

Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines

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Abstract

Tropical forests will experience relatively large changes in temperature and rainfall towards the end of this century. Little is known about how tropical trees will respond to these changes. We used tree rings to establish climate-growth relations of a pioneer tree, *Mimosa acantholoba*, occurring in tropical dry secondary forests in southern Mexico. The role of large-scale climatic drivers in determining interannual growth variation was studied by correlating growth to sea surface temperature anomalies (SSTA) of the Atlantic and Pacific Oceans, including the El Niño-Southern Oscillation (ENSO). Annual growth varied eightfold over 1970–2007, and was correlated with wet season rainfall ($r = 0.75$). Temperature, cloud cover and solar variation did not affect growth, although these climate variables correlated with growth due to their relations with rainfall. Strong positive correlations between growth and SSTA occurred in the North tropical Atlantic during the first half of the year, and in the Pacific during the second half of the year. The Pacific influence corresponded closely to ENSO-like influences with negative effects of high SSTA in the eastern Pacific Niño3.4 region on growth due to decreases in rainfall. During El Niño years growth was reduced by 37%. We estimated how growth would be affected by the predicted trend of decreasing rainfall in Central America towards the end of this century. Using rainfall predictions of two sets of climate models, we estimated that growth at the end of this century will be reduced by 12% under a medium (A1B) and 21% under a high (A2) emission scenario. These results suggest that climate change may have repercussions for the carbon sequestration capacity of tropical dry forests in the region.

Keywords: climate change, climate-growth relations, El Niño, rainfall, tree rings, tropical dry forest

Received 24 April 2009; revised version received 17 July 2009 and accepted 28 July 2009

Introduction

Tropical dry forests are predicted to experience strong changes in climatic conditions in the near future due to global warming: mean temperatures are projected to increase by $\sim 3^\circ\text{C}$ towards the end of this century (Christensen *et al.*, 2007), precipitation patterns will change (Held & Soden, 2006; Neelin *et al.*, 2006), and El Niño events may become more severe and occur at

higher frequency (Timmermann *et al.*, 1999; IPCC, 2007, but see Collins, 2005). Knowledge of the impact of climate change on the dynamics of dry forests has global relevance as these forests cover about 40% of the tropical and subtropical forest area (Murphy & Lugo, 1986), contain large amounts of carbon (Jaramillo *et al.*, 2003; Read & Lawrence, 2003) and provide a wide range of important ecosystem services for society (Wright, 2005).

Trees in tropical dry forests may be particularly sensitive to climatic changes, especially to drying. Tropical dry forests occur at the driest end of where forests can exist, and lower rainfall and/or higher temperatures increase water stress and may slow tree growth

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and raise mortality rates (Condit *et al.*, 2004; Nath *et al.*, 2006). However, inferences on the likely impact of climatic changes for tropical dry forest trees are impossible to make without a thorough understanding of the climate–growth relations of these trees. Few studies have related tree growth in dry tropical forests to climate. These studies revealed reduced tree growth during years with low rainfall (Bullock, 1997; Fichtler *et al.*, 2004; Nath *et al.*, 2006; Schöngart *et al.*, 2006; Gebrekirstos *et al.*, 2008) or temperature-sensitivity of tree growth (Devall *et al.*, 1995; Fichtler *et al.*, 2004; Trouet *et al.*, 2006). Yet, the implications of these findings for responses of tropical dry forest trees to future climatic changes are little studied. Inter-annual variation in local climate in tropical areas is modulated by large-scale climatic forces such as anomalies in sea surface temperature anomalies (SSTA) of the Atlantic and Pacific Ocean (Giannini *et al.*, 2000; Trenberth & Stepaniak, 2001; Taylor *et al.*, 2002). The best-known global climate fluctuation is the El Niño–Southern Oscillation (ENSO). It causes anomalous dry and warm conditions over large parts of the tropics during El Niño events (Allan *et al.*, 1996; Lyon, 2004; Malhi & Wright, 2004). These large-scale climatic phenomena have been shown to affect tree growth over very long distances ('teleconnections', Jacoby & D'Arrigo, 1990; Stahle *et al.*, 1998; Schöngart *et al.*, 2004).

Here we report climate–growth relations of *Mimosa acantholoba* (Willd.) Poir. (Fabaceae), a fast-growing, abundant and widespread tree in secondary dry forests of Mexico and Central America. We used tree ring analysis to reconstruct diameter increment over a 37-year period, and related these growth data to local climate variability and to large-scale climatic drivers. We specifically addressed the following questions (i) To what extent do local climatic variables (e.g. rainfall, temperature, cloud cover, and incoming solar radiation) explain inter-annual variation in growth? (ii) How do large-scale climatic drivers, such as SSTA in the equatorial Pacific (ENSO) and North tropical Atlantic indirectly influence tree growth through their effects on local climate? (iii) What changes in tree growth can be expected under climate change towards the end of the present century? In our analysis, we explicitly include relations between large-scale climatic drivers and local climate variability and unravel the direct and indirect effects of these large-scale climatic forces on tree growth.

Materials and methods

Study area and climate of the region

The study area is located on the Pacific slope of the Isthmus of Tehuantepec, close to the village of Nizanda

in the state of Oaxaca, South Mexico (16°39'N, 95°00'W). The natural vegetation consists of tropical deciduous dry forest (Pérez-García *et al.*, 2001). Mean annual temperature in the study region is 26 °C and total annual rainfall is ~ 930 mm. Rainfall is highly seasonal with a pronounced dry season from November until May (<50 mm month⁻¹), and a wet season from June until October that accounts for 90% of the annual rainfall (Fig. 1).

