Direct and Indirect Effects of Long-Term Field Warming Methods on the Physical Environment and Biological Responses in a Subtropical Forest

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Tree growth may be affected by rising temperature. We conducted two long-term, independent warming experiments in a subtropical forest; one experiment used translocation warming and one experiment used infra-red (IR) warming. Both warming techniques are designed to increase air and soil temperatures (T_{air} and T_{soil}), but may also differentially affect other environmental variables, including soil volumetric water content (SVWC), air relative humidity (RH) and vapor pressure deficit (VPD). Hence, tree response ascribed to T_{air} and T_{soil} may be dependent on the indirect effects of the warming techniques. We experimentally tested these ideas on three native tree species (*Machilus breviflora*, *Syzygium rehderianum,* and *Schima superba*), which occurred at all experimental sites, in subtropical China. We translocated trees from higher elevation sites to lower elevation sites in the coniferous and broadleaf mixed forest (T_{air} was $0.68 \pm 0.05°C$ higher; 8 years) and mountain evergreen broadleaf forest (T_{air} was $0.95 \pm 0.06°C$ and $1.63 \pm 0.08°C$ higher; 8 years). IR warming was imposed at an experimental site in a monsoon evergreen broadleaf forest (T_{air} was $1.82 \pm 0.03°C$ higher; 5 years). We found that both methods directly increased T_{air} and T_{soil} (although to varying degrees), while translocation warming indirectly dried the soil (lower SVWC) and IR warming indirectly dried the air (lower RH and higher VPD). *Machilus breviflora* exposed to translocation warming exhibited lower photosynthesis due to higher T_{soil} and lower SVWC, leading to declining growth. Higher T_{air} and T_{soil} due to translocation warming increased photosynthesis and growth for *S. superba*. Trees exposed to IR

warming exhibited reduced photosynthesis due to lower RH (*M. breviflora*) and to lower stomatal conductance (g_s) as a function of higher T_{air} (*S. rehderianum* and *S. superba*). This study highlights the potential direct and indirect effects of different warming techniques on the physical environment of forest ecosystems, and subsequently their impacts on biological traits of trees. Hence, different warming techniques may provide different outcomes when assessing the impact of warming on trees in future climates.

Keywords: environmental variables, long-term field warming, infra-red warming, translocation warming, physiological plasticity, subtropical forest, tree growth

INTRODUCTION

The global average air temperature is predicted to increase by 1.5°C during 2030-2052 (IPCC, 2018). Tropical forests play a vital role in the global carbon cycle, accounting for more than one-third of terrestrial net primary productivity, due to high metabolic activity and species diversity (Slot and Winter, 2017). Warming conditions put tropical forests at risk, since increasing temperatures could be approaching the high-temperature threshold associated with narrower temperature tolerances in tropical trees (Cunningham and Reed, 2002). Given our limited understanding of tropical forest response to warming conditions, field warming experiments will greatly improve our knowledge regarding the adaptability of tropical trees to higher temperatures (Cavaleri et al., 2015; Kimball et al., 2018).

The patterns of forest ecosystem response may vary based on different warming treatments (Natali et al., 2011). Numerous warming methods, including greenhouses, open top chambers, infra-red (IR) heaters, cables and studies along elevation gradients, have been employed to investigate warming effects on tree physiology in forest ecosystems (Booth, 1988; De Frenne et al., 2010; Wang et al., 2017; Kimball et al., 2018). Translocating plants and soils from cooler high elevation sites to warmer low elevation sites may achieve changes in environmental variables, containing air temperature (T_{air}), soil temperature (T_{soil}) and soil volumetric water content (SVWC), anticipated in a warmer world, that more accurately reflect the potential effects of altered environmental variables on plant and soil processes (Luan et al., 2014; Nottingham et al., 2019; Wu et al., 2020b). Higher T_{air} and T_{soil} under translocation warming may alleviate lower temperature limitations to stomatal conductance (g_s) (Strand et al., 2002; Li et al., 2016) and photosynthetic capacity (Zhou et al., 2018), thereby facilitating plant growth. In contrast, some studies reported that warming temperatures reduced photosynthesis due to stomatal limitation induced by lower SVWC (Wertin et al., 2012; Reich et al., 2018). The reductions in nutrient availability and absorption, due to increasing T_{soil} and declining SVWC, could decrease foliar nutrient concentrations, leading to non-stomatal limitations to photosynthesis and inhibition of plant growth (Leon-Sanchez et al., 2019).

Infra-red (IR) heaters are commonly used to directly increase T_{air} and T_{soil}, but they may also indirectly increase leaf-to-air vapor pressure deficit (VPD) by reducing air relative humidity (RH) in the field (Kimball et al., 2008; de Boeck and Nijs, 2011). In these studies, photosynthetic capacity and rate may decline with increasing T_{air}, which may generate leaf temperatures that exceed the optimum temperature (T_{opt}), reduce leaf chlorophyll (Dusenge et al., 2020) and Rubisco concentrations (Stinziano and Way, 2017). In addition, increased VPD due to IR warming, can directly reduce g_s and photosynthesis independent of temperature, eventually limiting tree growth (Restaino et al., 2016; Grossiord et al., 2020). However, IR manipulation may have limited impact on T_{soil} in some tropical forests, due to canopy interception of radiation by high vegetation cover (Rich et al., 2015); changes in T_{soil} might also be buffered in soils with higher SVWC (McDaniel et al., 2013) and depth (Luo et al., 2010).

Previous studies have demonstrated that environmental variables other than T_{air} and T_{soil} regulate plant physiological response to warming (Day, 2000; Reich et al., 2018), but few studies have assessed the impact of different warming techniques on the physical environment and subsequent biological responses in tropical forest ecosystems. Greater understanding of tree response to altered environmental variables in the field, and whether these responses change with warming technique, will increase our capacity to predict the responses of tropical forest ecosystems to warming (Shaver et al., 2000; Wan et al., 2002). In 2012, we initiated field warming experiments in the subtropical forest of China (Dinghushan) by translocation (initiated in 2012) and IR (initiated in 2015) warming techniques, which increased T_{air} and T_{soil} by 1–2°C. Our previous results showed that biomass of *S. superba* was enhanced, while that of *S. rehderianum* and *Machilus breviflora* were not influenced by translocation warming in the coniferous and broadleaf mixed forest (CBMF) (Li et al., 2017). Translocation warming increased photosynthesis and growth of *S. superba* and *S. rehderianum*, but reduced that for *M. breviflora* in the mountain evergreen broadleaf forest (MEBF) (Wu et al., 2020a,b). Infra-red warming reduced photosynthesis of *Schima superba*, but not for *Syzygium rehderianum* in the monsoon evergreen broadleaf forest (MEBMF) (Wu et al., 2018).

In this study, we analyzed the impacts of two independent experiments that compared two warming techniques – translocation (CBMF and MEBF) and IR (MEBMF) – on the physical environment and subsequent impacts on plant physiology and growth for the three common tree species (*M. breviflora*, *S. rehderianum,* and *S. superba*). We recognize that it would have been ideal to conduct a single experiment that directly compared translocation and IR warming within the same biological community in identical soils, but that was not possible given restrictions on using IR warming within the biological reserve. However, the two experiments reported here provide insight into potential, differential indirect effects of these warming techniques on the physical environment. Here,

we report physiological data (last 3 years) and growth data (last 5 years) from the two experimental warming treatments. Our objectives were to determine the direct and indirect effects of the warming techniques on the air and soil environment, and if they differed, to determine whether this had variable impacts on tree physiology and growth. Importantly, we need to know if the warming technique affects the outcome of studies on tree responses to future climate change scenarios.

MATERIALS AND METHODS

Study Site

This study was conducted at the Dinghushan Biosphere Reserve (DBR, 23°09'N–23°11'N, 112°30'E–112°33'E) in southern China, which exhibits a typical tropical monsoon climate. 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) (Liu et al., 2017; Wu et al., 2020a). There are three major tropical forest types in DBR, including the monsoon evergreen broadleaf forest (MEBMF, 30 m altitude above sea level), coniferous and broadleaf mixed forest (CBMF, 300 m altitude above sea level) and mountain evergreen broadleaf forest (MEBF, 600 m altitude above sea level). During 1954–2009, the mean annual temperature at the DBR has increased by approximately 1°C (Zhou et al., 2011).

