Long-term increases in intrinsic water-use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand

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Abstract

Rising atmospheric carbon dioxide [CO_2] can accelerate tree growth by stimulating photosynthesis and increasing intrinsic water-use efficiency (iWUE). Little evidence exists, however, for the long-term growth and gas-exchange responses of mature trees in tropical forests to the combined effects of rising [CO_2] and other global changes such as warming. Using tree rings and stable isotopes of carbon and oxygen, we investigated long-term trends in the iWUE and stem growth (basal area increment, BAI) of three canopy tree species in a tropical monsoon forest in western Thailand (*Chukrasia tabularis*, *Melia azedarach*, and *Toona ciliata*). To do this, we modelled the contribution of ontogenetic effects (tree diameter or age) and calendar year to variation in iWUE, oxygen isotopes, and BAI using mixed-effects models. Although iWUE increased significantly with both tree diameter and calendar year in all species, BAI at a given tree diameter was lower in more recent years. For one species, *C. tabularis*, differences in crown dominance significantly influence stable isotopes and growth. Tree ring $\Delta^{18}O$ increased with calendar year in all species, suggesting that increasing iWUE may have been driven by relatively greater reductions in stomatal conductance – leading to enrichment in $\Delta^{18}O$ – than increases in photosynthetic capacity. Plausible explanations for the observed declines in growth include water stress resulting from rising temperatures and El Niño events, increased respiration, changes in allocation, or more likely, a combination of these factors.

Keywords: carbon dioxide, carbon isotopes, intrinsic water-use efficiency, oxygen isotopes, stable isotopes, temperature, topical monsoon forest, tree growth, tree rings

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Introduction

The tropics are very underrepresented in studies of the response of forests to rising atmospheric carbon dioxide [CO_2] (only 11% of studies, Körner, 2009), despite the importance of feedbacks between rising [CO_2] and tropical forest growth for the global carbon cycle (Denman *et al.*, 2007). Empirical evidence for the response of tropical forests to rising [CO_2] has predominantly come from monitoring of forest inventory plots established in recent decades. Recent findings from networks of plots in the Amazon and Africa suggest that pan-tropical fertilization by [CO_2] may have accelerated tropical tree growth there (Phillips *et al.*, 2008; Lewis *et al.*, 2009). But the extent to which [CO_2] fertilization is limited by other concurrent global changes, and/or confounded with changes in forest disturbance patterns remains uncertain (Chambers & Silver, 2004; Wright, 2005; Chave *et al.*, 2008; Fisher *et al.*, 2008).

In addition to rising [CO_2], other global changes are occurring and likely acting upon tropical forests (Wright, 2005). Tropical surface temperatures are rising on average by 0.26 °C per decade (Malhi & Wright, 2004), possibly driving a deceleration of tree growth in some tropical forests by increasing water stress, and/or rates of respiration (Chambers & Silver, 2004; Feeley *et al.*, 2007; Clark *et al.*, 2009). Warmer surface temperatures may also trigger more frequent and extreme El Niño-Southern Oscillation events (Timmer-

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mann *et al.*, 1999), which in many tropical forests cause severe drought conditions that can greatly reduce tree growth (Nepstad *et al.*, 2004; Phillips *et al.*, 2009; Vincent *et al.*, 2009). In addition, recent observations of leaf gas exchange and eddy covariance show that net carbon assimilation is reduced in the upper and most productive canopy leaves of tropical trees during the warmest periods of the day, suggesting high temperatures could have negative effects on tree growth (Doughty & Goulden, 2008).

Free-air CO_2 enrichment (FACE) field experiments have played a key role in addressing uncertainties in forest responses to elevated $[CO_2]$ (reviewed in Ainsworth & Long, 2005). Yet FACE experiments in tropical forests are lacking, and are unlikely in the near future. Thus, empirical evidence for the long-term growth and gas-exchange responses of mature tropical trees to rising $[CO_2]$, as well as manifold global changes, is notably absent. Intrinsic water-use efficiency (iWUE) – the ratio of net CO_2 assimilation and stomatal conductance (A/g_s) – has received much attention because an integrated measure of iWUE can be indirectly estimated from $\delta^{13}C$ based on well known relationships among $\delta^{13}C$, the leaf internal CO_2 concentration (C_i), and the effects of g_s and A on C_i (Farquhar *et al.*, 1982). Further, $\delta^{13}C$ records from tree rings can provide an annual archive of gas-exchange and growth responses that is substantially longer than that provided by FACE experiments or forest inventory plot monitoring, and moreover, document trees responses to the historic rise in $[CO_2]$, in contrast to large-step increases in ambient CO_2 (Barber *et al.*, 2000; Penuelas *et al.*, 2008).

Although the study of long-term trends in $\delta^{13}C$ in tree rings is now common (McCarroll & Loader, 2004), few data exist for tropical trees. Measurements of $\delta^{13}C$ from annual growth rings of the tropical trees *Cedrela odorata* L. and *Swietenia macrophylla* King have shown that iWUE increased during the last century concurrent with the effects of rising $[CO_2]$ (Hietz *et al.*, 2005). Similar long-term increases in iWUE ($\sim$20%) were detected in mature *Araucaria angustifolia* Bertol., but its basal area increment (BAI, $cm^2\,yr^{-1}$) did not also increase (Silva *et al.*, 2009). Thus, it remains uncertain whether increases in iWUE necessarily lead to increases in stem growth in tropical trees. Furthermore, evidence from Mediterranean and boreal forests where temperatures are rising suggests that gains in iWUE resulting from increased $[CO_2]$ may be insufficient to compensate for the deleterious effects of warming and water stress, leading to significant declines in stem wood production (Barber *et al.*, 2000; Penuelas *et al.*, 2008; Linares *et al.*, 2009).

In addition to $\delta^{13}C$, the analysis of oxygen isotope ratios ($\delta^{18}O$) can provide valuable information in stu- dies of iWUE because $\delta^{13}C$ alone does not provide any indication of whether changes in iWUE are due to proportionally greater changes in A or g_s (Scheidegger *et al.*, 2000). After accounting for source water uptake, $\delta^{18}O$ fractionation within plants mostly varies with changes in g_s and vapour pressure deficit (VPD), and therefore leaf water loss via transpiration (Barbour *et al.*, 2002). For example, a decrease in g_s will increase evaporative enrichment in ^{18}O by decreasing evaporative leaf cooling, while also leading to decreased discrimination (increased ^{13}C, increased iWUE) because of reduced CO_2 supply. Although dual isotope studies of tree rings could partially fill the data gap for the long-term gas-exchange and growth responses of mature trees to environmental change (Sternberg *et al.*, 1989; Scheidegger *et al.*, 2000; Sidorova *et al.*, 2009), their application in the tropics is still very limited, even though many opportunities exist to obtain tree ring chronologies with an annual resolution from tropical species in forest regions where seasonal rainfall (dry season) or flooding result in an annual cessation of tree growth and annual growth rings (Worbes, 2002).

In western Thailand, concurrent with increasing $[CO_2]$, El Niño droughts have become more frequent and severe since the 1980s, and surface temperatures have increased significantly since 1950, with no corresponding increase in precipitation (Limsakul & Goes, 2008). For these reasons, in this study, we developed tree-ring chronologies and also analysed both carbon and oxygen isotope trends to investigate the long-term responses of gas exchange, iWUE, and stem growth in three tropical species to the multiple global change drivers. Specifically, we sought to determine whether iWUE increased over time; if stem growth increased concurrent with increasing iWUE; and whether changes in iWUE were driven by changes in A or g_s, while also quantifying effects not related to long-term environmental changes but to ontogeny and competition.

