Title: Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees

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Abstract

Climate change effects on growth rates of tropical trees may lead to alterations in carbon cycling of carbon-rich tropical forests. However, climate sensitivity of broad-leaved lowland tropical trees is poorly understood. Dendrochronology (tree-ring analysis) provides a powerful tool to study the relation between tropical tree growth and annual climate variability. We aimed to establish climate-growth relations for five annual-ring forming tree species, using ring-width data from 459 canopy and understory trees from a seasonal tropical forest in western Thailand. Based on 183/459 trees, chronologies with total lengths between 29 and 62 years were produced for four out of five species. Bootstrapped correlation analysis revealed that climate-growth responses were similar among these four species. Growth was significantly negatively correlated with current year maximum and minimum temperatures and positively correlated with dry season precipitation levels. Negative correlations between growth and temperature may be attributed to a positive relation between temperature and autotrophic respiration rates. The positive relation between growth and dry season precipitation levels likely reflects the strong water demand during leaf flush. Mixed-effect models yielded results that were consistent across species: a negative effect of current wet season maximum temperatures on growth, but also additive positive effects of for example prior dry season maximum temperatures. Our analyses showed that annual growth variability in tropical trees is determined by a combination of both temperature and precipitation variability. With rising temperature, the predominantly negative relation between temperature and growth may imply decreasing growth rates of tropical trees as a result of global warming.

Introduction

Tropical forests are currently experiencing some of the most rapid rates of warming in recent geological times (Marcott et al. 2013). And not only are temperatures rising around the world, there are indications that temperature anomalies are becoming more frequent (Hansen et al. 2012). The response of tropical forests to global warming may potentially have large impacts on global carbon cycling (Corlett 2011). Warming may reduce leaf–level photosynthesis (Doughty 2011), increase autotrophic respiration rates (Lloyd and Farquhar 2008) and increase evaporative demand (Galbraith et al. 2010), resulting in reduced tree growth. As tropical forests contain one of the largest terrestrial carbon pools (Dixon et al. 1994; Malhi and Grace 2000), it is crucial to understand their response to warming (Clark et al. 2003).

In the absence of *in situ* tree-level warming experiments in the tropics, analysis of temporal tree growth variability in relation to annual climatic variation can be the next best source of information on global warming effects on tropical trees (Brienen et al. 2010; Clark et al. 2010; Pumijumnong 2012). Repeated diameter measurements of tropical trees has shown that temporal variation in diameter growth was negatively correlated with temperature (Clark et al. 2003; Dong et al. 2012; Clark et al. 2013). However, due to the multi-year census interval of most permanent plot studies (e.g., Dong et al. 2012), the power of correlation analyses is generally low and the multi-year census interval requires an integration of yearly climate parameters over the census interval.

Tropical dendrochronology (tree-ring analysis) can provide long-term, high-resolution tropical tree growth data to complement plot–based repeated diameter measurements (Worbes 1995; Zuidema et al. 2013). Tropical tree species that form reliable annual growth rings provide annual-resolution growth data at multi-decadal to centennial scales, which enhance the detectability of climatic influences on growth variation in tropical trees (Zuidema et al. 2012). Multi-species tree-ring studies on climate-growth relations of broad-leaved trees from moist lowland tropical forests are rare, but studies in the Amazon (Dünisch et al. 2003; Brienen and Zuidema 2005) and West Africa (Schöngart et al. 2006) have shown that temporal variation in growth was positively correlated with total annual precipitation. In lowland tropical forests in Southeast Asia, analysis of the relation between climate and ring width has mainly focussed on teak (*Tectona grandis*) (Pumijumnong et al. 1995; Buckley et al. 2007) and only a few examples of other species exist (e.g., Zuidema et al. 2011). Besides the generally low representation of lowland moist tropical forest trees species in climate-growth studies, the focus has traditionally been on precipitation correlations (Jacoby 1989; Rozendaal and Zuidema 2011; Pumijumnong 2012) and effects of temperature anomalies on annual growth variability were often not evaluated (Dünisch et al. 2003; Brienen and Zuidema 2005; Schöngart et al. 2006) or determined non-significant (Couralet et al. 2010). However, whereas there is large uncertainty regarding predicted rainfall changes for the tropics, a clear warming trend across most of the tropics is undisputed (IPCC 2007; Wright et al. 2009).

Here we use tree-ring analyses to evaluate tree growth sensitivity to climatic variation in Southeast Asia. We took tree ring samples from over 450 individuals belonging to five species known to form annual rings (Baker and Bunyavejchewin 2006). These species represent three different families, vary in leaf phenology and represent several ecological guilds. The availability of >60 years of high quality climate data from a nearby meteorological station allowed us to address questions and hypotheses on the relationship between climate variability and tree growth. Specifically we addressed the following questions: (1) Is tree growth correlated with minimum and maximum temperature? (2) Is tree growth correlated with precipitation? Furthermore we used linear mixed-effects models to assess the relative importance of various seasonal climate indices on standardized diameter growth rates.

Materials and methods

Study area and species

The study area was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani province, western Thailand (15.60 N 99.20 E), approximately 550 m above sea-level. Climate in Huai Kha Khaeng is strictly seasonal with a marked dry season from November to April (Fig. 1a). Mean annual rainfall in HKK is 1473 mm and mean annual temperature is 23.5 ºC (Bunyavejchewin et al. 2009). Soils are highly weathered, slightly acidic ultisols and soil textures are sandy loam at the surface and sandy clay-loam in the subsurface horizons (Bunyavejchewin et al. 2009). The vegetation in the area is classified as seasonal dry evergreen and mixed deciduous forest (Bunyavejchewin et al. 2009). Canopy height in the forest is around 30 m, with occasional emergent trees reaching over 50 m tall. Members of the family Dipterocarpaceae dominate the area in total basal area; other well-represented families include Annonaceae, Euphorbiaceae and Meliaceae (Bunyavejchewin et al. 2001).

We sampled five tree species: *Afzelia xylocarpa (*Kurz) Craib (Fabaceae), *Chukrasia tabularis* A. Juss. (Meliaceae), *Melia azedarach* L. (Meliaceae), *Neolitsea obtusifolia* Merr. (Lauraceae) and *Toona ciliata* M. Roem. (Meliaceae). See Table 1 for a summary of the species' characteristics. All five species were known to form annual rings following a cambial wounding experiment over the period 1988-1998 (Baker et al. 2005). *Afzelia*, *Melia* and *Toona* have a distinctly deciduous leaf phenology, whereas *Chukrasia* is classified as brevi-deciduous and

Neolitsea is evergreen (Williams et al. 2008). All five species are canopy trees, reaching maximum heights of 30-45 m.