Warming Experiment Design

Translocation Warming Experiment

T_{air} and T_{soil} of CBMF and MEBF were increased by translocation warming. Coniferous and broadleaf mixed forest was translocated from the altitude of 300 m (current climate) to 30 m (T_{air} was 0.68 ± 0.05°C higher). The three plots of CBMF were constructed at 300 m elevation site and the other three plots of CBMF were constructed at 30 m elevation site. MEBF was translocated from the altitude of 600 m (current climate) to 300 (T_{air} was 0.95 ± 0.06°C higher) and 30 m (T_{air} was 1.63 ± 0.08°C higher). The three plots of MEBF were constructed at 600 m, 300 m, and 30 m elevation sites, respectively (**Figure 1**). The site was in an open area where they were exposed to full natural sunlight and rain. Each chamber had an edge length of 3 m, with a 0.8-m-deep belowground section. The belowground section was surrounded by a concrete brick wall covered with ceramic tiles to prevent lateral and vertical movement of water and nutrients from the surrounding soil. There was a hole at the top and another hole at the bottom of the wall. The holes (inner diameter: 2 cm) were connected to stainless-steel water collection boxes to collect surface and ground water samples. Both holes were capped by a 2-mm plastic net to prevent losses other than leachates.

In April 2012, soils from three different layers (0–20, 20–40, and 40–70 cm) were collected from the CBMF at approximately 300 m altitude, homogenized separately, and then transplanted by individual layers into the macrocosm model CBMF (300 and 30 m), resulting in 6.3 m^3 of soil in each chamber. Soils were allowed to settle and develop structure for one year before

seedlings were added to the plots. Similarly, soils were collected from the MEBF at approximately 600 m altitude, and then translocated to model MEBF (600, 300 and 30 m). In May 2013, 1-year old seedlings of *M. breviflora*, *S. rehderianum*, and *S. superba* (similar size, stem basal diameter was approximately 4 mm and height was approximately 30 cm) were collected in the field, according to their occurrence and distribution in CBMF (300 m) and MEBF (600 m). Then, six individuals per species were randomly transplanted into model CBMF and MEBF at each elevation. Each individual plant was transplanted in a randomized block design so that all plants received approximately equal light. A litter trap (0.3 × 0.3 m) with a mesh size of 1 mm was randomly placed in each plot about 0.3 m above the soil surface to collect litter from June 2014. Further details of the experimental design can be found in Liu et al. (2017). Here, we present data on physiological traits (last 3 years) and growth (last 5 years) of the experiment.

T_{air}, RH and water vapor pressure (e) of CBMF and MEBF were monitored and recorded at each elevation, using a HMP155A temperature probe. T_{soil} at 5-cm depth was automatically recorded in each chamber using Campbell 109 constantan-copper thermocouples (Campbell Scientific, Logan, UT, United States). SVWC at 5-cm depth was measured at the same depth using time domain reflectometer probes (CS616). Vapor pressure deficit (VPD) was calculated as: e/RH – e (e: water vapor pressure; RH: air relative humidity). Photosynthetically active radiation (PAR) and rainfall were recorded at each elevation. All data on microclimate were recorded every half hour using data loggers (CR1000, Cambell Scientific) and analyzed for the last 5 years.

Infra-Red Warming Experiment

T_{air} and T_{soil} of MEBMF were increased by IR heaters. At an altitude of 30 m, three plots of MEBMF were sealed by transparent glass to form open top chambers (OTCs, 3 m in height, T_{air} was 1.82 ± 0.03°C higher) in March 2012, which were heated by forced air blown over closed-loop resistance wires surrounding the OTCs at 1.5 m in height to simulate a warming environment in 2014; the remaining three plots were used as controls (Wu et al., 2018) (**Figure 1**). Three different soil layers and seedlings of *M. breviflora*, *S. rehderianum* and *S. superb* were collected from the MEBMF at an altitude of 30 m. Soil filling and seedlings planting were taken in MEBMF as indicated in CBMF and MEBF (shown above). Here, we present data on physiological traits (last 3 years) and growth (last 5 years) of the experiment.

T_{air}, RH and e of MEBMF (controls) were monitored and recorded at 30 m elevation, and air environmental variables of MEBMF (+ 1.82°C, warming treatment) were monitored and recorded in each chamber. T_{soil} and SVWC at 5-cm depth were automatically recorded in each chamber. Data were recorded hourly using data loggers (CR1000, Campbell Scientific) and analyzed for the last 5 years.

We were not allowed to use IR warming at the CBMF and MEBF sites, located within the core area of the Biosphere Reserve, due to potential fire risk from faulty IR heaters. Therefore, we translocated seedlings of *M. breviflora*, *S. rehderianum* and *S. superb* and soils from the CBMF (300 m) and MEBF

FIGURE 1 | (A) Schematic of the long-term filed warming experiments in Dinghushan, China: higher temperatures for coniferous and broadleaf mixed forest (CBMF) and mountain evergreen broadleaf forest (MEBF) were achieved by translocation warming; while higher temperatures for monsoon evergreen broadleaf forest (MEBMF) was achieved by infrared (IR) warming. **(B)** the conceptual diagram for the effects of environmental variables caused by translocation and infrared warming on biological traits. Tranloscation warming increased T_{air} and T_{soil} but decreased SVWC; IR warming enhanced T_{air} and VPD but reduced RH.

(600 m) sites to lower elevations to achieve natural increases in temperatures. However, we were able to use IR warming at the MEBMF site because it was not located within the core of the Reserve. Although this was not an ideal experimental design, it still allowed us to assess the indirect effects of the two warming treatments on the physical environment and subsequent biological response.

Leaf Gas Exchange Measurements

The net assimilation rate-intercellular CO_2 concentration (A-C_i) curves were generated on fully expanded leaves from three or four seedlings per chamber per species ($n = 3$–4) between 0900 and 1400 h on clear days in August 2019 and 2020 (last 2 years), using a portable open path gas exchange system (Licor-6400, Li-Cor, Lincoln, NE, United States) equipped with a leaf

chamber fluorometer (6400-40). A-C_i curves were generated at saturating PAR of 1500 μmol m^{-2} s^{-1}, leaf temperature (25°C) and ambient relative humidity inside the leaf chamber (~60%). A-C_i curves were generated using leaf chamber CO_2 values of (in order): 400, 200, 100, 50, 400, 400, 600, 800, 1200, 1400, 1600, and 1800 μmol mol^{-1}. The maximum rate of photosynthetic Rubisco carboxylation (V_{max}, μmol m^{-2} s^{-1}) and apparent maximum rate of photosynthetic electron transport (J_{max}, μmol m^{-2} s^{-1}) were estimated from A-C_i curves.

Leaf light-saturated photosynthesis (A_{sat}, μmol m^{-2} s^{-1}), stomatal conductance (g_s, mol m^{-2} s^{-1}) and transpiration rate (E, mmol m^{-2} s^{-1}) were measured in August 2018, 2019 and 2020 (last 3 years), at saturating PAR of 1500 μmol m^{-2} s^{-1}, CO_2 of 400 μmol mol^{-1} and leaf temperature (25 °C). Instantaneous water-use efficiency (iWUE, μmol m mol^{-1}) was calculated as A_{sat}/g_s.

Measurements of Nutrient and Chlorophyll Concentrations

For gas exchange measurements, opposite leaves were harvested for chemical analyses in August 2019 and 2020 (last 2 years). Five leaf discs (6 mm diameter) from one individual per treatment per chamber were cut and dipped into 5 mL of 80% acetone to determine the chlorophyll concentrations [$Chl_{(a+b)}$, μg cm^{-2}] (Arnon, 1949).

Some leaves were used to determine leaf area (LA, cm^2), with petioles removed, using a leaf area meter (Li-3000A; Li-Cor, Lincoln, NE, United States). The leaves were oven-dried for one week at 65°C, and dry biomass (LD, g) was determined. Leaf mass area (LMA, g cm^{-2}) was calculated as LD/LA. Oven-dried foliar samples were ground to fine powder in a ball mill. Leaf mass-based nitrogen (N) concentration (N_{mass}, g kg^{-1}) was measured using the Kjeldahl method (Bremner and Mulvaney, 1982). Leaf mass-based phosphorus (P) concentration (P_{mass}, g kg^{-1}) was measured photometrically after samples were digested with H_2SO_4-H_2O_2 (Anderson and Ingram, 1989). Leaf area-based N concentration (N_a, mg cm^{-2}) was calculated as $N_{mass} \times$ LMA, and leaf area-based P concentration (P_a, mg cm^{-2}) was calculated as $P_{mass} \times$ LMA.