Methods

Study site and species

The Huai Kha Khaeng (HKK, 15°40′N, 99°10′E) 50 ha forest dynamics plot is situated in west-central Thailand in a seasonally dry evergreen forest (Bunyavejchewin *et al.*, 2009). Mean tree density is 438 per ha ($\geq$10 cm dbh), mean canopy height is >45 m, and mean stand basal area is 30 $m^2\,ha^{-1}$ (for more details, see Baker *et al.*, 2005; Bunyavejchewin *et al.*, 2009). Previous research suggests that in the mid-1800s catastrophic disturbance resulted in the synchronous establishment of many of the trees now dominating canopy, and subsequent widespread disturbances of variable intensity have occurred at least three times: in the 1910s, 1940s, and 1960s (Baker *et al.*, 2005). Windstorms, fire and drought are the most likely types of

Table 1 Characteristics of the three *Meliaceae* species studied, number of trees sampled for growth and stable isotopes (N), and crown dominance of individuals (dominant, codominant, suppressed)

Species	Shade tolerance	Phenology	Wood density (kg m^{-3})	N	Crown dominance (d, c, s)
Chukrasia tabularis	Intolerant/intermediate	Evergreen	620	36*	13, 14*, 9
Melia azedarach	Very intolerant	Deciduous	480	22	11, 9, 2
Toona ciliata	Intolerant	Deciduous	470	14	10, 2, 2

Phenology from Williams *et al.* (2008). Wood density from Nock *et al.* (2009).
*Sample trees and sample sizes were identical for growth and stable isotope analyses in *Melia* and *Toona*, but in *Chukrasia* only 13 codominant trees were analyzed for stable isotopes.

disturbance to have occurred (details in Baker *et al.*, 2005). Soils in the area are Typic Vermustolls (mollisols) (Lauprasert, 1988), which are relatively fertile for tropical forest soils, although soil depth rarely exceeds 1–2 m. Elevation within the plot ranges from 550 to 640 m asl.

Three canopy tree species in the Meliaceae family – *Chukrasia tabularis* A. Juss., *Melia azedarach* L., and *Toona ciliata* M.Roem. – were selected because they form readily identifiable annual growth rings in response to a dry season generally lasting from November to April (<85 mm of rainfall per month). The annual nature of the growth rings was previously determined in a cambial wounding experiment (described in Baker *et al.*, 2005). Both *Melia* and *Toona* are drought deciduous, but *Chukrasia* is not (Table 1, Williams *et al.*, 2008). The three species vary in their light requirements: *Melia* is a pioneer that is generally found in large canopy gaps, whereas *Toona* and *Chukrasia* are relatively more shade-tolerant, but also require gaps to establish and ascend into the canopy (Baker & Bunyavejchewin, 2006). All comprise an important component of the forest community, are represented by a sufficient number of individuals of varying sizes and ages for statistical modelling, and their life history is well characterized (Table 1, Baker *et al.*, 2005; Baker & Bunyavejchewin, 2006; Williams *et al.*, 2008; Nock *et al.*, 2009).

Climate data and CO$_2$ records

Climate data were obtained from the Royal Thai Meteorological Department for Nakhon Sawan (~100 km east of HKK, 15.48°N, 100.10°E, Fig. 1a–c). The data were nearly complete (only 0.2% missing) and were checked for quality and consistency (Limsakul & Goes, 2008). Average annual values for atmospheric CO$_2$ concentrations were obtained from the Mauna Loa (for after 1958) and Law Dome datasets (20-year spline version, Etheridge *et al.*, 1998, available at http://cdiac.ornl.gov/trends/co2).

Dendrochronological analysis

To distinguish between the effects of ontogeny and long-term environmental changes on stable isotopes ratios and tree growth, trees were selected nonrandomly so all size classes >10 cm diameter at breast height (dbh) were represented (e.g. 20, 30, 40, 50, >50). This design yielded measurements of tree growth (as well as iWUE, Δ^{18}O) at a given diameter or age,
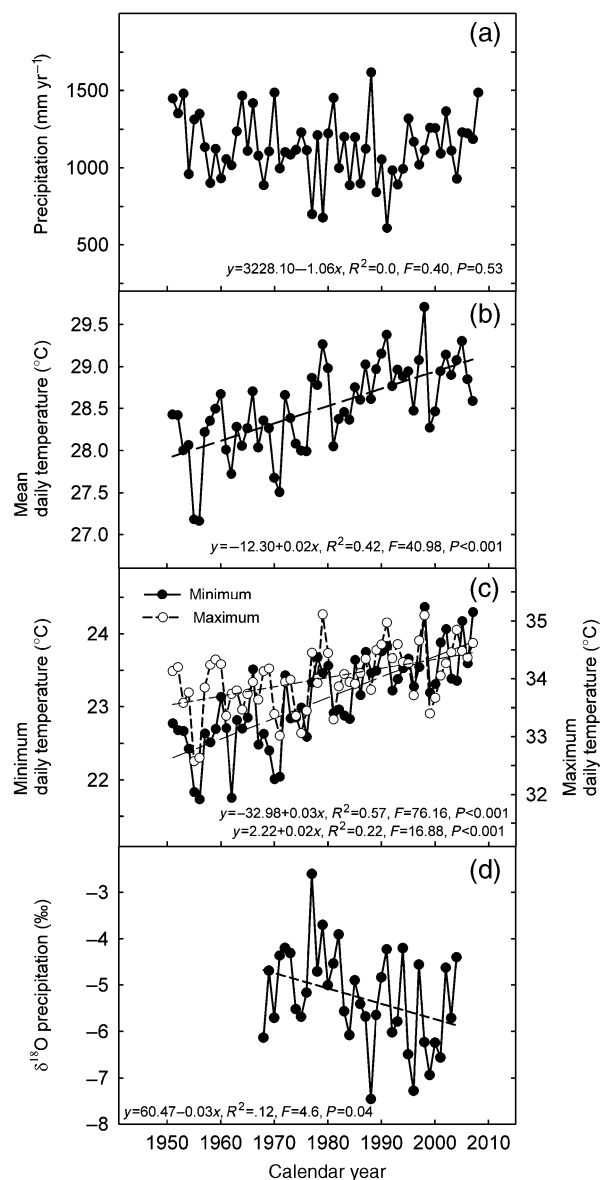

Fig. 1 Annual observations of climate for Nakhon Sawan, Thailand and oxygen isotopes in precipitation (δ^{18}O) for Bangkok, Thailand. (a) Total annual precipitation, (b) mean annual temperature, (c) mean annual minimum and maximum daily temperature, (d) mean annual δ^{18}O of precipitation for the wet season.

across multiple calendar years. Generally, individuals of each species were interspersed throughout the plot. Trees were cored (three per tree) using a 5 mm increment borer in April 2007: so the last complete year of growth was 2006. For a few smaller individuals, less than three cores were collected. We avoided coring trees with highly irregular stems, which were few, because rings can be very difficult to measure and cross-date. Crown exposure was scored qualitatively based on three categories: dominant, codominant, and suppressed. Finally, leaves were collected from the canopy using a sling shot to quantify the offset between leaf and stem carbon isotope composition (described below).

In the laboratory, cores were sanded until the tree rings were clearly visible using a succession of finer grained papers (highest 600 grit) and scanned at high resolution (1200 pixels per inch). Scans were measured in an image analysis program using a subroutine developed to calculate ring widths (0.01 mm resolution; SIGMASCAN PRO v.5.0.0, Systat Software Inc., San Jose, CA, USA). Tree ring series were first visually cross-dated by comparing measurements from the same tree and then from different trees, and then COFECHA – which calculates the correlation between individual ring-width series and a master ring-width series for each species – was used to check dating, find errors in individual series, and improve cross-dating accuracy (Holmes, 1983). After this procedure, only a small proportion of tree-ring series from each species poorly matched the master chronology despite the correction of traceable dating errors.

If cores did not include the pith, distance to the pith was estimated using a geometric method (based on ring arcs) in order to more accurately estimate tree age (Duncan, 1989). For a small number of cores, it was necessary to estimate the pith location as the difference between the sample length and half of the measured tree diameter (trees were generally round). The number of missing rings was calculated by dividing the missing distance (cm) by the average growth rate (cm yr^{-1}) in the adjacent five growth rings. Tree ages were then adjusted by the age estimate from the core with the least distance missing. Age estimates for an individual from different cores were mostly within 1–2 years of each other.

Stable isotope analysis of $\delta^{13}C$ and $\delta^{18}O$

For each tree, we identified the ring series most strongly correlated to the species master chronology, and from each corresponding core cut a thin slice of wood from groups of rings (decades) for grinding and cellulose extraction (e.g. 1981–1990, 1991–2000, 2001–2006). The decadal mid-point was used to quantify the independent variables year, tree size, and tree age for analysis of isotope trends.

To extract cellulose from wood powder, we used the procedure described in Hietz *et al.* (2005). The carbon and oxygen isotopic composition of three replicate samples of ca. 1 mg were measured with a high temperature reactor (HT-O, HEKAtech GmbH, Wegberg, Germany) coupled to a DELTAplus XP Mass Spectrometer (ThermoFinnigan, Thermo Fisher Scientific Inc., Waltham, MA, USA) using a modified high-temperature conversion (HTC) method (Knöller *et al.*, 2005). Samples and

standard materials were placed into tin capsules, dried overnight at 60 °C, and stored in a dry cabinet. The high temperature conversion was carried out at 1425 °C in a hot ceramic tube containing a glassy carbon tube filled with glassy carbon chips.