Sampling and measurements

Wood samples for tree-ring analysis were collected from 459 trees during the period between December 2010 and December 2011. All samples were collected within a ~300 ha area of mixed deciduous and seasonal dry evergreen forest. Samples from the locally more abundant species, *Neolitsea* and *Chukrasia*, were mainly collected following a clustered sampling design. These trees were sampled in a 50 m radius around a randomly assigned location in the ~300 ha area that was retrieved using a GPS device (Garmin GPSMAP 60C Sx). Because *Afzelia*, *Melia* and *Toona* were (locally) rare in the area, these species were sampled more opportunistically, by collecting additional samples from trees that were encountered in the forest. We aimed to gather a random subset of the local population of the five target species, therefore we took samples of all trees >5 cm dbh, irrespective of for example canopy position. At a height of approximately 1 m on the stem, we manually extracted wood cores with a 5.0 mm diameter Suunto (Vantaa, Finland) or a 5.15 mm diameter Haglöf (Långsele, Sweden) increment borer. Depending on the diameter of the tree we used borers with lengths varying between 40 and 70 cm. From trees <40 cm dbh two cores were taken, because the borer would go straight through the tree and we therefore obtained two complete radii per core. From all larger trees we took three cores, because only one complete radius per core was obtained. Taking multiple cores allowed us to measure rings over at least three different radii, thereby correcting for radial variation in diameter increment and facilitating the detection of very narrow and partially missing rings (Stokes and Smiley 1968). Extraction areas were left untreated (Dujesiefken et al. 1999).

The increment cores were glued to wooden mounts and cut perpendicular to the ring boundaries with a large sliding microtome (WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland). Digital images (1600 dpi) of the tree cores were obtained using a high-resolution flatbed scanner (Epson Expression 10000 XL) and analyzed in the WinDENDRO program for tree-ring analysis (version 2009b; Regent Instruments Canada Inc.). All tree-ring boundaries were marked manually on the screen by identifying the ring boundaries and measured to the nearest 0.001 mm. Identification of the growth rings, following standard procedures (Worbes and Junk 1989; Worbes 2002), was facilitated by (1) within–ring variations in the size and density of vessels for the ring-porous species *Melia* and *Toona*, (2) bands of marginal parenchyma delineating each ring in *Afzelia* and *Chukrasia* and (3) intra-annual wood-density variation in *Neolitsea* (Fig. S1).

Chronology development

Tree ring data quality was checked by visually crossdating tree ring series in WinDENDRO. For trees sampled during the growing season of 2011, this year was excluded from analysis because this ring did not represent a full growing season. After visually crossdating the tree-ring series, we checked for dating errors using the computer program COFECHA (Holmes 1983). This iterative process of crossdating greatly reduces the number of false and missing rings, both of which are known to occur in tropical species (Worbes 1995). Ring-width series that correlated poorly with the master chronology—for example, due to prolonged growth suppressions—were removed from the dataset prior to chronology development (Pederson et al. 2004). We used the dendrochronology program library in R (dplR; Bunn 2008) to produce species–specific chronologies from the previously selected tree-ring series. Ring–width indices were obtained by detrending the raw ring-width series using a 20–

year cubic spline. A 20–year cubic spline was chosen because it showed the best result in removing low-frequency trends (e. g., related to ontogeny and canopy-dynamics), while preserving the high frequency variation in growth. Next all ring-width series were prewhitened using autoregressive modeling to remove any effect of temporal autocorrelation in growth. Upper and lower 95% confidence intervals around the mean chronologies were based on a 1000 bootstrap replicates (Bunn 2008). Residual ring widths after detrending were normally distributed in all species as recommended for climate correlations (Cook et al. 1990).

Crossdating of annual growth rings was successful for four out of five species (Fig. 2a-d). However, for the non-ring-porous species (*Afzelia*, *Chukrasia*), this lead to the exclusion of a large fraction of trees (>60%) from their respective species–specific chronologies (Table 2). Because of high dating uncertainty remaining after attempting to crossdate *Neolitsea* ring-width series, we excluded this species from all further analyses. For the other four species a species–specific chronology was produced (Fig. 2e-h). Out of the total sample size the proportion of trees included in the chronology was 38% for *Afzelia*, 27% for *Chukrasia*, 89% for *Melia* and 79% for *Toona* (see Fig. S2 for diameter distributions of trees included in the chronologies). In *Afzelia* and *Chukrasia,* false, wedging and generally indistinct rings were frequently observed, especially in periods when growth was suppressed, resulting in higher rejection rates. The resulting chronologies were cut off when the running expressed population signal (EPS) was <0.85 (Wigley et al. 1984; Speer 2010). The EPS is used to assess how well a chronology of a finite number of trees estimates the hypothetical (noise-free) population chronology (Wigley et al. 1984). When the EPS value is <0.85 the chronology starts to be dominated by the individual tree-level signal, rather than the stand level signal and is therefore less useful for climate-growth analysis (Speer 2010).

Climate data

We used monthly climate data from the Nakhon Sawan meteorological station (15.80N, 100.20E) for the climate-growth analysis. All climate data were obtained from the KNMI Climate Explorer website (Trouet and Van Oldenborgh 2013). The Nakhon Sawan meteorological station is situated ~100 km east of the sampling area. Because the climate station is situated at a lower elevation, mean yearly temperatures are on average 5 ºC higher in Nakhon Sawan and mean annual precipitation 350 mm lower compared to the study site. The temperature dataset from the Nakhon Sawan station was nearly complete for the period 1951-2010 (<0.5% of the data points were missing), monthly precipitation data were missing for <4% of the months (1951-2010). Any missing values were replaced by gridded climate data for the location of the climate station (Trouet and Van Oldenborgh 2013). Significant positive trends in the annual maximum temperature data (0.011 ºC, $P < 0.01$) and annual minimum temperatures (0.025 ºC, $P < 0.001$) were found (Fig.1b). Because this study did not aim to analyze growth response to long-term climate change, but instead focusses on drivers of annual variability in growth, all climate data was linearly detrended prior to analysis (Fig. 1b). Therefore all climate parameters were expressed as deviations from the long–term trend. After detrending we found no evidence for temporal autocorrelation in the climate data.

Climate-growth analysis

All statistical analyses were performed in the R program environment for statistical computing, version 3.0.0 (R Core Team 2013). The climate response of each species was determined by correlating mean standardized ring–width series (chronologies) with monthly climate indices. All monthly correlations were performed using a 24-month window, from

January in the prior growing season to December in the current growing season. We included prior year climate variables in the analysis because a lagged effect of climate on tree growth has frequently been found for both temperate and tropical tree species (Pederson et al. 2004; Brienen and Zuidema 2005; Buckley et al. 2007). To test climate-growth relationships, Pearson correlations were calculated using 1000 bootstrapped correlations by random extraction with replacement of values in the climate dataset, following the DENDROCLIM approach (Biondi and Waikul 2004), as applied in the bootRes package in R (Zang and Biondi 2013).

To compare the relative contribution of temperature and rainfall on diameter growth, we used mixed-effects models, with a second order autocorrelation structure and individual trees as a random factor (nlme package in R; Pinheiro et al. 2011). The second order autocorrelation structure was added to the model to account for the effect of growth in year t_{-2} and year t_{-1} on growth in year t_0. A total of four different models was used, because each species was included in a separate model. First, we reduced the number of initial fixed factors to be included in the model by calculating mean 6–month seasonal indices from the monthly precipitation data, minimum- and maximum temperature data. We defined the dry season as November_{t-1} to April_{t0} and the wet season as May_{t0} to October_{t0}. In the analysis both the current dry and wet season indices were included as well as prior year dry and wet season indices. This resulted in a total of 12 initial variables to be included as fixed factors in the full model. All seasonal climate variables were linearly detrended prior to analysis and the variance was stabilized. Only standardized diameter growth rates for those trees that were also included in the chronology were used as dependent variables. In this way only those trees that had a strong common signal in growth were used. The full model was subsequently simplified by step-wise removal of the least significant variables and the model with the lowest Akaike's Information Criterion (AIC) value was selected (Zuur et al. 2009).