Measurement of Anatomical Traits

Three leaves of each species from randomly selected individuals per chamber were measured for stomatal anatomical traits in June 2019 and 2020 (last 2 years), using image analysis software (OPTPro 2012 4.0, Optec XTS20, Chongqing Optec Instrument, China). Stomatal density (SD), guard cell width (W, μm) and length (L, μm) were also measured using the image analysis software. Stomatal size (SS, μm^2) was defined as L * 2 * W (Franks and Beerling, 2009; Wu et al., 2018).

Soil Properties

We collected soils (0–10 cm) in the wet season (June) from 2015 to 2019. Soil cores (inner diameter: 3.5 cm) from each layer of each chamber were combined, homogenized. There were three replicates per treatments for each forest type.

A soil subsample was air-dried before determination of pH, total N (TN, g kg^{-1}), total P (TP, g kg^{-1}), soil available N concentration (AN, mg kg^{-1}) and soil available P concentration (AP, mg kg^{-1}). Soil pH was measured at a soil-to-water ratio of 1:2.5. After digestion with concentrated sulfuric acid, TN was determined by the Kjeldahl method (Bremner and Mulvaney, 1982) and TP by an ultraviolet spectrophotometer (Lambda650/250, PE, United States) (Anderson and Ingram, 1989). After soil was extracted with 1 M KCl solution, AN was determined colorimetrically (Liu et al., 2017). AP was extracted with 0.03 M NH_4F and 0.025 M HCl and measured by inductively coupled plasma optical emission spectrometer (ICP-OES) (Optima 2000 DV, Perkin Elmer, United States) (Bray and Kurtz, 1945).

Growth Measurements

The stem basal diameter (D, mm) and height (H, cm) of all seedlings per species in each chamber were measured in June (wet season) and December (dry season) from 2015 to 2019. The stem volume (V, cm^3) of all seedlings per species in each chamber was also calculated as 3.14 * (D/2) $\hat{}$ 2 * H.

Statistical Analysis

Data were assessed using Kolmogorov-Smironv 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 warming effect on T_{air}, T_{soil}, RH, SVWC, VPD, PAR and rainfall in the wet and dry seasons in the three forest types. Significant differences in foliar morphological, physiological traits and soil properties among the treatments were analyzed using a one-way ANOVA, followed by Tukey's multiple comparison test. A repeated measures general liner model was used to evaluate the effects of warming and time on D^2H for the four tree species. Data were analyzed using SPSS 24.0 (SPSS Inc., Chicago, IL, United States). The mixed liner model was used to analyze the main effects of environmental variables on the responses of photosynthetic capacity (J_{max} and V_{max}), gas exchange (A_{sat}, g_s, E and iWUE), biochemistry (concentrations of $Chl_{(a+b)}$, N_a and P_a) and stomatal morphology (SD and SS). Differences were considered to be statistically significant at $P < 0.05$. Data were analyzed using R (R 3.5.3). We calculated the response ratio (RR) of AN and AP with warming (mean value measured in the warmed environment divided by the mean value measured in the control environment).

The relative importance of stomatal traits (g_s, SD and SS), biochemistry [concentrations of $Chl_{(a+b)}$, N_a and P_a], concentrations of soil nutrient availability (AN and AP) and soil types (lateritic soil and yellow soil) in explaining variations in photosynthesis (J_{max}, V_{max} and A_{sat}), was determined using variation partitioning analysis (VPA) and redundancy analysis (RDA) using the "varpart" function in the "Vegan" package in R (R 3.5.3).

RESULTS

Environmental Variables

Under translocation warming, T_{air} in CBMF at 30 m was $0.86 \pm 0.07°C$ (wet season), $0.52 \pm 0.02°C$ (dry season) and $0.68 \pm 0.05°C$ (annual) higher compared to temperatures at 300 m, but they were not significantly different (**Figure 2A**). T_{soil} in CBMF at 30 m was $1.35 \pm 0.01°C$ (wet season) higher compared to temperature at 300 m, and although it was higher ($0.68 \pm 0.01°C$) in the dry season, it was not significantly different (**Figure 2B**). T_{air} in MEBF at 300 m was $1.01 \pm 0.01°C$ (wet season) and $0.95 \pm 0.06°C$ (annual) higher, and at 30 m was $1.87 \pm 0.08°C$ (wet season) and $1.63 \pm 0.08°C$ (annual) higher compared to temperatures at 600 m. T_{air} trended higher at 300 m ($0.78 \pm 0.10°C$) and 30 m ($1.3 \pm 0.08°C$) compared to temperature at 600 m in the dry season, but it was not significantly different (**Figure 2C**). T_{soil} in MEBF at 300 m was $0.78 \pm 0.01°C$ (wet season) and $1.46 \pm 0.01°C$ (dry season) higher, and at 30 m was $2.22 \pm 0.01°C$ (wet season) and $2.50 \pm 0.01°C$ (dry season) higher compared to temperatures at 600 m (**Figure 2D**). In MEBF and CBMF, the average monthly

soil SVWC was significantly lower at 30 m compared to 600 and 300 m, in the wet and dry seasons ($P < 0.05$, **Table 1**).

During the last 5 years of the IR warming experiment, T_{air} in MEBMF in the warming treatment was $1.59 \pm 0.01°C$ (wet season), $2.12 \pm 0.05°C$ (dry season) and $1.82 \pm 0.03°C$ (annual) higher compared to temperatures in the control plots (**Figure 2E**). T_{soil} in the IR warming treatment was $1.06 \pm 0.02°C$ (dry season) higher compared to temperature in the control plots, and although it trended higher ($0.38 \pm 0.01°C$) in the wet season, it was not significantly different (**Figure 2F**). Infra-red warming treatments significantly reduced the average monthly air RH, **and** increased VPD, of MEBMF in the wet and dry seasons ($P < 0.05$, **Table 1**).

Physiological, Stomatal Anatomical and Plant Chemical Traits

In CBMF, $0.68°C$ of translocation warming induced higher g_s for *S. superba*, but no effects on stomatal density and smaller stomatal size for *M. breviflora* and *S. rehderianum* (**Figures 3A–C**). The $0.68°C$ translocation warming treatment reduced transpiration of *M. breviflora* but enhanced that of

