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Research paper

Disentangling the effects of atmospheric CO₂ and climate on intrinsic water-use efficiency in South Asian tropical moist forest trees

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Due to the increase in atmospheric CO₂ concentrations, the ratio of carbon fixed by assimilation to water lost by transpiration through stomatal conductance (intrinsic water-use efficiency, iWUE) shows a long-term increasing trend globally. However, the drivers of short-term (inter-annual) variability in iWUE of tropical trees are poorly understood. We studied the inter-annual variability in iWUE of three South Asian tropical moist forest tree species (*Chukrasia tabularis* A.Juss., *Toona ciliata* M. Roem. and *Lagerstroemia speciosa* L.) derived from tree-ring stable carbon isotope ratio ($\delta^{13}\text{C}$) in response to variations of environmental conditions. We found a significantly decreasing trend in carbon discrimination ($\Delta^{13}\text{C}$) and an increasing trend in iWUE in all the three species, with a species-specific long-term trend in intercellular CO₂ concentration (C_i). Growing season temperatures were the main driver of inter-annual variability of iWUE in *C. tabularis* and *L. speciosa*, whereas previous year temperatures determined the iWUE variability in *T. ciliata*. Vapor pressure deficit was linked with iWUE only in *C. tabularis*. Differences in shade tolerance, tree stature and canopy position might have caused this species-specific variation in iWUE response to climate. Linear mixed effect modeling successfully simulated iWUE variability, explaining 41–51% of the total variance varying with species. Commonality analysis revealed that temperatures had a dominant influence on the inter-annual iWUE variability (64–77%) over precipitation (7–22%) and atmospheric CO₂ concentration (3–6%). However, the long-term variations in iWUE were explicitly determined by the atmospheric CO₂ increase (83–94%). Our results suggest that the elevated CO₂ and concomitant global warming might have detrimental effects on gas exchange and other physiological processes in South Asian tropical moist forest trees.

Keywords: Bangladesh, iWUE, moist tropical forest, Rema-Kalenga Wildlife Sanctuary, stable carbon isotope, tree-ring.

Introduction

Atmospheric CO₂ is one of the main greenhouse gases affecting life forms and their surrounding environments (Anderson et al. 2016). Since the industrial revolution, atmospheric CO₂ concentration has been rising exponentially, with a sharp increase in the most recent decades (Keeling et al. 1976, 1995, Betts et al. 2016). As recorded in the Mauna Loa Earth Observatory in Hawaii, atmospheric CO₂ concentration increased by nearly 29% during the past 65 years. This consistent rise in atmospheric CO₂ resulted in many environmental changes,

including a rise in global temperatures, and the occurrence of extreme climatic events around the world (IPCC 2013). These environmental changes have already been proved to affect the physiology, ecology and biology of plants from individual to biome scale (Silva and Anand 2013, Swann et al. 2016). Most studies conducted on plants' responses to environmental changes have focused on the short-term response in manipulation experiments (Körner 2006, Leuzinger et al. 2011, Norby and Zak 2011). However, long-term responses of plants to global environmental changes are poorly studied so far due to

the lack of long-term experimental data (Hovenden and Newton 2018). Nevertheless, understanding the long-term physiological responses of plants, especially trees in tropical regions, is important because tropical trees are a crucial component of global biogeochemical cycles (Zuidema et al. 2013).

In the absence of long-term ecophysiological experiments in the tropics, tree-ring stable isotopes provide a good proxy to study the long-term responses of trees to environmental changes (McCarroll and Loader 2004, Zuidema et al. 2013, van der Sleen et al. 2017b) from multi-decadal to centennial scale. During carbon sequestration and water uptake by roots and subsequent wood formation processes, heavier isotopes are discriminated against the lighter ones. However, the rate of discrimination is influenced by the prevailing environmental condition and thus may imprint the environmental signal in tree-rings (McCarroll and Loader 2004). It is important to note that discrimination rate is also affected influenced by the variation in intercellular CO₂ concentration (C_i), which is driven by stomatal conductance and photosynthesis (Farquhar et al. 1982). Thus, variations in stable carbon isotopes ($\delta^{13}\text{C}$) in tree-rings provide deeper insight into changes in intrinsic water-use efficiency (iWUE), which is the ratio of carbon fixed by assimilation to water lost by transpiration through stomatal conductance (Farquhar et al. 1982, McCarroll and Loader 2004).

Intrinsic water-use efficiency derived from tree-ring stable carbon isotope ratios ($\delta^{13}\text{C}$) has already been used as a potential proxy for the past physiological responses of tropical trees to environmental changes (Hietz et al. 2005, Brienen et al. 2011, Gebrekirstos et al. 2011, Nock et al. 2011, van der Sleen et al. 2014). Nonetheless, how changes in the $\delta^{13}\text{C}$ -derived iWUE in tropical trees are related to climate has not been adequately understood so far. Besides, the large and rapid on-going changes in atmospheric CO₂ concentrations may also be reflected in iWUE trends in tropical tree-rings (van der Sleen et al. 2014). Yet, the relative importance of climate and atmospheric CO₂ in determining the iWUE variability has not been explored for many tropical trees and ecosystems, although it is crucial for advancing our understanding of long-term physiological responses of tropical trees to elevated CO₂ and climatic changes.

Long-term physiological responses of trees to environmental changes may vary across biomes, sites, species and even within the individual tree level (Peñuelas et al. 2011, Silva and Anand 2013, Battipaglia et al. 2014, Rahman et al. 2019b). Water-use efficiency response to environmental changes varied between species (Martínez-Sancho et al. 2018, Liu et al. 2019), within the species distributed in mesic and xeric sites (Lévesque et al. 2014) and between different forest management practices (Rezaie et al. 2018). It is thus important to study how tropical tree species of different functional types differ in their water-use response to elevated CO₂ and climate. The currently available studies on the impact of climate on iWUE variability of tropical trees were mostly conducted in dry tropical regions (e.g.,

Gebrekirstos et al. 2011), highlighting the research gap in moist tropical forests.

