulic characteristics of peach (*Prunus persica* L.) seedlings under different soil moisture conditions. *J For Res* 25:365–375.
- Zhao XX, Tian QX, Huang L, Lin QL, Wu JJ, Liu F (2022) Fine-root functional trait response to nitrogen deposition across forest ecosystems: a meta-analysis. *Sci Total Environ* 844:157111. <https://doi.org/10.1016/j.scitotenv.2022.157111>.
- Zheng MH, Zhang W, Luo YQ, Li DJ, Wang SH, Huang J, Lu XK, Mo JM (2018) Stoichiometry controls symbiotic nitrogen fixation and its response to nitrogen inputs in a nitrogen-saturated forest. *Ecology* 99:2037–2046.
- Zheng MH, Chen H, Li DJ, Luo YQ, Mo JM (2020) Substrate stoichiometry determines nitrogen fixation throughout succession in southern Chinese forests. *Ecol Lett* 23:336–347.
- Zhou GY, Wei XH, Wu YP et al. (2011) Quantifying the hydrological responses to climate change in an intact forested

- small watershed in Southern China. *Glob Chang Biol* 17: 3736–3746.
- Zhou GY, Houlton BZ, Wang WT et al. (2014) Substantial reorganization of China's tropical and subtropical forests: based on the permanent plots. *Glob Chang Biol* 20:240–250.
- Zhou SX, Medlyn B, Sabate S, Sperlich D, Prentice IC (2014) Short-term water stress impacts on stomatal, mesophyll and biochemical limitations to photosynthesis differ consistently among tree species from contrasting climates. *Tree Physiol* 34: 1035–1046.