Our continuous-flow isotope ratio mass spectrometric (CF-IRMS) measurements generally followed the principle of identical treatment for reference materials and samples. Normalization of the raw $\delta^{18}O$ values vs. the VSMOW-SLAP scale was achieved by using a two-point calibration of in-house cellulose standards that have been calibrated against the international reference materials IAEA-601 and IAEA-602. The $\delta^{13}C$ values of the cellulose samples were obtained by normalizing raw delta values into the VPDB (Vienna Pee Dee belemnite) scale using a calibration against the international reference standards IAEA-CH-3 and IAEA-CH-6. IAEA-C3 and an in-house cellulose standard (synthetic microcrystalline cellulose, Merck) were used as control reference materials. Mean (SD) for the three replicates was 0.19‰ for $\delta^{13}C$ and 0.23‰ for $\delta^{18}O$. Isotopic values of carbon and oxygen are expressed relative to VPDB and VSMOW (Vienna standard mean ocean water).

Offset between wood cellulose and leaf material $\delta^{13}C$

Stem wood is generally 1‰–3‰ more enriched in $\delta^{13}C$ compared with leaves (reviewed in Cernusak *et al.*, 2009). Because the Farquhar *et al.* model (1982) is valid for CO_2 uptake but does not account for later discrimination, we adjusted wood cellulose $\delta^{13}C$ for the offset between the $\delta^{13}C$ of leaf material collected in 2007 (four to six trees per species), and recent wood cellulose (averaged from 2001 to 2006 rings), assuming that the offset between wood and leaf remained constant through time. Approximately, 1 mg of bulk leaf material was analysed. Differences were approximately 1‰, 1.5‰, and 0.5‰ for *Chukarasia*, *Toona*, and *Melia*, respectively ($\delta^{13}C_{stem} - \delta^{13}C_{leaf}$).

Calculation of $\Delta^{13}C$ and iWUE

Following Farquhar *et al.* (1982) we calculated carbon isotope discrimination, $\Delta^{13}C$, as

$$\Delta^{13}C = \frac{(\delta_{air} - \delta_{plant})}{(1 - \delta_{plant}/1000)},$$

and accounted for the decline in $\delta^{13}C_{air}$ over time resulting from increasing combustion of ^{13}C depleted fossil fuels (details in Saurer *et al.*, 1997b; Francey *et al.*, 1999; McCarroll & Loader, 2004).

Carbon isotope discrimination during CO_2 fixation in the leaves of C_3 plants is related to the ratio of intercellular to atmospheric CO_2 concentration (C_i/C_a)

$$\Delta^{13}C = a + (b - a)\left(\frac{C_i}{C_a}\right),$$

where a is the discrimination due to slower diffusion of $^{13}CO_2$ through stomata ($a = 4.4‰$) and b is fractionation discrimination by Rubisco against $^{13}CO_2$ ($b = 27‰$, Farquhar *et al.*, 1982).

Given that leaf conductance to water vapour (g_{H_2O}) is 1.6 times the conductance to CO_2, $\Delta^{13}C$ can be converted to iWUE,

defined as (Osmond et al., 1980)

$$iWUE = \frac{A}{g_s} = \left[1 - \left(\frac{\Delta - a}{b - a}\right)\right]\frac{C_a}{1.6},$$

which can be simplified to

$$\frac{A}{g_s} = \frac{(C_a - C_i)}{1.6}.$$

It follows from above that any variation in $\Delta^{13}C$ and iWUE may come from either relatively greater changes in A or g_s.

Accounting for source water effects on tree ring oxygen isotope enrichment

Variation in tree ring oxygen isotope composition is primarily due to source water effects, leaf level enrichment effects, and dampening of the leaf level signal in the stem before wood cellulose is synthesized (McCarroll & Loader, 2004). The $\delta^{18}O$ value of tree source water is primarily influenced by the $\delta^{18}O$ of precipitation, and to a lesser extent by plant interception, evaporation from surface retention, and soil evaporative en-

richment (McCarroll & Loader, 2004). We were primarily interested in isolating the leaf level effect on oxygen isotope enrichment in tree rings. Therefore, tree ring $\Delta^{18}O$ was calculated by subtracting the mean decadal value of $\delta^{18}O$ in precipitation from our decadal $\delta^{18}O$ tree ring values. In calculating the mean decadal value of $\delta^{18}O$ in precipitation, following Saurer et al. (1997a), values for the growing season were used (March–October for HKK).

Annual measurements of $\delta^{18}O$ (1968–2004) in precipitation were obtained from the Global Network of Isotopes in Precipitation program (GNIP, Fig. 1d, IAEA/WMO 2006; http://www.naweb.iaea.org/napc/ih/GN-IP/IHS_GNIP.html). Patterns of $\delta^{18}O$ in precipitation in the study region are dominated by large-scale moisture transport, so the GNIP data (from Bangkok, $\sim 240\,km$ south of HKK) are likely representative for the HKK site too (Yoshimura et al., 2003; He et al., 2006; Ichiyanagi, 2007).

Statistical analysis

Mixed-effects models are well suited to the repeated measures structure of tree ring and isotope data, as they can account for
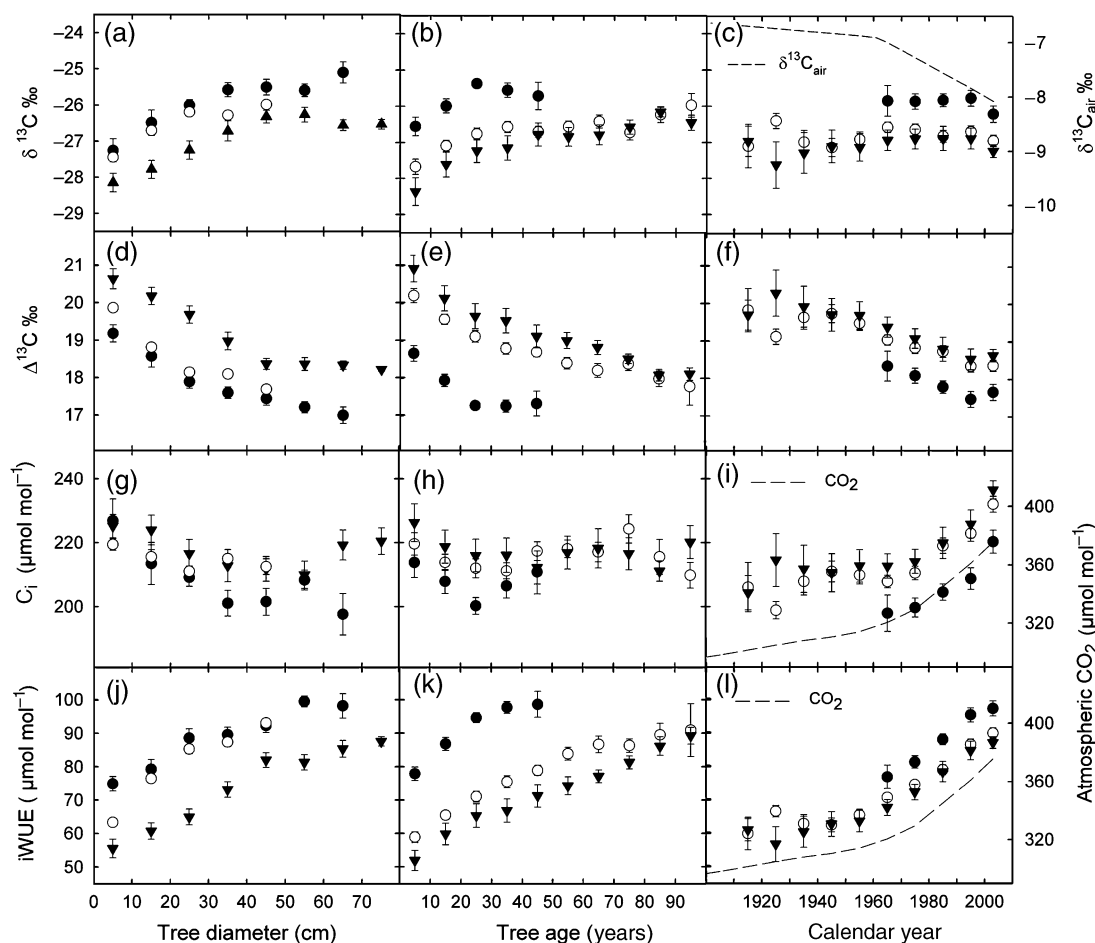

