

Increasing intrinsic water-use efficiency over the past 160 years does not stimulate tree growth in southeastern China

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ABSTRACT: Understanding the responses of tree growth and intrinsic water-use efficiency (iWUE) to anthropogenic CO₂ increase and climate warming provides important benchmarks for evaluating future forest dynamics under different scenarios of warming and CO₂ changes. Relative to the short period of instrumental data of the past few decades, long-term tree-ring width and stable carbon isotopic ($\delta^{13}\text{C}$) data are invaluable in fully comprehending their interactions during the entire industrial era, since ~1850. Here, we present a tree-ring width chronology (1856 to 2015) and $\delta^{13}\text{C}$ series (1876–2015) of *Pinus massoniana* for Yongtai county of Fujian province, in humid subtropical China, a 'green island' relative to other dry subtropical areas of the world. Tree growth was limited by precipitation of the hydrological year (previous November to current October) ($r = 0.568$, $p < 0.001$), and the stable carbon isotope discrimination ($\Delta^{13}\text{C}$) was strongly correlated with relative humidity in September–October ($r = -0.677$, $p < 0.001$) of the current growing season. We found that the iWUE increased by 40.9% since 1876. Specifically, we found that the $c_i:c_a$ ratio decreased during the study period whereas intercellular CO₂ concentration (c_i) increased. The negative relationship between basal area increment (BAI) and iWUE indicated that increasing iWUE may not lead to long-term enhancement of tree growth. Our results indicated a drought-induced limitation to tree growth in response to rising CO₂, and that trees may mitigate the negative effects of a decrease in water availability through a reduction in stomatal conductance.

KEY WORDS: Tree-ring · Stable carbon isotope · Intrinsic water-use efficiency · *Pinus massoniana* · Humid subtropical China

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1. INTRODUCTION

The increase in atmospheric CO₂ concentration (c_a) and the resulting climate change are coupled with forest dynamics, since forests are the largest carbon sink in terrestrial ecosystems (Huang et al. 2007, Bonan 2008, Frank et al. 2010). Their couplings can be indirect and complex via, for example, the intrinsic water use efficiency (iWUE). The iWUE is deter-

mined by the ratio between net photosynthesis (A) and leaf conductance (g) (Farquhar et al. 1982). Controlled experiments have demonstrated that iWUE increases as a result of the enhanced CO₂ assimilation and decreased stomatal conductance in response to CO₂ increase (Picon et al. 1996). Monitoring studies are very useful in revealing the responses of tree growth to CO₂ fertilization and climate warming, but these generally short-term studies may not be able to

fully reveal the adaption of forests to long-term increases in CO₂ concentrations and warming trends. This situation can be alleviated using long-term tree-ring proxy data (Saurer et al. 2004). Tree-ring width data are not only a useful indicator of tree growth, but also of past climate changes over the last few hundred to thousands of years (Li et al. 2007, Cook et al. 2010, Fang et al. 2012). Carbon and water exchange at the leaf level are intimately coupled, and thus the iWUE can be inferred from carbon exchange data. The stable carbon isotope ratio ($\delta^{13}\text{C}$) in a tree ring is proportional to the ratio of the intercellular CO₂ concentration (c_i) and c_a , offering an effective tool to trace long-term changes in iWUE (Farquhar et al. 2003). Therefore, tree-ring width and $\delta^{13}\text{C}$ can be used to disentangle the linkages among CO₂ concentration, climate, iWUE and forest dynamics in a historical context. This can shed light on forest responses to different scenarios of future CO₂ concentration and climate warming.

Recent studies have focused on tree-growth response to rising CO₂ concentration and climate warming at local or regional scales (Andreu-Hayles et al. 2011, Lévesque et al. 2014, Dietrich et al. 2016). A rise in CO₂ concentration and the associated increase in iWUE are expected to stimulate tree growth in arid regions, where trees are limited by drought (e.g. Soulé & Knapp 2006, Linares & Camarero 2012, Liu et al. 2014). However, other studies found that tree growth did not increase significantly in arid regions despite the enhanced CO₂ concentration and iWUE (Andreu-Hayles et al. 2011, Wang et al. 2012, Lévesque et al. 2014, Wu et al. 2015, Dietrich et al. 2016, Fernández-De-Uña et al. 2016). The linkages among CO₂ concentration, climate, iWUE, and tree growth can be even more complex in environments where tree-growth conditions are favourable, such as humid and subtropical/tropical forests. A number of studies showed that tree growth had a positive trend in tropical forests that is attributable to the CO₂ fertilization effect (Lloyd & Farquhar 2008, Lewis et al. 2009). Others found no obvious trend of tree growth in subtropical/tropical forests (Nock et al. 2011, Xu et al. 2014, van der Sleen et al. 2015).

Our study region in the western bank of the Taiwan Strait supports the world's largest subtropical evergreen broadleaf forests, facilitated by the East Asian summer monsoon (Sheng et al. 2010). However, despite abundant precipitation, drought stress in tree growth during summer has been reported due to high temperatures and relatively low precipitation during this season (Chen et al. 2012, Li et al. 2016). This suggests that tree rings could potentially be

used for studying climate change and iWUE in this region. Currently, most of the tree-ring based climate studies in China have focused on arid and cold areas (Zhang et al. 2003, Gou et al. 2008, Li J et al. 2017). Although a few studies have been conducted in subtropical China (Zheng et al. 2012, Duan et al. 2013, Chen et al. 2015, Shi et al. 2015, Cai & Liu 2016), tree-ring data are sparse, in particular those based on stable carbon isotopes. Relationships between tree rings, climate and iWUE are poorly understood in humid subtropical eastern Asia, where fewer tree-ring studies have been conducted. To our knowledge, there is only one tree-ring carbon isotopic series published from southwestern Fujian province (Li D et al. 2017), which found that the relationships between tree rings, climate and iWUE were similar to that in arid China. However, these tree-ring width sites and the tree growth of recent decades at the Niulin site have been influenced by the removal of resin. Therefore, our study selected the Fangguangyan site, where soil depth is shallower and tree growth is expected to be more drought-stressed. In addition, there was no removal of resin at our study site. We found that our tree rings show higher correlations with drought than previously studied sites. The increasing CO₂ concentration since the beginning of the industrial era at ~1850 provides an important background to reveal the responses of forest dynamics to CO₂ increase. The objectives of this study were to (a) develop the first tree-ring width and $\delta^{13}\text{C}$ series for Yongtai county in Fujian province, and (b) assess the interactions between the increase in CO₂ concentration, climate, iWUE and tree growth since the beginning of the industrial era.

2. DATA AND METHODS

2.1. Study site

The tree-ring samples were taken from *Pinus massoniana* trees at the site of Fangguangyan (site code FGY; 25° 53' N, 119° 11' E) on the western bank of the Taiwan Strait in Yongtai county of the Fuzhou area (Fig. 1). FGY is a protected area for historical relics (a temple) in Fujian Province. Old growth *P. massoniana* trees can be found in such locations because logging is often prohibited near temples due to tradition. The region is characterised as a typical subtropical monsoon climate. According to observations from Fuzhou meteorological Stn (26° 05' N, 119° 17' E, 84 m a.s.l.) during 1953–2015, the average annual total precipitation was 1377 mm and the average