Historical local climate data were obtained from several sources. Data from the nearest weather station of (Ixtepec, 16°33'N, 95°06'W, 14 km from research site) were used for rainfall (1970–2006) and for cloud cover (1970–2003; CONAGUA, 2003). As the Ixtepec temperature records showed irregularities, we used monthly gridded temperature anomaly data (1970–2007) from GISSTEMP (Hansen *et al.*, 1999). Average daily solar radiation data at earth surface (kWh m⁻² day⁻¹; 1983–2005) were also obtained from a gridded dataset (NASA; <http://eosweb.larc.nasa.gov>).

As a proxy for large-scale, interannual drivers of climate we used SSTA from the extended SSTA-dataset until 2003 of Kaplan *et al.* (1998). Data of the Southern Oscillation Index (SOI), a meteorological index based on air pressure difference between Tahiti and Darwin that is often used to characterize the strength of El Niño events (Trenberth & Caron, 2000), were obtained from the National Centre for Atmospheric research (<http://www.cgd.ucar.edu/cas/catalog/climind/soi.html>). We define El Niño years as those with 3-monthly means of Niño3.4 SSTA exceeding +0.5 for at least five consecutive months (*sensu* National Oceanic and Atmospheric

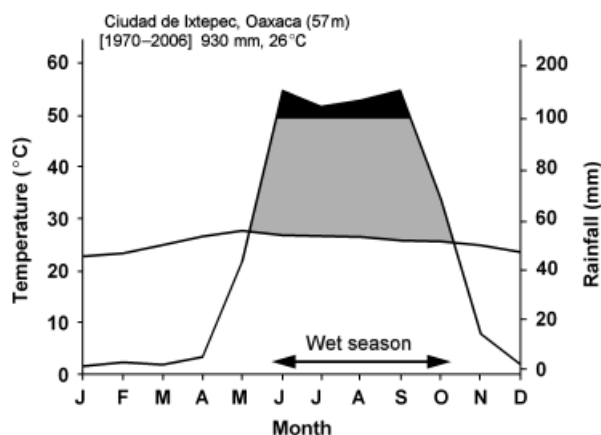


Fig. 1 Climate diagram Ixtepec, 14 km from study site. Data source CONAGUA (2003). The black area indicates months with more than 100 mm rain, the gray area those with <100 mm, and months where rainfall undercuts the temperature line can be considered dry.

Administration, <http://www.cgd.ucar.edu/cas/ENSO/enso.html>).

Study species, sample collection and tree ring analysis

We performed tree ring analysis on *M. acantholoba* (Willd.) Poir. (Fabaceae), a common dry-forest pioneer tree that reaches up to 7 m in height, ca. 20 cm in diameter and has a maximum age of ca. 40 years. In the study area, *M. acantholoba* accounts for about half of the basal area of secondary forest stands <40 years old, and often forms mono-dominant stands in abandoned agricultural fields (Lebrija-Trejos *et al.*, 2008). *M. acantholoba* is strictly deciduous, shedding leaves at the end of the wet season, between early November and late December, depending on the amount of rain at the start of the dry season. Leaf flushing occurs usually after the first rains, in late May to early June.

M. acantholoba forms distinct annual rings characterized by a higher density of vessels and larger vessel size at the beginning of each growth zone (i.e., semi-ring porous growth zones, Brienen *et al.*, 2009).

We collected 50 entire stem discs between November 2006 and February 2008 from secondary forest stands aged 10–64 years (Lebrija-Trejos *et al.*, 2008; Brienen *et al.*, 2009). For this study, we selected trees >10 years old with regular and round stems (31 trees). On these trees, rings were dated to calendar year and ring widths were measured along two to three radii to the nearest 0.001 mm using a computer-compatible tree ring measuring system (Velmex Inc., Bloomfield, NY, USA) and a $\times 40$ stereomicroscope. We averaged ring widths over radii (simple arithmetic mean) and converted radial growth to mean diameter growth rates. In our final analysis, three additional trees were left out due to low correlation with other growth series. We could not detect any dating errors in those trees.

For climate growth correlations, we first standardized growth values of each tree and then calculated yearly growth indices by averaging standardized growth rates of all 28 trees included in our analysis. Standardization of growth values was performed to obtain equal variances among trees and to avoid influences of variation in mean growth rates and the length of records between trees (Cook & Kairiukstis, 1989). Growth data were standardized as follows:

$$g_{i,stand} = (g_i - \hat{g})/\sigma, \quad (1)$$

where $g_{i,stand}$ = standardized growth rate at year i , g_i = growth rate at year i , \hat{g} = mean growth rate of the tree, and σ = standard deviation of all growth data of the tree. It is common practice to also remove variation in growth rates due to tree age or size, using detrending techniques (Cook & Kairiukstis, 1989), but this was not

necessary in our case as no age- or diameter-dependent growth trends were observed. Lack of such trends may be due to the pioneer character of the species and the high light conditions.