Fig. 2 Variation in mean $\delta^{13}C$, $\Delta^{13}C$, C_i, and intrinsic water-use efficiency (iWUE) with calendar year, tree diameter, and tree age for *Toona* (triangles), *Chukrasia* (open circles), and *Melia* (closed circles) trees in western Thailand. Whiskers indicate standard errors. Means and standard errors were calculated by decade, by 10 cm diameter classes, and by 10-year age classes.

random effects or variation at the individual tree level, and also can include flexible modelling of autocorrelation. We developed linear mixed-effects models to test for ontogenetic (tree diameter and tree age) and long-term effects (i.e. calendar year) on iWUE, ΔO^{18} and BAI – assuming that variation with calendar year reflects the cumulative effects of any global changes such as increasing surface temperatures and/or atmospheric $[CO_2]$ (Fig. 1b and c, $[CO_2]$ in Fig. 2i). The number of trees analysed for both growth and isotopic trends was 36, 22, and 14 for *Chukrasia*, *Melia*, and *Toona*, respectively; except for *Chukrasia*, there was one less tree for isotope analysis (35 trees, Table 1). Linear regression was used to determine significant trends in climate (Fig. 1).

To model tree growth, we converted ring widths (annual increment, $cm\,yr^{-1}$) to BAI ($cm^2\,yr^{-1}$), and log-transformed BAI and the explanatory variables (calendar year, tree age, and tree diameter) after visual assessment of bivariate plots. We did so in order to obtain linear relationships, stabilize the variance and satisfy assumptions of normality. In addition, we also mean-centred the variable calendar year to reduce collinearity. Temporal autocorrelation of within-tree errors in BAI models was modelled with a continuous first-order autoregressive process.

For each of iWUE, $\Delta^{18}O$ and BAI, the most parsimonious model was selected from a series of competing models by first evaluating the significance of the fixed effects terms with Wald tests and likelihood-ratio test, and then the significance of the random-effects terms and error autocorrelation using likelihood-ratio tests. Finally, we compared models using Akaike's information criteria (AIC, model selection in Tables S1, S3 and S5). $\Delta AIC < 2$ was taken as substantial evidence in support of a model over competing models. Crown competitive status was initially included in models of iWUE, $\delta^{18}O$ and BAI for all species, but was only significant for *Chukrasia*, which had greater numbers of trees in the varying classes (Table 1). Differences between codominant and dominant were not significant, so a binary factor (suppressed or not) was included in models of iWUE, $\delta^{18}O$, and BAI. Inspection of ring-series for low increment growth confirmed observations of crown suppression.

All predicted values were calculated using the fixed effect portion of models only. Because the sample size and the range of tree sizes declined with increasing time before present (shown in Fig. 5), we only predicted values of the response (iWUE, BAI, $\Delta^{18}O$) for calendar years in which our sample included individuals spanning the range of diameters for which the response was predicted. Model fit was assessed by plotting predicted values vs. the observed data (Fig. S1, a–c), and statistical assumptions were examined graphically (Pinheiro & Bates, 2000). Pseudo r^2 values for the fixed effects were calculated as the squared correlation between the observed data and their predicted values. All analyses were done in R, version 2.6.2 (R foundation for Statistical Computing, Vienna, Austria), using the package NLME (Pinheiro & Bates, 2000).

Results

Trends in tree ring carbon isotope composition and iWUE

Overall relationships between $\delta^{13}C$, $\Delta^{13}C$, C_i, and iWUE and tree diameter, calendar year, and tree age were similar for the three species (Fig. 2a–l). $\delta^{13}C$ increased with tree diameter and tree age by 1‰ in *Melia*, and by 1.5‰ in *Toona* and *Chukrasia* (Fig. 2a and b). No change in $\delta^{13}C$ was observed with calendar year, although $\delta^{13}C_{air}$ decreased due to fossil fuel burning (Fig. 2c). Accordingly, carbon isotope discrimination ($\Delta^{13}C$) relative to the atmosphere declined with tree diameter, tree age and calendar year in all three species (Fig. 2d–f).

C_i increased with calendar year, and generally declined with tree diameter, but showed no relationship with tree age (Fig. 2g–i). For *Melia*, C_i increased with calendar year from 200 to 220 $\mu mol\,mol^{-1}$ for the period 1960–2003 (Fig. 2i). For *Toona* and *Chukrasia*, C_i was relatively constant before 1960, and then increased strongly, concurrent with the rapid increase in atmospheric CO_2 from approximately 210 to 230 $\mu mol\,mol^{-1}$ (Fig. 2i). The increases in C_i since ~1960 were quite similar in the three species – roughly 5 $\mu mol\,mol^{-1}$ per decade (Fig. 2i).

For all species their iWUE increased with tree diameter, tree age, and calendar year, suggesting an influence of each on iWUE (Fig. 2j–l). For *Melia*, iWUE increased by ~27% from ~75 to ~95 $\mu mol\,mol^{-1}$ with calendar year (1960–2006, Fig. 2l), tree age (Fig. 2k), and tree diameter (Fig. 2j). For *Chukrasia*, iWUE increased from ~60 to 90 $\mu mol\,mol^{-1}$, or by ~50% with calendar year (~1910 to 2006, Fig. 2l), with tree age (Fig. 2k), and with tree diameter (Fig. 2j). For *Toona*, iWUE also increased by ~50%, from ~60 to 90 $\mu mol\,mol^{-1}$ with calendar year (1910–2006, Fig. 2l), with tree age (Fig. 2k), and with tree diameter (Fig. 2j). iWUE increased only slightly with calendar year before 1960 in *Toona* and *Chukrasia* (data for *Melia* was not available before 1960), and then increased at a faster rate, concurrent with the increase in atmospheric CO_2 and air temperatures (Figs 1b, c and 2l).

Across all species model comparison indicated greater support for iWUE models that included tree diameter and calendar year, compared with models that included tree age and calendar year (ΔAIC, Table S1). Likelihood-ratio tests indicated the addition of random effects significantly improved model fit in all species (Table S2). The best models included the following parameters for the species: *Toona*: calendar year, tree diameter, and their interaction; *Chukrasia*: calendar year, tree diameter, crown dominance, and calendar year × tree diameter interaction; and *Melia*: calendar year and tree diameter (Table 2, model selection in Table S1).

Predicted increases in iWUE with calendar year were greatest in *Chukrasia*, ~5% per decade; followed by *Toona*, ~3.5% per decade; and *Melia*, ~3% per decade (Fig. 3a–c, Table 2). Overall, iWUE was greatest in *Melia*, followed by *Chukrasia*, and then *Toona* (Fig. 3a–c, Table 2). A marginal but significant interaction between year
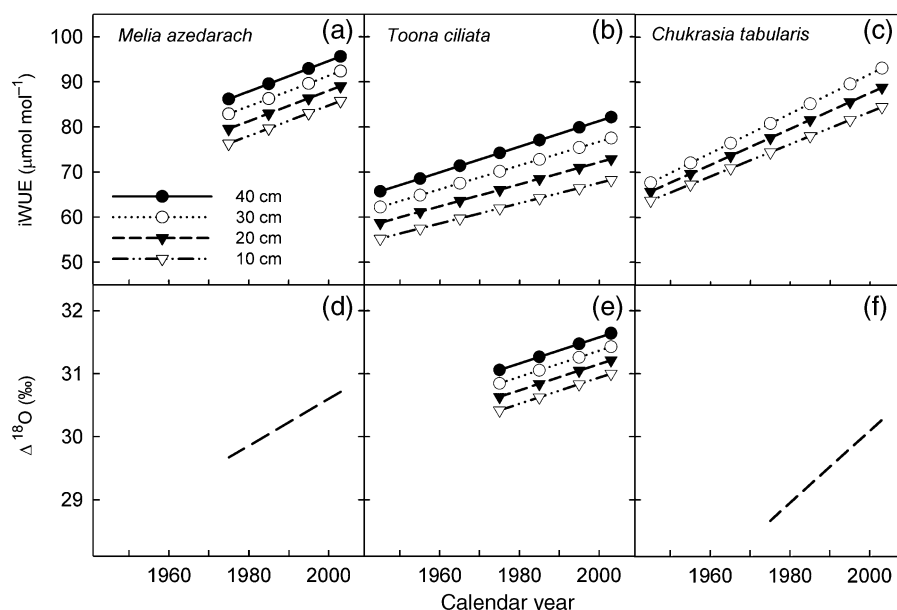
Fig. 3 Changes in intrinsic water-use efficiency (iWUE), and tree ring oxygen isotope composition ($\Delta^{18}O$) for *Toona*, *Melia*, and *Chukrasia* trees in western Thailand expressed as a function of calendar year and tree diameter as predicted by the most parsimonious maximum likelihood models for each species* (Tables 2 and 3; for model selection see Tables S1 and S3). Panels arranged vertically by species. Response predicted using values of 40, 30, 20, and 10 cm for tree diameter. *Note: For *Toona*, a number of models for $\Delta^{18}O$ had equal support. Predicted values based on the model with the lowest AIC. Details for the full models including random effects are given in Tables S2 and S4.

