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

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2 trees

3

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16

17 **Key words:** climate-growth relation; global change; Thailand; tree rings; tropical tree

Author contributions: MV, PAZ, PJB, SB conceived and designed the study. MV performed the collection of samples and ring-width measurements. MV analyzed the data. MV, PAZ, PJB wrote the manuscript.

18 **Abstract**

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

## 39 **Introduction**

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

49 In the absence of *in situ* tree-level warming experiments in the tropics, analysis of  
50 temporal tree growth variability in relation to annual climatic variation can be the next best  
51 source of information on global warming effects on tropical trees (Brienen et al. 2010; Clark et  
52 al. 2010; Pumijumnong 2012). Repeated diameter measurements of tropical trees has shown that  
53 temporal variation in diameter growth was negatively correlated with temperature (Clark et al.  
54 2003; Dong et al. 2012; Clark et al. 2013). However, due to the multi-year census interval of  
55 most permanent plot studies (e.g., Dong et al. 2012), the power of correlation analyses is  
56 generally low and the multi-year census interval requires an integration of yearly climate  
57 parameters over the census interval.

58 Tropical dendrochronology (tree-ring analysis) can provide long-term, high-resolution  
59 tropical tree growth data to complement plot-based repeated diameter measurements (Worbes  
60 1995; Zuidema et al. 2013). Tropical tree species that form reliable annual growth rings provide

61 annual-resolution growth data at multi-decadal to centennial scales, which enhance the  
62 detectability of climatic influences on growth variation in tropical trees (Zuidema et al. 2012).  
63 Multi-species tree-ring studies on climate-growth relations of broad-leaved trees from moist  
64 lowland tropical forests are rare, but studies in the Amazon (Dünisch et al. 2003; Brien and  
65 Zuidema 2005) and West Africa (Schöngart et al. 2006) have shown that temporal variation in  
66 growth was positively correlated with total annual precipitation. In lowland tropical forests in  
67 Southeast Asia, analysis of the relation between climate and ring width has mainly focussed on  
68 teak (*Tectona grandis*) (Pumijumnong et al. 1995; Buckley et al. 2007) and only a few examples  
69 of other species exist (e.g., Zuidema et al. 2011). Besides the generally low representation of  
70 lowland moist tropical forest trees species in climate-growth studies, the focus has traditionally  
71 been on precipitation correlations (Jacoby 1989; Rozendaal and Zuidema 2011; Pumijumnong  
72 2012) and effects of temperature anomalies on annual growth variability were often not  
73 evaluated (Dünisch et al. 2003; Brien and Zuidema 2005; Schöngart et al. 2006) or determined  
74 non-significant (Couralet et al. 2010). However, whereas there is large uncertainty regarding  
75 predicted rainfall changes for the tropics, a clear warming trend across most of the tropics is  
76 undisputed (IPCC 2007; Wright et al. 2009).

77         Here we use tree-ring analyses to evaluate tree growth sensitivity to climatic variation in  
78 Southeast Asia. We took tree ring samples from over 450 individuals belonging to five species  
79 known to form annual rings (Baker and Bunyavejchewin 2006). These species represent three  
80 different families, vary in leaf phenology and represent several ecological guilds. The availability  
81 of >60 years of high quality climate data from a nearby meteorological station allowed us to  
82 address questions and hypotheses on the relationship between climate variability and tree  
83 growth. Specifically we addressed the following questions: (1) Is tree growth correlated with

84 minimum and maximum temperature? (2) Is tree growth correlated with precipitation?  
85 Furthermore we used linear mixed-effects models to assess the relative importance of various  
86 seasonal climate indices on standardized diameter growth rates.

## 87 **Materials and methods**

### 88 **Study area and species**

89 The study area was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai  
90 Thani province, western Thailand (15.60 N 99.20 E), approximately 550 m above sea-level.  
91 Climate in Huai Kha Khaeng is strictly seasonal with a marked dry season from November to  
92 April (Fig. 1a). Mean annual rainfall in HKK is 1473 mm and mean annual temperature is 23.5  
93 °C (Bunyavejchewin et al. 2009). Soils are highly weathered, slightly acidic ultisols and soil  
94 textures are sandy loam at the surface and sandy clay-loam in the subsurface horizons  
95 (Bunyavejchewin et al. 2009). The vegetation in the area is classified as seasonal dry evergreen  
96 and mixed deciduous forest (Bunyavejchewin et al. 2009). Canopy height in the forest is around  
97 30 m, with occasional emergent trees reaching over 50 m tall. Members of the family  
98 Dipterocarpaceae dominate the area in total basal area; other well-represented families include  
99 Annonaceae, Euphorbiaceae and Meliaceae (Bunyavejchewin et al. 2001).