FIGURE 2 | Monthly mean air temperature (T_{air}, °C) and monthly mean soil temperature (T_{soil}, °C) at **(A,B)** coniferous and broadleaf mixed forest (CBMF), **(C,D)** mountain evergreen broadleaf forest (MEBF) and **(E,F)** monsoon evergreen broadleaf forest (MEBMF) from 2015 to 2020.
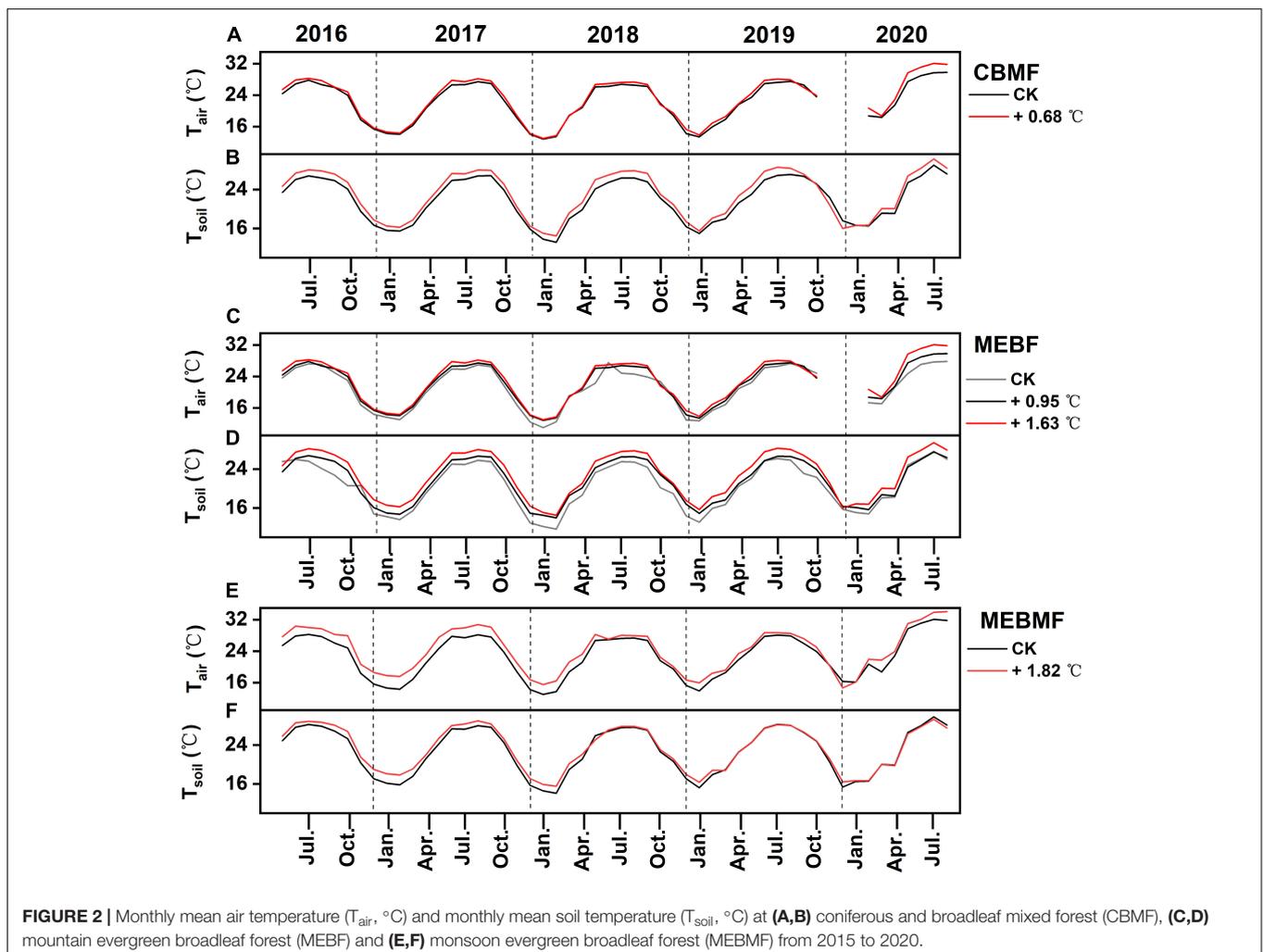
TABLE 1 | The average monthly air temperature (T_{air}, °C, $n = 24$), soil temperature (T_{soil}, °C, $n = 72$), air relative humidity (RH, %, $n = 24$), soil volumetric water content (SVWC, $m^3\ m^{-3}$, $n = 72$), vapor pressure deficit (VPD, kPa, $n = 24$), photosynthetically active radiation (PAR, $\mu mol\ m^{-2}\ s^{-1}$, $n = 24$) and rainfall (mm, $n = 24$) in the wet and dry seasons from 2016 to 2020 for coniferous and broadleaf forest (CBMF), mountain evergreen broadleaf forest (MEBF) and monsoon evergreen broadleaf forest (MEBMF).

	Translocation-CBMF			Translocation-MEBF			IR-MEBMF	
	Wet	**Drought**		**Wet**	**Drought**		**Wet**	**Drought**
T_{air}			**T_{air}**			**T_{air}**		
			600 m	**24.98 ± 0.45**[b]	16.59 ± 0.86			
300 m	25.99 ± 0.46	17.37 ± 0.76	300 m	**25.99 ± 0.46**[ab]	17.37 ± 0.76	Control	**26.85 ± 0.53**[b]	**17.89 ± 0.78**[b]
30 m	26.85 ± 0.53	17.89 ± 0.78	30 m	**26.85 ± 0.53**[a]	17.89 ± 0.78	Warming	**28.44 ± 0.54**[a]	**20.01 ± 0.73**[a]
T_{soil}			**T_{soil}**			**T_{soil}**		
			600 m	**24.09 ± 0.27**[b]	**16.48 ± 0.37**[b]			
300 m	**25.13 ± 0.27**[b]	18.27 ± 0.38	300 m	**24.87 ± 0.26**[b]	**17.94 ± 0.37**[a]	Control	26.33 ± 0.27	**18.59 ± 0.38**[b]
30 m	**26.48 ± 0.27**[a]	18.95 ± 0.38	30 m	**26.31 ± 0.26**[a]	**18.98 ± 0.38**[a]	Warming	26.71 ± 0.26	**19.65 ± 0.36**[a]
RH			**RH**			**RH**		
			600 m	88.09 ± 2.11	81.91 ± 3.36			
300 m	84.44 ± 1.09	81.59 ± 1.53	300 m	84.44 ± 1.09	81.59 ± 1.53	Control	**84.44 ± 1.09**[a]	**81.59 ± 1.53**[a]
30 m	85.11 ± 1.39	82.55 ± 1.26	30 m	85.11 ± 1.39	82.55 ± 1.26	Warming	**76.02 ± 1.69**[b]	**71.94 ± 0.73**[b]
SVWC			**SVWC**			**SVWC**		
			600 m	**0.20 ± 0.01**[a]	**0.16 ± 0.01**[a]			
300 m	**0.20 ± 0.01**[a]	**0.16 ± 0.02**[a]	300 m	**0.20 ± 0.01**[a]	**0.16 ± 0.01**[a]	Control	0.17 ± 0.01	0.12 ± 0.01
30 m	**0.18 ± 0.01**[b]	**0.12 ± 0.01**[b]	30 m	**0.15 ± 0.01**[b]	**0.12 ± 0.01**[b]	Warming	0.17 ± 0.01	0.11 ± 0.01
VPD			**VPD**			**VPD**		
			600 m	0.39 ± 0.07	0.37 ± 0.07			
300 m	0.47 ± 0.03	0.40 ± 0.04	300 m	0.47 ± 0.03	0.40 ± 0.04	Control	**0.55 ± 0.06**[b]	**0.41 ± 0.03**[b]
30 m	0.55 ± 0.06	0.41 ± 0.03	30 m	0.55 ± 0.06	0.41 ± 0.03	Warming	**0.78 ± 0.05**[a]	**0.63 ± 0.03**[a]
PAR			**PAR**			**PAR**		
			600 m	**454.24 ± 31.70**[a]	**360.29 ± 33.76**[a]			
300 m	306.47 ± 13.01	232.45 ± 17.92	300 m	**306.47 ± 13.01**[b]	**232.45 ± 17.92**[b]	Control	335.32 ± 36.83	246.70 ± 30.14
30 m	335.32 ± 36.83	246.70 ± 30.14	30 m	**335.32 ± 36.83**[ab]	**246.70 ± 30.14**[ab]	Warming	335.32 ± 36.83	246.70 ± 30.14
Rainfall			**Rainfall**			**Rainfall**		
			600 m	316.25 ± 34.06	101.38 ± 21.75			
300 m	353.45 ± 32.71	114.17 ± 23.55	300 m	353.45 ± 32.71	114.17 ± 23.55	Control	318.03 ± 36.64	105.12 ± 17.81
30 m	318.03 ± 36.64	105.12 ± 17.81	30 m	318.03 ± 36.64	105.12 ± 17.81	Warming	318.03 ± 36.64	105.12 ± 17.81

Different lowercase letters above the bold values indicate significant differences in T_{air}, T_{soil}, RH, SVWC, VPD, PAR and rainfall between control and warming treatments in the wet and dry seasons, respectively.

S. superba (**Figure 3D**). Declining iWUE was observed in *S. rehderianum* and *S. superba* (**Figure 3E**). In MEBF, g_s of *M. breviflora* was increased by 0.95°C of translocation warming, but that was reduced by 1.63°C of translocation warming. *S. rehderianum* and *S. superba* had higher g_s under 0.95°C and 1.63°C of translocation warming (**Figure 3F**). Warming did not affect stomatal density for the three tree species (**Figure 3G**). Stomatal size of *S. rehderianum* was decreased by 1.63°C translocation warming (**Figure 3H**). Transpiration of *M. breviflora* was increased by 0.95°C translocation warming, but reduced by 1.63°C translocation warming. *S. rehderianum* and *S. superba* had higher transpiration under 0.95°C and 1.63°C translocation warming (**Figure 3I**). iWUE for the three tree species were not affected by warming (**Figure 3J**).