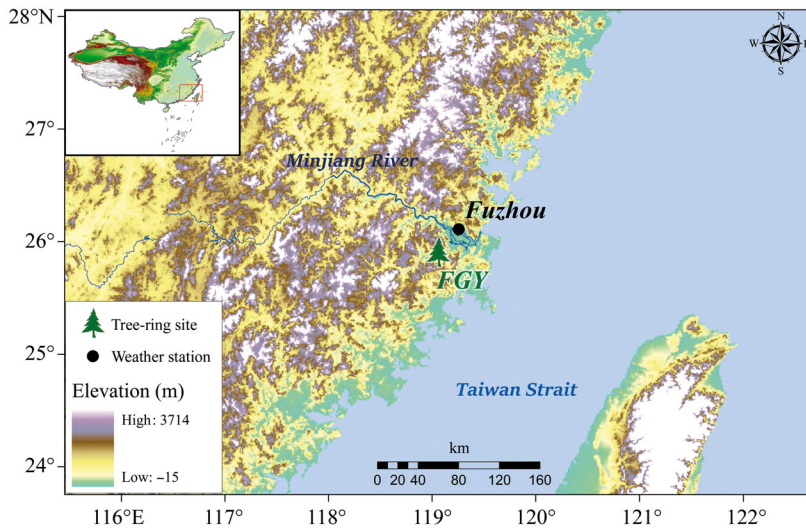


Fig. 1. Tree-ring sampling site, meteorological station and sampling site in eastern Fujian province

annual mean temperature was 20.0°C. Precipitation peaks in May and June, while temperature peaks in July and August (Fig. 2a). Summers on the western bank of the Taiwan Strait are relatively dry due to the dominance of the western Pacific subtropical high (Li et al. 2016). From 1953 to 2015, the mean temperature increased significantly ($r^2 = 0.52$; $p < 0.001$) while the atmospheric relative humidity displayed a significant declining trend ($r^2 = 0.35$; $p < 0.001$). Sunshine hours also decreased significantly ($r^2 = 0.42$; $p < 0.001$, 1961–2015) (Fig. 2e). The study region is covered by Humic Acrisols soil, and soil coverage at the sampling site is shallow. The study region is dominated by evergreen broadleaf forests with scattered *P. massoniana* trees. The trees at FGY grow on a northeast-facing slope (within an inclination of 20°). The samples were collected from the biggest trees of similar size and age, being consistently older than 120 yr.

2.2. Tree-ring width chronology

In April 2015, 2 to 3 cores were collected at breast height (1.3 m) using 5 mm diameter increment borers from each of 100 sampled living *P. massoniana* trees at FGY. Following standard dendrochronological methodology, tree cores were mounted, air dried and polished (Stokes & Smiley 1968). Visual cross-dating was conducted to ensure accurate matching of ring-width patterns among all tree cores using a LINTAB 6.0 measuring station, with a precision of 0.001 mm. The quality of the cross-dating was assessed from

the correlations among dated tree-ring width series using the program COFECHA (Holmes 1983). Dimensionless tree-ring index series, with age-related growth trends removed, were produced by dividing the raw measurements by the growth curves of a smoothed cubic spline curve with a 50% frequency cutoff of 2/3 of the length of the series. A standard tree-ring width chronology was developed by averaging the dimensionless tree-ring indices from the individual trees (Cook 1985). Expressed population signal (EPS) is defined by the mean inner-series correlation of all the series, and increasing EPS was tacitly associated with a more accurate estimation of climate–growth relationships (Wigley et al. 1984). To account for the decreased

sample number in the early period of the chronology, we used the EPS over 0.85 to determine the reliable portion of standard chronology.

In addition, we developed a frequency-based chronology following a recently introduced method (Fang et al. 2017). This method was introduced to address the fact that the ratio of growth disturbance relative to the total number of tree rings at interdecadal timescales is often higher than at interannual timescales. Thus the interdecadal variations are less likely to be averaged out when treated the same way as the interannual variations of the tree ring. The dimensionless tree-ring series were separated by high- ($f > 0.1$) and low-pass ($f < 0.1$) filters. A high-frequency chronology was produced by averaging the high-passed tree-ring indices. A low-frequency chronology was then generated by averaging the series with coherent interdecadal variations. In this study, we selected 28 series with high loadings (> 0.5) on the first principal component of all the interdecadal variations of the 68 series. The final chronology is the mean of the high- and low-frequency chronologies.

2.3. Tree radial growth

Tree-ring width decreases with age in mature trees. If a decline in growth caused by environmental factors is suspected, the age trend may make it impossible to detect this effect based only on the changes of ring width. To overcome this problem, tree-ring width was converted into basal area increment (BAI) parameter, calculated forward from the

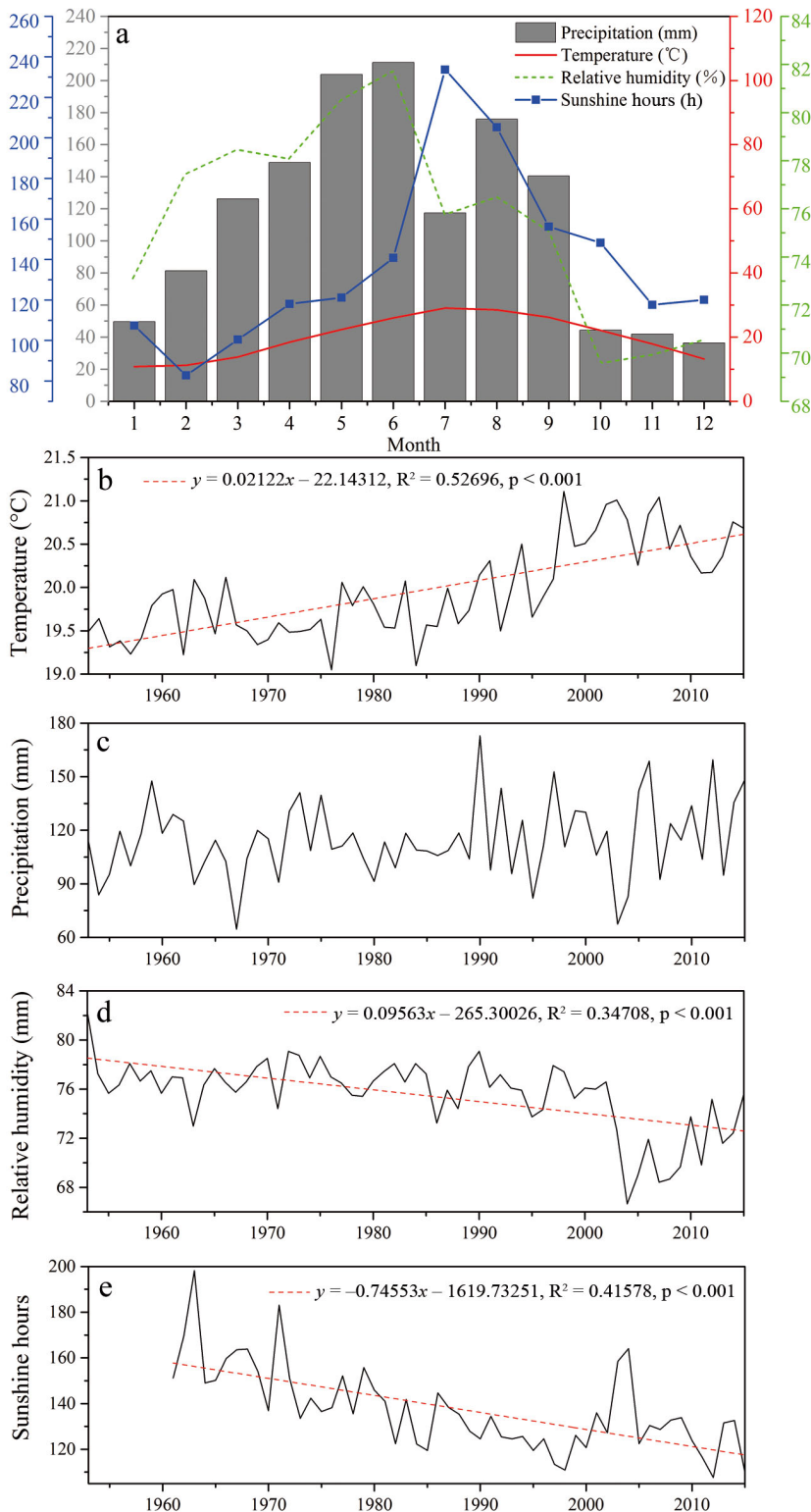


Fig. 2. (a) Comparison of mean monthly temperature, precipitation, relative humidity (each 1953–2015) and sunshine hours (1953–2015) in the research area, based on Fuzhou meteorological Stn. Trends in (b) mean temperature, (c) precipitation, (d) relative humidity for the period of 1953–2015 and (e) sunshine hours from 1961–2015. Red dashed lines: $p < 0.001$ for linear regression

pith and not considering the bark, from the raw ring widths based on the assumption of concentrically distributed tree rings (Phipps & Whitton 1988):

$$BAI = \pi \times (r_n^2 - r_{n-1}^2) \quad (1)$$

where r is the radius of the tree, and n is the yr of tree-ring formation.