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

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

## 108 **Sampling and measurements**

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

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

### 139 **Chronology development**

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

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

158         Crossdating of annual growth rings was successful for four out of five species (Fig. 2a-d).  
159 However, for the non-ring-porous species (*Afzelia*, *Chukrasia*), this lead to the exclusion of a  
160 large fraction of trees (>60%) from their respective species-specific chronologies (Table 2).  
161 Because of high dating uncertainty remaining after attempting to crossdate *Neolitsea* ring-width  
162 series, we excluded this species from all further analyses. For the other four species a species-  
163 specific chronology was produced (Fig. 2e-h). Out of the total sample size the proportion of trees  
164 included in the chronology was 38% for *Afzelia*, 27% for *Chukrasia*, 89% for *Melia* and 79% for  
165 *Toona* (see Fig. S2 for diameter distributions of trees included in the chronologies). In *Afzelia*  
166 and *Chukrasia*, false, wedging and generally indistinct rings were frequently observed, especially  
167 in periods when growth was suppressed, resulting in higher rejection rates. The resulting  
168 chronologies were cut off when the running expressed population signal (EPS) was <0.85  
169 (Wigley et al. 1984; Speer 2010). The EPS is used to assess how well a chronology of a finite  
170 number of trees estimates the hypothetical (noise-free) population chronology (Wigley et al.  
171 1984). When the EPS value is <0.85 the chronology starts to be dominated by the individual  
172 tree-level signal, rather than the stand level signal and is therefore less useful for climate-growth  
173 analysis (Speer 2010).

## 174 **Climate data**

175           We used monthly climate data from the Nakhon Sawan meteorological station (15.80N,  
176 100.20E) for the climate-growth analysis. All climate data were obtained from the KNMI  
177 Climate Explorer website (Trouet and Van Oldenborgh 2013). The Nakhon Sawan  
178 meteorological station is situated ~100 km east of the sampling area. Because the climate station  
179 is situated at a lower elevation, mean yearly temperatures are on average 5 °C higher in Nakhon  
180 Sawan and mean annual precipitation 350 mm lower compared to the study site. The temperature  
181 dataset from the Nakhon Sawan station was nearly complete for the period 1951-2010 (<0.5% of  
182 the data points were missing), monthly precipitation data were missing for <4% of the months  
183 (1951-2010). Any missing values were replaced by gridded climate data for the location of the  
184 climate station (Trouet and Van Oldenborgh 2013). Significant positive trends in the annual  
185 maximum temperature data (0.011 °C,  $P < 0.01$ ) and annual minimum temperatures (0.025 °C,  $P$   
186  $< 0.001$ ) were found (Fig.1b). Because this study did not aim to analyze growth response to long-  
187 term climate change, but instead focusses on drivers of annual variability in growth, all climate  
188 data was linearly detrended prior to analysis (Fig. 1b). Therefore all climate parameters were  
189 expressed as deviations from the long-term trend. After detrending we found no evidence for  
190 temporal autocorrelation in the climate data.

## 191 **Climate-growth analysis**

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

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

203 To compare the relative contribution of temperature and rainfall on diameter growth, we  
204 used mixed-effects models, with a second order autocorrelation structure and individual trees as  
205 a random factor (nlme package in R; Pinheiro et al. 2011). The second order autocorrelation  
206 structure was added to the model to account for the effect of growth in year  $t_2$  and year  $t_1$  on  
207 growth in year  $t_0$ . A total of four different models was used, because each species was included  
208 in a separate model. First, we reduced the number of initial fixed factors to be included in the  
209 model by calculating mean 6-month seasonal indices from the monthly precipitation data,  
210 minimum- and maximum temperature data. We defined the dry season as November $_{t-1}$  to April $_{t0}$   
211 and the wet season as May $_{t0}$  to October $_{t0}$ . In the analysis both the current dry and wet season  
212 indices were included as well as prior year dry and wet season indices. This resulted in a total of  
213 12 initial variables to be included as fixed factors in the full model. All seasonal climate  
214 variables were linearly detrended prior to analysis and the variance was stabilized. Only  
215 standardized diameter growth rates for those trees that were also included in the chronology were  
216 used as dependent variables. In this way only those trees that had a strong common signal in  
217 growth were used. The full model was subsequently simplified by step-wise removal of the least

218 significant variables and the model with the lowest Akaike's Information Criterion (AIC) value  
219 was selected (Zuur et al. 2009).

220

## 221 **Results**

### 222 **Tree-ring chronologies**

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

### 237 **Correlation between ring width and climate**

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

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

251 When correlating monthly maximum temperatures and growth similar patterns arise as  
252 those for monthly minimum temperatures. All four species showed significant negative  
253 correlations with current year wet season maximum temperatures (Fig. 5). To illustrate the strong  
254 synchrony between temperature and growth, we plotted anomalies in current-year wet-season  
255 maximum temperature and growth of *Melia* (Fig. 6), the species with the strongest temperature-  
256 growth correlation (Fig 5c). *Toona* also showed significant negative correlations between growth  
257 and current-year dry season maximum temperatures (Fig. 5d). In addition, both *Chukrasia*,  
258 *Melia* and *Toona* also showed significant positive correlations between growth and prior dry  
259 season monthly maximum temperatures (Fig. 5b-d). It is highly unlikely that the significantly  
260 negative correlation between mean current year December maximum temperatures and *Afzelia*

261 growth (Fig. 5a) has a direct causal relation, because by December the ring has already been  
262 completely formed. The significant correlation most likely resulted from temporal  
263 autocorrelation in mean monthly maximum temperatures, as it can be seen that the preceding  
264 months also show a trend towards negative correlations.