We assessed the degree of correspondence of inter-annual growth variation among trees by calculating the mean Pearson's correlation coefficient of all pair-wise combinations of trees (r'). This mean intertree correlation was used to determine the expressed population signal (EPS), which indicates the degree to which samples represent the population signal and to calculate the subsample signal strength (SSS). EPS and SSS were calculated according to Wigley *et al.*, (1984):

$$EPS = (Nr')/(1 + (N - 1)r'), \quad (2)$$

$$SSS = n(1 + (N - 1)r')/N(1 + (n - 1)r'), \quad (3)$$

where N = actual sample size, n = arbitrary subsample of N , and r' = mean inter-tree correlation.

Climate-growth analyses

We studied relations between large-scale climatic drivers (SSTA) and local climatic variables and dissected their influences on tree growth using path analysis. To get insight into the regions of the oceans that modulated tree growth and during which seasons, we correlated standardized growth with 3-monthly means of gridded fields of SSTA (Kaplan extended SSTA until 2003; Kaplan *et al.*, 1998) using the climate explorer (van Oldenborgh & Burgers, 2005). SSTA-data from those regions in the Pacific and Atlantic Oceans that most strongly correlated with tree growth were used in further analysis, and correlated to local climate and growth during different seasons.

We then assessed how local climate variability influenced growth. To provide detailed insight into the influence of rainfall during different months on growth, we correlated growth with 3-monthly rainfall means, running from July of the previous year to December of the current year. Growth was also correlated with annual (from November until October) and seasonal (dry and wet season, cf. Fig. 1) averages of rainfall, temperature, cloud cover and solar radiation. The previous wet season was included as it may have important influences on current growth (Fritts, 1976). To correct for possible correlations between climate variables, we also calculated partial correlations, which allowed us to study the effect of each climate variable on tree growth, while controlling for the effects of other climate variables.

Using path analysis, we integrated all relations between large-scale climatic drivers, local climate and

growth. We included all possible paths from large-scale climatic drivers to local climate variables, from large-scale climatic drivers to tree growth, and from local climate variables to tree growth. Path analysis allowed us to dissect direct and indirect influences of climate on growth. Direct effects consist of direct relations between a predictor variable (e.g., climate) and growth, and are given as standardized partial regression coefficients or path coefficients (Kline, 1998). Indirect effects occur when a predictor variable (e.g., SSTA) is correlated with growth through its correlation with other predictors (e.g., rainfall) that have a direct effect on growth. The strengths of indirect effects can be calculated as the product of corresponding path coefficients. Both indirect and direct effects indicate the change in a criterion variable (growth), expressed in standard deviation units, as a result of a change of one standard deviation in its predictor. Total effects were calculated as the sum of the direct and indirect effects. The following SSTA variables were selected as they produced the highest correlations with local climate and tree growth: dry-season SSTA of the tropical northwest Atlantic and wet-season SSTA in the central equatorial Pacific. We included the central equatorial Pacific region, i.e., the Niño3.4 region, instead of west Pacific as this is the traditional region used to assess the strength of El Niño events (Trenberth & Stepaniak, 2001).

We chose to include all paths in the analysis, also those which were non-significant to illustrate all relationships. This approach may reduce statistical reliability of the model as the number of paths is relatively large compared with the sample size (Kline, 1998), but results did not change when we reduced the number of relations by removing non-significant paths. The comparative fit index (CFI) and the root mean square error of approximation (RMSEA) were used to assess the fit of the model (Kline, 1998).

Finally, we also tested for the influence of El Niño events on tree growth, using correlations of growth and southern oscillation index (SOI), and *t*-test for differences between El Niño and 'non-Niño' years. Our relatively short dataset did not allow spectrum analysis, a common tool to test for ENSO cycles in ring width patterns (cf. Stahle *et al.*, 1998; Fichtler *et al.*, 2004; Schöngart *et al.*, 2004; Therrell *et al.*, 2006).

Path analysis was conducted with AMOS 7.0 (Arbuckle, 2003), and all other statistical analyses were done in SPSS 15.0.

Growth projections for 2080–2099, and long-term growth trends

We evaluated how tree growth would be influenced by future changes in rainfall. To this end, we developed a

multiple regression model between growth and rainfall during the dry and wet seasons for 1980–1999, and used predictions of rainfall for the end of this century to estimate growth during this period. Results from two sets of climate models were used to calculate the degree of rainfall reduction under two emission scenarios: medium (A1B) and high-emission scenario (A2). Estimation of rainfall reductions for the A1B-emission scenario were obtained from the regional climate projections for Central America of the IPCC-working group 1 (Christensen *et al.*, 2007), which predict area-averaged rainfall changes between the periods of 1980–1999 and 2080–2099 based on a set of 21 models. Estimations of rainfall reductions under the A2 emission scenario were obtained from Neelin *et al.* (2006), in which a set of 10 climate models was used to predict rainfall change per decade for the months June–August. As rainfall decreases during these months are indicative for decreases over the entire year (Neelin *et al.*, 2006), we applied the percentage rainfall decrease during June–August to calculate rainfall during 2080–2099.