Results

Tree-ring chronologies

Total chronology lengths ranged from 29 to 62 years (running EPS > 0.85), with the longest chronology spanning the period between 1950 and 2011 for *Toona*. The independently constructed chronologies were significantly positively correlated among all pairs of species (*Pearson r*, $P < 0.05$), except for *Afzelia* and *Toona* ($P < 0.10$). This similarity in year-to-year variation in growth is also expressed by the occurrence of synchronous marker years (years of abnormally low growth) in the chronologies, such as 1972,1990 and 1997 (Fig. 2). Both the high correlation among chronologies and the simultaneous occurrence of marker years provides strong evidence for the presence of an external factor driving annual variability in growth. We used the Monsoon Asia Drought Atlas (MADA) data (Cook et al. 2010) as an independent reference chronology to verify dating accuracy of the four chronologies constructed in this study. We found that *Melia* and *Toona* chronologies were highly significantly positively correlated with the MADA chronology ($P < 0.01$), $R^2 = 0.19$ and $R^2 = 0.34$ respectively. However, the *Afzelia* chronology was only marginally correlated with the MADA chronology ($P = 0.07$) and the *Chukrasia* chronology was not significantly correlated with the MADA chronology ($P = 0.36$).

Correlation between ring width and climate

We started the climate growth analysis by correlating standardized ring-width indices with monthly climate indices of the current and prior year. Significant positive correlations between total monthly precipitation and ring-width index values were found in all species. A significant correlation with current year April precipitation was found in *Chukrasia* and *Toona*, indicating that growth may be positively influenced by early growing season rainfall (Fig. 3b,d). *Melia* and *Toona* ring–width indices were also significantly positively influenced by prior year rainfall (Fig. 3c,d). We tested the correlation between total current-year precipitation and chronologies of the four species, but this revealed no significant correlations.

Afzelia, *Chukrasia*, *Melia* and *Toona* all showed strong negative correlations with current wet season monthly minimum temperatures (Fig. 4). *Chukrasia* and *Toona* also showed significant negative correlations between growth and current dry season minimum temperatures. Positive correlations between growth and minimum temperature of the prior dry season were only found for *Melia* (Fig. 4c).

When correlating monthly maximum temperatures and growth similar patterns arise as those for monthly minimum temperatures. All four species showed significant negative correlations with current year wet season maximum temperatures (Fig. 5). To illustrate the strong synchrony between temperature and growth, we plotted anomalies in current-year wet-season maximum temperature and growth of *Melia* (Fig. 6), the species with the strongest temperature-growth correlation (Fig 5c). *Toona* also showed significant negative correlations between growth and current–year dry season maximum temperatures (Fig. 5d). In addition, both *Chukrasia*, *Melia* and *Toona* also showed significant positive correlations between growth and prior dry season monthly maximum temperatures (Fig. 5b-d). It is highly unlikely that the significantly negative correlation between mean current year December maximum temperatures and *Afzelia* growth (Fig. 5a) has a direct causal relation, because by December the ring has already been completely formed. The significant correlation most likely resulted from temporal autocorrelation in mean monthly maximum temperatures, as it can be seen that the preceding months also show a trend towards negative correlations.

We used linear mixed-effect models for each species to determine the additive effects of climate on diameter growth (Fig. 7). AIC values of the selected models were 0.34-1.98 units lower than that of the model with one-but-lowest AIC value. For *Afzelia* the model explaining diameter growth revealed that current year dry season minimum temperature was positively related with diameter growth, whereas the effect of wet season maximum temperatures was negative (Fig. 7a). Prior year dry season maximum temperature had a positive effect on *Afzelia* growth and dry season precipitation, minimum temperature and wet season minimum temperature were all negatively related with *Afzelia* growth.

Selected models for *Chukrasia*, *Melia* and *Toona* were relatively similar (Fig. 7b,c,d). Current year dry season precipitation was positively related with diameter growth, whereas there was a negative relation between diameter growth and wet season maximum temperatures. Models for *Melia* and *Toona* also included a significant effect of current year wet season precipitation, which was negatively related with diameter growth. *Chukrasia*, *Melia* and *Toona* showed a positive relation with prior year dry season maximum temperature and prior year wet season precipitation levels. We also selected best fit linear mixed-effects models in which we modelled raw annual diameter growth based on seasonal climate indices (results not presented). By using relations established in these models (modelling raw growth data instead of detrended growth data) we determined that an increase of wet season maximum temperatures with 1 °C was associated with a reduction in mean diameter growth of 0.3 mm for *Afzelia*, 0.9 mm for *Chukrasia*, 2.3 mm for *Toona* and 3.0 mm for *Melia* (see also Fig. 6).

Discussion

Species suitability for climate-growth analyses

We showed that *Afzelia*, *Chukrasia*, *Melia* and *Toona* rings can be used for climate-growth analysis. Unfortunately, poor crossdating precluded *Neolitsea* from climate-growth analysis, although a cambial wounding experiment has independently demonstrated the annual nature of *Neolitsea* rings (Baker et al. 2005). The frequent association of *Neolitsea* with non-dominant canopy positions, in contrast to the other four species (Vlam, M. *unpublished results*), may have resulted in an overriding effect of local stand dynamics on annual growth variability (Denslow 1980; Druckenbrod et al. 2013) resulting in the more frequent occurrence of false rings. The highly significant correlations of the *Melia* and *Toona* chronologies with the independently constructed MADA-chronology (Cook et al. 2010) further supported our confidence in the dating accuracy of these two species. Unfortunately, *Melia* and *Toona* are relatively short–lived, limiting the establishment of century-long climate-growth relations. The chronology length of *Afzelia* and *Chukrasia* was mainly confined by dating uncertainty and limited crossdating success prior to 1970. For tropical tree species with such complex wood anatomy and high potential for dating errors, tree-ring analyses would ideally be performed on whole stem cross-sections.

We are aware that our study species are a non-random selection and small subset of the most abundant species at our study site. They represent just two families and do not include the most dominant family (Dipterocarpaceae), but they do differ in for example ecological guild and the degree of deciduousness. The number of species fore which tree-ring analyses can be done at a given site will likely increase when recently tested techniques to reconstruct annual growth patterns of (apparently) ring-less species become more accessible (Poussart et al. 2004; Loader et al. 2011).