2.4. Tree-ring $\delta^{13}\text{C}$ and intrinsic water-use efficiency

We selected 14 cores from 14 trees for isotopic analysis. The ‘juvenile effect’ in tree-ring stable carbon isotope points to a rising trend in $\delta^{13}\text{C}$ series. Possible causes of the ‘juvenile effect’ include ^{13}C -depleted CO_2 near the ground from soil respiration (canopy effect) (Schleser & Jayasekera 1985), reduced light (Farquhar et al. 1982), actual juvenile wood (crown wood) with different physical and anatomical characteristics than mature wood (Monserud & Marshall 2001), and hydraulic conductivity (McCarroll & Loader 2004). To avoid the possible ‘juvenile’ age effect on tree-ring $\delta^{13}\text{C}$, we removed the first 20 yr of each core before pooling the woody material. The cores had no missing rings and had regular ring boundaries. The whole, dated, annual rings from the cores were cut off using a dissecting scalpel under a binocular microscope. Then all the rings formed in the same calendar yr were mixed together (pooled) and stored in microcentrifuge tubes (Leavitt 2008). Then α -cellulose of the annual tree rings was extracted following a modification of the method by Green (1963) and Loader et al. (1997). In order to homogenize the cellulose, an ultrasonic water bath (JY92-2D, Scientz Industry) was used to break the cellulose fibers (Laumer et al. 2009). The α -cellulose was then freeze-dried for 3 d prior to isotope analysis.

The tree-ring carbon isotope ratio ($\delta^{13}\text{C}$) values were measured using a

Flash Elemental Analyzer (Flash 2000) coupled with a Thermo Scientific MAT 253 (Thermo Electron Corporation) at the Key Laboratory of Humid Subtropical Eco-geographical Process (Ministry of Education), Fujian Normal University. Each sample was repeatedly measured 2 to 4 times, and the robust measurement was determined as a minor deviation of these measurements. The mean of these measurements was used for further analyses. By convention, the ratio of stable carbon isotope ($^{13}\text{C}:^{12}\text{C}$) is expressed by delta (δ) as deviations from the Vienna Pee Dee Belemnite (VPDB) standard (Coplen 1995), and the result is expressed in ‰:

$$\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (2)$$

where R_{sample} is the $^{13}\text{C}:^{12}\text{C}$ ratio for the tree-ring α -cellulose sample and R_{standard} is the $^{13}\text{C}:^{12}\text{C}$ ratio in VPDB standard. SD of the isotope measurements was $<0.07\text{‰}$ for repeated samples.

The carbon isotope discrimination ($\Delta^{13}\text{C}$) in C_3 plants is expressed as follows (Farquhar et al. 1982):

$$\Delta^{13}\text{C} = (\delta^{13}\text{C}_a - \delta^{13}\text{C}_p)/(1 + \delta^{13}\text{C}_p/1000) \quad (3)$$

where the $\Delta^{13}\text{C}$ was expressed as a result of preferential use of ^{12}C over ^{13}C during photosynthesis. $\delta^{13}\text{C}_a$ and $\delta^{13}\text{C}_p$ are the isotopic value of atmospheric CO_2 and plant material (tree ring), respectively. The $\delta^{13}\text{C}_a$ values for the period 1976 to 2004 were taken from McCarroll & Loader (2004), $\delta^{13}\text{C}_a$ values for 2005 to 2015 were observations from Mauna Loa Observatory, Hawaii, and the measured $\delta^{13}\text{C}_p$ values were used to calculate $\Delta^{13}\text{C}$.

$\Delta^{13}\text{C}$ is also a function of the difference between the intercellular and atmospheric CO_2 :

$$\Delta^{13}\text{C} = a + (b - a) (c_i/c_a) \quad (4)$$

where a ($\sim 4.4\text{‰}$) represents the discrimination that occurs during diffusion of CO_2 through the stomata and b ($\sim 27\text{‰}$) is the fractionation due to carboxylation, c_i and c_a are the intercellular and atmospheric CO_2 concentration, respectively.

The intrinsic water-use efficiency (iWUE) is the ratio of the CO_2 assimilation rate (A) to stomatal conductance (g) for water vapour, which represents the cost of assimilation per unit of water (Ehleringer & Cerling 1995). iWUE was introduced to compare photosynthetic properties independent of evaporative demand, and has been widely associated with long-term trends in the internal regulation of carbon uptake and water loss in plants (McCarroll & Loader 2004, Robertson et al. 2008). It is given as follows:

$$\text{iWUE} = A/g = (c_a - c_i)/1.6 = c_a (1 - c_i/c_a)/1.6 \quad (5)$$

In a theoretical context, Saurer et al. (2004) proposed 3 primary plant responses to rising CO_2 in tree-ring isotope values: (a) c_i constant, (b) $c_i:c_a$ ratio constant (an active response), and (c) $c_a - c_i$ constant (a passive response). The scenarios differ in the degree to which an increase in c_i corresponds to an increase in c_a : either (a) not at all, (b) in a proportional way or (c) at the same rate. In our study, these 3 scenarios were used to account for observed iWUE trends (Linares & Camarero 2012).

2.5. Climate data and analyses

Pearson's correlation coefficient (r) was used to examine the relationship between observed monthly climate variables from Fuzhou meteorological Stn and the tree-ring width chronologies, tree-ring $\Delta^{13}\text{C}$ and iWUE. All the correlations were calculated using both raw and first-order differenced data. First-order differenced data were calculated as the residual between the tree-ring data of successive years. We calculated the first-order differenced data to remove the autocorrelation, and to highlight their interannual variability. The coherence of variability of BAI and iWUE was calculated through a 31 yr moving correlation analysis. Due to the potential influence of previous growing seasons' climate on tree growth, we calculated climate–growth correlations from previous February (the start of previous growing season) to current October (the end of current growing season). Correlations, linear regressions and time-series analyses were conducted using the SPSS 11.0 statistical package.

3. RESULTS

3.1. Tree-ring width chronology and climate–growth relationship

The standard chronology using traditional methods with an EPS > 0.85 spans from 1856 to 2015 (Fig. 3a). Tree growth showed no obvious trend for the entire period. The frequency-based chronology has more pronounced interdecadal variations than the standard chronology (Fig. 3a). As shown in Fig. 3b, the frequency-based chronology, developed from selected tree-ring series with coherent interdecadal variations, showed somewhat stronger interdecadal variability than the standard chronology based on all tree-ring series, including some series with divergent interdecadal variations. Nonetheless, interdecadal