We calculated the growth change towards the end of the century as:

$$\Delta G = 100(G_{\text{now}} - G_{\text{pred}})/G_{\text{pred}}, \quad (4)$$

where ΔG = percentage growth change, G_{now} = model estimate of growth 1980–1999, G_{pred} = model estimate of growth 2080–2099. Associated 95% confidence limits ($C_{2.5\%}$, $C_{97.5\%}$) of ΔG were calculated as follows:

$$C_{2.5\%, \Delta G} = (C_{2.5\%, G_{\text{now}}} - C_{2.5\%, G_{\text{pred}}})/C_{2.5\%, G_{\text{pred}}}, \quad (5)$$

where $C_{2.5\%, \Delta G}$ = lower confidence limit of ΔG , $C_{2.5\%, G_{\text{now}}}$ = lower confidence limit of G_{now} , $C_{2.5\%, G_{\text{pred}}}$ = lower confidence interval of G_{pred} . The upper confidence interval $C_{97.5\%, \Delta G}$ was calculated in exactly the same way. The lower (and upper) confidence limits of G were calculated by subtracting (or adding) $1.96 \times$ standard error to each coefficient in the multiple regression model and using corresponding rainfall values for each of the periods.

An important requirement for projecting growth over time periods outside the calibration period is a successful validation of the climate-growth model (Fritts, 1976). We therefore tested the predictive *skills* of our climate-growth model using the 'leave-one-out' cross validation (Michaelsen, 1987), a procedure especially appropriate when time-series are short as in our study. In this procedure, a series of regression models is fitted, each time omitting a certain year from the calibration set and using the model to predict growth for the omitted year. We thus obtained a predicted growth value for each year, which were compared with the observed value for that year. The reduction of error (RE) was used as a measure of the predictive *skill* of the model (Fritts,

1976), i.e. the model's accuracy compared with a random prediction. Following Fritts (1976), we calculated RE as:

$$RE = 1 - \left(\frac{\sum_{i=1..n} (y_{obs,i} - y_{pred(i)})^2}{\sum_{i=1..n} (y_{obs,i} - \hat{y})^2} \right), \quad (6)$$

where $y_{obs,i}$ = observed growth during year i , $y_{pred(i)}$ = predicted growth for year i (i.e. without using data for year i), and \hat{y} , the calibration-period mean of growth. Positive RE values are indicative for a regression model with predictive skill (Fritts, 1976).

Results

Intertree correlation and tree ring statistics

Mean annual diameter growth varied eightfold across years, from 0.17 to 1.32 cm yr⁻¹, with an average of 0.50 cm yr⁻¹ ($\sigma = 0.29$ cm yr⁻¹). Temporal growth variation was rather similar among sampled trees, as indicated by a mean inter-tree correlation of 0.69 ($n = 28$ trees, 1970–2007). The EPS of 0.98 was particularly high, and shows that our samples capture 98% of the inter-annual growth variation in the population. Over the entire period of analyses (1970–2007) our sample size was higher (3–28 trees) than that minimally required (2.4) to reach the acceptable level of 0.85 for SSS (Cook & Kariukstis 1989).

Correlations between large-scale climate drivers and local climate

Annual rainfall varied five-fold over the analyzed period (1970–2006), ranging from 380 to 1850 mm. We found that SSTA in the Pacific and Atlantic oceans were the principal drivers of this year-to-year climate variability (Table 1), in accordance with climate studies in the region (Enfield & Alfaro, 1999; Giannini *et al.*, 2000; Taylor *et al.*, 2002). Specifically, positive SSTA in the tropical northwest Atlantic region (25°N–10°S, 20°–50°W) during the dry season resulted in higher annual rainfall, higher wet season cloud cover, and reduced solar radiation during the wet season. Temperature was positively affected during the dry season.

During the wet season the influence of SSTA in the Pacific was more pronounced (cf. Taylor *et al.*, 2002). Effects of west and central Pacific SSTA on local climate were in general opposite: negative west and positive central equatorial Pacific SSTA (during El Niño's) resulted in lower annual rainfall, higher temperature (differs for seasons), and higher solar radiation during the wet season (Table 1). Cloud cover during the wet season was only affected by west Pacific SSTA.

We found similar responses of rainfall, temperature and solar radiation to the SOI (Table 1), a different measure of the strength of El Niño–Southern Oscillation derived from atmospheric pressure data instead of Pacific SSTA (Trenberth & Caron, 2000). Wet season

Table 1 Pearson correlations between large-scale and local climate variables

Large-scale climatic variables	Annual rain [†]	Local climate variables			
		Mean temperature		Mean cloud cover	Mean solar radiation
		Dry [‡]	Wet [§]	Wet [§]	Wet [§]
Central equatorial Pacific SSTA [¶] (wet season)	–0.60***	0.05	0.59***	–0.16	0.52*
West Pacific SSTA (wet season)	0.61***	0.42**	–0.22	0.49**	–0.58**
Southern Oscillation Index (SOI), wet season	0.60***	0.07	–0.54**	0.26	–0.45*
Atlantic SSTA ^{††} (dry season)	0.43*	0.44*	0.07	0.70***	–0.45*

Sea surface temperature anomalies (SSTA) in the Pacific and Atlantic Ocean and the Southern Oscillation Index (SOI) were averaged over wet (June–October) or dry season (November–May). High SSTA in the central equatorial Pacific (Niño3.4 region) and low SOI correspond to El Niño-years.

*** $P < 0.001$,

** $P < 0.01$,

* $P < 0.05$.

[†]Annual = November–October.

[‡]Dry season = November–May.

[§]Wet season (> 50 mm) = June–October.

[¶]Niño 3.4 region (5°N–5°S, 120°–170°W).

^{||}(0°N–20°N, 120°–150°E).