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

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

283 was associated with a reduction in mean diameter growth of 0.3 mm for *Afzelia*, 0.9 mm for  
284 *Chukrasia*, 2.3 mm for *Toona* and 3.0 mm for *Melia* (see also Fig. 6).

## 285 **Discussion**

### 286 **Species suitability for climate-growth analyses**

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

302 We are aware that our study species are a non-random selection and small subset of the  
303 most abundant species at our study site. They represent just two families and do not include the  
304 most dominant family (Dipterocarpaceae), but they do differ in for example ecological guild and

305 the degree of deciduousness. The number of species for which tree-ring analyses can be done at  
306 a given site will likely increase when recently tested techniques to reconstruct annual growth  
307 patterns of (apparently) ring-less species become more accessible (Poussart et al. 2004; Loader et  
308 al. 2011).

### 309 **Climate correlations**

310 Both the correlation analyses and linear mixed-effects models showed that tree growth  
311 was strongly driven by climate variability and growth responses were often similar among  
312 species. The correlation analysis showed that growth variability in all four species was strongly  
313 negatively correlated with current year minimum and maximum temperatures. This finding is  
314 similar to that of Clark et al. (2003), who showed that growth rates of trees in an old-growth  
315 tropical rain forest in Costa Rica were negatively correlated with current year daily minimum  
316 temperatures. Furthermore, Dong et al. (2012) showed that growth anomalies of whole tropical  
317 forest stands in Malaysia, Panama and Thailand were negatively correlated with five-year-  
318 averaged temperature anomalies. In addition, similar negative effects of temperature on tree  
319 growth were found in tropical sites with higher latitude and elevation (e.g., Buckley et al. 2007).  
320 The mechanism for a negative relation between temperature and tree growth in the tropics may  
321 be through higher temperatures leading to reduced carbon assimilation rates, by having both a  
322 direct negative impact on photosynthesis rates (Galbraith et al. 2010) and increasing autotrophic  
323 respiration rates (Clark 2007; Feeley et al. 2007). Maintenance costs of plant tissue increase with  
324 higher ambient temperatures (Lloyd and Farquhar 1996). For tropical forests it has been shown  
325 that an air temperature increase of 10 °C leads to roughly a doubling of respiration rates (Meir et  
326 al. 2008). However, this was contrasted by Doughty (2011) finding little evidence of enhanced  
327 respiration rates in an *in situ* warming experiment with tropical trees. It has also been shown for

328 deciduous temperate trees that leaf respiration rates show rapid acclimation to increased air  
329 temperature (Lee et al. 2005). Temperature also influences leaf-to-air vapour pressure deficit and  
330 tree evapotranspiration rates (Galbraith et al. 2010; Choat et al. 2012). When evaporative  
331 demand increases due to higher temperatures, the leaf stomata tend to close to reduce water loss,  
332 resulting in lower CO<sub>2</sub>-uptake and decreased carbon assimilation rates (Lloyd and Farquhar  
333 2008). Because the majority of annual net primary production of trees in a seasonal forest is  
334 concentrated in the months with high rainfall (April-October in HKK), it is likely that growth is  
335 most sensitive to temperature variability during this time of the year. And thirdly, temperature is  
336 negatively correlated with rainfall (Devall et al. 1995). Thus, both increased evaporative demand  
337 leading to lower carbon assimilation rates, increased respiration costs and reduced precipitation  
338 rates during warm years could potentially be driving negative correlations between tree growth  
339 and current wet season temperature.

340           Unlike previously described climate-growth relations for seasonal tropical forests  
341 (Dünisch et al. 2003; Brienen and Zuidema 2005; Schöngart et al. 2006; Couralet et al. 2010),  
342 the mixed model analysis showed that the relation between growth and temperature were  
343 generally stronger than those between growth and precipitation. Weak correlations between  
344 single-year drought and tree growth were also found in two large-scale drought experiments in  
345 the Amazon (Brando et al. 2008; Metcalfe et al. 2010). Both studies provided evidence that net  
346 primary productivity of trees declined during the simulated drought, but this reduction was  
347 relatively modest in the first year. But as expected a period of consecutive years with low  
348 rainfall, such as the period 1989-1993 in western Thailand, did result in one of the clearest  
349 reductions in growth rates among the four species. The positive relation between growth and  
350 early growing season precipitation levels has been commonly found in tropical

351 dendrochronological studies (Pumijumnong et al. 1995; Buckley et al. 2007; Rozendaal and  
352 Zuidema 2011; Soliz-Gamboa et al. 2011). This strong relation likely reflects the importance of  
353 adequate water amounts for the flushing of new leaves (Brando et al. 2008), which occurs around  
354 the spring equinox for most species in HKK (Williams et al. 2008). The absence of long-term  
355 climate data from the HKK study site forced us to use of data recorded at the Nakhon Sawan  
356 meteorological station (~100 km east of HKK) for all climate-growth analyses. Although most of  
357 the rainfall during the wet season in HKK originates from the Asian summer monsoon system  
358 (Wang and Ho 2002), regional variability in rainfall is comparatively higher than regional  
359 variability in temperature. The high local variability in rainfall amounts, combined with a ~100  
360 km distance between to the meteorological station, may have led to an underestimation of the  
361 positive growth-precipitation correlations.