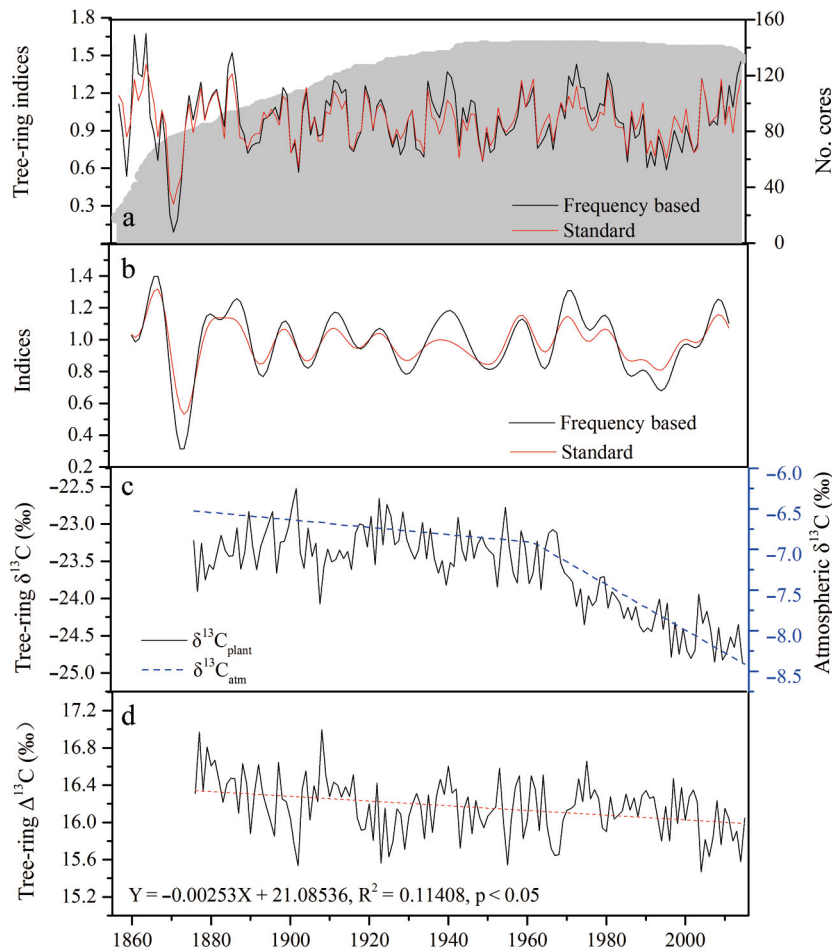


Fig. 3. (a) Comparisons between the standard chronology, the frequency-based chronology and the sample size (shaded area) of *Pinus massoniana* cores for the period of 1856–2015. The standard chronology was developed using traditional methods by averaging all the cross-datable tree-ring indices while removing age-related growth trends. The frequency-based chronology was produced by averaging the mean of the interannual and the interdecadal tree-ring series. (b) Comparisons among the interdecadal ($f < 0.1$) variations of the frequency-based chronology and the standard chronology. Chronologies of (c) tree-ring $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{plant}}$) and atmospheric $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{atm}}$), and (d) the corrected tree-ring $\delta^{13}\text{C}$ ($\Delta^{13}\text{C}$) based on the method of McCarroll & Loader (2004). The values of $\delta^{13}\text{C}_{\text{atm}}$ were derived from Francey et al. (1999). Dashed red lines: results of linear regression fitted to the data

variations of the 2 tree-ring chronologies agree well with each other. As the standard chronology was developed from more tree-ring data than the frequency-based one, we consider the standard chronology to be more robust.

As shown in Fig. 4a, the standard chronology was significantly ($p < 0.05$) and negatively correlated with temperature of current May and June. Significant and positive correlations between tree-ring width standard chronology and precipitation were found for May, July, September and October (Fig. 4b). The tree-ring chronology was significantly and negative-

ly correlated with relative humidity of previous April and June, but positively correlated with relative humidity of current February and September (Fig. 4c). Positive correlations with sunshine hours were observed for previous June while their negative correlations were seen with current May (Fig. 4d). In addition, we calculated correlations between tree growth and seasonal combinations of climate variables, and found the highest correlation with precipitation of a hydrological yr from previous November to current October ($r = 0.568$, $p < 0.001$). The correlations based on the first-order differenced data are generally stronger than those derived from the raw data.

3.2. Tree-ring stable carbon isotopic variability and its responses to climate

A downward trend in atmospheric $\delta^{13}\text{C}$ is observed due to the emission of CO_2 from fuels with low ^{13}C , as well as deforestation since the beginning of the industrial era ~1850 (Feng 1998). Our $\delta^{13}\text{C}$ values show a decreasing trend (a slope of the linear regression: -0.009) since 1876, which is due to the trend in atmospheric $\delta^{13}\text{C}$ (Fig. 3c). We thus applied an optimal correction method to remove the decreasing trend in tree-ring $\delta^{13}\text{C}$ series (Farquhar et al. 1982). The tree-ring $\delta^{13}\text{C}$ chronology spans 140 yr from 1876 to 2015 (Fig. 3d), with a mean value of -23.6‰ and SD of 0.55.

As shown in Fig. 5, the tree-ring $\Delta^{13}\text{C}$ values were significantly ($p < 0.05$) and negatively correlated with temperature in previous August, November, and current May, but positively correlated with current January and October precipitation in the raw data. The $\Delta^{13}\text{C}$ chronology showed positive correlation with relative humidity in previous March, August, October, September, December and current January, April, May, June, July, August, September, October. Peak correlation between the $\Delta^{13}\text{C}$ and relative humidity was found for September–October of the current yr ($r = 0.677$, $p < 0.001$).