The moist tropical forests in Bangladesh are rich in tree diversity (Sobuj and Rahman 2011a, 2011b, Rahman et al. 2012, Sarker et al. 2015), but are highly vulnerable to climate change (Khaine and Woo 2015). It is therefore of high relevance to test if different moist forest tree species in Bangladesh show variable responses in iWUE to environmental changes. We conducted a tree-ring based stable carbon isotope study on three tropical moist forest tree species (*Chukrasia tabularis* A.Juss., *Toona ciliata* M. Roem. and *Lagerstroemia speciosa* L.) in a moist tropical forest in Bangladesh, which differ in their shade tolerance, growth rates, xylem porosity and growing habitat preferences. *Chukrasia tabularis* is an intermediate shade-tolerant, fast-growing, diffuse-porous species. *Toona ciliata* is a shade-intolerant, fast-growing, (semi)ring-porous species, while *L. speciosa* is a shade-tolerant, slow-growing, ring-porous species. The main objective of this study was to investigate the short-term (inter-annual) variability and long-term patterns of iWUE in the three species in response to elevated CO₂ and climate. We tested the following hypotheses:

- (i) In response to rising atmospheric CO₂ concentration (C_a), there is a species-independent long-term positive trend in stable carbon isotope ratios ($\delta^{13}\text{C}$), carbon discrimination ($\Delta^{13}\text{C}$), intercellular CO₂ concentration (C_i) and iWUE.
- (ii) Climate exerts an overriding influence on inter-annual variability of iWUE over atmospheric CO₂, whereas atmospheric CO₂ shapes the long-term pattern of iWUE.

Materials and methods

Study sites and climate

The study was conducted in the 1795 ha large nature reserve Rema-Kalenga Wildlife Sanctuary (RKWS) (24°06'–24°14'N and 91°36'–91°39'E) in Bangladesh. Tree sampling was conducted in Rema, Kalenga and Chonbari forest reserves within the RKWS, which is a part of the Indo-Burma biodiversity hotspot (Brooks et al. 2002). The study sites consist of floodplain areas and hills up to 100 m above the sea level. Hill tops are represented by sandy loamy soils, whereas flood plain areas comprise of clay loamy soils. The study sites experience a humid monsoon climate with total annual precipitation of 2363 mm and mean annual temperature of 24.8 °C calculated over 1950–2015. There is a distinct seasonality, with a dry season (monthly precipitation <100 mm) extending from November to February (Figure 1A). Taking the climate seasonality pattern and the phenological behavior of trees into account, we assumed that March–October is the growing season of our studied species. The main monsoon season extends from May to August. March–April is the pre-monsoon and September–October is the post-monsoon season in our study area.

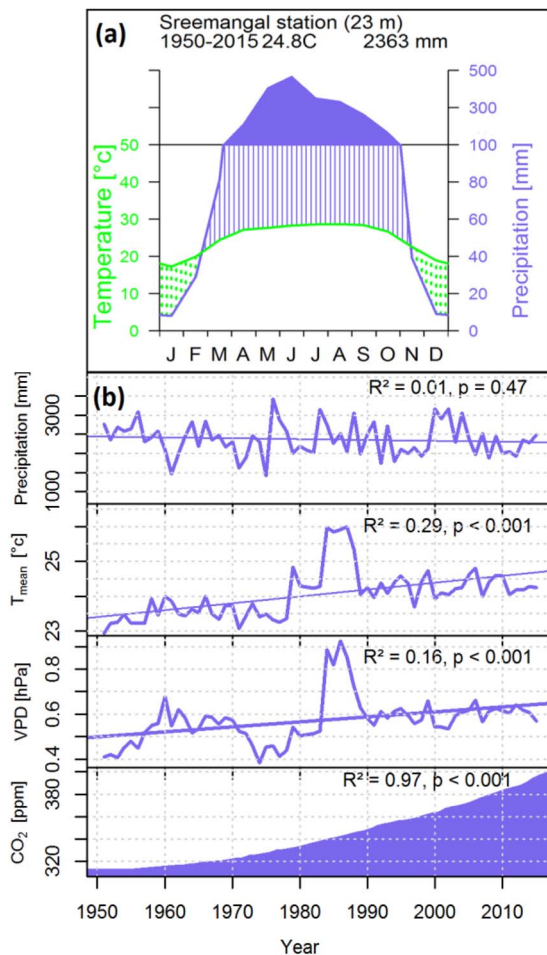


Figure 1. (A) Climate diagram based on the climate data over 1950–2015 recorded at the nearest climate station Sreemangal, 23 km away from the study site. Green dotted areas represent the dry season with monthly precipitation < 100 mm. Dark shaded areas represent the wet season with monthly precipitation > 100 mm. (B) Inter-annual variability and long-term trends in precipitation, mean temperature, vapor pressure deficit (VPD) and atmospheric CO₂ concentration from 1950 to 2015.

Study species and wood sample collection

Recent studies on several species in Bangladeshi moist tropical forests revealed species-specific growth responses to the climate change (Rahman et al. 2018). Species-specific drought resilience and hydraulic conductivity response to water stress were observed in the functionally different moist forest species in Bangladesh (Islam et al. 2018, Rahman et al. 2019a). We therefore selected two species from the top canopy (*C. tabularis* and *T. ciliata*, Meliaceae), and one species from the middle canopy (*L. speciosa*, Lythraceae). Species selection was based on the formation of distinct wood anatomical growth-ring boundaries, xylem porosity, ecological guild and their wide distribution in tropics. All three species form fairly distinct and annual growth-ring boundaries (Rahman et al. 2018). The main characteristics of the species are described in Table 1.

We collected 210 increment cores from 105 trees, and one stem disc of *C. tabularis*. Cores were extracted at breast height

Table 1. Characteristics of three South Asian tropical moist forest tree species.

Species name	Family	Distribution ¹	Phenology ²	Shade tolerance ³	Max. height (m)	Growth-ring boundary features ⁴	Wood density (g cm ³)	Growth rate
<i>Chukrasia tabularis</i>	Meliaceae	SA, EA, SEA	(Kalinganire and Pinyopusarek 2000; Williams et al. 2008; Orwa et al. 2009)	(Kalinganire and Pinyopusarek 2000; Williams et al. 2008; Orwa et al. 2009)	40	MP	0.59	Fast growing
<i>Toona ciliata</i>	Meliaceae	SA, SEA, Af, A	Deciduous	P	45	P, MP, FWT	0.38	Fast growing
<i>Lagerstroemia speciosa</i>	Lythraceae	SA, EA, SEA	Deciduous	ST	30	P, MP, FWT	0.64	Slow growing

¹SA, South Asia; EA, East Asia; SEA, South-East Asia; A, Australia; Af, Africa.

²Deciduous: tree leafless for > 4 weeks; brevi-deciduous: tree briefly or only partially leafless.

³P, pioneer; PST, partially shade tolerant; ST, shade tolerant.

⁴MP, marginal parenchyma band (terminal or initial); P, porosity; FWT, thick-walled latewood fibers.