In MEBMF, g_s of *M. breviflora*, *S. rehderianum* and *S. superba* were reduced by the 1.82°C IR warming treatment (**Figure 3K**). *Schima superba* exhibited reduced stomatal density under 1.82°C of IR warming (**Figure 3L**). The 1.82°C IR warming treatment enhanced stomatal size for *M. breviflora*, but decreased that of *S. rehderianum* (**Figure 3M**). Decreasing transpiration had been observed in *M. breviflora* and *S. rehderianum* under the 1.82°C

IR warming treatment (**Figure 3N**), but iWUE of *M. breviflora* was enhanced by 1.82°C of IR warming (**Figure 3O**).

In CBMF, *S. rehderianum* had higher $Chl_{(a+b)}$ concentration in the 0.68°C translocation warming treatment (**Figure 4A**). N_a for the three tree species were not affected by translocation warming (**Figure 4B**). P_a of *S. superba* was enhanced by 0.68°C of translocation warming (**Figure 4C**). In MEBF, the concentrations in $Chl_{(a+b)}$, N_a and P_a for *M. breviflora*, *S. rehderianum* and *S. superba* were not affected by warming (**Figures 4D–F**). In MEBMF, warming exerted no effects on the concentrations in $Chl_{(a+b)}$ and Na for the three tree species (**Figure 4G,H**).

Photosynthetic Capacity and Light-Saturated Rates

In CBMF, J_{max} and V_{max} of *S. superba* in the 0.68°C translocation warming treatment were significantly increased by 106.2% and 43.6%, respectively (**Figures 5A,B**). The 0.68°C translocation warming treatment did not affect J_{max}/V_{max} for *M. breviflora*, *S. rehderianum* and *S. superba* (**Figure 5C**). The 0.68°C translocation warming treatment decreased A_{sat} of *M. breviflora* by 26.9%, but increased that of *S. superba* by 33.4%

FIGURE 3 | (A,F,K) Stomatal conductance (g_s, mol m^{-2} s^{-1}, $n = 12$), **(B,G,L)** stomatal density (SD, 10^{-4}, $n = 15$), **(C,H,M)** stomatal size (SS, μm^2, $n = 50$), **(D,I,N)** transpiration rate (E, mmol m^{-2} s^{-1}, $n = 12$) and **(E,J,O)** instantaneous water use efficiency (iWUE, μmol m mol^{-1}, $n = 12$) of *Machilus breviflora*, *Syzygium rehderianum* and *Schima superba* exposed to various warming treatments in coniferous and broadleaf mixed forest (CBMF), mountain evergreen broadleaf forest (MEBF) and monsoon evergreen broadleaf forest (MEBMF). Different lowercase letters above the error bars (standard errors) indicate significant differences in g_s, SD, SS, E and iWUE from August 2018 or 2019 to August 2020.

(**Figure 5D**). In MEBF, J_{max} for the three tree species were not influenced by warming (**Figure 5E**). V_{max} of *S. superba* under the 1.63°C translocation warming treatment was enhanced by 56.1% (**Figure 5F**). The 1.63°C translocation warming treatment

decreased J_{max}/V_{max} for *S. superba* (**Figure 5G**). The 0.95°C translocation warming treatment enhanced A_{sat} of *M. breviflora* by 43.9%, but the 1.63°C translocation warming treatment decreased A_{sat} by 17.4%. The 0.95°C and 1.63°C translocation

FIGURE 4 | (A,D,G) The total concentrations of chlorophyll a and chlorophyll b [Chl$_{(a+b)}$, μg cm^{-2}, $n = 6$], **(B,E,H)** the area-based nitrogen concentrations in the leaves (N$_a$, mg cm^{-2}, $n = 6$) and **(C,F,I)** area-based phosphorus concentrations in the leaves (P$_a$, mg cm^{-2}, $n = 6$) of *Machilus breviflora*, *Syzygium rehderianum* and *Schima superba* exposed to various warming treatments in coniferous and broadleaf mixed forest (CBMF), mountain evergreen broadleaf forest (MEBF) and monsoon evergreen broadleaf forest (MEBMF). Different lowercase letters above the error bars (standard errors) indicate significant differences in Chl$_{(a+b)}$, N$_a$ and P$_a$ from August 2018 or 2019 to August 2020.

warming treatments enhanced A$_{sat}$ of *S. rehderianum* and *S. superba* by approximately 40.0% (**Figure 5H**).

In MEBMF, 1.82°C of IR warming significantly reduced J$_{max}$ and V$_{max}$ of *M. breviflora* by 34.4% and 26.1%, respectively (**Figures 5I,J**). Lower J$_{max}$/V$_{max}$ for *S. superba* was observed in MEBMF (**Figure 5K**). A$_{sat}$ of *M. breviflora*, *S. rehderianum* and *S. superba* in the 1.82°C IR warming treatment were decreased by 36.3%, 23.1%, and 23.8%, respectively (**Figure 5L**).

The Soil Types, Soil Chemistry and Nutrient Availability in the Three Forest Types

The soil type of CBMF and MEBMF was lateritic soil, and that of MEBF was yellow soil. The concentrations of TN and TP, and pH for CBMF, MEBF and MEBMF were not significantly influenced by warming (**Table 2**). In CBMF, AN

was significantly increased by 0.68°C of translocation warming, while AP showed decreasing trends to warming (**Supplementary Figure 1A**). In contrast, the 0.95°C and 1.63°C translocation warming treatments in MEBF significantly decreased AN but had no significant effects on AP (**Supplementary Figure 1B**). In MEBMF, AN and AP were not significantly affected by IR warming (**Supplementary Figure 1C**).

Impacts of Environmental Variables on Physiology Under Translocation and Infra-Red Warming Treatments

In the translocation warming treatment, lower A$_{sat}$ for *M. breviflora* was mainly driven by higher T$_{soil}$ and lower SVWC. Stomatal size of *M. breviflora* was significantly decreased by higher T$_{air}$. Higher T$_{air}$ significantly increased g$_s$ for *S. rehderianum*, but decreased its stomatal size. The

FIGURE 5 | (A,E,I) The area-based maximum rate of photosynthetic electron transport (J_{max}, μmol m^{-2} s^{-1}, $n = 6$), **(B,F,J)** the area-based maximum rate of photosynthetic Rubisco carboxylation (V_{max}, μmol m^{-2} s^{-1}, $n = 6$), **(C,G,K)** the ratio of the area-based maximum rate of photosynthetic electron transport and area-based maximum rate of photosynthetic Rubisco carboxylation (J_{max}/V_{max}, $n = 6$) and **(D,H,L)** the light-saturated photosynthetic rate (A_{sat}, μmol m^{-2} s^{-1}, $n = 12$) of *Machilus breviflora*, *Syzygium rehderianum* and *Schima superba* exposed to various warming treatments in coniferous and broadleaf mixed forest (CBMF), mountain evergreen broadleaf forest (MEBF) and monsoon evergreen broadleaf forest (MEBMF). Different lowercase letters above the error bars (standard errors) indicate significant differences in J_{max}, V_{max}, J_{max}/V_{max} and A_{sat} from August 2018 or 2019 to August 2020.

enhancements in photosynthetic capacity and gas exchange for *S. superba* were significantly driven by higher T_{air} and T_{soil} (**Table 3**, $P < 0.05$).

In the 1.82°C IR warming treatment, lower RH significantly decreased gas exchange for *M. breviflora*. Stomatal size of *M. breviflora* was significantly increased

by higher T_{air} and lower RH. g_s of *S. rehderianum* and *S. superba*, and stomatal size of *S. rehderianum* were mainly reduced by increasing T_{air}. Transpiration of *S. rehderianum* was decreased by higher T_{air} and VPD. The reduction in P_a for *S. superba* was driven by T_{air}, RH and VPD. Stomatal density of *S. superba* was significantly

TABLE 2 | The soil types, concentrations of total nitrogen (TN, g kg^{-1}, $n = 9$) and phosphorus (TP, g kg^{-1}, $n = 9$), and pH in the substrate soil (0–10 cm) in the wet season from 2017 to 2019 for coniferous and broadleaf forest (CBMF), mountain evergreen broadleaf forest (MEBF) and monsoon evergreen broadleaf forest (MEBMF).