^{††}(25°N–10°S, 20°–50°W).

rainfall was reduced by 45% (t -test -4.881 , $P < 0.001$, $df = 35$) during El Niño years between 1970 and 2006.

Teleconnections between large-scale climate drivers and tree growth

Tree growth was correlated both with the Pacific and the Atlantic SSTA, but during different periods of the year (Fig. 2). In the first half of the year Atlantic SSTA exhibited the strongest influence on growth (Fig. 2a and b), while in the second half of the year growth was mainly affected by the Pacific SSTA (Fig. 2c and d). For the Atlantic, the west equatorial area between 25°N–10°S and 20°–50°W had the highest influence on growth. In this region, growth showed positive correlations with SSTA for various seasons, but most strongly during the dry season (Table 2). For the Pacific, we observed negative relations of growth with central equatorial SSTA in the Niño3.4 region (5°N–5°S, 120°–170°W) and

positive relations with west SSTA (0°N–20°N, 120°–150°E). These Pacific regions influence ENSO events.

We also found positive correlations of growth with the SOI (Table 2). This showed that growth was negatively affected by El Niño-episodes. The total reduction in diameter growth during El Niño years between 1970 and 2007 was 37% ($t = -2.32$, $P < 0.05$, $df = 36$). Notwithstanding such a strong influence of El Niño, not all El Niño-episodes led to lower rainfall and hence not all El Niño's were visible in the ring-width pattern. For example, rainfall and growth during 1997, one of the strongest El Niño episodes of the last decades, were not particularly low, although rainfall and growth were both slightly lower compared with previous and following years (cf. Fig. 3).

Correlations between local climate and growth

Diameter growth was positively correlated with rainfall for all months during the wet season and for some

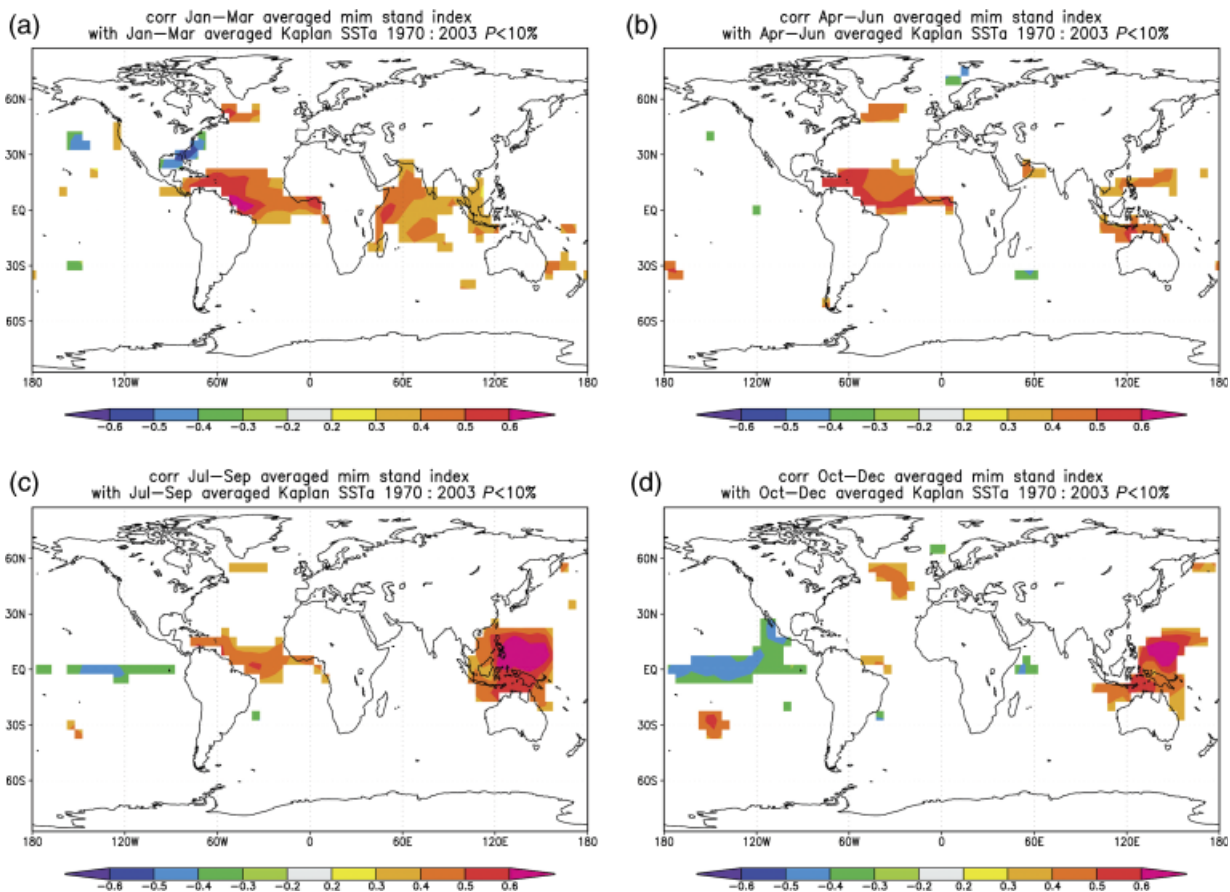


Fig. 2 Correlations between standardized growth of *Mimosa acantholoba* and gridded sea surface temperature-anomalies (SSTA) during January–March (a), April–June (b), July–September (c), and October–December (d). Orange and red colors indicate positive relations, and green and blue colors indicate negative correlations ($P < 0.01$). Hence, North tropical Atlantic SSTA correlated positively with growth, while central equatorial Pacific SSTA during the end of the year correlated negatively with growth. The analysis was done by using the Climate explorer of the KNMI (van Oldenborgh & Burgers, 2005) and covers the time-period 1970–2003. SSTA data are from the Kaplan extended SSTA-dataset until 2003 (Kaplan *et al.*, 1998).