(1.3 m) using a 5-mm Suunto increment borer (Vantaa, Finland). After air drying in the laboratory, cross-sectional surface of the cores were sanded by increasingly fine sand papers (80–2000 grit) until growth-rings were visible with the naked eye (Stokes and Smiley 1968). To improve the contrast of vessels from the surrounding tissues, we used white chalk on the wood surface to fill the vessels. The stem disc and cores were then scanned with a flatbed scanner (Epson Expression 10000XL, Long Beach) at a resolution of 2000 d.p.i.

Ring-width measurement and cross-dating

Ring-width measurement was performed on polished wood surface using Lintab 6 and on the scanned images using the CooRecorder image analysis software (Cbis, Saltsjöbaden, Sweden) at a precision level of 0.01 mm. First, two or three cores or disc radii of a tree were cross-dated using the TSAP-Win software (Rinntech, Heidelberg, Germany). Cross-dating of cores from different directions within a tree allowed identifying false rings, wedging rings and missing rings (Worbes et al. 2002). Cross-dating within trees was statistically checked using *t*-test and GLK values (Eckstein and Bauch 1969). Cross-dating accuracy was checked by computer program COFECHA (Grissino-Mayer 2001). Finally, we successfully cross-dated 115 cores from 70 trees of three species.

Cellulose extraction, stable carbon isotope measurements and analysis

We selected a subset of five to six trees samples of each species that showed high cross-correlations with the species-specific ring-width chronologies over the past three decades (1986–2015). The size (diameter at breast height (DBH) and height) and the canopy position of the trees are presented in Table S1 available as Supplementary Data at *Tree Physiology* Online. We focused on studying the recent three decades because by this selection, the juvenile wood formed in the early life stage of trees was removed and thus a possible juvenile effect in the tree-ring isotope series (Duffy et al. 2017) was avoided. Wood slices were cut into fine pieces to increase the contact surface for the solvent during cellulose extraction. From raw wood samples, cellulose was extracted following the Jayme–Wise method (Wieloch et al. 2011). The cellulose extraction process involved the following three main steps: (i) alkaline extraction treatment with 5% NaOH solution for 2 h at 60 °C to remove resin, tannin and other essential oils from the sample; (ii) chlorination treatment with acidified NaClO₂ (7%) to remove lignin from the samples; (iii) second alkaline extraction treatment with 17% NaOH solution for 2 h at room temperature to remove short-chained cellulose products as well as other impurities including xylan and mannan. After the extraction, the cellulose was homogenized using an ultrasonic homogenization system (Laumer et al. 2009). The homogenized cellulose samples were then freeze dried for 72 h. The dried samples were weighed and ~250 ± 10 µg cellulose was loaded into a tin capsule

for δ¹³C measurement. The cellulose samples were analyzed with an elemental analyzer at the stable isotope laboratory of the Institute of Geography, University of Erlangen-Nuremberg. The analyzer operates in continuous-flow mode interfaced to a Stable Isotope Ratio Mass Spectrometer (Delta V Advantage, Thermo Fisher, Waltham). The carbon isotope composition (δ¹³C) was calculated by the following formula:

$$\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where *R* represents the ratio of ¹³C/¹²C wood samples and an internationally recognized standard material (Vienna-Pee Dee Belemnite). The δ¹³C values were corrected for changes in atmospheric ¹³CO₂, which has increased over the last two centuries due to the combustion of isotopically light fossil fuels. The δ¹³C_{air} values up to 2004 were obtained from McCarroll and Loader (2004) and the values for the period over 2005–15 were obtained following a recent study (Graven et al. 2017). The discrimination against ¹³C (Δ¹³C) by plants was calculated as:

$$\Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{tree}}) / (1 + \delta^{13}\text{C}_{\text{tree}}/1000) \quad (2)$$

Carbon discrimination during CO₂ fixation of C₃ plants is linearly related to the ratio of intercellular CO₂ concentration in the leaves (C_i) to the atmospheric CO₂ concentration (C_a) and can be expressed as following equation (Francey and Farquhar 1982):

$$\delta^{13}\text{C} = a + (b - a) (C_i/C_a) \quad (3)$$

where, *a* is the discrimination against ¹³C that takes place due to the slower diffusion of ¹³CO₂ relative to ¹²CO₂ (*a* = 4.4%) and *b* is the discrimination by Rubisco against ¹³CO₂ (*b* = 27%) (Farquhar et al. 1982). From the Eq. (3) and using direct measurements of atmospheric CO₂ (https://www.esrl.noaa.gov/gmd/ccgg/trends/gl_data.html), C_i was calculated as follows:

$$C_i = ((\Delta^{13}\text{C} - a) C_a) / (b - a) \quad (4)$$

The iWUE is defined as the ratio of assimilation rate (*A*) to water loss due to stomatal conductance (*g_s*) and can be estimated using the following equation (Farquhar et al. 1989):

$$\text{iWUE} = A/g_s = (C_a - C_i) / 1.6 = C_a (1 - C_i/C_a) / 1.6 \quad (5)$$

Data preparation

To develop standard chronologies, we detrended iWUE time series by fitting a 10-year cubic smoothing spline curve with a 50% frequency response (*f* = 0.50) using dplR package in R (Bunn 2008). For long-term analysis, we used a conservative detrending method (mean) to retain the low frequency signals in the chronology (Nock et al. 2011, Sullivan et al. 2016). The 'mean' function fits a horizontal line using the mean value of the series, thus indexing them while preserving all low-frequency