Forest Types	Soil Types	Warming Sites	TN	TP	pH
CBMF	Lateritic soil	300 m	1.15 ± 0.08	0.12 ± 0.01	4.33 ± 0.03
		30 m	1.02 ± 0.05	0.12 ± 0.01	4.27 ± 0.07
MEBF	Yellow soil	600 m	1.02 ± 0.04	0.25 ± 0.01	4.27 ± 0.07
		300 m	1.15 ± 0.13	0.27 ± 0.01	4.37 ± 0.07
		30 m	0.99 ± 0.14	0.26 ± 0.01	4.42 ± 0.06
MEBMF	Lateritic soil	Control	1.06 ± 0.04	0.15 ± 0.01	4.37 ± 0.03
		Warming	1.11 ± 0.03	0.15 ± 0.01	4.43 ± 0.02

TABLE 3 | Summary report of effects of air temperature (T_{air}, °C), soil temperature (T_{soil}, °C) and soil volumetric water content (SVWC, m^3 m^{-3}) on photosynthetic capacity, gas exchange, biochemistry for *Machilus breviflora*, *Syzygium rehderianum,* and *Schima superba* in last 2 or 3 years under translocation warming by the mixed liner model.

Variables	M. breviflora			S. rehderianum			S. superba		
	T_{air}-F (P)	T_{soil}-F (P)	SVWC-F (P)	T_{air}-F (P)	T_{soil}-F (P)	SVWC-F(P)	T_{air}-F (P)	T_{soil}-F (P)	SVWC-F (P)
Photosynthetic capacity									
J_{max}	1.62 (0.23)	0.14 (0.72)	0.19 (0.67)	0.36 (0.56)	**4.94 (0.04)**	1.07 (0.31)	1.73 (0.20)	0.84 (0.37)	0.19 (0.67)
V_{max}	**5.98 (0.03)**	1.67 (0.21)	0.55 (0.46)	0.33 (0.57)	3.72 (0.07)	0.83 (0.37)	1.19 (0.29)	1.34 (0.26)	0.01 (0.97)
Gas exchange									
A_{sat}	0.47 (0.49)	2.72 (0.10)	1.28 (0.26)	3.86 (0.05)	3.53 (0.06)	**6.74 (0.01)**	**8.40 (0.005)**	**12.73 (< 0.001)**	1.17 (0.28)
g_s	0.11 (0.74)	0.33 (0.57)	0.54 (0.47)	**7.47 (0.007)**	0.64 (0.42)	0.01 (0.98)	**19.65 (< 0.001)**	**20.26 (< 0.001)**	0.06 (0.81)
E	0.04 (0.85)	0.31 (0.58)	0.88 (0.35)	1.99 (0.16)	3.34 (0.07)	0.96 (0.33)	**4.28 (0.04)**	3.95 (0.05)	0.23 (0.63)
iWUE	0.90 (0.35)	4.00 (0.05)	0.07 (0.80)	1.62 (0.21)	2.52 (0.11)	**8.93 (0.003)**	2.68 (0.10)	0.45 (0.50)	**4.94 (0.03)**
Biochemistry									
$Chl_{(a+b)}$	0.90 (0.35)	2.74 (0.11)	0.96 (0.33)	**22.76 (< 0.001)**	**6.69 (0.01)**	0.03 (0.85)	0.37 (0.55)	1.98 (0.17)	1.19 (0.28)
N_a	1.19 (0.29)	0.05 (0.82)	1.15 (0.29)	0.01 (0.93)	2.15 (0.15)	0.06 (0.81)	**6.36 (0.02)**	0.87 (0.36)	0.01 (0.96)
P_a	3.88 (0.06)	0.04 (0.84)	0.01 (0.92)	0.37 (0.55)	0.14 (0.71)	0.22 (0.64)	**5.91 (0.02)**	1.83 (0.19)	0.07 (0.79)
Stomatal morphology									
SD	1.25 (0.27)	0.25 (0.62)	1.08 (0.30)	0.02 (0.89)	**4.69 (0.03)**	0.14 (0.70)	0.09 (0.77)	0.01 (0.93)	0.18 (0.69)
SS	**9.63 (0.002)**	0.41 (0.52)	1.71 (0.19)	**19.92 (< 0.001)**	1.95 (0.16)	0.01(0.96)	2.96 (0.09)	0.03 (0.87)	**5.09 (0.03)**

Photosynthetic capacity: the area-based maximum rate of photosynthetic electron transport (J_{max}, µmol m^{-2} s^{-1}), the area-based maximum rate of photosynthetic Rubisco carboxylation (V_{max}, µmol m^{-2} s^{-1}). Gas echange: the light-saturated photosynthetic rate (A_{sat}, µmol m^{-2} s^{-1}), stomatal conductance (g_s, mol m^{-2} s^{-1}), transpiration rate (E, mmol m^{-2} s^{-1}) and instantaneous water use efficiency (iWUE, µmol m^{-2} mol^{-1}). Biochemistry: the total concentrations of chlorophyll a and chlorophyll b [$Chl_{(a+b)}$, µg cm^{-2}], the area-based nitrogen contents in the leaves (N_a, mg cm^{-2}) and area-based phosphorus contents in the leaves (P_a, mg cm^{-2}). Stomatal mophology: stomatal density (SD) and stomatal size (SS, µm^2). The bold values indicate significant differences.

decreased by declining RH and increasing VPD (**Table 4**, $P < 0.05$).

The Effects of Stomatal Traits, Biochemistry, Nutrient Availability and Soil Types on Photosynthesis Traits for the Three Tree Species Between Coniferous and Broadleaf Mixed Forest and Mountain Evergreen Broadleaf Forest

The change in photosynthesis trait for *M. breviflora* between CBMF and MEBF was mainly correlated with soil type, stomatal traits and nutrient availability, and their ratios were 43%, 26%, and 16%, respectively (**Supplementary Figure 2A**). The soil type explained the 10% changes in photosynthesis trait for *S. rehderianum* between CBMF and

MEBF (**Supplementary Figure 2B**). Biochemistry was main factor inducing the shift in photosynthesis trait for *S. superba* between CBMF and MEBF (**Supplementary Figure 2C**).

Growth

In CBMF, the 0.68°C translocation warming treatment reduced stem volume of *M. breviflora* and *S. rehderianum* by 6.2% and 6.3%, respectively (**Figures 6A,B**). The stem volume of *S. superba* was increased by 117.8% (**Figure 6C**). In MEBF, the 1.63°C translocation warming treatment significantly decreased the stem volume of *M. breviflora* by 54.9% (**Figure 6D**). The 0.95°C and 1.63°C translocation warming treatments significantly increased the stem volume of *S. rehderianum* in MEBF by 26.5% and 106.5%, respectively (**Figure 6E**). The 0.95°C and 1.63°C translocation warming treatment significantly enhanced stem volume in MEBF by 33.5% and 119.7% (**Figure 6F**).

In MEBMF, the 1.82°C IR warming treatment reduced stem volume of *S. rehderianum* by 42.8% (**Figure 6H**). The 1.82°C IR

TABLE 4 | Summary report of effects of air temperature (T_{air}, °C), air moisture (RH,%) and vapor pressure difference (VPD, kPa) on photosynthetic capacity, gas exchange, biochemistry and stomatal morphology for *Machilus breviflora*, *Syzygium rehderianum*, and *Schima superba* in last 2 or 3 years under infrared warming by the mixed liner model.