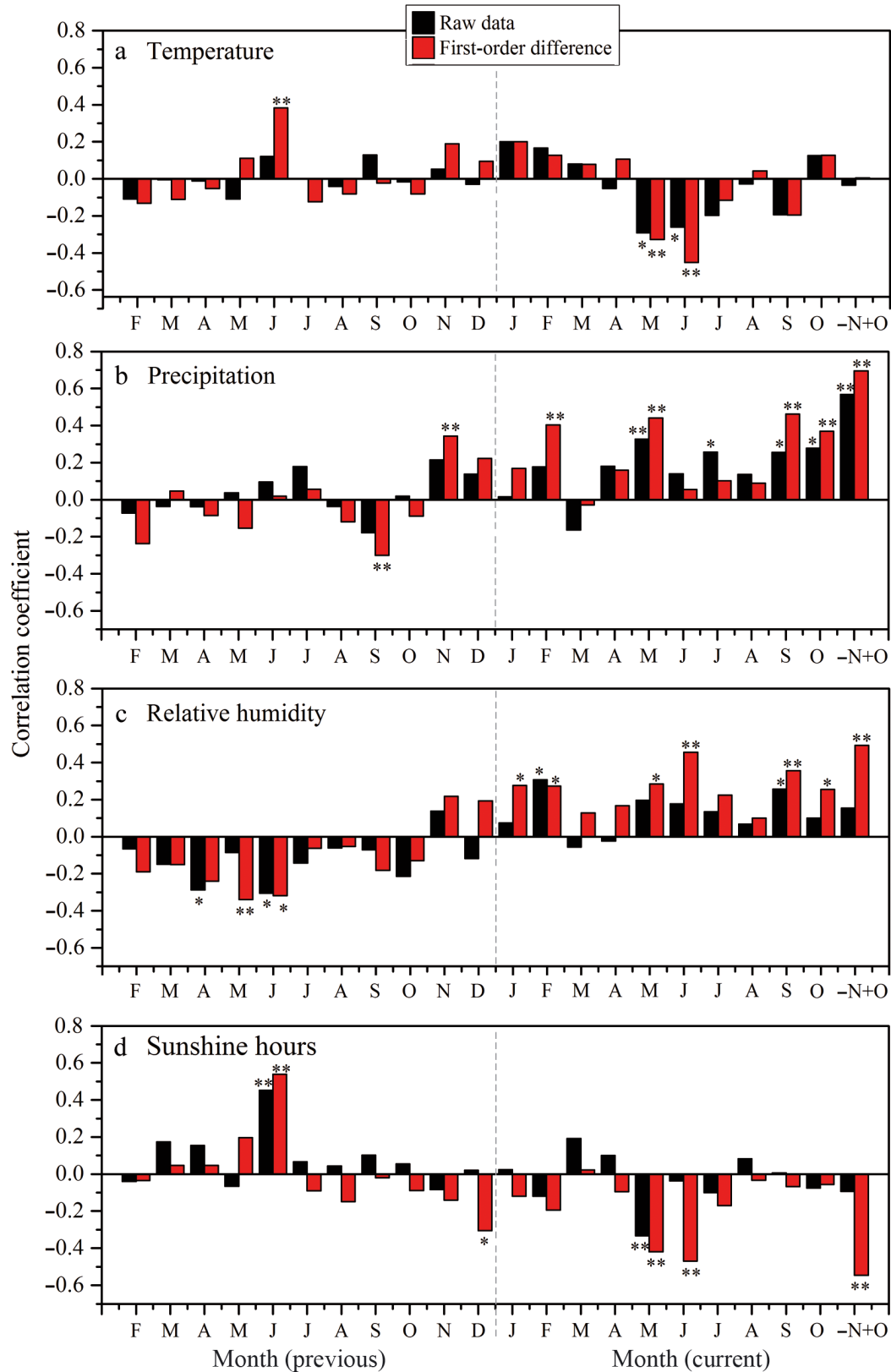


Fig. 4. The raw and first-order differenced data correlation relationship between the tree-ring standard chronology and climate variables from the previous growing season (previous February) to the current growing season (current October). Correlated with (a) monthly mean temperature, (b) monthly total precipitation, (c) relative humidity, (d) sunshine hours; (a–c) 1953–2015, (d) 1961–2015. –N+O: period from previous November to current October. * and ** represent the 95 and 99% significance levels

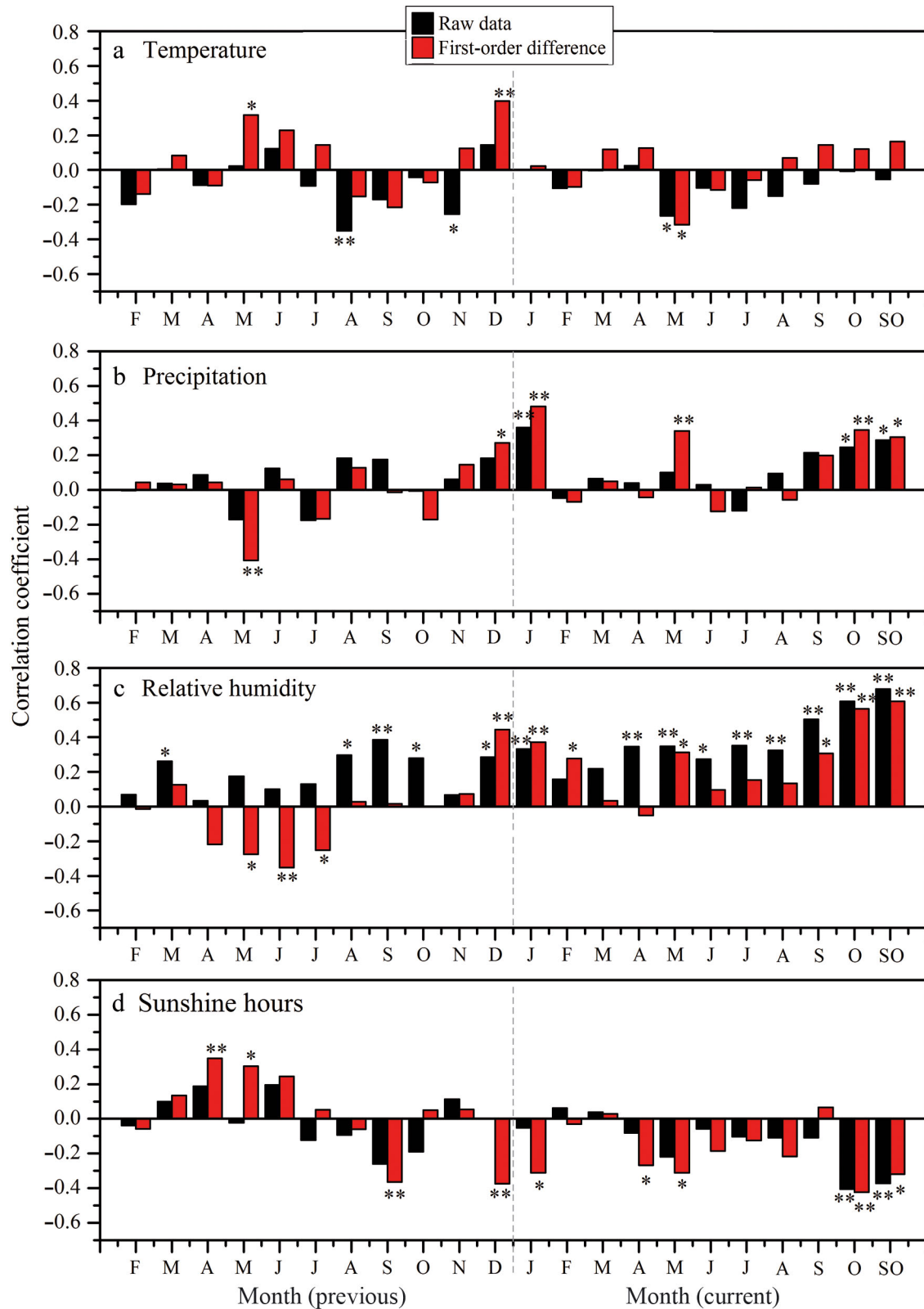


Fig. 5. The raw and first-order differenced data correlation relationship between tree-ring carbon isotope discrimination ($\Delta^{13}\text{C}$) and climate variables from the previous growing season (previous February) to the current growing season (current October). Correlated with (a) monthly mean temperature, (b) monthly total precipitation, (c) relative humidity, (d) sunshine hours; (a–c) 1953–2015, (d) 1961–2015. SO: period from September to October. * and ** represent the 95 and 99% significance levels