Table 2 Maximum likelihood parameter estimates for mixed models describing the effects of calendar year (Y), tree diameter (D) and crown dominance (C, for *Chukrasia* only) on intrinsic water use efficiency for *Toona*, *Melia* and *Chukrasia*

Model	Parameters	Estimate (SE)	df	*t*-value	*P*-value
Toona					
	Intercept	55.58 (0.54)	95	21.87	<0.000
	Y	0.20 (0.07)	95	2.58	0.011
	D	0.39 (0.06)	95	5.65	<0.000
	Y × D	0.002 (0.0008)	95	3.21	0.002
Melia					
	Intercept	77.15 (1.79)	59	43.08	<0.000
	Y	0.34 (0.05)	59	6.25	<0.000
	D	0.32 (0.04)	59	8.47	<0.000
Chukrasia					
	Intercept	70.73 (1.35)	196	52.20	<0.000
	Y	0.32 (0.04)	196	7.92	<0.000
	D	0.31 (0.06)	196	5.32	<0.000
	C	−8.19 (1.71)	33	−4.80	<0.000
	Y × D	0.004 (0.001)	195	3.38	0.001

Pseudo r^2-values were 0.67, 0.62 and 0.79, respectively. Calendar year was mean-centred. Fixed effects parameters are shown. See Table S1 for model selection (models: t8.s, m7.s, c8.C.s) and Table S2 for random effects details.

and tree diameter was found for *Toona* and *Chukrasia*, with slightly greater increases in iWUE over time in larger diameter trees (Fig. 3b and c; Table 2). Finally,

iWUE was significantly lower in suppressed *Chukrasia* trees relative to nonsuppressed *Chukrasia* trees (term C, −8.19, $P < 0.000$, Table 2).

Trends in oxygen isotope composition

Variation in $\delta^{18}O$ and $\Delta^{18}O$ was much less pronounced than in $\delta^{13}C$ and $\Delta^{13}C$ (compare Figs 2a–f and 4a–f). After accounting for the effects of a negative trend in $\delta^{18}O$ in precipitation with calendar year on tree ring $\delta^{18}O$, we found greater changes in $\Delta^{18}O$ than in $\delta^{18}O$ with calendar year (Fig. 4c vs. Fig. 4f).

The $\Delta^{18}O$ model with the lowest AIC for *Toona* included the effects of tree diameter and calendar year, a random intercept, and explained slightly more of the variation in the data (pseudo $r^2 = 0.20$, Table S3), compared with the model with the next lowest AIC (pseudo $r^2 = 0.17$, Table S3). We note, however, that ΔAIC values indicated equal support for models including the following fixed effects: only tree age, only tree diameter, and only calendar year (differences in AIC < 2, Table S3), and that the fixed effect for calendar year in the selected model bordered significance (term Y, Table 3, $P = 0.055$).

For *Chukrasia*, the model with the lowest AIC included significant effects of tree diameter, calendar year and crown dominance, and a random intercept

term (Table 3, for random effects see Table S4). Much of the variation in $\Delta^{18}O$ was explained by the model (pseudo $r^2 = 0.64$, Table 3), and ΔAIC indicated considerably less support for alternative models (AIC>3, Table S3).

A significant effect of calendar year on $\Delta^{18}O$ was also found for *Melia* ($P<0.001$, Table 3), but model selection indicated little evidence for ontogenetic effects (Table

Table 3 Maximum likelihood parameter estimates for mixed models describing the effects of calendar year (Y), tree diameter (D) and crown dominance (C, for *Chukrasia* only) on $\Delta^{18}O$ for *Toona*, *Melia* and *Chukrasia*

Model	Parameters	Estimate (SE)	df	t-value	P-value
Toona					
	Intercept	29.97 (0.45)	37	66.17	<0.000
	Y	0.02 (0.01)	37	1.98	0.055
	D	0.02 (0.01)	37	2.01	0.051
Melia					
	Intercept	30.13 (0.11)	49	282.39	<0.000
	Y	0.04 (0.01)	49	7.10	<0.000
Chukrasia					
	Intercept	28.57 (0.08)	102	346.22	<0.000
	Y	0.06 (0.003)	102	17.87	<0.000
	C	−0.40 (0.12)	33	−3.38	0.002

Pseudo r^2-values were 0.20, 0.28 and 0.64, respectively. Calendar year was mean centred. Fixed effects parameters are shown. See Table S3 for model selection (models: t.Ox.7, m.Ox.6, c.Ox.6.C), and Table S4 for random effects details.

S3). The model fit reasonably well, with a pseudo r^2 of 0.28, although the model under predicted $\Delta^{18}O$ at low values and over predicted $\Delta^{18}O$ at high values (Fig. S1b). A random intercept significantly improved model fit (Table S4).

Predicted changes in $\Delta^{18}O$ for were positive for all species (Fig. 3d–f). The greatest increase was found in *Chukrasia*, ~1.5‰, followed by *Melia*, 1‰, and *Toona*, <1‰ (Fig. 3d–f). For *Chukrasia*, suppressed trees were slightly less enriched in $\delta^{18}O$ (C term, −0.33, $P<0.000$, Table 3). Finally, for *Toona* tree ring $\Delta^{18}O$ increased slightly with increasing tree diameter (Fig. 3e, Table 3).

Variation in BAI with tree size, age, and calendar year

Large temporal changes in growth were evident, with both large declines in BAI in a number of years (e.g. ~1990, 1997–1998; 2002; Fig. 5a, d and g), and large increases in others (Fig. 5a, d and g; e.g. 2000, 2006). BAI at a given tree age was highest in *Melia*, followed by *Toona* and then *Chukrasia* (Fig. 5b, e and h). For a given diameter BAI was also highest in *Melia*, and was slightly higher in *Toona* than in *Chukrasia* (Fig. 5c, f and i).

Likewise for carbon and oxygen composition, the mixed-models for BAI with the lowest AIC included tree diameter and calendar year, whereas equivalent models based on tree age and calendar year had little support (Table 4, model selection in Table S5). For *Toona*
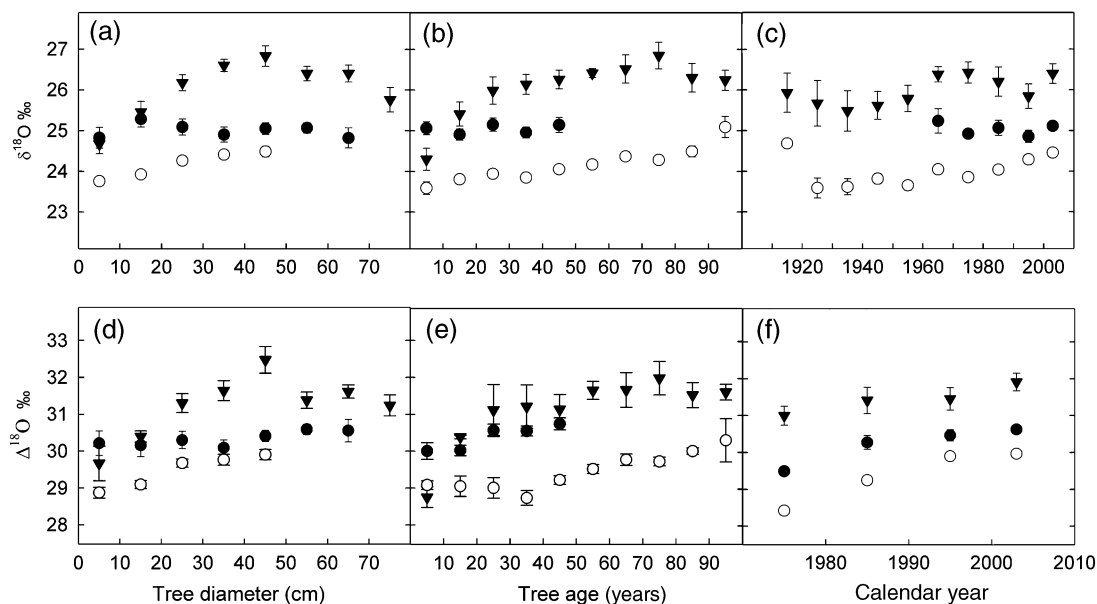