Variables	M. breviflora			S. rehderianum			S. superba		
	T_{air}-F (P)	RH-F (P)	VPD-F (P)	T_{air}-F (P)	RH-F (P)	VPD-F (P)	T_{air}-F (P)	RH-F (P)	VPD-F (P)
Photosynthetic capacity									
J_{max}	0.33 (0.59)	5.50 (0.06)	0.02 (0.88)	0.16 (0.71)	0.41 (0.55)	0.98 (0.37)	0.34 (0.58)	3.07 (0.13)	0.29 (0.61)
V_{max}	0.57 (0.48)	1.54 (0.26)	0.22 (0.65)	0.02 (0.88)	0.30 (0.61)	1.22 (0.32)	0.19 (0.68)	3.00 (0.14)	0.06 (0.81)
Gas exchange									
A_{sat}	0.01 (0.94)	**11.29 (0.002)**	1.24 (0.27)	0.05 (0.82)	3.42 (0.07)	1.38 (0.25)	1.18 (0.28)	3.19 (0.08)	0.01 (0.97)
g_s	0.89 (0.35)	**12.35 (0.002)**	0.03 (0.86)	**6.06 (0.02)**	0.24 (0.63)	2.52 (0.12)	2.80 (0.10)	0.79 (0.38)	1.49 (0.23)
E	0.26 (0.61)	**21.27 (< 0.001)**	0.32 (0.57)	**4.81 (0.03)**	0.34 (0.56)	**4.92 (0.03)**	1.46 (0.23)	0.71 (0.40)	1.33 (0.25)
iWUE	0.01 (0.93)	**21.70 (< 0.001)**	0.09 (0.76)	0.01 (0.99)	2.33 (0.13)	**5.65 (0.02)**	**8.94 (0.005)**	1.26 (0.27)	3.07 (0.09)
Biochemistry									
$Chl_{(a+b)}$	0.99 (0.34)	0.02 (0.88)	0.10 (0.76)	0.06 (0.81)	1.57 (0.24)	0.62 (0.45)	0.44 (0.52)	0.02 (0.88)	0.47 (0.51)
N_a	**7.60 (0.03)**	0.63 (0.45)	0.03 (0.87)	**13.21 (0.005)**	2.82 (0.13)	0.13 (0.73)	**23.11 (0.001)**	0.03 (0.86)	2.04 (0.19)
P_a	0.45 (0.53)	1.45 (0.28)	0.26 (0.63)	**17.37 (0.003)**	0.88 (0.37)	0.19 (0.69)	**11.94 (0.006)**	**26.17 (< 0.001)**	**6.07 (0.03)**
Stomatal morphology									
SD	0.59 (0.45)	0.22 (0.64)	**5.20 (0.03)**	0.53 (0.47)	0.86 (0.36)	0.62 (0.44)	2.58 (0.12)	**14.66 (< 0.001)**	**8.13 (0.008)**
SS	**4.99 (0.03)**	**11.29 (< 0.001)**	0.12 (0.73)	2.05 (0.16)	1.01 (0.32)	0.95 (0.33)	**7.27 (0.008)**	**21.09 (< 0.001)**	3.06 (0.08)

Photosynthetic capacity: the area-based maximum rate of photosynthetic electron transport (J_{max}, $\mu mol\ m^{-2}\ s^{-1}$) and the area-based maximum rate of photosynthetic Rubisco carboxylation (V_{max}, $\mu mol\ m^{-2}\ s^{-1}$). Gas echange: the light-saturated photosynthetic rate (A_{sat}, $\mu mol\ m^{-2}\ s^{-1}$), stomatal conductance (g_s, $mol\ m^{-2}\ s^{-1}$), transpiration rate (E, $mmol\ m^{-2}\ s^{-1}$) and instantaneous water use efficiency (iWUE, $\mu mol\ m^{-2}\ mol^{-1}$). Biochemistry: the total concentrations of chlorophyll a and chlorophyll b ($Chl_{(a+b)}$, $\mu g\ cm^{-2}$), the area-based nitrogen contents in the leaves (N_a, $mg\ cm^{-2}$) and area-based phosphorus contents in the leaves (P_a, $mg\ cm^{-2}$). Stomatal mophology: stomatal density (SD) and stomatal size (SS, μm^2). The bold values indicate significant differences.

warming treatment had no significant effect on the stem volume of *M. breviflora* and *S. superba* (**Figures 6G,I**).

DISCUSSION

We designed our experiment to increase T_{air} and T_{soil} in a subtropical forest using two common techniques – translocation and IR warming– but which also differentially affected other environmental variables, including SVWC, RH and VPD. We found that the warming methods differed in their impacts on the physical environment. In general, both methods directly increased T_{air} and T_{soil} (although to varying degrees), while translocation warming indirectly dried the soil (lower SVWC) and IR warming indirectly dried the air (lower RH and higher VPD). This study highlighted the direct and indirect effects of different warming techniques on the physical environment of forest ecosystems, and subsequently, the complex and variable biological impacts on trees. Hence, different warming techniques may provide different outcomes when assessing the impact of warming on trees in future climates.

The Impacts of Translocation and Infra-Red Warming on the Physical Environment

Translocation experiments utilize natural temperature gradients to increase T_{air} and T_{soil} (Dunne et al., 2004; Salinas et al., 2011), but may indirectly reduce soil moisture, leading to lower SVWC (Hu et al., 2016; Fang et al., 2020). Although some studies have analyzed the impact of few environmental variables on

biological traits in response to translocation treatments, few have investigated the full suite of physical environmental variables and subsequent impacts on biological traits (Budge et al., 2011; Li et al., 2016; Soderberg et al., 2020; Lie et al., 2021).

The IR heaters directly increased T_{air} and T_{soil} in the dry (but not wet) season in MEBMF. The IR heaters also dried the air, leading to lower RH and higher VPD, as has been observed in other studies, with observations of some impacts on the plants (Amthor et al., 2010; de Boeck et al., 2012). However, most studies using IR heaters did not address the potential impacts of the underlying indirect effects of reduced RH and increased VPD, although it was biological relevant (Aronson and McNulty, 2009). Overall, the main difference between the two warming methods was that translocation warming indirectly dried the soil, while IR warming indirectly dried the air.

Direct Effects of Higher T_{air} and T_{soil} on Plant Physiology and Growth

The 0.68°C (CBMF) and 1.63°C (MEBF) of translocation warming decreased A_{sat} for *M. breviflora* in the wet season, inhibiting its growth. In contrast, translocation warming increased A_{sat} for *S. rehderianum* in the wet season in MEBF, and increased J_{max}, V_{max} and A_{sat} for *S. superba* in the wet season in CBMF and MEBF, leading to more rapid growth. *M. breviflora* in CBMF exhibited smaller stomatal size in response to 0.68°C of translocation warming, which may have contributed to lower A_{sat} (Zhu et al., 2020). A_{sat} for *M. breviflora* in CBMF and MEBF were mainly reduced by the direct effect of higher T_{soil}, subsequently leading to lower water uptake