Table 2 Pearson correlations between standardized growth and Sea Surface Temperature anomalies (SSTA) in the Pacific and Atlantic Ocean and the Southern Oscillation Index (SOI), averaged over wet (June–October) or dry season (November–May)

	Previous wet†	Dry‡	Current wet†	Annual§
Central equatorial Pacific SSTA¶ (wet season)	0.27	0.16	−0.48**	−0.20**
West Pacific SSTA (wet season)	0.16	0.19	0.73***	0.56**
Southern Oscillation Index (SOI), wet season	−0.29	−0.11	0.44**	0.20
Atlantic SSTA†† (dry season)	0.46**	0.63***	0.38*	0.55**

High SSTA in the Central equatorial Pacific (Niño3.4 region) and low SOI correspond to El Niño-years.

*** $P < 0.001$,

** $P < 0.01$,

* $P < 0.05$.

†Wet season (> 50 mm) = June–October.

‡Dry season = November–May.

§Annual = November–October.

¶Niño 3.4 region (5°N–5°S, 120°–170°W).

|| (0°N–20°N, 120°–150°E).

†† (25°N–10°S, 20°–50°W).

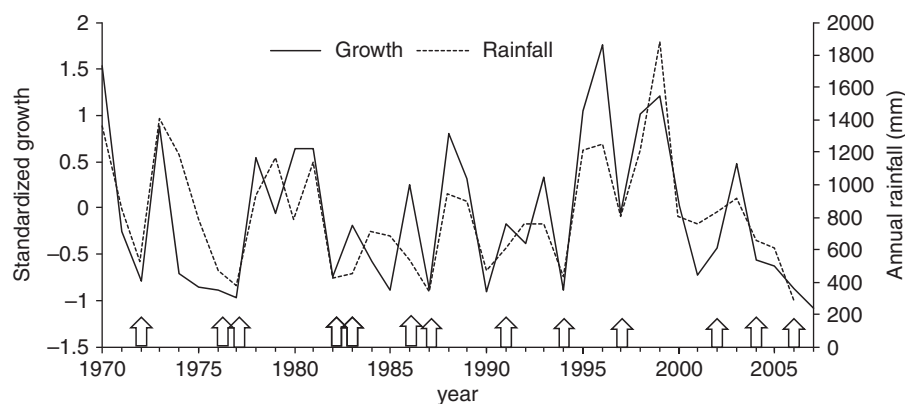


Fig. 3 Temporal variation in growth rates of *Mimosa acantholoba* (bold line) and annual rainfall (broken line). El Niño-years (*sensu* NOAA, cf. <http://www.cgd.ucar.edu/cas/ENSO/enso.html>) are indicated with arrows.

months during the preceding dry season (Fig. 4). We also found a positive correlation of tree growth with cloud cover during the wet season, and negative correlations with wet season temperature and solar radiation (Table 3). Among all climate variables considered, tree growth showed the strongest correlations with rainfall, as is illustrated by a highly synchronous pattern between growth and rainfall in Fig. 3. When correcting for the strong effect of wet-season rainfall on growth, using partial correlation, all correlations between growth and other climate variables disappeared (Table 3). Thus, negative correlations between growth on one hand and temperature, cloud cover and solar radiation on the other were entirely due to correlations of these climate variables with wet season rainfall. Similarly, correlations between growth and rainfall in November and December of the previous year (cf. Fig. 4), were due to correlations of rainfall in these months with rainfall during the following wet season (Pearson's $r = 0.36$,

$P < 0.05$). When correcting for the influence of wet season rainfall, we found a positive effect of dry-season rainfall on growth. However, dry-season rainfall added little to the total variation in growth rate explained by wet season rainfall (cf. Table 3).

Path analysis: from large-scale climate drivers to local climate and tree growth

The influence of Pacific and Atlantic SSTA on local climate and growth is illustrated by the path diagram in Fig. 5. Consistent with the results presented above, this diagram shows that both ocean basins influenced rainfall and temperature, but that only rainfall significantly affected tree growth.

High central equatorial Pacific SSTA (during El Niño-years) negatively affected rainfall and thereby reduced growth. The path diagram shows that there is no significant direct effect of the Pacific on growth (i.e., path