Climate correlations

Both the correlation analyses and linear mixed-effects models showed that tree growth was strongly driven by climate variability and growth responses were often similar among species. The correlation analysis showed that growth variability in all four species was strongly negatively correlated with current year minimum and maximum temperatures. This finding is similar to that of Clark et al. (2003), who showed that growth rates of trees in an old-growth tropical rain forest in Costa Rica were negatively correlated with current year daily minimum temperatures. Furthermore, Dong et al. (2012) showed that growth anomalies of whole tropical forest stands in Malaysia, Panama and Thailand were negatively correlated with five–year–averaged temperature anomalies. In addition, similar negative effects of temperature on tree growth were found in tropical sites with higher latitude and elevation (e.g., Buckley et al. 2007). The mechanism for a negative relation between temperature and tree growth in the tropics may be through higher temperatures leading to reduced carbon assimilation rates, by having both a direct negative impact on photosynthesis rates (Galbraith et al. 2010) and increasing autotrophic respiration rates (Clark 2007; Feeley et al. 2007). Maintenance costs of plant tissue increase with higher ambient temperatures (Lloyd and Farquhar 1996). For tropical forests it has been shown that an air temperature increase of 10 °C leads to roughly a doubling of respiration rates (Meir et al. 2008). However, this was contrasted by Doughty (2011) finding little evidence of enhanced respiration rates in an *in situ* warming experiment with tropical trees. It has also been shown for deciduous temperate trees that leaf respiration rates show rapid acclimation to increased air temperature (Lee et al. 2005). Temperature also influences leaf-to-air vapour pressure deficit and tree evapotranspiration rates (Galbraith et al. 2010; Choat et al. 2012). When evaporative demand increases due to higher temperatures, the leaf stomata tend to close to reduce water loss, resulting in lower CO_2-uptake and decreased carbon assimilation rates (Lloyd and Farquhar 2008). Because the majority of annual net primary production of trees in a seasonal forest is concentrated in the months with high rainfall (April-October in HKK), it is likely that growth is most sensitive to temperature variability during this time of the year. And thirdly, temperature is negatively correlated with rainfall (Devall et al. 1995). Thus, both increased evaporative demand leading to lower carbon assimilation rates, increased respiration costs and reduced precipitation rates during warm years could potentially be driving negative correlations between tree growth and current wet season temperature.

Unlike previously described climate-growth relations for seasonal tropical forests (Dünisch et al. 2003; Brienen and Zuidema 2005; Schöngart et al. 2006; Couralet et al. 2010), the mixed model analysis showed that the relation between growth and temperature were generally stronger than those between growth and precipitation. Weak correlations between single–year drought and tree growth were also found in two large–scale drought experiments in the Amazon (Brando et al. 2008; Metcalfe et al. 2010). Both studies provided evidence that net primary productivity of trees declined during the simulated drought, but this reduction was relatively modest in the first year. But as expected a period of consecutive years with low rainfall, such as the period 1989-1993 in western Thailand, did result in one of the clearest reductions in growth rates among the four species. The positive relation between growth and early growing season precipitation levels has been commonly found in tropical dendrochronological studies (Pumijumnong et al. 1995; Buckley et al. 2007; Rozendaal and Zuidema 2011; Soliz-Gamboa et al. 2011). This strong relation likely reflects the importance of adequate water amounts for the flushing of new leaves (Brando et al. 2008), which occurs around the spring equinox for most species in HKK (Williams et al. 2008). The absence of long-term climate data from the HKK study site forced us to use of data recorded at the Nakhon Sawan meteorological station (~100 km east of HKK) for all climate-growth analyses. Although most of the rainfall during the wet season in HKK originates from the Asian summer monsoon system (Wang and Ho 2002), regional variability in rainfall is comparatively higher than regional variability in temperature. The high local variability in rainfall amounts, combined with a ~100 km distance between to the meteorological station, may have led to an underestimation of the positive growth-precipitation correlations.

Evidence for a lagged climate-growth response is commonly found in dendrochronological investigations across the tropics (e.g., Dünisch et al. 2003; Brienen and Zuidema 2005). Both misdating of the rings and temporal autocorrelation in the growth data have been suggested as methodological causes for observed lagged responses (Soliz-Gamboa et al. 2011). However, temporal autocorrelation in the tree-ring and climate data was low and dating certainty, especially of *Melia* and *Toona*, was high, both were therefore unlikely to have caused the observed lagged responses. Alternatively, physiological pathways leading to lagged climate-growth responses in tropical trees have been suggested but remain poorly investigated so far. In temperate trees the presence of preformed shoots in trees with strong seasonality in leaf formation has been suggested to lead to lagged growth responses because growth for the first flush is set during bud formation in the prior year (Oliver and Larson 1996; Pederson et al. 2004). Also favorable conditions in the current year may promote the formation of reserves, rather than growth in the current year and these reserves can then be used in the beginning of the next growing season (Dünisch et al. 2003; Pederson et al. 2004). For instance, the three deciduous species in our study (*Afzelia*, *Melia* and *Toona*) completely rely on reserve materials for the flushing of new leaves and possibly also for the initial stages of xylem formation (Ohashi et al. 2009). We do not understand how prior-year temperatures may have a positive effect on growth in our study species.

Tropical tree growth and climate change

Daily maximum temperatures in western Thailand have been steadily rising over recent decades (Trouet and Van Oldenborgh 2013) . The combination of rising temperature and a strong negative relation between diameter growth and current growing season maximum temperatures in all four study species, may indicate that tree growth rates will likely decrease over time. These reduced diameter growth rates may result in a reduced carbon sequestration capacity of the forest as a whole (Brienen et al. 2010). However, historical growth responses to annual climate variability, e.g. linking past negative growth anomalies with relatively warm years, should not be translated into oversimplified projections of long term growth responses to long term changes in climate (Zuidema et al. 2013). Trees may for example respond to a structural increase in temperatures and drought through physiological acclimation of both photosynthesis and respiration (Galbraith et al. 2010), potentially reducing the long term effect of increased temperature on growth. The negative effect of rising temperatures may also be compensated by a CO_2-fertilization effect (Baker et al. 2004; Lloyd and Farquhar 2008) through a strong increased water-use-efficiency of trees (Hietz et al. 2005; Nock et al. 2011). The extent of this CO_2-fertilization effect on tropical tree growth is the subject of ongoing scientific debate (rner 2003; Clark 2004; Lloyd and Farquhar 2008; Körner 2009) and requires further in-depth investigation (Zuidema et al. 2013). Analyses of tree rings, climate-growth relations and isotope analyses of tree species from tropical lowland forests can assist in predicting tropical forest dynamics under global change.

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Tables

Table 1 Study species characteristics (Nguyen et al. 1996; Nghia 1998; Kalinganire and Pinyopusarek 2000; Williams et al. 2008; LaFrankie 2010).

Species	**Family**	**Light**	**Leaf habit (months leafless)**	**Ring structure (ID quality)**	**Natural distribution range**
Afzelia xylocarpa	Fabaceae	Shade intolerant	Deciduous (1.5)	Marginal parenchyma (+)	Mainland Southeast Asia
Chukrasia tabularis	Meliaceae	Shade intolerant; moderately shade tolerant	Evergreen/ brevi-deciduous	Marginal parenchyma (+/-)	South Asia, Southeast Asia
Melia azedarach	Meliaceae	Shade intolerant	Deciduous (2)	Ring porous (++)	South Asia, Southeast Asia, Australia
Neolitsea obtusifolia	Lauraceae	Shade tolerant	Evergreen	Density gradient (-)	Mainland Southeast Asia
Toona ciliata	Meliaceae	Shade intolerant: moderately shade tolerant	Deciduous (0.5)	Ring porous (++)	South Asia, Southeast Asia, Australia

Table 2 Descriptive statistics of the ring-width series. All the statistics displayed concern only those series that were used for the chronology production.