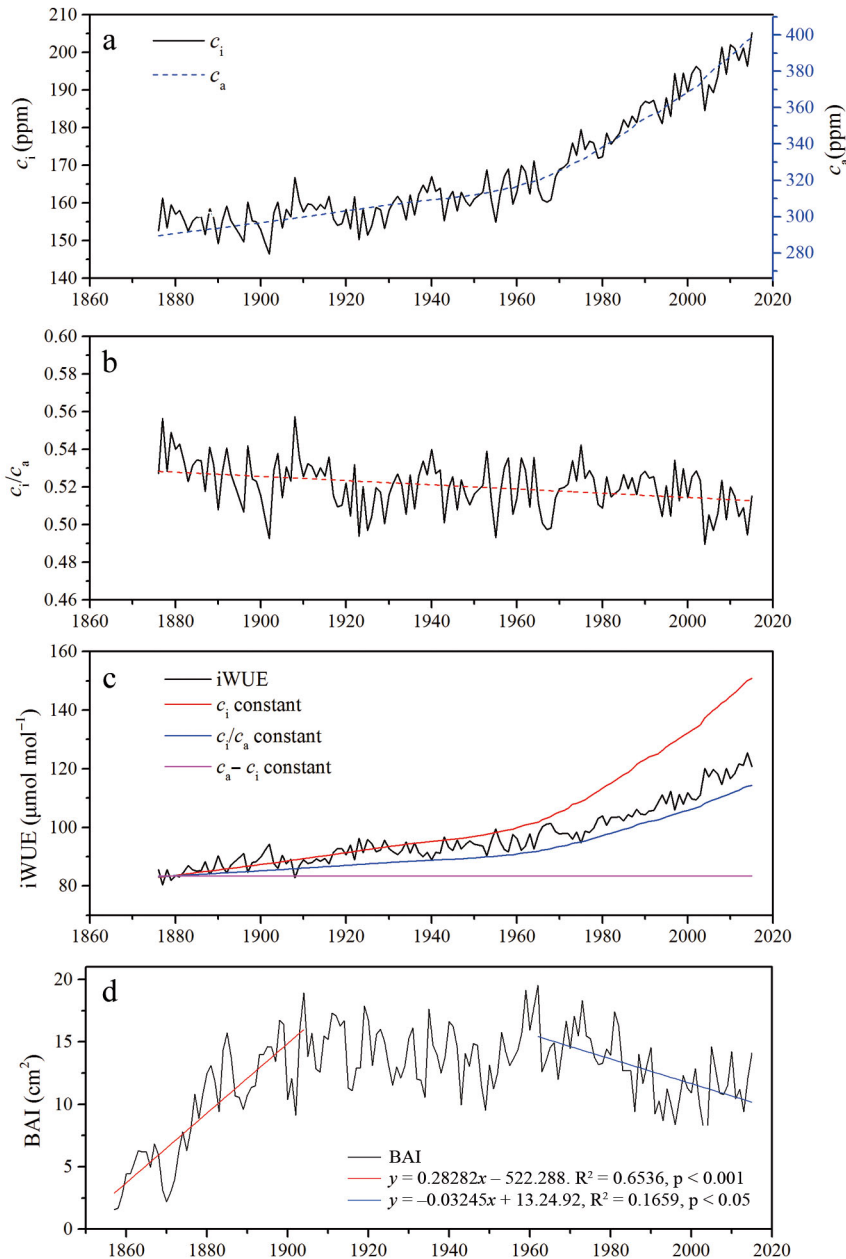


Fig. 6. (a) Leaf intercellular CO₂ concentration (c_i) and ambient CO₂ concentration (c_a), (b) $c_i:c_a$ ratio; dashed line: linear fit for this period, (c) different scenarios of intrinsic water-use efficiency (iWUE) in response to increasing c_a , 1876–2015. Atmospheric CO₂ concentrations derived from McCarroll & Loader (2004). (d) Basal area index (BAI), 1857–2015

In addition, $\Delta^{13}\text{C}$ was positively correlated with previous May sunshine hours, but significantly and negatively correlated with sunshine hours in current October. The correlations based on the first-order differenced data between the tree-ring $\Delta^{13}\text{C}$ and climate factors were similar to those derived from the raw data.

3.3. Trends in iWUE and BAI

As expected, the c_i generally increased with rising c_a , ranging from 152.7 ppm to 205.3 ppm (Fig. 6a). The $c_i:c_a$ ratio has a clear decreasing trend ($Y = -0.0001X + 0.528$, $R^2 = 0.120$, $p < 0.001$, where $X = \text{yr}$) during the studied period (Fig. 6b). The iWUE increased markedly by about 40.9% from 1876 to 2015 (Fig. 6c). Long-term variations in stem BAI did not reveal an overall linear trend (Fig. 6d). In the early phase of the sampled period (1857 to 1904), BAI increased steadily, from initial values well below the long-term mean to a value greater than the mean. From 1905 to 1960, BAI gradually decreased with some fluctuations. This was followed by a rapid decrease to a value smaller than the long-term mean: 26.8% from 1960 to 2015. The 31 yr moving correlations revealed negative correlations between BAI and iWUE under increasing atmospheric CO₂ (Fig. 7). Significant negative correlations between BAI and iWUE are found in the 1930s–40s and 1970s–90s (raw).

4. DISCUSSION

4.1. Effects of precipitation of a hydrological year on tree growth

Tree growth of our sampling site is mainly limited by precipitation during a hydrological yr from previous November to current October. Moisture limitation of tree growth for a hydrological yr is widely found in arid and semi-arid regions surrounding the Tibetan Plateau (Fang et al. 2015), but has not been reported for humid subtropical China. In arid regions, ring width formation often ends in August and subsequent precipitation is used for tree growth of the next yr (Fang et al. 2012, X. Gou et al. unpubl.). Tree growth integrates precipitation of the non-growing and growing seasons, usually showing the highest correlation with precipitation of a hydrological yr from previous August to current July (Li J et al. 2017). In the warm subtropical region of southeastern China, the growing season is longer than

further north, and ring width formation can continue until October (Zhang et al. 2016). This would explain why tree growth seen in this study had its strongest response to precipitation from previous November to current October.

Post growing season precipitation can be retained in the soil and facilitate tree growth for the coming yr (Fang et al. 2012). Li et al. (2012) speculate that this could be the case for arid regions surrounding the Tibetan Plateau, because snow in the cold regions can be retained for a long period. In addition, precipitation in the early-growing season in these areas is low, causing a need for retention of moisture from before the growing season (Fang et al. 2015). However, this may not be the case for our study region, since precipitation in the non-growing season is less likely to be retained for a long period, and the precipitation in the early growing season is high. Instead, the influence of the non-growing season precipitation likely exists because sufficient precipitation before the growing season can produce sufficient nutrients or carbohydrates (X. Gou et al. unpubl.), which can be used for tree growth during the growing season.

The absence of the strongest responses to hydrological year precipitation in the tree-ring data from Fujian province may be because tree growth at these sites is less sensitive to drought. To our knowledge, tree growth at FGY showed higher correlations with precipitation relative to other tree-ring data of Fujian province (Chen et al. 2012, 2015, Li et al. 2016). A drought-stressed condition may exist due to the shallow soil at FGY, which is not able to retain precipita-

tion well. The soil depth at the sampling points ranges from 20 cm (some roots grew on bare stones) to 130 cm. The soil water storage of the mountains in the north Fujian province is from 225.28 to 398.56 mm yr⁻¹ (Han et al. 2011). Tree rings at FGY show high correlations with precipitation in early growing seasons in May and June, which is not observed in other nearby sites with deeper soil (Cao et al. 2016, Li D et al. 2017). This is probably because moisture of the early growing season is crucial for ring width formation, and the shallow soil at FGY is not able to retain precipitation well, even though precipitation in this season is high (Li D et al. 2017). Our study highlights that moisture limitation of a hydrological yr for tree growth is not only a common feature in arid regions but can also been seen in a humid region if the site has a low ability to retain soil moisture.

4.2. Limitation of autumn relative humidity on tree-ring $\Delta^{13}\text{C}$

The mean $\delta^{13}\text{C}$ value at FGY (-23.95‰) is lower than that from a nearby site in Quanzhou area (-22.95‰ ; $25^{\circ}25' \text{N}$, $117^{\circ}56' \text{E}$; Li D et al. 2017). The strongest correlation observed between FGY tree-ring $\Delta^{13}\text{C}$ records and relative humidity in autumn (September to October) is in agreement with previously published tree-ring carbon isotopic series from the Quanzhou area, about 110 km southwest of FGY (Li D et al. 2017). This indicates that the influence of autumn relative humidity on tree $\Delta^{13}\text{C}$ might be a

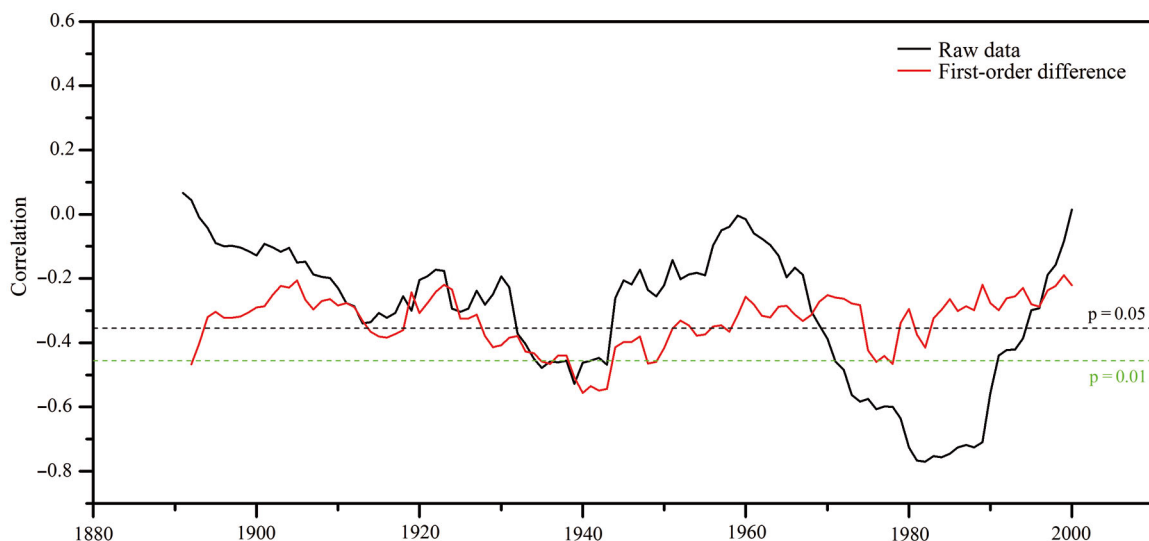


Fig. 7. Running correlations based on a 31 yr window of the basal area index (BAI) and intrinsic water-use efficiency (iWUE). Black (green) horizontal dashed lines: 95% (99%) confidence levels