Fig. 4 Variation in mean tree ring $\delta^{18}O$ and $\Delta^{18}O$ for *Toona* (triangles), *Chukrasia* (open circles), and *Melia* (closed circles) trees in western Thailand. Whiskers indicate standard errors. Means and standard errors were calculated by decade, by 10 cm diameter classes, and by 10-year age classes. *Note:* Calculation of $\Delta^{18}O$ requires data for the $\delta^{18}O$ in precipitation and thus could only be calculated for 1970–2006.
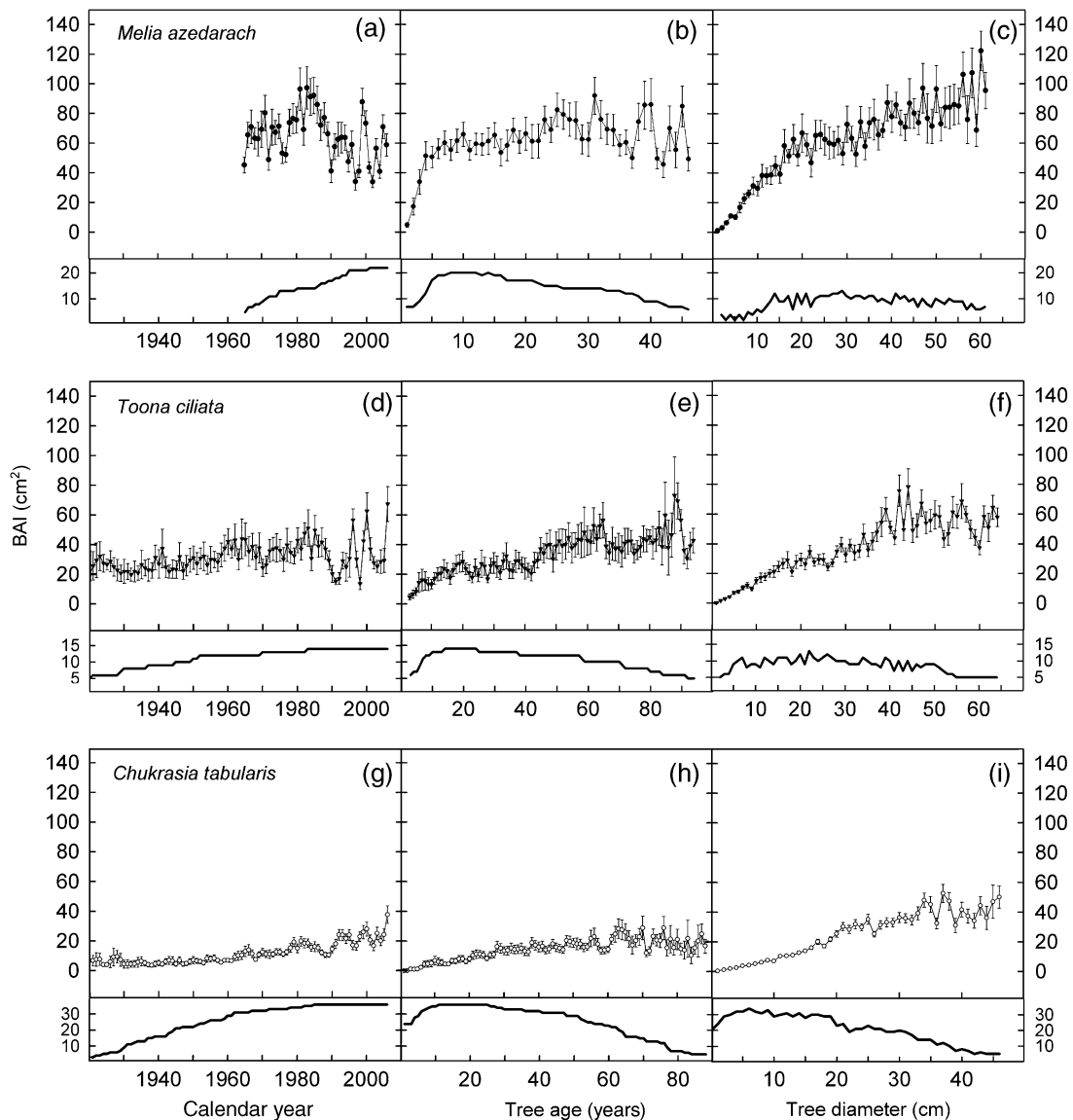
Fig. 5 Variation in mean basal area increment growth (BAI) by calendar year, tree age, and tree diameter for three canopy tree species in western Thailand. Whiskers indicate standard errors. Number of trees indicated in the lower portion of each panel. Panels arranged horizontally by species.

and *Chukrasia*, the differences between the best model and alternatives were substantial ($\Delta AIC > 3$, Table S5). For *Melia*, we found equal support for two models, which differed in their random effects, so the simpler model was used (Table S5). In the final models for *Melia* and *Toona*, the fixed effects included calendar year and tree diameter (Table 4, Table S5); for *Chukrasia* additional parameters significantly improved model fit, including: crown dominance, and an interaction between calendar year and tree diameter (Table 4, Table S5). Random intercepts were significant in all models, and a random slope was significant for *Toona* (Table S6).

Model terms for calendar year for all species indicated significant declines in BAI in more recent years in all size classes (Fig. 6a–c, Table 4). Declines in growth with calendar year were greatest in *Melia*: predicted BAI during the period 1970–2006 declined by ~50% (Fig. 6a, Table 4). For *Toona*, the decline in BAI with calendar year from 1940–2006 was ~50% (Fig. 6b, Table 4). In *Chukrasia*, a similar magnitude of BAI decline was observed as for *Toona* (Fig. 6c, Table 4), but the decline was slightly less at smaller diameters (Fig. 6c; term $Y \times D$, $P = 0.05$, Table 4). Finally, crown dominance also had an important effect on growth in *Chukrasia*: as anticipated,
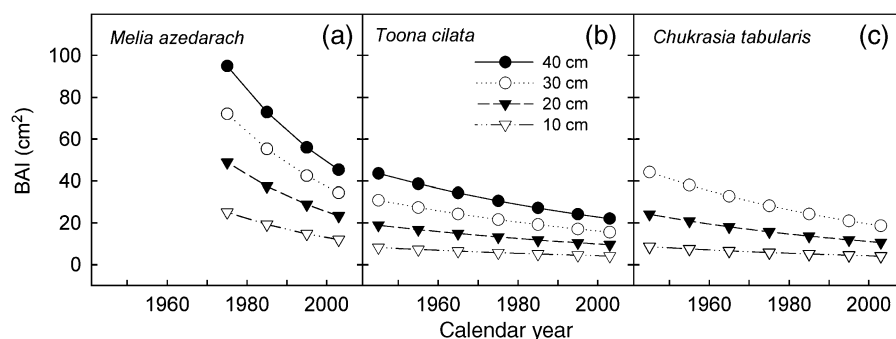
Fig. 6 Changes in basal area increment expressed as a function of calendar year and tree diameter for three canopy tree species in western Thailand as predicted by the most parsimonious maximum likelihood model for each species (Table 4, for model selection see Table S5). Response predicted using values of 40, 30, 20, and 10 cm for tree diameter. *Note:* predicted growth for *Chukrasia* is for nonsuppressed trees. Growth of suppressed *Chukrasia* individuals was lower (Table 4). The full model description including random effects is given in Table S6.