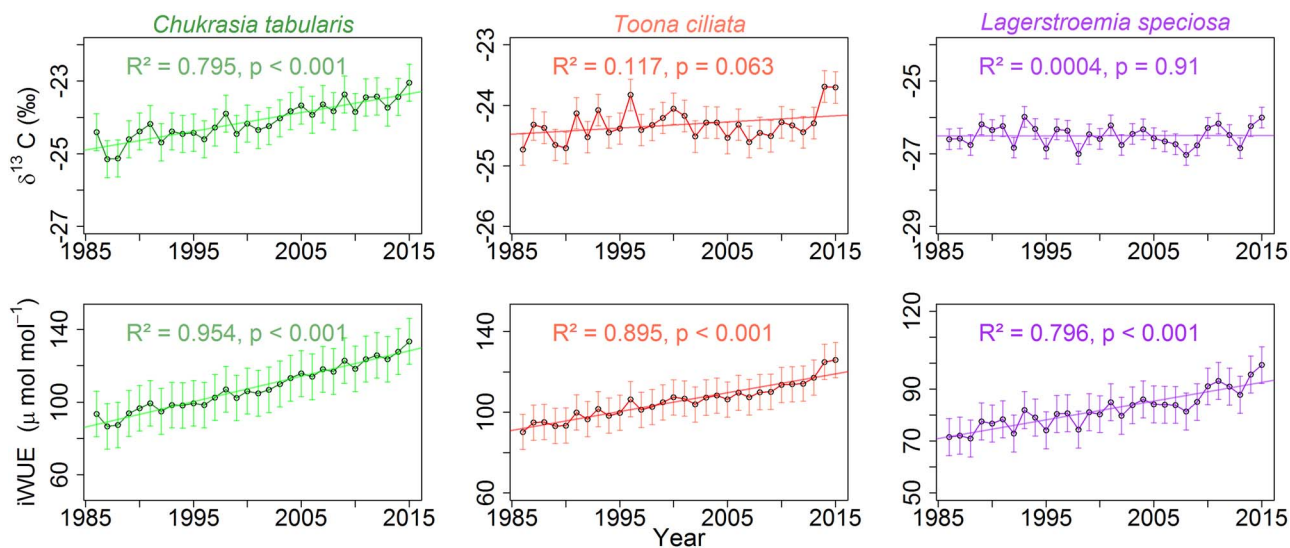


Figure 2. Annual variability and long-term trends in $\delta^{13}\text{C}$ (corrected for atmospheric CO_2 increase) and intrinsic water-use efficiency (iWUE) of three South Asian tropical moist forest tree species.

variations contained in the original data. Thus, we worked with two data sets: spline-filtered chronologies and mean-indexed original chronologies. Spline-filtered chronologies were used for dendroclimatic analysis, modeling and commonality analysis (CA). Mean-indexed chronologies were used to calculate long-term trends in tree-ring variables (Bunn 2008). Inter-series correlation between individual trees ($r_{\text{bar.bt}}$) and expressed population signal (EPS) were calculated using the commonly accepted equations (Briffa and Jones 1990).

Data analyses

We analyzed monthly mean temperatures, vapor pressure deficit (VPD) and annual precipitation data for the period after 1950. Temperature and precipitation data were collected from the nearby meteorological station Sreemangal, which is 23 km away from the study site. The VPD was calculated from monthly temperature and relative humidity data following the equation: $\text{VPD} = ((100 - \text{RH})/100) \times \text{SVP}$, where saturated vapor pressure ($\text{SVP}) = 0.610 \exp \times ((17.27 \times T)/(T + 237.3))$, T = temperature and RH = relative humidity.

To test if the tree-ring time series have any long-term trends, we performed simple linear regression analysis of the mean chronologies of all the tree-ring variables. Pearson correlation analysis was performed to explore the association between iWUE and climate variables. Intrinsic water-use efficiency was simulated using linear mixed effect (LME) modeling, taking climate variables as fixed factors and tree-height and DBH as random factors. Tree-height can influence estimates of iWUE (Brienen et al. 2017) and was reconstructed applying height-diameter allometric equations developed from the region–environment–structure model (Feldpausch et al. 2011). Best model selection was based on the Akaike information criterion (AIC), Bayesian information criterion (BIC) and log

likelihood ratio (loglik). The best model results in the lowest AIC and BIC and the highest loglik values. Commonality analysis was performed to disentangle the effects of multiple factors (temperature, precipitation and atmospheric CO_2) on iWUE. One of the advantages of CA is that it can separate the relative contribution of a particular predictor in explaining the variance of response variable as well as providing the relative contribution shared by multiple predictors (Huang et al. 2017). All analyses were performed within the R statistical programming environment (R Development Core Team 2016).

Results

Long-term trends in $\delta^{13}\text{C}$, $\Delta^{13}\text{C}$, C_i and iWUE

We observed a significantly increasing trend in $\delta^{13}\text{C}$ in *C. tabularis* ($R^2 = 0.80$, $P < 0.001$) over the past three decades. In contrast, *T. ciliata* and *L. speciosa* did not show any significant long-term trends in $\delta^{13}\text{C}$ (Figure 2). However, all three species showed a significantly decreasing trend in $\Delta^{13}\text{C}$, with *C. tabularis* displaying the highest decrease in $\Delta^{13}\text{C}$ (14%). In contrast to the decreasing trend in carbon discrimination, we observed strongly significant increasing trend in iWUE in all three species (Figure 2). The iWUE of *C. tabularis* showed the highest increase, by 29–46%. Nonetheless, divergent long-term trends were observed in C_i , with *C. tabularis* showing decreasing trend, whereas *T. ciliata* and *L. speciosa* showing increasing trends. The percentage change in C_i in *L. speciosa* was almost double (9%) that in the other two species. The descriptive statistics of all tree-ring variables are presented in Table 2.

Climatic influences on iWUE

A significant increasing trend was observed in mean temperature and VPD concurrent with the increasing atmospheric CO_2

Table 2. Descriptive statistics of the tree-ring variables of three South Asian tropical moist forest tree species.

Species	Variables	Minimum	Maximum	Mean	SD
<i>C. tabularis</i>	$\delta^{13}\text{C}$	-25.15	-23.05	-24.10	0.51
	$\Delta^{13}\text{C}$	14.96	17.98	16.49	0.77
	C_i	187.34	208.84	197.72	5.03
	iWUE	86.58	133.46	107.98	12.56
<i>T. ciliata</i>	$\delta^{13}\text{C}$	-24.73	-23.69	-24.32	0.26
	$\Delta^{13}\text{C}$	15.65	17.57	16.72	0.43
	C_i	190.57	211.20	201.73	5.26
	iWUE	90.20	125.87	105.47	8.72
<i>L. speciosa</i>	$\delta^{13}\text{C}$	-27.03	-25.98	-26.50	0.28
	$\Delta^{13}\text{C}$	18.05	19.64	19.00	0.40
	C_i	225.10	255.99	239.11	7.84
	iWUE	71.03	99.27	82.11	7.11

T, temperature; P, precipitation; VPD, vapour pressure deficit; py = previous year.

concentration over 1950–2015 (Figure 1B). However, local precipitation showed a high inter-annual variability but did not show a significant trend over 1950–2015.

The high inter-series correlations ($r_{\text{bar},\text{bt}}$) and EPS values of $\delta^{13}\text{C}$ chronologies (Table S2 available as Supplementary Data at *Tree Physiology Online*) indicate that the iWUE chronologies, which are derived from the mean $\delta^{13}\text{C}$ series (detrended by fitting a smooth spline curve) of all the three species are robust and contain a common signal which can be related to climate variables. Both T_{mean} and VPD in the current year April had negative associations with iWUE in *C. tabularis* (Figure 3). Water-use efficiency was also inversely related with previous year precipitation (August and November). The current year June temperature was negatively correlated with iWUE in *T. ciliata*. However, the strongest correlation of iWUE in *T. ciliata* was observed with previous year June temperature (Figure 3). Precipitation and VPD had no significant influence on iWUE in *T. ciliata* in our study sites. Water-use efficiency in *L. speciosa* was strongly negatively connected with the current year June temperature ($r = 0.64$, $P < 0.001$) and August precipitation. Overall, climate variables explained 41–51% of the total variation in iWUE, depending on species. The highest and lowest amounts of variation were explained for *L. speciosa* and *C. tabularis*, respectively (Figure 4). The LME model results are shown in Table 3.