common feature of the western bank of the Taiwan Strait. High tree-ring $\Delta^{13}\text{C}$ means more ^{12}C uptake by trees as a result of a high rate of photosynthesis and high stomatal conductance (Farquhar et al. 1982, McCarroll & Loader 2004). Stomatal activity was reduced to prevent excessive water loss, leading to reduced influx of CO_2 into the intercellular space, a lower c_i and a decrease in ^{13}C -discrimination. This explains the positive response of tree-ring $\Delta^{13}\text{C}$ to relative humidity in autumn at FGY. Similar results have been reported for other subtropical areas (Lv et al. 2002). Precipitation also played a role in tree-ring carbon isotope discrimination in current October. The relation between $\Delta^{13}\text{C}$ and rainfall is well understood for dry sites in the subtropics, where moisture stress is pronounced and can be explained by stomatal responses to soil moisture and relative humidity. A strong influence of precipitation on tree oxygen stable isotope discrimination was also found in western Fujian, since precipitation can modulate stomatal conductance and thus tree oxygen isotopes (Xu et al. 2013). In some cool and high-elevation areas, carbon isotopes in tree rings tend to be dominated by variables that control the assimilation rate, mainly sunshine hours and temperature (McCarroll & Pawellek 2001, Gagen et al. 2007). In tropical dry forest trees, however, temperature and irradiance may also indirectly influence stomatal behaviour, and thereby the carbon isotope signal, through their effects on water vapour pressure deficit across stomata (Brienen et al. 2011). This may be the reason for the negative correlation between sunshine hours and $\Delta^{13}\text{C}$.

4.3. Physiological responses to increased c_a

The magnitude of the increase in iWUE at FGY is higher than that for arid regions (Liu et al. 2008, Wang et al. 2012), but similar to that for tropics areas (Brienen et al. 2011, Nock et al. 2011). In a subtropical forest of southern China, the iWUE of *P. massoniana* increased about 38% in the past 130 yr (Sun et al. 2010). Previous results indicated a similar rate of increase (38.4%) of iWUE in the Quanzhou area (Li D et al. 2017). These different increases in iWUE showed that differences in temperature, air humidity and soil water availability were important factors that caused the differences in the physiological responses of plants to increased c_a .

As expected, the increase in iWUE was not strong (slope of 0.13) and the changes in iWUE were close to the scenario with constant c_i before ~1960 (Fig. 6c, Fig. A1 in the Appendix). Short-term experiments

also show constant c_i for a variety of species (Sage 1994), representing a strong response to increasing atmospheric CO_2 (Saurer et al. 2004). The scenario with constant c_i may indicate tree adaptation to increased c_a through decreasing leaf conductance (Brienen et al. 2011). Both the increases in c_i and c_a become stronger after ~1960 (Fig. 6a), which may be due to increasing global industrial activities. From 1960 to 2015, the iWUE showed a rapidly increasing trend (slope of 0.51), which closely followed the scenario with a constant $c_i:c_a$ ratio (Fig. 6c). Previous studies also found that trees may switch from near-constant c_i towards a near-constant $c_i:c_a$ ratio (Huang et al. 2017). The increase in iWUE may be attributed to high net photosynthesis and/or low stomatal conductance (McCarroll & Loader 2004), which has been documented by experimental studies (Luo et al. 1996). Thus, increases in iWUE during the 2 periods may have been forced by different physiological mechanisms, implying that a dynamic leaf gas-exchange strategy may exist as a response to increasing c_a (Voelker et al. 2016). Furthermore, the $\Delta^{13}\text{C}$ series had a slight declining trend ($Y = -0.0023X + 17.11$, $r^2 = 0.09$) at a rate of 0.023‰ per decade during the past 140 yr.

4.4. Correlations between BAI and iWUE

Long-term trends in BAI for *Pinus massoniana* since 1856 increased for many decades, but decreased in recent decades. These trends have been widely reported in both tropical and subtropical forests (Sun et al. 2010, Nock et al. 2011). Widespread declines in tree BAI in recent years have demonstrated a warming-induced growth decline despite increasing iWUE for forest systems at dry sites (Andreu-Hayles et al. 2011, Linares & Camarero, 2012, Lévesque et al. 2014).

iWUE has positive correlations with sunshine hours and negative correlations with relative humidity for the first-order difference data (Fig. A2 in the Appendix). Our finding of no tree growth stimulation by the increase in iWUE agrees with previous studies in arid Mediterranean areas (Linares et al. 2009, Lévesque et al. 2014) as well as northwestern China and eastern Canada (Wu et al. 2015, Dietrich et al. 2016). A study based on a global-scale dataset revealed that increased iWUE did not necessarily lead to enhanced tree growth, and that half of the sample sites from 47 major forest biome types showed decreased tree growth or no change (Peñuelas et al. 2011).

Theoretically, an increase in iWUE can stimulate tree growth, particularly where trees are drought-stressed. The lack of tree growth stimulation by the increasing iWUE may be attributed to 2 types of factors. (1) An increase in tree growth may not be revealed in the ring-width series. For example, increased iWUE may only stimulate height growth rather than radial growth, and will consequently not be revealed in the tree-ring width data. (2) Our results indicated that the influence of increasing iWUE on tree growth is more pronounced during autumn, which is a period of low ring width formation (Li et al. 2016). Moreover, the long-term trend is often difficult to establish, because there is no method to fully distinguish these tree-growth trends and age-related growth trends. It is difficult to explicitly assess the stimulation of increasing iWUE on tree growth due to the influence of other environmental factors that may be more important (Silva & Anand 2013). A drying trend is observed at FGY, which may counteract the stimulation of the drought-stressed trees by the increase in iWUE. It should be noted that the stimulation of iWUE on tree growth is mainly revealed at centennial or longer timescales because the increase in CO₂ concentration and thus the iWUE does not have marked interannual and interdecadal variability. Interannual and interdecadal changes of iWUE may be caused by climate variations. However, the relationships of climate and iWUE with tree growth may be reversed. For example, dry conditions can cause stomatal closure, which may be associated with a high iWUE but low tree growth. This explains the negative correlations between iWUE and tree growth for the first-order differenced data.

5. CONCLUSIONS

We present the first tree-ring width chronology (1856 to 2015) and stable carbon isotopic series ($\delta^{13}\text{C}$) (1876 to 2015) from Yongtai county, southern China, western bank of the Taiwan Strait. *Pinus massoniana* tree-ring width formation in the studied region was mainly limited by precipitation during a hydrological year, which is more in agreement with drought-stressed trees in arid regions than at more humid subtropical sites. This indicates that precipitation can limit tree growth, including in humid areas, if the trees are moisture sensitive. The iWUE showed a strong increasing trend in response to the steady increase in atmospheric CO₂ concentrations since the beginning of the industrial era. The c_i remained constant before ~1960, but started to increase thereafter,

following a constant $c_i:c_a$ ratio. This was probably because trees did not maintain a constant c_i , due to the very sharp increase in c_a after ~1960. This study shows no apparent increase in tree growth in response to increased iWUE, which is similar to findings in other studies in hot and humid regions. Our results provide insights for the evaluation of the potential impacts of global warming and drought stress on plant carbon–water relationships in forests of subtropical China.