Table 4 Maximum likelihood parameter estimates for mixed effects models describing the effects of calendar year (Y), tree diameter (D) and crown dominance (C, for *chukrasia* only) on basal area increment for *Toona*, *Melia* and *Chukrasia*

Model	Parameter	Estimate (SE)	df	*t*-value	*P*-value
Toona					
	Intercept	−0.40 (0.07)	1014	−5.65	<0.000
	Year	−23.25 (7.16)	1014	−3.24	<0.000
	Diameter	1.21 (0.05)	1014	25.02	0.001
Autocorrelation		0.46		208.91	<0.000
Melia					
	Intercept	0.30 (0.09)	667	3.24	0.001
	Year	−52.54 (5.89)	667	−8.92	0.000
	Diameter	0.96 (0.06)	667	15.51	0.000
Autocorrelation		0.47		137.77	<0.000
Chukrasia					
	Intercept	−0.66 (0.06)	2229	−10.70	0.000
	Year	−16.67 (6.81)	2229	−2.44	0.014
	Diameter	1.44 (0.04)	2229	32.39	0.000
	C	−0.15 (0.07)	34	−2.20	0.035
	Y × D	−8.66 (4.47)	2229	−1.94	0.052
Autocorrelation		0.36		290.91	<0.000

Pseudo r^2-values were 0.65, 0.47 and 0.75, respectively. Autocorrelation was modelled using an autoregressive model with an order of 1 (AR1). Fixed effects parameters are shown. See Table S5 for model selection (models: t7.g.s, m7.g, c8.g.C), and Table S6 for random effects details.

individuals who were suppressed grew slower (term C, $P < 0.05$, Table 4).

iWUE in relation to temperature, precipitation and atmospheric CO_2

Regressions relating iWUE to changes in mean annual temperature and atmospheric [CO_2] were significant for all species (Fig. 7a and b). In addition, regressions for both mean annual temperature and atmospheric [CO_2] provided very similar fits, and slopes were quite similar for all the species (Fig. 7a and b). However, we did not find a relationship between iWUE and total annual precipitation (Fig. 7c).

Discussion

The role of tree age and diameter for ontogenetic variation in iWUE and growth

We found significant evidence in favour of models for the variation in iWUE that included tree diameter, compared with equivalent models including tree age (Table S1). Changes in isotope ratios with ontogeny are often referred to as 'age-related effects', although both
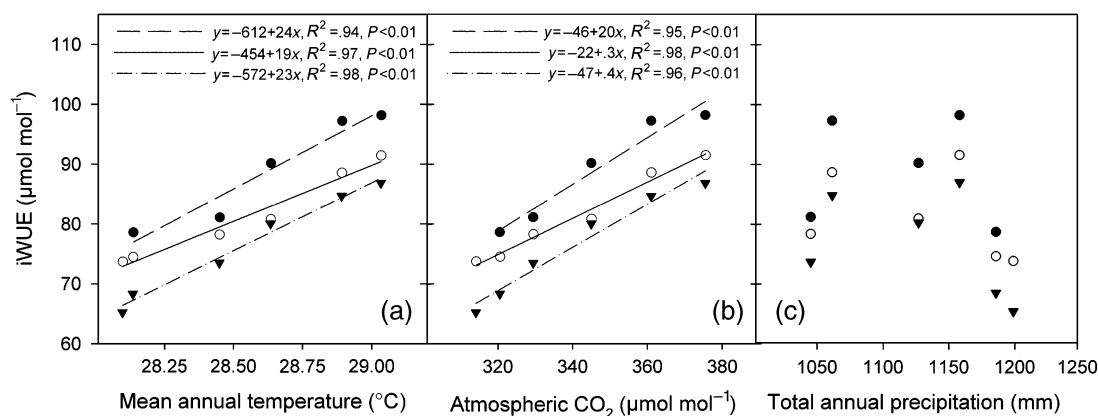
Fig. 7 Mean decadal values of intrinsic water-use efficiency (iWUE) vs. corresponding mean values for atmospheric CO_2 concentration, mean annual temperature, and total annual precipitation for *Toona* (triangles), *Chukrasia* (open circles), and *Melia* (closed circles) trees in western Thailand. Significant regressions shown for atmospheric CO_2 concentration and mean annual temperature. *Note:* Data excluded for tree diameter <10 cm to minimize juvenile effects. This approximately corresponded to the minimum diameter of a canopy tree.

age-related developmental effects on iWUE ($\delta^{13}C$) as well as microclimatic effects that may be more closely related to tree size have received attention (McCarroll & Loader, 2004). In the present study, variation in iWUE with tree diameter likely reflects a number of cooccurring influences that include: assimilation of $\delta^{13}C$ depleted air near the forest floor (Schleser & Jayasekera, 1985), changes in irradiance and photosynthetic capacity (Francey & Farquhar, 1982; Duquesnay *et al.*, 1998), and changes in the VPD with height in the canopy (Sternberg *et al.*, 1989). For example, trees which increase in diameter at a faster rate would likely assimilate $\delta^{13}C$ depleted air near to the forest floor for a shorter time period. Although determining the importance of individual microclimatic variables on iWUE ($\delta^{13}C$) is challenging because light, vapour pressure, wind, and other factors all vary with height in the canopy, our results serve to highlight the necessity of disentangling ontogenetic effects from long-term environmental trends (e.g. warming, CO_2; Bert *et al.*, 1997).

Recent research suggests that competition between trees may also have an important influence on iWUE. Mediterranean fir trees subjected to less competition from neighbouring trees exhibited higher growth and iWUE, probably due to an influence of greater light interception in dominant trees (Linares *et al.*, 2009). Similarly, we found growth and iWUE were greater in *Chukrasia* trees which were in more dominant canopy positions (Tables 2 and 4), which is also consistent with a greater influence of microclimatic effects on iWUE, as opposed to age-related factors.

In agreement with our findings for iWUE, we found tree diameter was a better predictor of BAI than tree age in all species (Table S5). Although few studies have compared the relation of tree age and tree diameter to

stem growth (BAI) in tropical trees, we believe that tree diameter, not tree age, is likely to be more closely related to important determinants of light capture such as tree height and crown size (King *et al.*, 2005).

Long-term trends in iWUE and stem BAI growth

For all three species in the present study, iWUE increased with calendar year by 3–5% per decade (Fig. 3). This result agrees with those from Hietz *et al.* (2005) for Brazilian *Cedrela odorata* (34%, ~3% per decade) and *Swietenia macrophylla* (52%, ~5% per decade), and from Silva *et al.* (2009) for *Araucaria angustifolia* (Bertol.) from southern Brazil (27%, ~3% per decade). Therefore, based on the limited evidence to date, it appears that long-term increases in iWUE may be common in tropical tree species. Indeed, increases in iWUE in forest trees during the last century have been documented on a global scale; studies in boreal (Saurer *et al.*, 2004), temperate (Bert *et al.*, 1997; Duquesnay *et al.*, 1998; Feng, 1999), and Mediterranean forests (Penuelas *et al.*, 2008; Linares *et al.*, 2009), have all revealed long-term increases in iWUE (range 17–40%, although see Marshall & Monserud, 1996), consistent with theorized increases in iWUE as a result of elevated CO_2.

And yet, while iWUE strongly increased with calendar year for all species, we found evidence of long-term declines in BAI with calendar year for all species (Fig. 6, Table 4). Recent studies of the response of gas exchange and stem growth to interactions among similar environmental changes – e.g. surface warming, water stress and rising [CO_2] – have also found that increasing iWUE ($\delta^{13}C$) can be associated with decreasing stem growth (Barber *et al.*, 2000; Penuelas *et al.*, 2008; Linares *et al.*, 2009), likely because the ameliorating effects of [CO_2] on

water stress cannot compensate for the effects of increasing aridity on gas exchange in some forests (Barber *et al.*, 2000; Penuelas *et al.*, 2008; Linares *et al.*, 2009). Indeed, in the present study regressions of iWUE vs. atmospheric [CO_2] and mean annual temperature suggested that both variables could have influenced iWUE (Fig. 7). Future analyses of annual variation in isotopes with annual variations in mean temperatures and precipitation can shed more light on the relative importance of [CO_2] and water stress for $\delta^{13}C$ and iWUE.

Although performing climate correlations was beyond the scope of this study because procedures for maximizing the climatic signal in tree rings involve statistical de-trending that may remove the long-term growth trends of interest, other research at HKK examining tree-ring and climate correlations has identified that *Melia* stem growth is negatively correlated with an index of El Niño severity, and that *Toona* growth is positively related to precipitation (P. J. Baker, unpublished results). Stem growth is expected to be the most sensitive component of NPP to drought because it is low on the carbon allocation hierarchy (Chapin *et al.*, 1990); thus, increasingly frequent and stronger El Niño droughts affecting Thailand (Limsakul & Goes, 2008), which in other forests have been shown to have community wide affects on growth (Vincent *et al.*, 2009), may have contributed to the growth declines detected in these species. Drought was recently also shown to have strong impacts on biomass accumulation in Amazonian forests and suggests much of the tropics could be vulnerable to moisture stress (Phillips *et al.*, 2009).