Relative contribution of C_a and climate in iWUE variability

We disentangled the effects of the climate variables and atmospheric CO_2 on iWUE by CA. Since iWUE was calculated from C_a , examining iWUE as a role of C_a is somewhat circular in reasoning. Therefore, we examined C_i/C_a instead of iWUE in CA and thus, the influence of C_a was factored out and changes in iWUE remained independent of long-term trend in C_a . Commonality analysis revealed a dominant influence of climate on the C_i/C_a of all the three species when analyzed with detrended data (Figure 5A). The relative contribution of temperature was higher than the other variables in explaining

C_i/C_a variability, ranging between 49 and 74% depending on the species. The pure effect of temperature was highest in *T. ciliata* (74%) and lowest in *C. tabularis* (49%). On the other hand, the highest and lowest pure effects of precipitation were found in *C. tabularis* and *T. ciliata*, respectively. The maximum pure effect of C_a was found in *L. speciosa* (11%), whereas the least pure effect of C_a was found in *C. tabularis* (0.5%). The joint effect of temperature and precipitation was highest in *C. tabularis* (31%) and lowest in *T. ciliata* (13%).

When long-term trends were retained in the iWUE values, the influence of C_a became prominent over the climate variables (Figure 5B). The pure effect of C_a ranged between 68 and 94%, with highest and lowest percentages in *T. ciliata* and *L. speciosa*. The highest pure effect of temperature was found in *L. speciosa* (25.1%). The maximum joint effect was shared by C_a and precipitation observed in *T. ciliata* (7%).

Discussion

Long-term changes in tree-ring variables

In general, we observed an increasing iWUE and a decreasing $\Delta^{13}\text{C}$ in our studied species. Increasing water-use efficiency is a common response to rising atmospheric CO_2 concentration observed in all studies conducted in different tropical forest sites (Silva and Anand 2013, van der Sleen et al. 2014). However, the magnitude of increase in iWUE varied across species and sites (Nock et al. 2011, Silva and Anand 2013, van der Sleen et al. 2014, Fu et al. 2017). In our studied species, iWUE increased between 29 and 46% over the past three decades. The high variation in the increase in iWUE might be attributed to the topographic variation of the species occurrence. *Chukrasia tabularis* grows on the slopes of hills, whereas *L. speciosa* is found in low lying flood plain areas. In the floodplain, *L. speciosa* likely optimized its carbon fixation without strong stomatal regulation due to sufficient water supply from high soil moisture content in the clayey loamy soils, resulting in low iWUE. On the other hand, *C. tabularis* growing on sandy loamy soils on

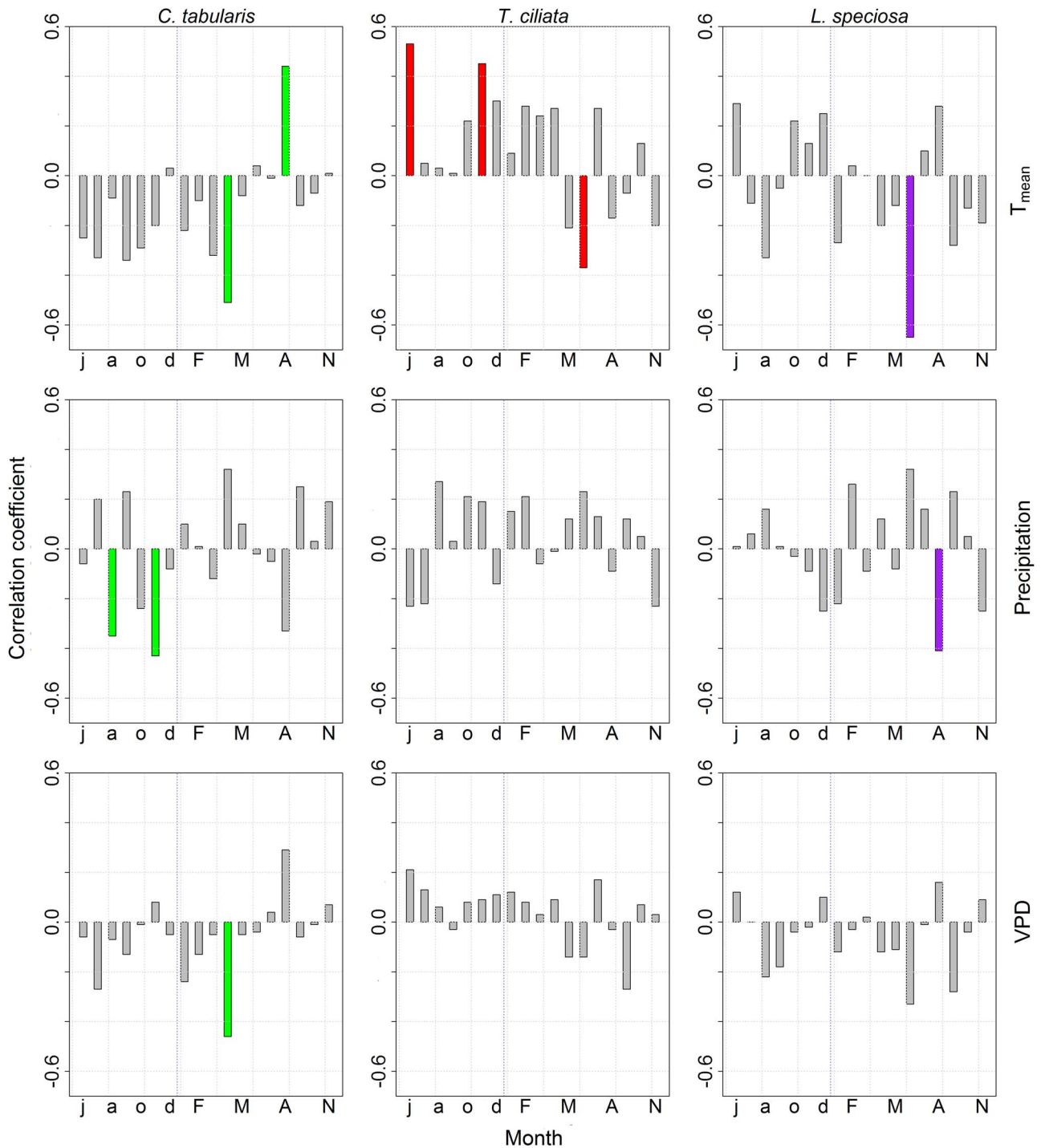


Figure 3. Relationships between climate variables and intrinsic water-use efficiency (iWUE) (detrended, spline-filtered chronologies) for three South Asian tropical moist forest tree species. The upper-case letters indicate months of the current year. The lower-case letters indicate months of the previous year.

hill slopes containing lower moisture content showed highest economic use of water for carbon gain, leading to a higher iWUE.