362 Evidence for a lagged climate-growth response is commonly found in  
363 dendrochronological investigations across the tropics (e.g., Dünisch et al. 2003; Brienen and  
364 Zuidema 2005). Both misdating of the rings and temporal autocorrelation in the growth data  
365 have been suggested as methodological causes for observed lagged responses (Soliz-Gamboa et  
366 al. 2011). However, temporal autocorrelation in the tree-ring and climate data was low and  
367 dating certainty, especially of *Melia* and *Toona*, was high, both were therefore unlikely to have  
368 caused the observed lagged responses. Alternatively, physiological pathways leading to lagged  
369 climate-growth responses in tropical trees have been suggested but remain poorly investigated so  
370 far. In temperate trees the presence of preformed shoots in trees with strong seasonality in leaf  
371 formation has been suggested to lead to lagged growth responses because growth for the first  
372 flush is set during bud formation in the prior year (Oliver and Larson 1996; Pederson et al.  
373 2004). Also favorable conditions in the current year may promote the formation of reserves,

374 rather than growth in the current year and these reserves can then be used in the beginning of the  
375 next growing season (Dünisch et al. 2003; Pederson et al. 2004). For instance, the three  
376 deciduous species in our study (*Azalia*, *Melia* and *Toona*) completely rely on reserve materials  
377 for the flushing of new leaves and possibly also for the initial stages of xylem formation (Ohashi  
378 et al. 2009). We do not understand how prior-year temperatures may have a positive effect on  
379 growth in our study species.

### 380 **Tropical tree growth and climate change**

381         Daily maximum temperatures in western Thailand have been steadily rising over recent  
382 decades (Trouet and Van Oldenborgh 2013) . The combination of rising temperature and a strong  
383 negative relation between diameter growth and current growing season maximum temperatures  
384 in all four study species, may indicate that tree growth rates will likely decrease over time. These  
385 reduced diameter growth rates may result in a reduced carbon sequestration capacity of the forest  
386 as a whole (Brienen et al. 2010). However, historical growth responses to annual climate  
387 variability, e.g. linking past negative growth anomalies with relatively warm years, should not be  
388 translated into oversimplified projections of long term growth responses to long term changes in  
389 climate (Zuidema et al. 2013). Trees may for example respond to a structural increase in  
390 temperatures and drought through physiological acclimation of both photosynthesis and  
391 respiration (Galbraith et al. 2010), potentially reducing the long term effect of increased  
392 temperature on growth. The negative effect of rising temperatures may also be compensated by a  
393 CO<sub>2</sub>-fertilization effect (Baker et al. 2004; Lloyd and Farquhar 2008) through a strong increased  
394 water-use-efficiency of trees (Hietz et al. 2005; Nock et al. 2011). The extent of this CO<sub>2</sub>-  
395 fertilization effect on tropical tree growth is the subject of ongoing scientific debate ( Körner  
396 2003; Clark 2004; Lloyd and Farquhar 2008; Körner 2009) and requires further in-depth

397 investigation (Zuidema et al. 2013). Analyses of tree rings, climate-growth relations and isotope  
398 analyses of tree species from tropical lowland forests can assist in predicting tropical forest  
399 dynamics under global change.

400

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577

578

579 **Tables**

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

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

582

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

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

585

586 <sup>a</sup> *r* is the mean series intercorrelation of every series with the master chronology as produced by  
 587 the program COFECHA (Holmes 1983).

588 <sup>b</sup> *ms* is the mean sensitivity, which is a measurement of the year-to-year variability in tree-ring  
 589 width as produced by the program COFECHA (Holmes 1983).

590 <sup>c</sup> Rbar.wt is the mean of the correlations between series from the same tree.

591 <sup>d</sup> Rbar.bt is the mean interseries correlation between all series from different trees.

592 <sup>e</sup> EPS is the expressed population signal.