Our results contrast with recent findings arguing that CO_2 fertilization has accelerated tropical tree growth (Phillips *et al.*, 2008; Lewis *et al.*, 2009), but they are consistent with other studies that have identified evidence of declining tree growth in tropical forests. For example, recently Clark *et al.* (2009) found that the diameter growth of six canopy tree species in Costa Rica was very sensitive to changes in water stress and to variation in mean annual nighttime temperature, but not to increasing atmospheric [CO_2]. Furthermore, another recent study of tree growth from two permanent inventory plots in Panama and Malaysia also suggests that tropical tree growth is declining, most likely also in response to increases in cloudiness and in the proportion of photosynthetic gains lost to respiration with increasing nighttime temperatures (Feeley *et al.*, 2007). In the present study, data from the closest weather station to HKK do not show any long-term changes in sunlight hours (Tebakari *et al.*, 2005), but they do show that along with mean annual daily temperature, mean daily minimum temperatures (night) have increased by 1.5 °C since ~1950 (Fig. 1). It is therefore possible that increasing respiratory costs contributed to the growth

declines we report here. However, the effects of respiration are still hotly debated, and a number of arguments have been presented against the respiration hypotheses: namely, that (a) that growth is not limited by carbon, (b) respiration rates invoked to explain growth declines may not be realistic, and (c) acclimation of respiration is likely (Lloyd & Farquhar, 2008 and references therein). Interestingly, because iWUE does not account for changes in the proportion of fixed carbon lost by processes such as respiration, relatively greater increases in respiration than in photosynthetic C fixation could also account for a decoupling of increased iWUE from increased stem growth.

We suggest that our results for tree ring $\Delta^{18}O$ also contrast with a CO_2 fertilization driven increase in tree growth. $\Delta^{18}O$ increased with calendar year in all of the species studied, although the change was not very large (Fig. 3d–f, Table 3). Based on the semi-quantitative model developed by Scheidegger *et al.* (2000), increasing $\Delta^{18}O$ in tandem with decreasing $\Delta^{13}C$ in tree rings and increasing iWUE (Grams *et al.*, 2007) suggests that g_s declined with calendar year. This is because reduced g_s increases evaporative enrichment in ^{18}O as evaporative cooling decreases, while $\delta^{13}C$ increases because of reduced discrimination from reduced CO_2 supply. Thus, we have provided tentative evidence that the change in iWUE was likely due to a greater change in g_s (reduction) rather than in A (stimulation). Nonetheless, we appreciate that it is difficult to account for all influences on the fractionation of $\delta^{18}O$ in long-term observational studies (e.g. we do not account for mixing of enriched leaf water and source water), and that both increasing CO_2 and increasing temperature and VPD could contribute to long-term reductions in g_s. In addition, if stomata are insensitive to changes in VPD, increasing VPD could independently contribute to increasing $\Delta^{18}O$ (Barbour *et al.*, 2002). Annual climate correlations between $\Delta^{18}O$ and weather could potentially resolve some of these uncertainties in the future. Finally, though it is not always possible to obtain data for $\delta^{18}O$ in precipitation, our results suggest it was important to account for the influence of $\delta^{18}O$ in precipitation on tree ring $\Delta^{18}O$ due to a declining trend over time (Figs 1d and 4).

Whatever the causes of declining growth in the three species of Meliaceae, both *Toona* and *Chukrasia* are important timber species in other areas of their range. Therefore any strong declines in tree growth could have significant implications for future use of the species. The forested landscapes of continental Thailand are mosaics of different forest types, with evergreen and deciduous forests intergrading in complex patterns. If declining growth does indeed reflect water stress, warming and more frequent and severe El Niño events

could potentially lead to an expansion of deciduous forest within the forest mosaic and long-term changes in vegetation patterns in Thailand, with unknown consequences for carbon storage and diversity (Boonpragob & Santisirisomboon, 1996).

Conclusions

Evidence for the long-term growth response of tropical forests to global change is mixed. Thus, the search for the factors responsible for positive or negative growth trends continues and is of great importance for predicting future global changes and its implications for management and conservation. We have shown that the analysis of tree rings and multiple stable isotopes can yield insights applicable to the long-term response of mature tropical trees to important drivers of global change that may have negative (warming, drought), or positive (CO_2 fertilization, N deposition) effects on tree growth. While increasing $[CO_2]$ generally results in more efficient water use and has been related to increased growth elsewhere, in this Thai monsoon forest changes in other limiting climatic factors appear to have exerted stronger opposing effects which may actually lead to declines in tree growth.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Assessment of model fits for the most parsimonious mixed effects maximum likelihood models describing the variation in iWUE, Δ^{18}O and BAI for three tropical tree species in western Thailand. 1:1 line shown in all plots. (a)Intrinsic water-use efficiency (models: *Toona*, t8.s; *Melia*, m7.s; *Chukrasia*, c8.C.s). (b) Oxygen isotope composition (large delta, Δ^{18}O) (models: *Toona*, t.Ox.7, *Melia*, m.Ox.6; *Chukrasia*, c.Ox.6.C). (c) Stem growth (BAI) (models: *Toona*, t7.g.s; *Melia*, m7.g; *Chukrasia*, c8.g.C).

Table S1. Selection of mixed models describing the variation in intrinsic water use efficiency (iWUE) with calendar year (Y), tree diameter (D), tree age (A) and crown dominance position in the canopy (C, for *Chukrasia* only: suppressed or not-suppressed). Terms in lower case were not significant ($P > 0.05$). ΔAIC not presented if higher order terms were not-significant. Random slope inclusion indicated by x. Calendar year was mean centered. All models fit better with a random intercept. Selected model indicated in bold. Abbreviations: log-likelihood (LL), Akaike's information criterion (AIC).

Table S2. Maximum likelihood parameter estimates for mixed models describing the effects of calendar year (Y), tree diameter (D), and crown dominance (C, for *Chukrasia* only) on intrinsic water use efficiency for *Toona*, *Melia* and *Chukrasia*. Pseudo r-squared values were 0.67, 0.62 and 0.79 respectively. Calendar year was mean centered. See Table S1 for model selection (models: t8.s, m7.s, c8.C.s).

Table S3. Selection of mixed models describing the variation in tree ring oxygen isotope composition (Δ^{18}O‰) with calendar year (Y), tree diameter (D), tree age (A) and crown dominance position in the canopy (C, for *Chukrasia* only: suppressed or not-suppressed). Terms in lower case were not significant ($P > 0.05$), or indicate the model did not converge (DNC). ΔAIC values not presented for models with non-significant higher order terms. Random slope inclusion indicated by x. Calendar year was mean centered. All models fit better with a random intercept. Selected model indicated in bold. Abbreviations: log-likelihood (LL), Akaike's information criterion (AIC).

Table S4. Maximum likelihood parameter estimates for mixed models describing the effects of calendar year (Y), tree diameter (D) and crown dominance (C, for *Chukrasia* only) on Δ^{18}O for *Toona*, *Melia*, *Chukrasia*. Pseudo r-squared values were 0.20, 0.28 and 0.64 respectively. Calendar year was mean centered. See Table S2 for model selection (models: t.Ox.7, m.Ox.6, c.Ox.6.C).

Table S5. Selection of mixed models describing the variation in basal area increment (BAI) with calendar year (Y), tree diameter (D), tree age (A) and crown dominance position in the canopy (C, for *Chukrasia* only: suppressed or not-suppressed). Terms in lower case were not significant ($P > 0.05$). ΔAIC values are not presented if higher order terms were not significant. Random slope inclusion indicated by x. Calendar year was log-transformed and centered by its mean value. BAI, D and A were log-transformed. All models fit better with a random intercept and an autoregressive error correlation component of order 1. Selected model indicated in bold. Abbreviations: log-likelihood (LL), Akaike's information criterion (AIC).

Table S6. Maximum likelihood parameter estimates for mixed effects models describing the effects of calendar year (Y), tree diameter (D) and crown dominance (C, for *Chukrasia* only) on basal area increment for *Toona*, *Melia* and *Chukrasia*. Pseudo r-squared values were 0.65, 0.47 and 0.75 respectively. Autocorrelation was modelled using an autoregressive model with an order of 1 (AR1). See Table S3 for model selection (models: t7.g.s, m7.g, c8.g.C).

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