The range of increase in iWUE in our studied species is much higher than the iWUE increase of 30–35% observed in an earlier study conducted on 12 tree species in three tropical forest sites and calculated over 150 years (van der Sleen et al. 2014). A

lower increase in iWUE (10–17%) over the period from 1950 to 2005 was also observed in subtropical forests in Brazil and Argentina (Silva et al. 2009, Sun et al. 2010). The difference in the magnitude of change in iWUE might be linked to differences in site conditions (e.g., annual precipitation amount) between tropical forest sites (Yu et al. 2005). It is also possible that

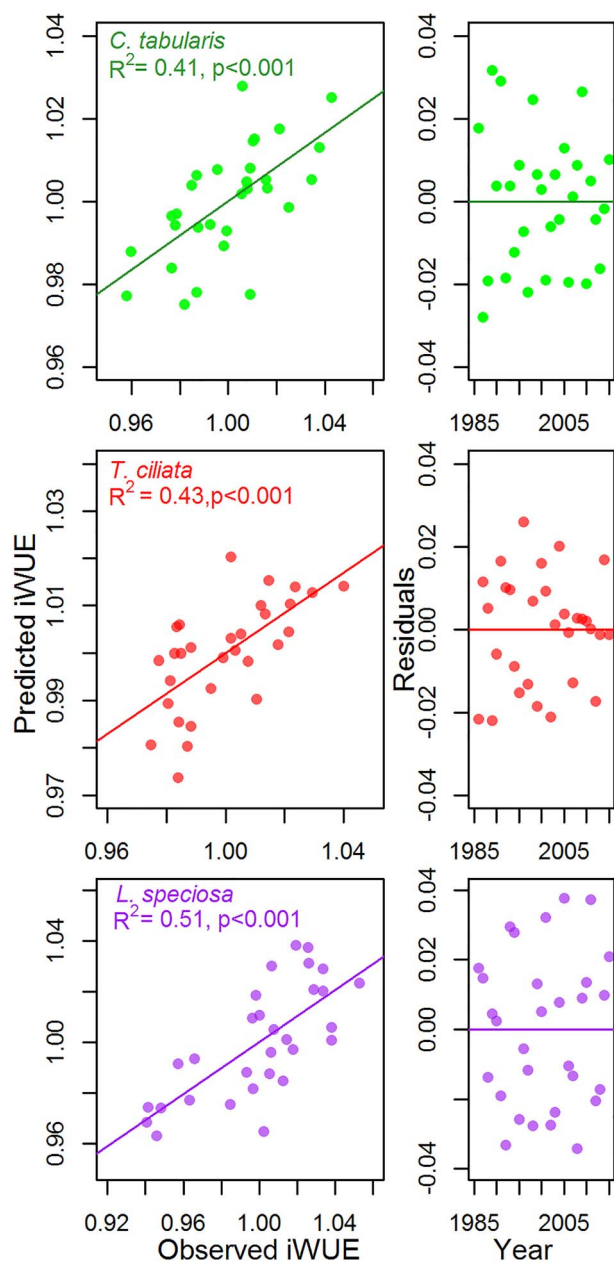


Figure 4. Relationships between observed and predicted intrinsic water-use efficiency (iWUE) and the residual values of the predicted models for three South Asian tropical moist forest tree species. Climate and atmospheric CO_2 were included as the fixed factors (see Table 3). Tree-height and diameter at breast height were considered as random factors in the mixed effect model for the three species.

differences in the methods to remove ontogenetic effects on iWUE might have caused this variation in iWUE trend between two studies. van der Sleen et al. (2014) followed the size-class isolation method to remove the effects of tree size (diameter) on iWUE. In our study, we detrended iWUE series by fitting a spline function and thus removed low frequency signals that are mostly associated with ontogenetic trends. We further used tree-height as a random factor in a mixed effect model to avoid effects of tree-height on iWUE, because tree-height strongly affects iWUE

in tropical trees (Brienen et al. 2017). With increasing tree-height, iWUE may double or even triple over a tree's lifespan (Brienen et al. 2017). A stronger increase in iWUE may also be caused by site degradation due to increasing disturbance intensity over time (Yu et al. 2005). However, our sampling sites represent the core zone of a nature reserve and thus were not subjected to large-scale anthropogenic disturbances. Consistent with our results, a similar magnitude of increase in iWUE (40%, during the past four decades) was found in *Mimosa acantholoba* from a tropical dry forest of the southern Mexico (Brienen et al. 2011), although the authors did not control for ontogenetic effects, and thus their estimate may contain a juvenile effect.

Increasing water-use efficiency in association with decreasing carbon discrimination generally implies that trees are growing under water-stress conditions at least for a part of growing season (Korol et al. 1999). It is, however, possible that decreasing carbon discrimination may be a result of atmospheric CO_2 increase, increase in photosynthesis rates or temperature effects on mesophyll conductance. Taking the mesophyll conductance effect into account improved model estimates for iWUE (Cintra et al. 2019). Their model took both mesophyll conductance and photorespiration effects together into account (Farquhar and Von Caemmerer 1982, Seibt et al. 2008), which is currently not addressed in our study. Nevertheless, von Caemmerer and Evans (2015) investigated the temperature response of mesophyll conductance for nine species, including both trees and herbs. Herb species showed strong responses to temperature, while cool environment and tropical trees were relatively insensitive to temperature. Quantification of the temperature effect on carbon isotope discrimination during diffusion through mesophyll in tropical trees therefore calls for further studies.

Most of the long-term variation in iWUE in our studied species was explained by rising atmospheric CO_2 concentration (Figure 5B). Explanation of nearly 86% of the total variation by C_a indicates that long-term iWUE trends are driven mainly by the increasing C_a and not by temperatures or precipitation changes. In line with our findings, increased assimilation rate due to rising atmospheric CO_2 drove long-term increase in iWUE in tropical (Nock et al. 2011, van der Sleen et al. 2014), temperate (Rezaie et al. 2018), boreal (Xu et al. 2018, Giguère-Croteau et al. 2019), Mediterranean (Granda et al. 2014, Martínez-Sancho et al. 2018) and subtropical forests (Li et al. 2017, Weiwei et al. 2018).