Species	*n* sampled (trees/radii)	*n* chronology (trees/radii)	Time span	*n* years	*r*[a]	*ms*[b]	Rbar.wt[c]	Rbar.bt[d]	EPS[e]
Afzelia	100/341	38/133	1976-2011	36	0.38	0.42	0.45	0.13	0.90
Chukrasia	104/330	28/70	1982-2010	29	0.46	0.57	0.46	0.18	0.88
Melia	90/330	71/252	1970-2011	42	0.48	0.42	0.51	0.20	0.96
Toona	61/220	46/168	1950-2011	62	0.50	0.65	0.64	0.26	0.95

[a] *r* is the mean series intercorrelation of every series with the master chronology as produced by the program COFECHA (Holmes 1983).

[b] *ms* is the mean sensitivity, which is a measurement of the year-to-year variability in tree-ring width as produced by the program COFECHA (Holmes 1983).

[c] Rbar.wt is the mean of the correlations between series from the same tree.

[d] Rbar.bt is the mean interseries correlation between all series from different trees.

[e] EPS is the expressed population signal.

Figure legends

Fig. 1 (a) Climate diagram for the Nakhon Sawan meteorological station, ~100 km east of the study site. (b) Annual precipitation and temperature observations from the Nakhon Sawan meteorological station. Upper line (Tmax, filled circles) represents the mean daily maximum temperature, middle line rainfall (triangles) and lower line (Tmin, open circles) is the mean daily minimum temperature. Linear regression models were fit to the temperature data and decadal regression coefficients are indicated in the figure (*,**,*** for $P < 0.05$,0.01 and 0.001 respectively).

Fig. 2 (a-d) Raw ring widths of all individual *Afzelia*, *Chukrasia*, *Melia* and *Toona* trees that were included in the chronology. (e-h) Chronologies of the study species. Black line represents the mean standardized ring-width index (chronology). Grey area indicates the 95% confidence envelop of the chronology based on 1000 time bootstrap analysis with replacement of individual series. Marker years (1972, 1990 and 1997) were indicated by the vertical dotted lines.

Fig. 3 Bootstrapped correlation between ring width index and detrended monthly precipitation data from prior January to current December. Solid black bars represent significant correlations at the $P > 0.05$ confidence level.

Fig. 4 Bootstrapped correlation between ring width index and detrended mean monthly minimum temperature data from prior January to current December. Solid black bars represent significant correlations at the $P > 0.05$ confidence level.

Fig. 5 Bootstrapped correlation between ring width index and detrended mean monthly maximum temperature data from prior January to current December. Solid black bars represent significant correlations at the $P > 0.05$ confidence level.

Fig. 6 An example of the strong synchrony between growth and temperature. Shown are mean annual raw diameter growth anomalies of *Melia* (*n* = 71) and current-year wet season maximum temperature anomalies for the period 1970-2011. Note that the temperature-axis is inverted.

Fig. 7 Linear mixed-effects model results of the best model explaining mean standardized diameter growth as a function of standardized seasonal climate indices for the current and prior year. “Prior dry” and “prior wet” refer to the six month dry and wet season of the prior year, “current wet” and “current dry” refer to the six month dry and wet season of the current year. Only parameters of the selected model with the lowest AIC value are shown.

Supporting information legend

Fig. S1 Ring structure of the five study species, direction of growth is from right to left. White arrows indicate ring boundaries.

Fig. S2 Boxplots showing the dbh distribution of all sampled trees and those trees included in the chronology.

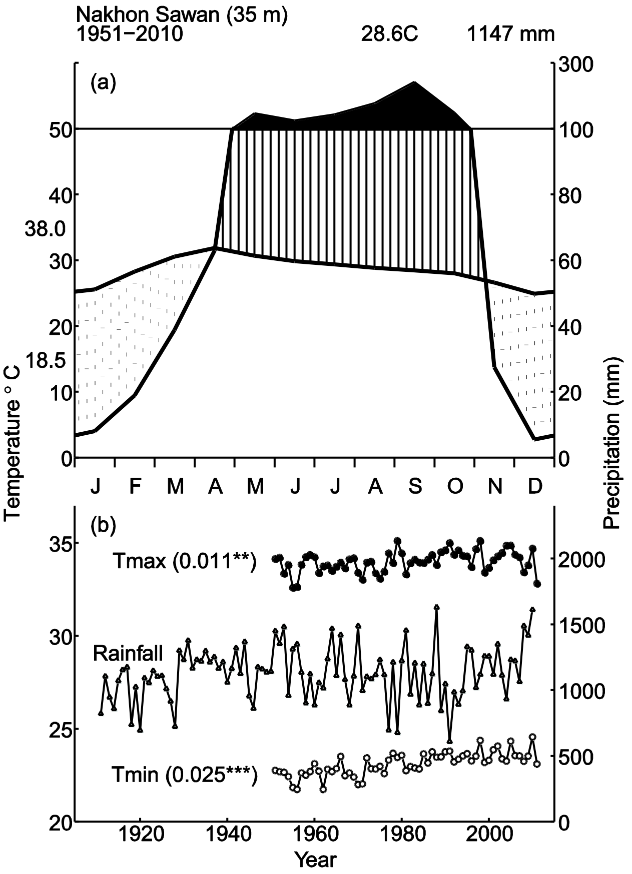
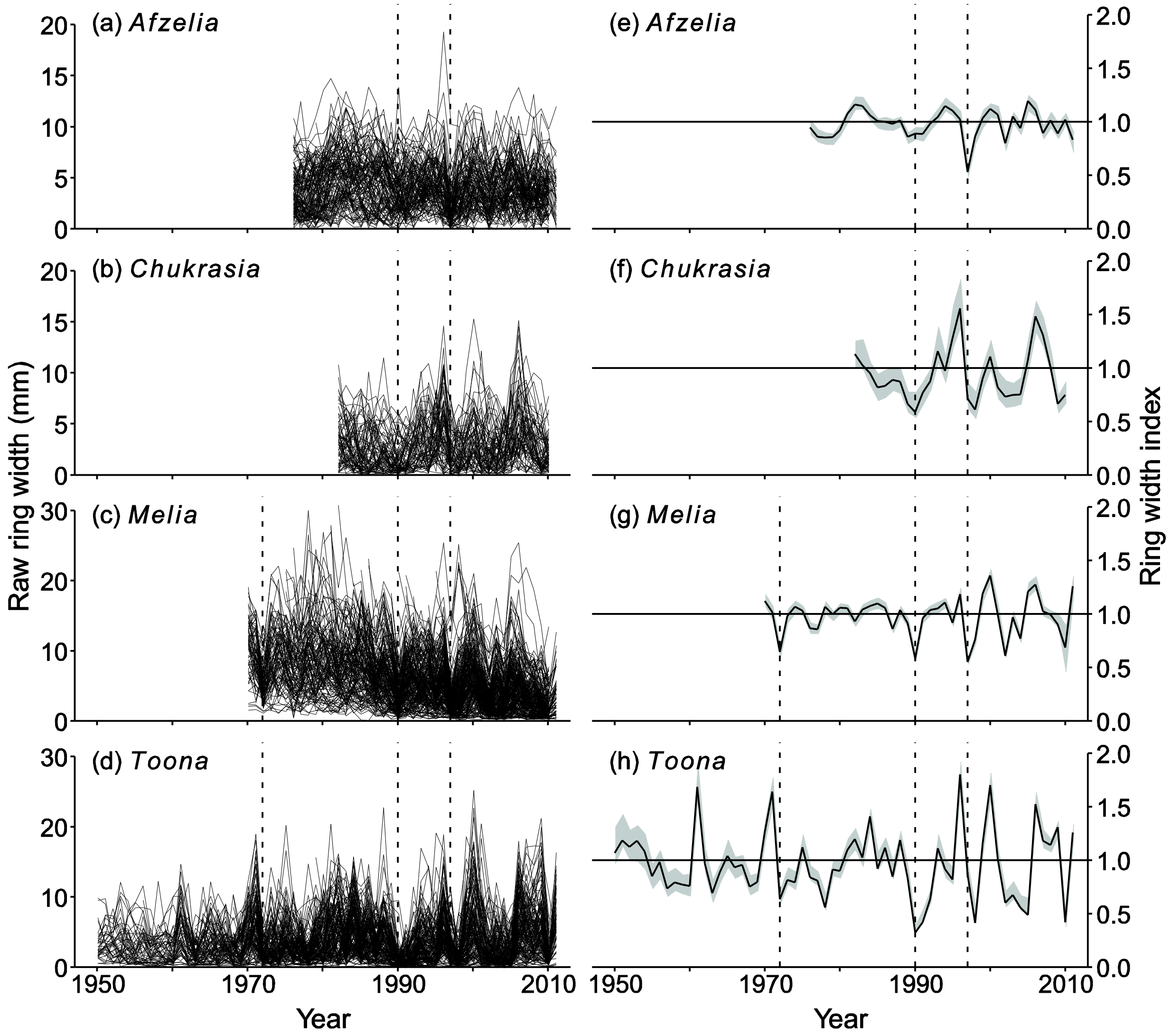