593 **Figure legends**

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

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

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

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

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

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

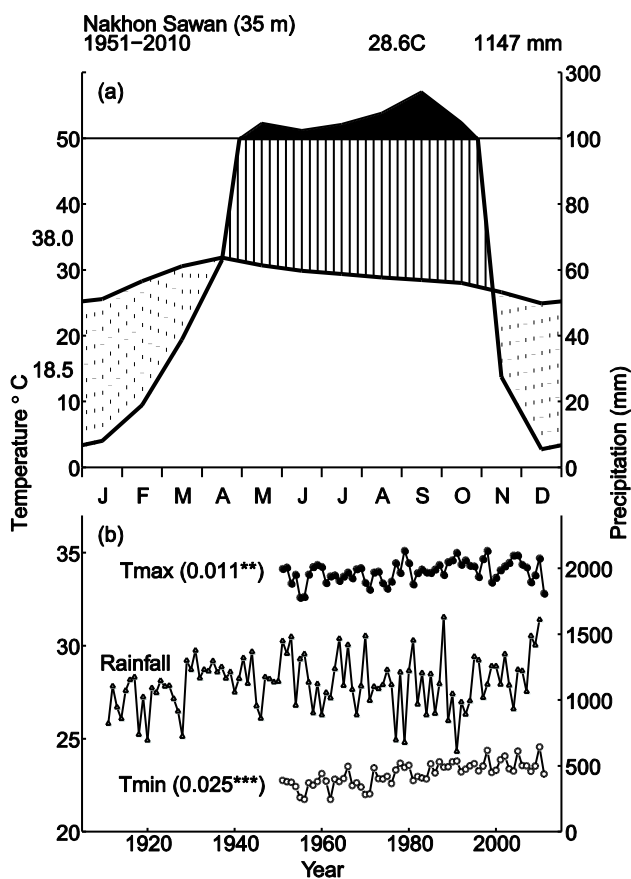
618 **Fig. 7** Linear mixed-effects model results of the best model explaining mean standardized  
619 diameter growth as a function of standardized seasonal climate indices for the current and prior  
620 year. “Prior dry” and “prior wet” refer to the six month dry and wet season of the prior year,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