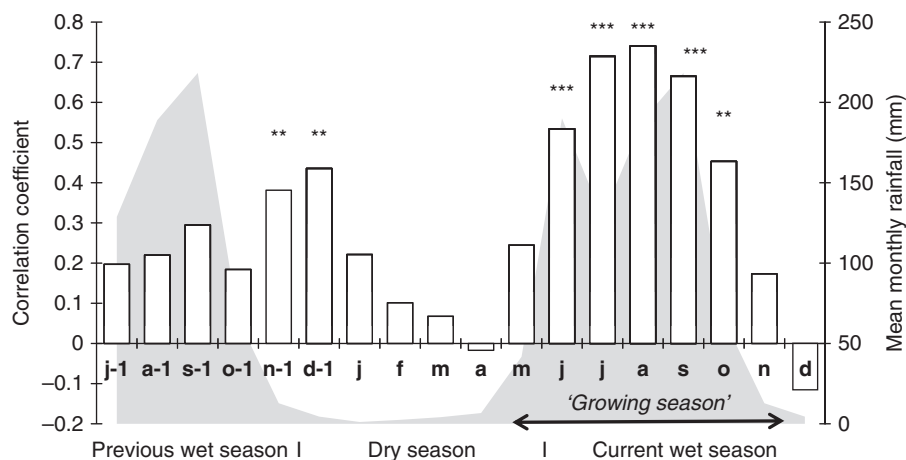


Fig. 4 Variation in monthly rainfall and its correlations with tree growth of *Mimosa acantholoba* in a Mexican dry forest. Correlations run from previous growing season (July; 'j-1') to the middle of following dry season (December; 'd'). Correlations were computed using three-monthly averages of rainfall for 1970–2006. Significance levels are indicated above or below the bars, *** $P < 0.001$, ** $P < 0.01$. The shaded area in the background is the mean total rainfall for each month.

Table 3 Correlations (and partial correlations) between standardized growth and rain, temperature and solar radiation during different seasons

	Previous wet†	Dry‡	Current wet†	Annual§
Rain	0.20 (–0.17)	0.23 (0.34*)	0.75*** (na)	0.78*** (na)
Mean temperature	0.25 (0.19)	0.19 (0.21)	–0.38* (0.00)	–0.05 (0.16)
Mean cloud cover	0.12 (–0.10)	0.26 (0.24)	0.47* (0.32)	0.41* (0.32)
Solar radiation	–0.13 (0.00)	0.27 (–0.01)	–0.52* (0.12)	–0.28 (–0.07)

Partial correlations are corrected for the influence of current wet season rainfall on growth. Values are Pearson correlation coefficients.

*** $P < 0.001$,

** $P < 0.01$,

* $P < 0.05$.

†Wet season (> 50 mm) = June–October.

‡Dry season = November–May.

§Annual = November–October.

coefficient is nearly zero), and that the entire influence of the Pacific on growth is therefore due to its effect on rainfall ($r_{\text{indirect}} = -0.32$).

The effect of the North tropical Atlantic Ocean was opposite: positive north Atlantic SSTA led to increased rainfall and increased growth. The relation between Atlantic SSTA and growth was only for a very small portion explained by its effects on local climate ($r_{\text{indirect}} = 0.16$), while there was a large direct effect of Atlantic SSTA on growth ($r_{\text{direct}} = 0.40$). The higher total effect of the Atlantic Ocean ($r_{\text{total}} = 0.55$) compared with the Pacific Ocean ($r_{\text{total}} = -0.36$) indicated a stronger impact of the former on tree growth, but a complete comparison with the degree to which both ocean basins influence growth should also include west Pacific SSTA. Overall performance of our model was good ($\chi^2 = 0.87$,

$df = 2$, $P = 0.35$, CFI = 1.00, RMSEA $< 10^{-4}$), and it explained a relative large portion of growth rate variation (70%).

Growth projections for 2080–2099

Rain during the preceding dry and current wet season was the best predictors for growth over 1980–1999, and was included in a regression model to predict growth towards the end of this century (Diameter growth = $-0.11 + 0.0026 \times \text{Rain}_{\text{dry}} + 0.00071 \times \text{Rain}_{\text{wet}}$; $R^2 = 0.78$, $F = 29.2$, $df = 19$, $P < 0.0001$). Validation of the regression model showed a high correlation ($r = 0.81$) between observed and predicted growth, and a good predictive skill as indicated by a relative high RE (RE = 0.65). These results suggest that the model may

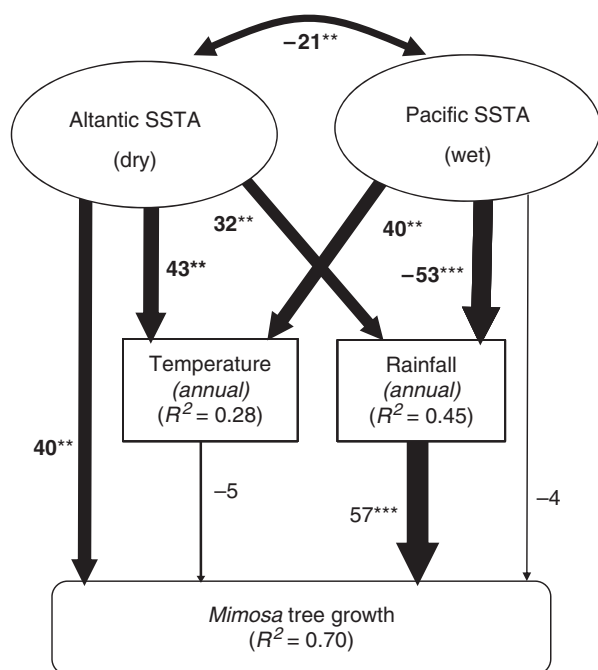


Fig. 5 Path diagram showing direct and indirect influences of Sea Surface Temperature anomalies (SSTA) in the North tropical Atlantic and central equatorial Pacific (Niño3.4-region) on *Mimosa acantholoba* tree growth in Mexico. Line width of arrows is proportional to the strength of the path coefficient. Path coefficients ($\times 100$) are included. The two-headed arrow represents a free correlation. $***P < 0.001$, $**P < 0.01$. Temperature and rainfall are annual averages, from November until October.