However, increasing iWUE and decreasing $\Delta^{13}\text{C}$ may not always be reflected by long-term trends in stem radial growth. Our previous studies on the radial growth of the same species found no sign of any long-term increase in tree growth (Rahman et al. 2017), but rather found strong negative relationships with temperatures and a projected tree growth decline with higher expected future temperatures (Rahman et al. 2018). The positive relationship between iWUE and tree growth was also absent in a previous study across the tropics

Table 3. Restricted maximum likelihood parameter estimates and model skills of linear mixed effect models (fixed effects) predicting iWUE of three South Asian tropical moist forest tree species.

Species	Estimates	Value	SEM	DF	t-value	P-value	R ²	AIC	BIC	logLik
<i>C. tabularis</i>	(Intercept)	0.73	0.35	25	2.09	0.05	0.41	−110.93	−101.18	63.47
	T_Apr	−0.19	0.13	25	−1.39	0.18				
	T_Aug	0.47	0.30	25	1.57	0.13				
	VPD_Apr	−0.01	0.03	25	−0.36	0.72				
	P_py_Nov	0.00	0.00	25	−1.20	0.24				
<i>T. ciliata</i>	(Intercept)	0.65	0.28	26	2.33	0.03	0.43	−144.20	−135.40	79.10
	T_py_Jun	0.43	0.18	26	2.43	0.02				
	T_Jun	−0.26	0.17	26	−1.47	0.15				
	T_py_Nov	0.17	0.09	26	1.98	0.06				
<i>L. speciosa</i>	(Intercept)	2.23	0.27	27	8.21	0.00	0.51	−105.06	−97.28	58.53
	T_Jun	−1.20	0.27	27	−4.37	0.00				
	P_Aug	0.00	0.00	27	−2.20	0.04				

T, temperature; P, precipitation; VPD, vapour pressure deficit; py = previous year.

(van der Sleen et al. 2017a), indicating either an absence of CO₂ fertilization in tropical trees, or that tree growth in tropical regions is limited by other factors than atmospheric CO₂. It is, however, important to note that detecting the CO₂ radial growth fertilization effect is not straightforward, since also multiple biases related to tree demography might influence long-term growth trends (Brienen et al. 2016)

Intrinsic water-use efficiency and climate: inter-annual variation

Overall, mixed models successfully simulated the iWUE in our studied species. Climate variables explained 41–51% of the total iWUE variability (Figure 4). Adjustment in water-use efficiency might be one of the adaptation strategies of plants to cope with water limitation (Tardieu et al. 2014, Blankenagel et al. 2018). Intrinsic water-use efficiency is a function of assimilation rate and water loss by stomatal conductance (Farquhar et al. 1982). Thus, the rising atmospheric CO₂ concentrations might be linked with tree-ring δ¹³C-derived iWUE (Battipaglia et al. 2013). However, water loss by transpiration can be influenced by stomatal conductance as well as by climatic conditions, particularly leaf-to-air VPD (Turner et al. 1984), suggesting that iWUE might also be linked with climate (Rezaie et al. 2018). We simulated iWUE, taking climate variables as the fixed factors and tree-height as the random factor in a mixed effect model and found that current and previous year temperature and precipitation as well as current year VPD significantly influenced iWUE in our studied species (Table 3).

In response to increasing temperature, ability to increase iWUE is a competitive advantage for C₃ plants (Tardieu et al. 2014). Some earlier studies reported positive relationships between iWUE and high air temperature (Seibt et al. 2008; Battipaglia et al. 2014). In contrast to earlier findings, our species negatively responded to higher temperatures (Figure 3). The iWUE in one of the studied species (*C. tabularis*) reacted negatively to high VPD. These findings are in line with

the results of an experimental study conducted in a reforestation site that reported negative relations of iWUE with VPD (Grossnickle et al. 2005). A strong negative correlation of iWUE with pre-monsoon and monsoon temperature and VPD likely implies that higher temperature might have caused photosynthetic limitation and higher evapotranspiration, leading to a decrease in iWUE (Seibt et al. 2008). Multiple evidences suggest that leaf-level photosynthesis in many tropical forests might already have reached a high temperature threshold (Mau et al. 2018, Pau et al. 2018). It was also reported that water limitation significantly suppressed leaf-level photosynthesis (Urban et al. 2017a). It is therefore possible that, in unusually warm years, elevated temperatures induce increased stomatal conductance, restrict photosynthesis and thus limit iWUE in our sites (Urban et al. 2017b).

The species-specific differences in iWUE responses to climate as observed in the current study might be linked with species-specific life history strategies. Nonetheless, there is evidence that shade-tolerant and light-demanding species do not differ in their leaf-level water-use efficiency (Poorter 2005), suggesting that both pioneer and climax species fix the same amount of carbon per unit water loss. It was also reported that fast-growing pioneer species show higher iWUE than slow-growing late successional tropical trees (Wang et al. 2013). In contrast, Bonal et al. (2000) found higher iWUE in shade-tolerant species than in pioneer species. These contradictory reports may imply that more studies are required to test the iWUE response to climate across the leaf and wood economic spectrum of tropical tree species.

According to the mixed model results, iWUE in *L. speciosa* showed the highest sensitivity to climate ($R^2 = 51$, $P < 0.001$). Possible causes might be linked with tree stature and canopy position in natural forest conditions. *Lagerstroemia speciosa* is a slow-growing, shade-tolerant species attaining a lower height than the two other studied light-demanding species. Existing evidence suggests that iWUE increases with tree-height