623

624 **Supporting information legend**

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

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



629

Fig. 1

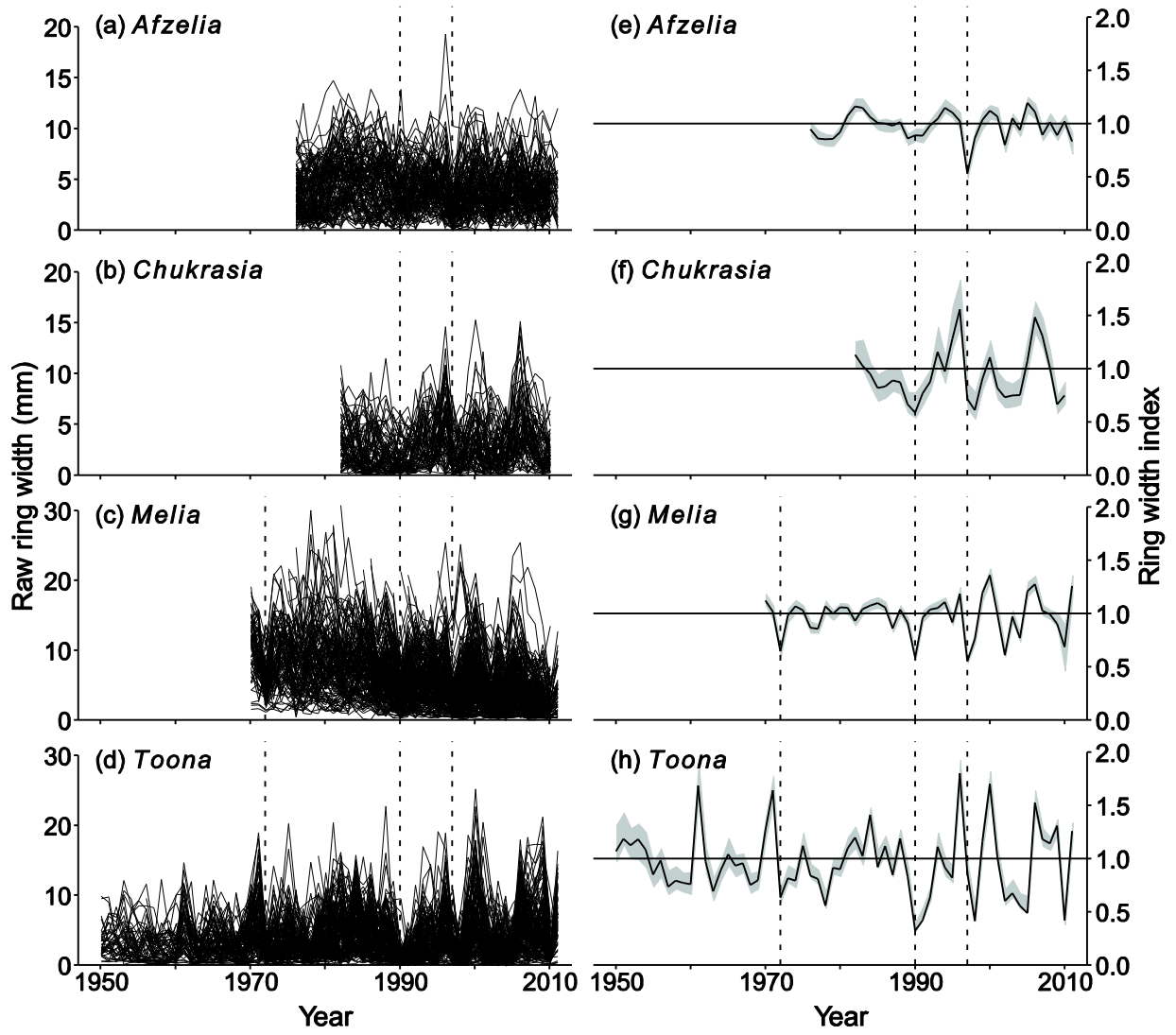
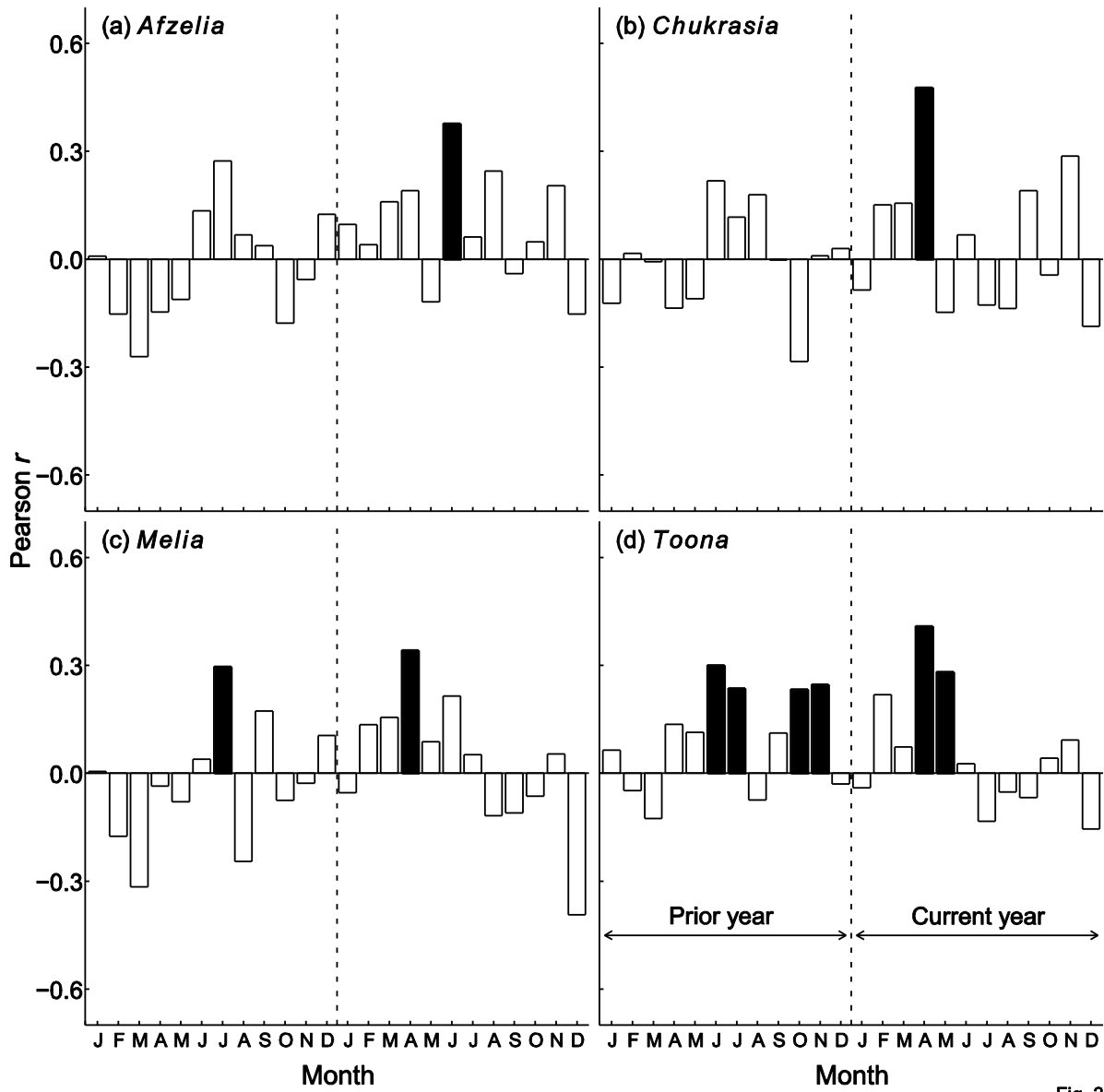
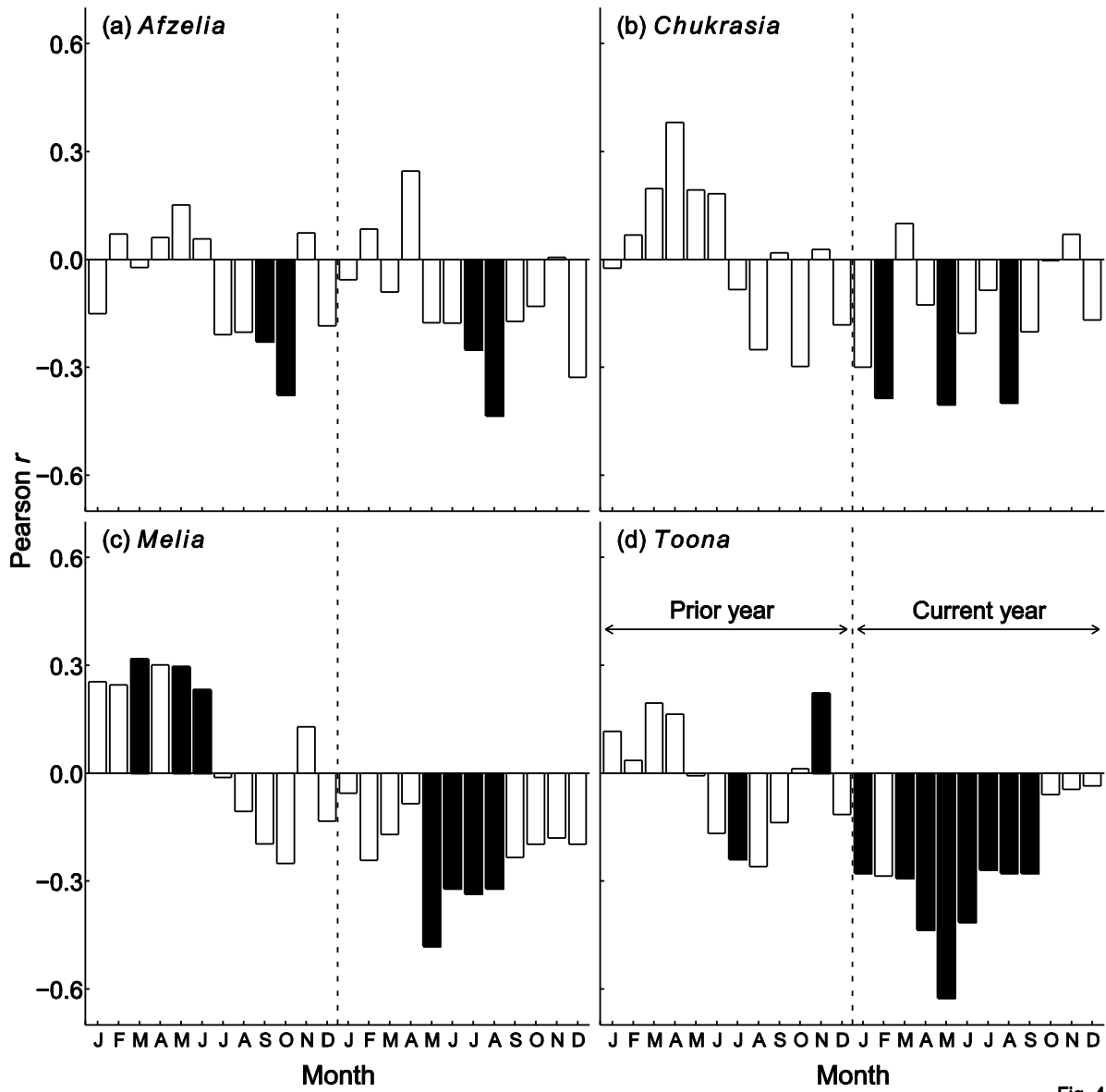