Fig. 1



(a) *Afzelia*
(b) *Chukrasia*
(c) *Melia*
(d) *Toona*
(e) *Afzelia*
(f) *Chukrasia*
(g) *Melia*
(h) *Toona*
Raw ring width (mm)
Ring width index
Year
Year
0
5
10
15
20
30
0.0
0.5
1.0
1.5
2.0
1950
1970
1990
2010

630

Fig. 2

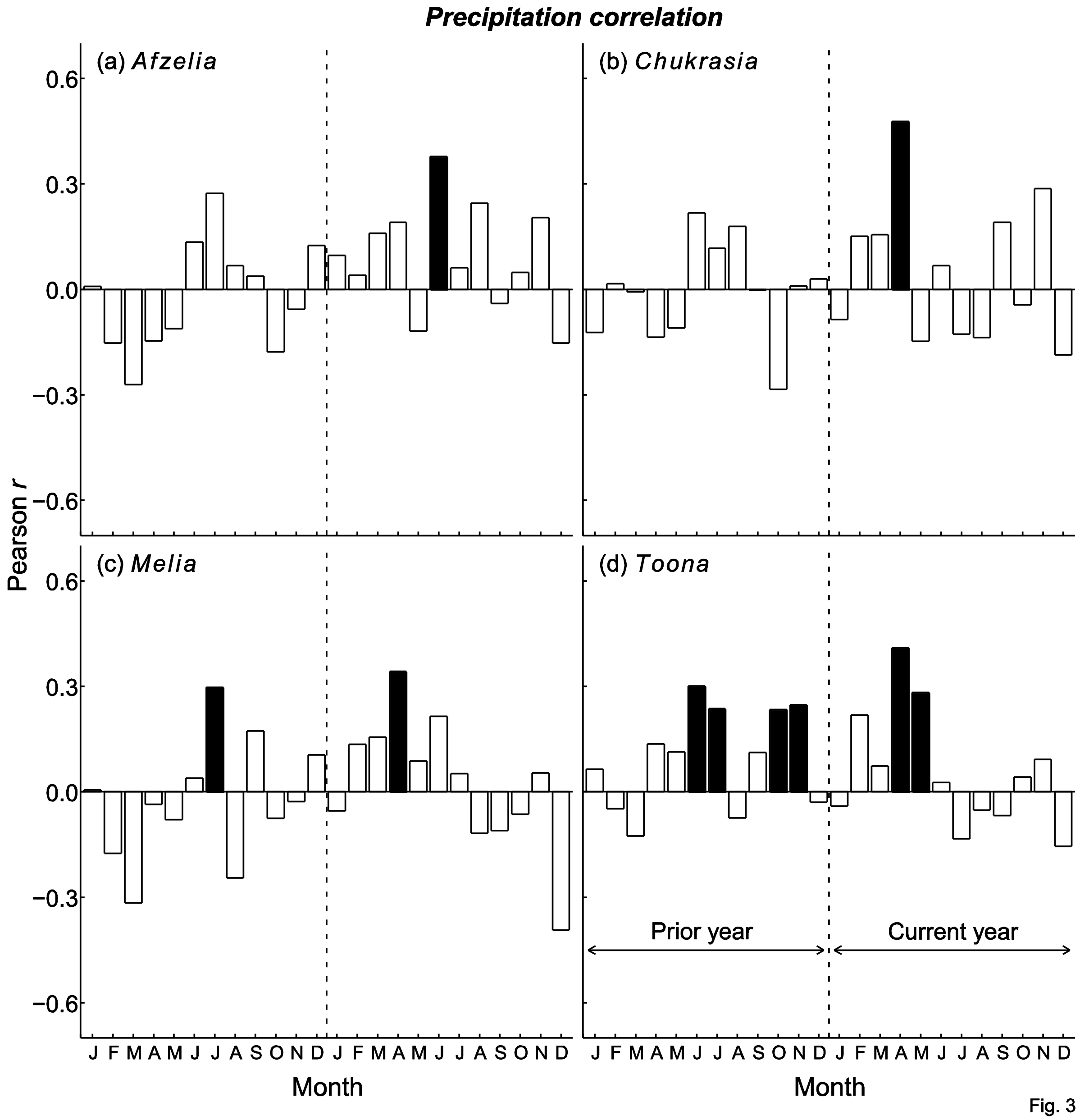
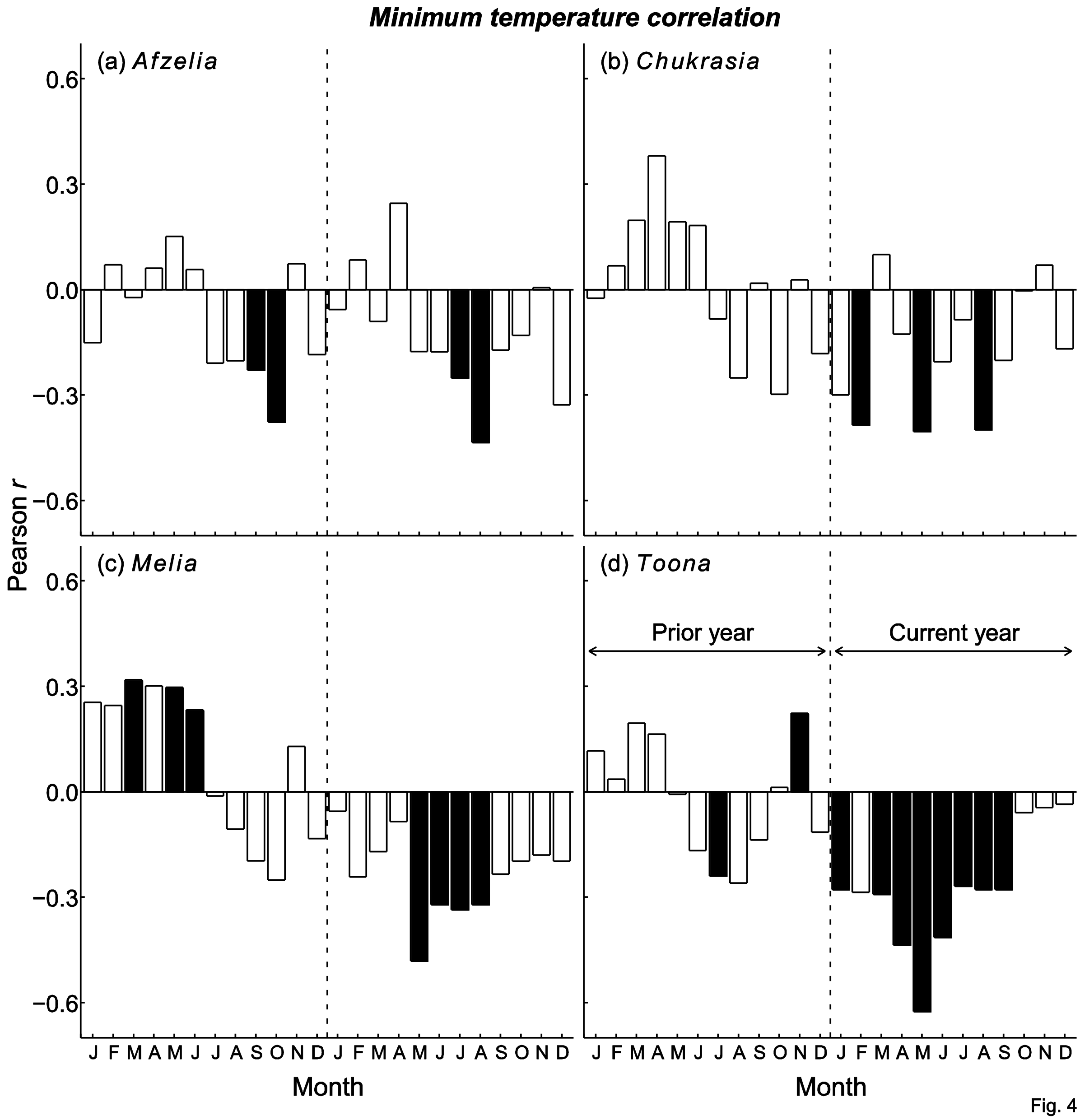
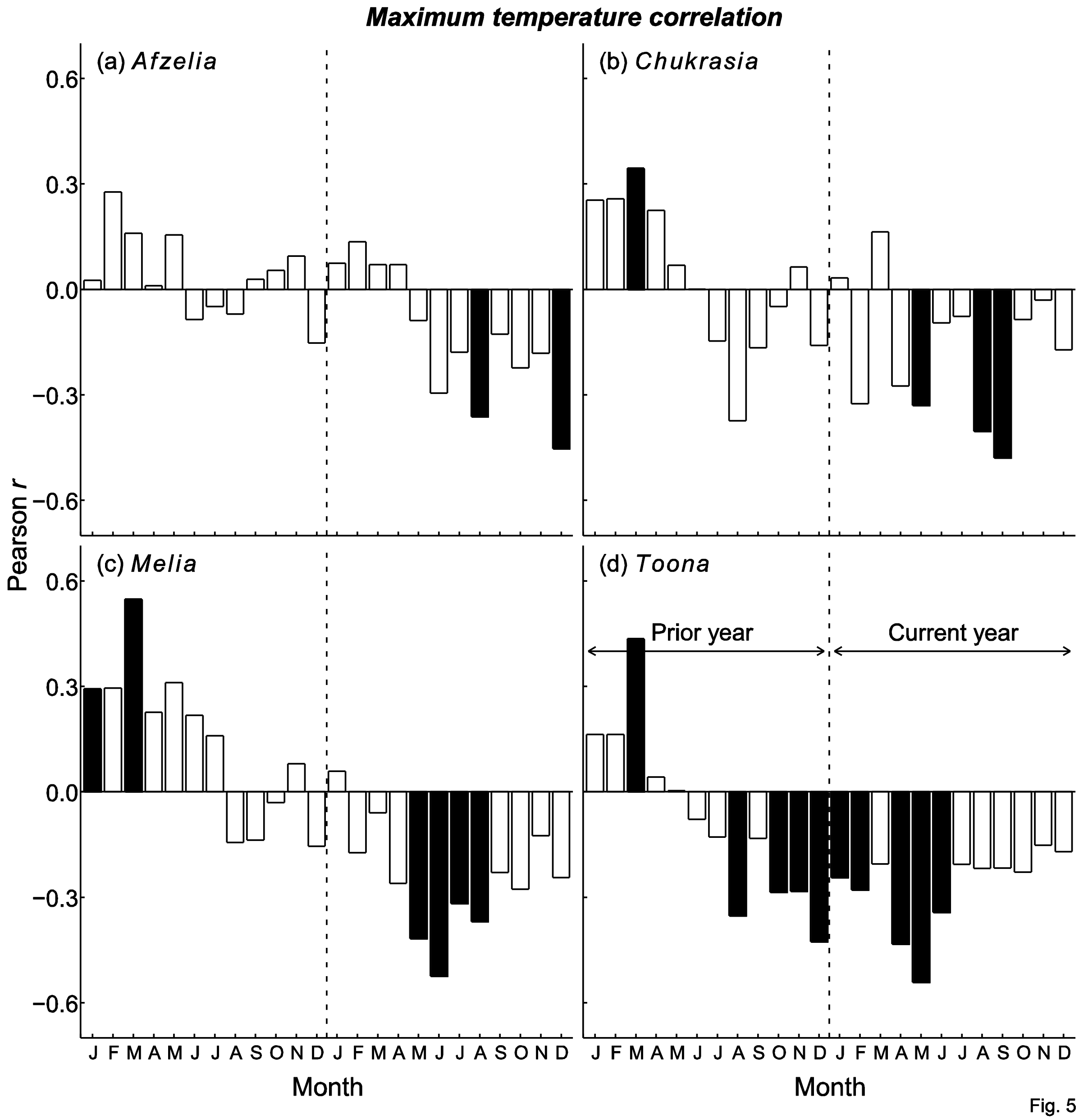

Precipitation correlation
(a) *Afzelia*
(b) *Chukrasia*
(c) *Melia*
(d) *Toona*
Pearson *r*
0.6
0.3
0.0
−0.3
−0.6
Prior year
Current year
J F M A M J J A S O N D J F M A M J J A S O N D
Month

Fig. 3


Minimum temperature correlation
(a) Afzelia
(b) Chukrasia
(c) Melia
(d) Toona
Pearson r
0.6
0.3
0.0
−0.3
−0.6
Prior year
Current year
J F M A M J J A S O N D J F M A M J J A S O N D
Month