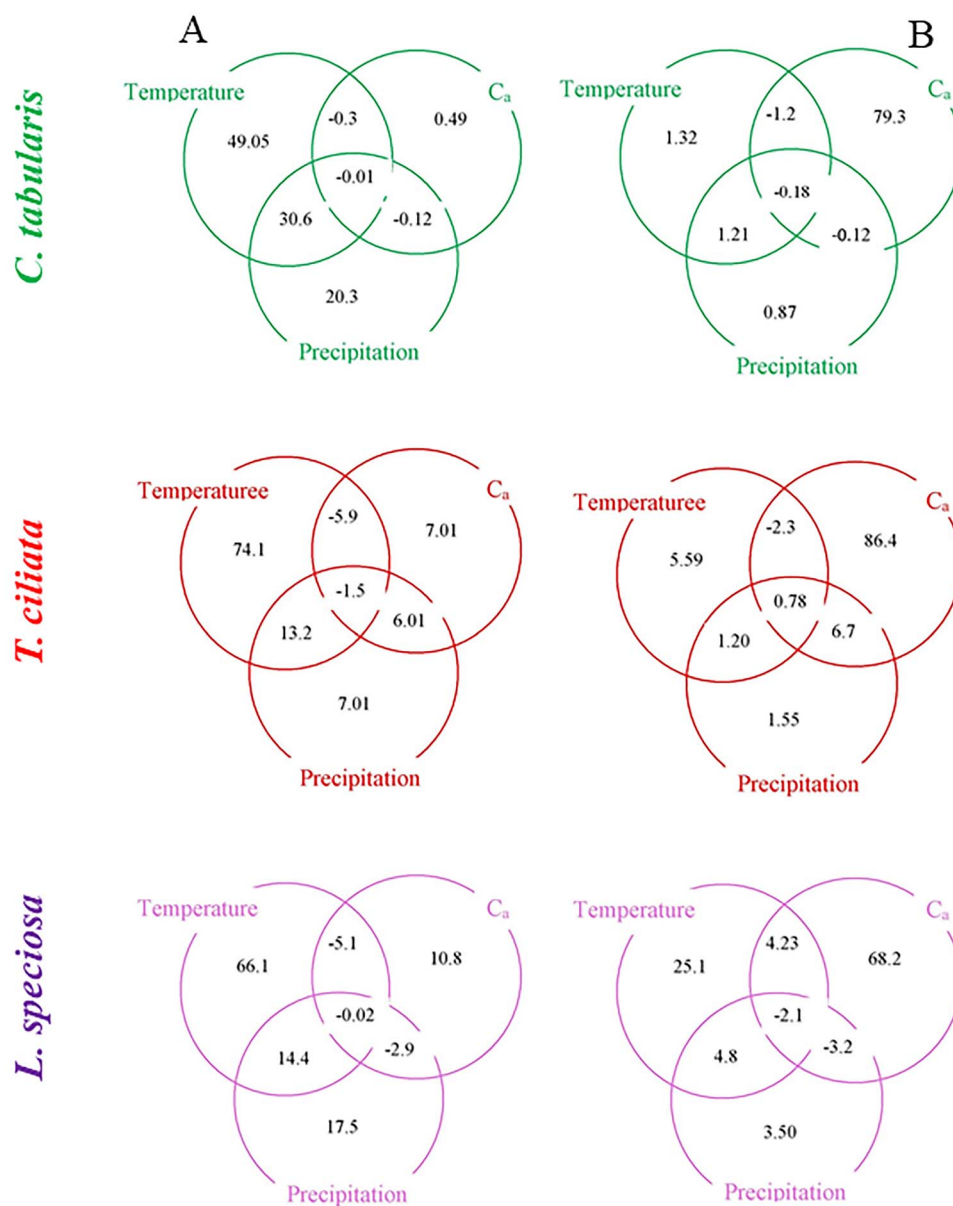


Figure 5. Commonality analysis results displaying the proportion of contribution (%) of temperature, precipitation and atmospheric CO₂ in explaining the variability of C_i/C_a three South Asian tropical moist forest tree species. In case of climate variables, only the monthly values that were significant in the direct correlations (Figure 3) were used. (A) C_i/C_a values were detrended to remove the long-term trend and retain the inter-annual variability (spline-filtered chronologies). (B) Non-detrended C_i/C_a (original values) and atmospheric CO₂ values were used.

(Brienen et al. 2017). Light availability also directly influences $iWUE$ (Navarro-Cerrillo et al. 2016, Brienen et al. 2017). It is thus likely that lower tree-height and light availability made *L. speciosa* more vulnerable to photosynthetic limitation. An increase in temperature above the optimal level for photosynthesis in the main growing season may further reduce assimilation, affecting $iWUE$ negatively as we observed in *L. speciosa* (Figure 3). Some studies suggest that many tropical forests have already reached the temperature threshold for leaf level photosynthesis (Mau et al. 2018, Pau et al. 2018). In our study site, the maximum temperature exceeded 32 °C on

>50% of the days during the wet season (April–October) (data not shown). It is therefore possible that $iWUE$ in *L. speciosa* (with height and canopy limitations) showed higher climate sensitivity. It is also likely that *L. speciosa* is more climate sensitive because of higher transpiration due to higher stomatal conductance. However, further studies are needed to support this hypothesis.

What triggers $iWUE$ variability in tropical trees: atmospheric CO₂, climate or both?

Temperature exerted a dominant influence on the inter-annual variability of C_i/C_a in all three study species as revealed by

the CA (Figure 5A). Temperature had the highest pure effects, although the relative importance of temperature, precipitation and C_a in explaining iWUE variability varied between species. The inter-species difference in the relative importance of each variable implies that tree's life history strategies (ecological guild) are important in determining gas exchange response of tropical trees to global change factors (Mastrotheodoros et al. 2017, Zhang et al. 2018). For instance, the strong light-demanding pioneer *T. ciliata* showed higher sensitivity of iWUE to temperature than the partial shade-tolerant *C. tabularis* and shade-tolerant *L. speciosa*. Likewise, precipitation sensitivity of C_i/C_a was higher in *C. tabularis* than in the two other species, likely because of lower tolerance of water logging in the late monsoon season (Orwa et al. 2009). The weaker influence of precipitation than of temperatures probably lies in the fact that our study sites receive ~2400 mm rainfall annually (Figure 1A), providing sufficient soil moisture for tree growth. However, higher temperatures might increase evapotranspiration, leading to soil moisture deficit (Rahman et al. 2019a), which results in higher sensitivity to water stress aggravated by elevated temperature in our studied species. A very small contribution of C_a (0.5–11%) in explaining inter-annual variability of iWUE in our studied species suggests that atmospheric CO₂ is not so important in explaining the short-term (inter-annual) variability in C_i/C_a .

Above all, we demonstrate that the ecophysiological responses to the past environmental changes can be reconstructed from the stable carbon isotope fractionation in South Asian tropical moist forests. We identified the driving factors of inter-annual variability and long-term patterns of iWUE in three tropical moist forest tree species in Bangladesh and disentangled their relative contributions. Inter-annual variability in iWUE was mainly triggered by climatic factors, whereas the long-term variation in iWUE was explained by atmospheric CO₂. Among the climatic factors, temperatures had the dominant influence on the inter-annual variability in iWUE in all the three species over precipitation. Our analysis suggests that the global warming is detrimental to the gas exchange response of South Asian tropical moist forest species.

Supplementary Data

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

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Conflict of interest

None declared.

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