Fig. 2

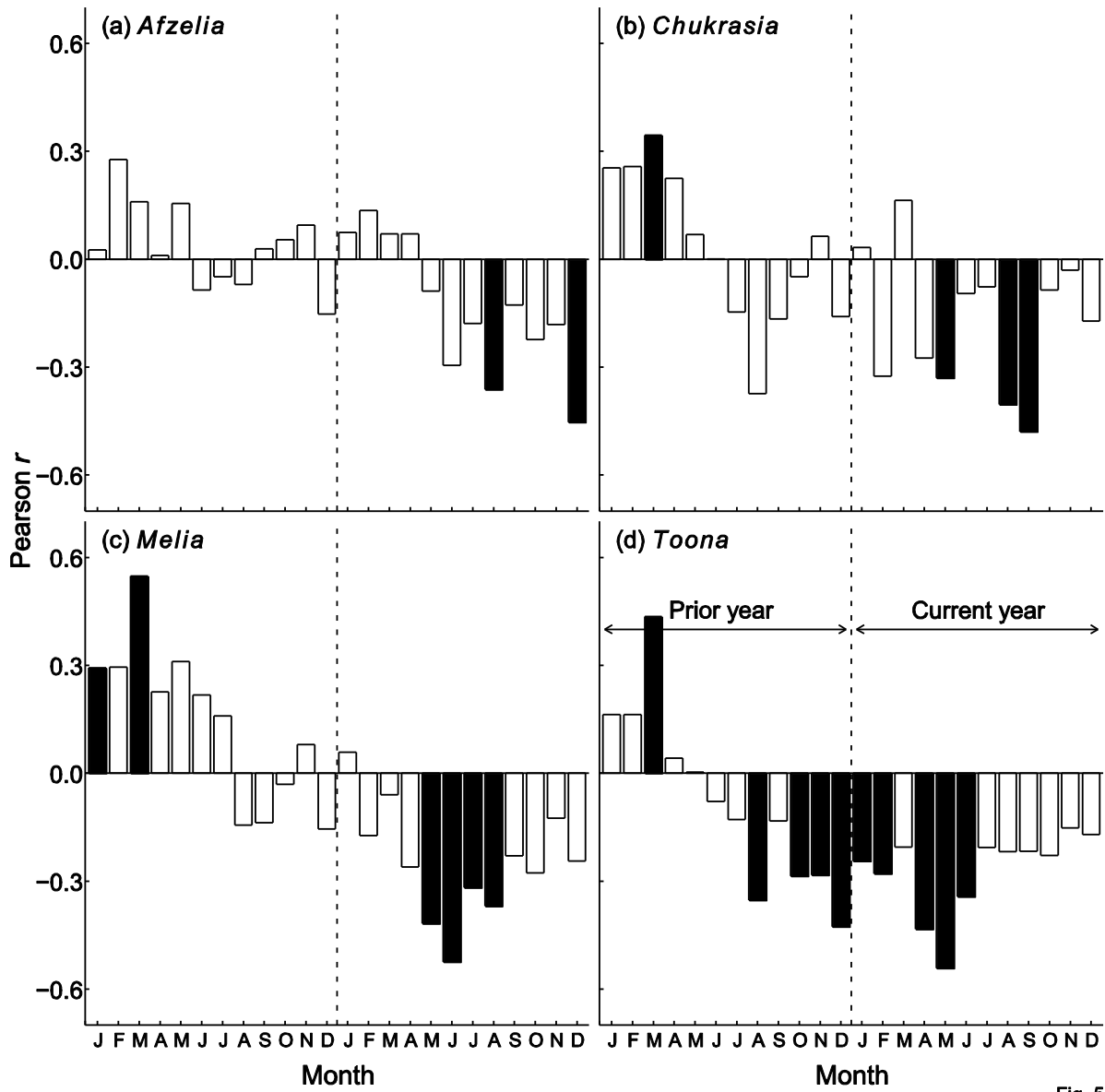
**Precipitation correlation**



**Minimum temperature correlation**



**Maximum temperature correlation**



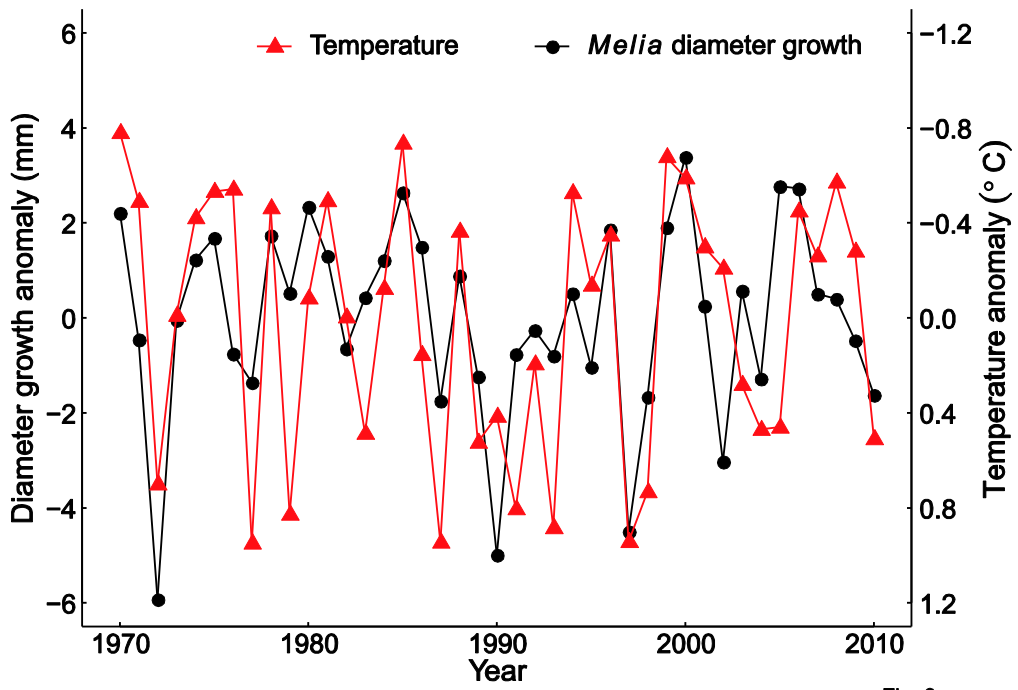


Fig. 6