FIGURE 6 | (A,D,G) The stem volume (V, cm³) of *Machilas breviflora* in coniferous and broadleaf mixed forest (CBMF), mountain evergreen broadleaf forest (MEBF) and monsoon evergreen broadleaf forest (MEBMF), from June 2015 to December 2019; **(B,E,H)** V of *Syzygium rehderianum* in CBMF, MEBF and MEBMF; **(C,F,I)** V of *Schima superba* in CBMF, MEBF and MEBMF.
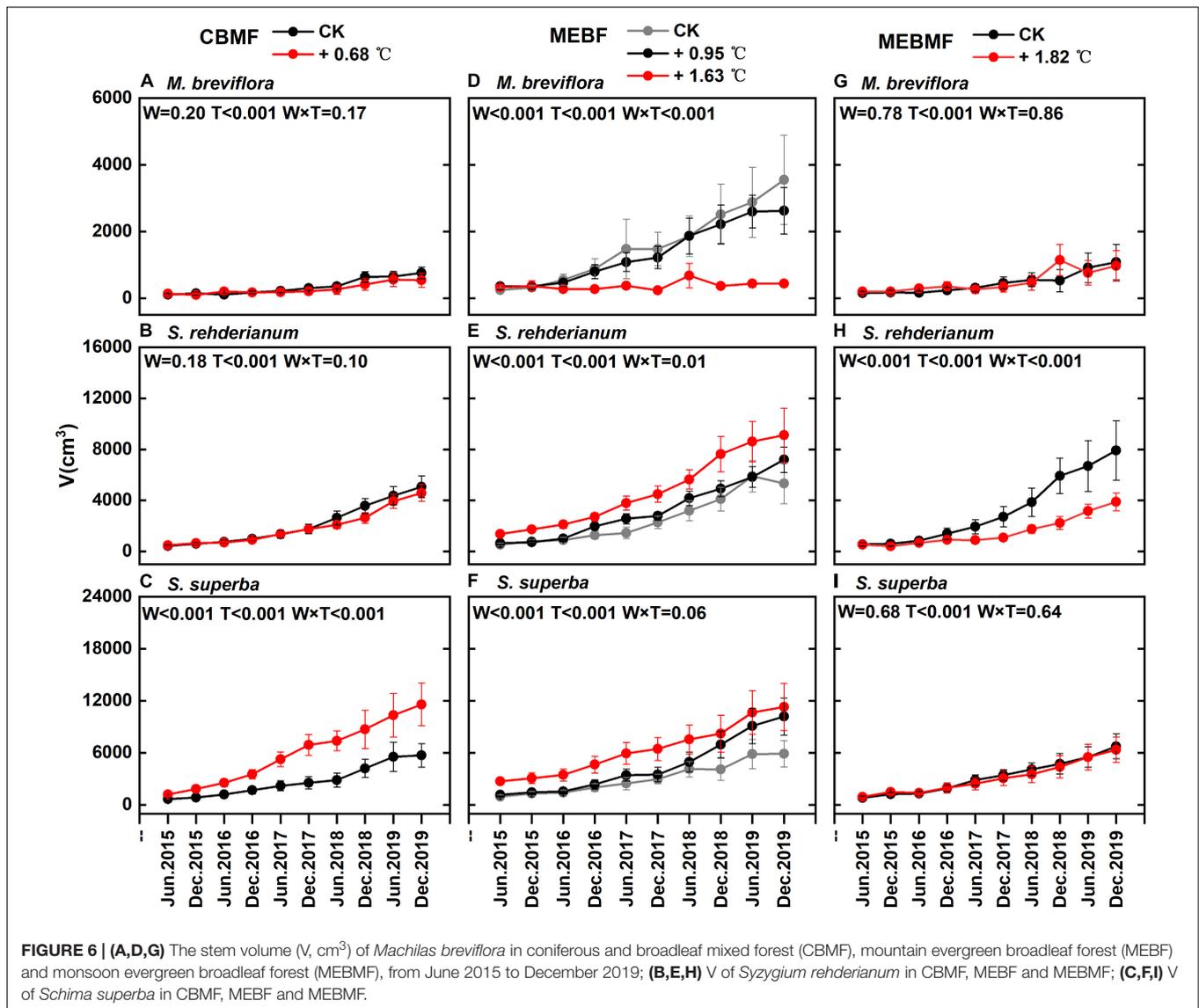
from the soil, and lower g_s. Higher T_{air} directly increased g_s of *S. rehderianum* in MEBF, leading to increasing A_{sat} and growth (Dai et al., 2021). However, growth of *S. rehderianum* in CBMF was lower due to translocation warming. The differential responses of photosynthesis for *S. rehderianum* in the CBMF and MEBF sites may be attributable to warming impacts on soil types and nutrient availability. *S. rehderianum* exhibited smaller stomatal size in response to increasing T_{air} caused by translocation and IR warming, which would be beneficial for lowering transpiration, as has been observed previously (Parkhurst, 1994; Pellizzari et al., 2017; Wu et al., 2020a). J_{max}, V_{max}, and A_{sat} for *S. superba* were increased by higher T_{air} and T_{soil} in both translocation warming sites. T_{air} at the translocation warming sites might be lower than T_{opt} of *S. superba*, which enhanced its photosynthetic capacity and rate due to increasing g_s (Way and Yamori, 2014; Slot and Winter, 2017). Higher T_{soil} could increase water uptake to

promote leaf water supply, thereby increasing g_s for *S. superba*, resulting in increased photosynthetic capacity and rate (Wu et al., 2012; Harrison et al., 2020; Wu et al., 2020b). Increased T_{air} induced by translocation warming resulted in higher transpiration for *S. superba*, which might be used to cool leaves (Drake et al., 2018).

IR warming reduced A_{sat} for *S. rehderianum* and *S. superba* in the wet season in MEBMF. g_s of *S. rehderianum* and *S. superba* in the wet season in MEBMF was mainly reduced by the direct effect of higher T_{air} under 1.82°C of IR warming, when T_{air} might exceed its T_{opt} (Taylor et al., 2019), which reduced A_{sat}. Additionally, *S. rehderianum* and *S. superba* under 1.82°C of IR warming might have limited capacity to alter T_{opt} to acclimate to higher T_{air} (Carter et al., 2021), resulting in declining g_s and A_{sat}. Thus, the 1.82°C IR warming treatment significantly decreased growth for *S. rehderianum* in MEBMF due to declining A_{sat}.

Indirect Effects of Soil Volumetric Water Content, Relative Humidity, and Vapor Pressure Deficit on Plant Physiology and Growth

Translocation warming indirectly reduced SVWC due to higher T_{soil}. Lower SVWC may decrease soil water availability, thereby increasing stomatal limitation to A_{sat} for *M. breviflora* in the wet season, and inhibiting its growth (Zhang et al., 2020). Similar to our results, Reich et al. (2018) found that warming impacts on photosynthesis was dependent on SVWC. In contrast, growth of *M. breviflora* was enhanced by translocation warming in MEBF, when SVWC was higher, leading to higher A_{sat}.

IR heaters indirectly reduced RH and increased VPD. The reductions in J_{max}, V_{max} and A_{sat} for *M. breviflora* in the wet season in MEBMF were attributable to indirect effect of declining RH rather than increasing T_{air} under 1.82°C of IR warming, which was also related to decreased g_s due to high stomatal sensitivity to dry air (Kitao et al., 2014). Xiao et al. (2020) also found that reduced g_s was driven by declining RH instead of increasing T_{air}. Higher T_{air} and lower RH both enhanced stomatal size for *M. breviflora*, which might be beneficial for increasing transpirational cooling to reduce leaf temperature in warmer environments (Miserere et al., 2021). Stomatal density for *S. superba* was decreased by the indirect effects of higher RH and lower VPD, which could reduce A_{sat} and water loss, similar to previous observations (Du et al., 2019; Fanourakis et al., 2020; Miserere et al., 2021). The IR warming treatment reduced leaf P_a concentration for *S. superba* due to lower transpiration, which further inhibited photosynthesis (Aliniaeifard and van Meeteren, 2013; Leon-Sanchez et al., 2019; Shrestha et al., 2021).

CONCLUSION

We found that biological responses to warming, in three tropical tree species, differed between translocation and IR warming due to differential impacts of the warming technique on the physical environment, including indirect effects on SVWC, RH, and VPD. Hence, different warming techniques may provide different outcomes when assessing the impact of warming on trees in future climates. Importantly, future experiments should directly compare the warming techniques at the same sites and in the same soils to test our findings. Subsequently, we should monitor a full suite of environmental variables in warming experiments to determine the mechanistic basis for the biological responses to warming, which will increase our predictive capacity regarding the impact of climate change on forests.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.877025/full#supplementary-material

Supplementary Figure 1 | (A) The response ratio (RR) of available N (AN) and available P (AP) in the substrate soil (0–10 cm) in the wet season from 2015/2016 to 2019 for **(A)** coniferous and broadleaf forest (CBMF), **(B)** mountain evergreen broadleaf forest (MEBF) and **(C)** monsoon evergreen broadleaf forest (MEBMF).

Supplementary Figure 2 | Variation partitioning analysis (VPA) showing the effects of stomatal traits, biochemistry, nutrient availability and soil types on photosynthesis traits for *Machilas breviflora* **(A)**, *Syzygium rehderianum* **(B)** and *Schima superba* **(C)** between coniferous and broadleaf mixed forest (CBMF) and mountain evergreen broadleaf forest (MEBF). Photosynthesis traits are represented by the area-based maximum rate of photosynthetic electron transport (J_{max}), the area-based maximum rate of photosynthetic Rubisco carboxylation (V_{max}), and the light-saturated photosynthetic rate (A_{sat}). Stomatal traits contain stomatal conductance (g_s), stomatal density (SD) and size (SS). Biochemistry includes the concentrations of chlorophyll a and b ($Chl_{(a+b)}$), and the concentrations of nitrogen and phosphorus in leaves (N_a and P_a). Nutrient availability contains nitrogen availability (AN) and phosphorus availability (AP). Soil types contain lateritic soil and yellow soil.

Supplementary Table 1 | Some data in this paper were previously published, but have been provided in this paper to support the comprehensive study of different warming techniques at different sites.

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