Acknowledgements. Constructive comments from 3 excellent reviewers are highly appreciated. We are grateful for the kind assistance from Zhuangpeng Zheng and Shiyin Chen in the field and the lab. This research was funded by the National Science Foundation of China (41471172, U1405231), fellowship for the National Youth Talent Support Program of China (Ten Thousand People Plan) and the innovation team project (IRTL1705). Support from the Swedish Formas (Future Research Leaders) is also acknowledged.

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Appendix. Additional data

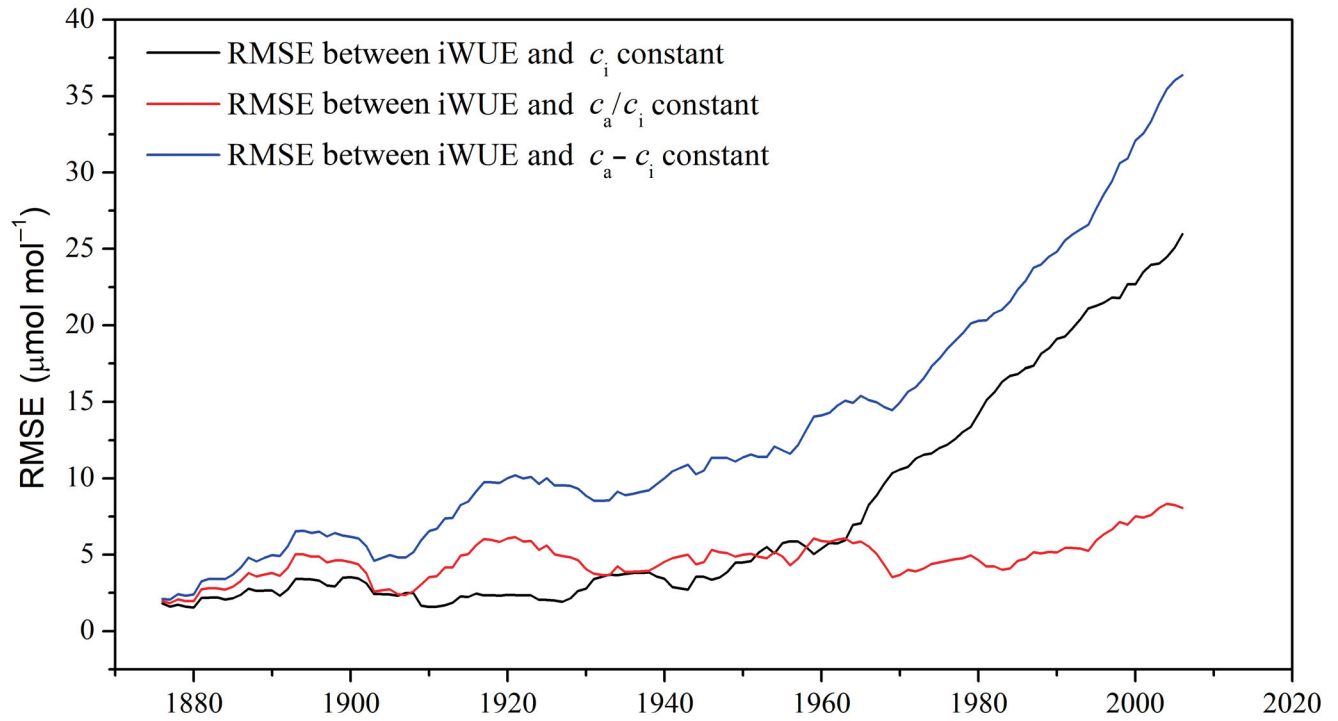


Fig. A1. Root mean square error (RMSE) between observed and predicted data in the 3 theoretical scenarios. The RMSE was calculated with a running window of 10 years

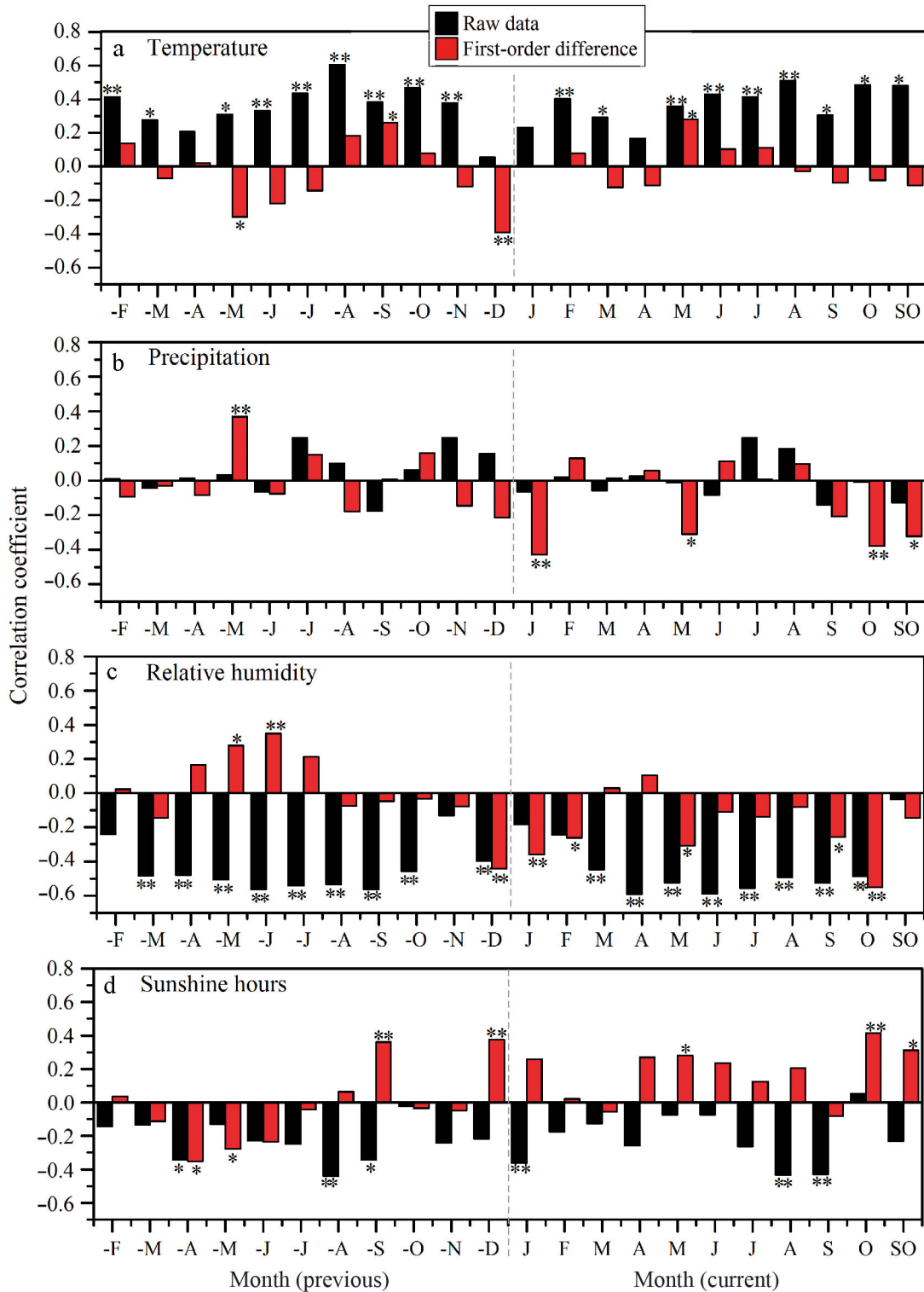


Fig. A2. Correlations between the intrinsic water-use efficiency (iWUE) and (a) monthly mean temperature, (b) monthly total precipitation, (c) relative humidity, (d) sunshine hours from previous February to current October based on the raw and first-order differenced data. Correlations calculated for (a–c) 1953–2015, (d) 1961–2015. * and ** represent the 95 and 99% significance levels