632

Fig. 4


Maximum temperature correlation
(a) *Afzelia*
(b) *Chukrasia*
(c) *Melia*
(d) *Toona*
Pearson *r*
0.6
0.3
0.0
−0.3
−0.6
Prior year
Current year
J F M A M J J A S O N D J F M A M J J A S O N D
Month

633

Fig. 5

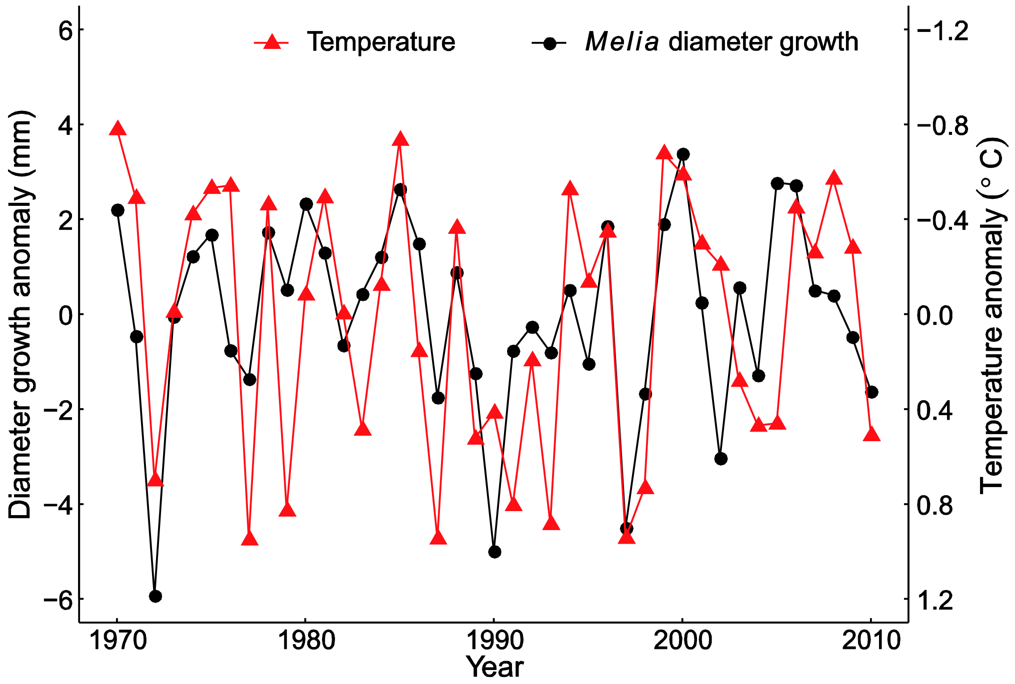
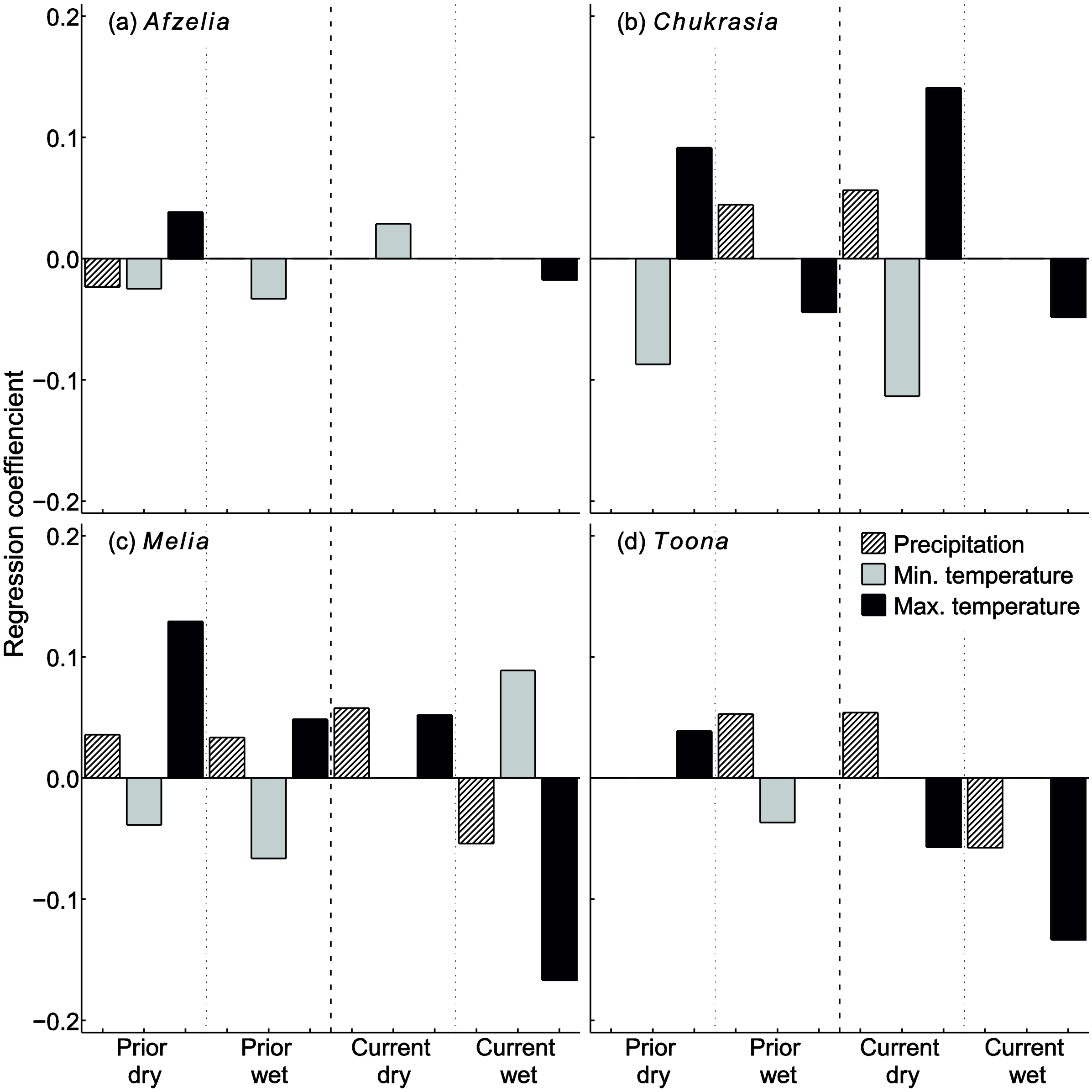

Temperature
Melia diameter growth
Diameter growth anomaly (mm)
6
4
2
0
−2
−4
−6
Temperature anomaly (° C)
−1.2
−0.8
−0.4
0.0
0.4
0.8
1.2
1970
1980
1990
2000
2010
Year

Fig. 6

635



(a) Afzelia
(b) Chukrasia
(c) Melia
(d) Toona
Regression coeffiencient
0.2
0.1
0.0
−0.1
−0.2
Precipitation
Min. temperature
Max. temperature
Prior dry
Prior wet
Current dry
Current wet

Fig. 7

Author/s:
Vlam, M;Baker, PJ;Bunyavejchewin, S;Zuidema, PA

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