be used to predict growth outside the calibrated time-period (Fritts, 1976). Using this regression model, we estimated that growth would be reduced by 12% (confidence interval = 10–34%) towards the end of this century (2080–2099) under the moderate emission scenario A1B, which projects rainfall decreases of 14% during the dry and 9% during the wet season (cf. Christensen *et al.*, 2007). Under the higher emission scenario A2, growth would be reduced by 21%, due to an annual rainfall decrease of 18% (confidence interval = 16–62%) derived from data in Neelin *et al.* (2006, see Materials and methods). Note that these estimates do not account for a possible influence of increased atmospheric CO₂ pressure on growth (see Discussion).

Discussion

Local climatic influences on tree growth

Of all local climatic factors, wet-season rainfall had the highest influence on diameter growth of *Mimosa* trees. Other studies on tree growth in tropical dry forests reported similar results (Bullock, 1997; Stahle *et al.*,

1999; Therrell *et al.*, 2006; Trouet *et al.*, 2006; Gebrekirstos *et al.*, 2008). A strong wet-season impact on growth is to be expected as $\sim 90\%$ of the annual rainfall falls during that season. Still, there was some effect of dry-season rainfall on growth, probably through the positive effect of elevated soil- or stem-water content for initial growth.

Interestingly, neither temperature nor solar radiation seemed to influence tree growth, after controlling for the effect of wet-season rainfall. The negative correlations between these variables and growth disappeared when the effect of rainfall was accounted for. For example, rainfall was strongly reduced during El Niño years, but temperature and solar radiation also tended to be higher. Such correlations among climate variables highlight the importance of including all relevant climatic factors simultaneously in climate-growth analyses.

The absence of a clear influence of temperature on growth in this study is consistent with the theoretical predictions of Lloyd & Farquhar (2008), but contrasts with findings of empirical studies in dry forest trees (Deval *et al.*, 1995; Fichtler *et al.*, 2004). However, the degree to which the results of these studies indicate real temperature effects on growth is not clear, as they did not simultaneously test for effects of temperature and rainfall. Differences between species in climate sensitivity may also explain these contrasts (e.g., Knight & Ackerly, 2003). *M. acantholoba* is characterized by a set of functional traits for controlling leaf temperature such as compound leaves, slender leaflets, and pulvini (Lebrija-Trejos *et al.*, in press), which may explain the lack of a clear effect of temperature on growth. Clearly, there is a need to perform thorough tests of climate-growth relations for more species and tropical forest types. Long-term datasets on growth and climate are essential in this respect (Clark, 2007) and may be obtained from tree ring analysis, a technique that has recently proven to be useful in the tropics (Fichtler *et al.*, 2004; Brienen & Zuidema, 2005; Schöngart, *et al.*, 2006; Trouet *et al.*, 2006).

Large-scale climatic effects on tree growth

We found teleconnections between *Mimosa* growth in Mexico and SSTA of the North tropical Atlantic and Pacific. This finding parallels the bimodal effects of the two oceans on climate in the region, with a tropical Atlantic influence during the early part of the rainy season and a Pacific influence at the end of the wet season (Enfield & Alfaro, 1999; Giannini *et al.*, 2000; Taylor *et al.*, 2002). The area of highest influence in the tropical (north) Atlantic coincides with the main convection centers for rainfall in the study region. With

positive SSTA, rainfall during the early rainy season is enhanced by stronger convection (Taylor *et al.*, 2002). During the wet season, the observed pattern of correlations with Pacific SSTA clearly demonstrates ENSO influences on growth. Correlations in the East and West Pacific are oppositely signed with reductions in growth during warm phase ENSO events (El Niño's) when the central equatorial Pacific (i.e., Niño3.4-region) is warmer and the west Pacific is cooler than usual. This east-west gradient in SSTA is correlated with the Pacific thermocline during El Niño's that leads to warmer waters in the east due to reduced cold water upwelling, and a relative cooling of the west Pacific (Trenberth & Caron, 2000).

Tree growth was partially governed by SSTA influences on local climate as showed by path analysis. The influence of central equatorial Pacific SSTA (ENSO) on tree growth was nearly entirely through its impact on rainfall and the strong rainfall-growth relation. However, the major part of the Atlantic SSTA influence on tree growth could not be explained fully by its effects on local climate factors included in our analysis. Hence, there are still some unaccounted effects of the Atlantic SSTA on climate which cause its influence on growth. Cloud cover and solar radiation were both affected by Atlantic SSTA (Table 1), but tree growth did not correlate with these factors (Table 2). Some part of the observed correlations of Atlantic SSTA may also emerge from teleconnections between the two ocean basins and their interactive, nonlinear effects on local climate (Enfield & Alfaro, 1999; Giannini *et al.*, 2000; Taylor *et al.*, 2002). Path analysis proved useful in dissecting and visualizing complex relations between large-scale and local climatic factors and their influences on growth.

Very few studies have shown growth decreases during El Niño events in dry forests (Condit *et al.*, 2004), and we know of none that quantified growth reductions during multiple El Niño events. The 37-year long dataset allowed us to assess ENSO effects on growth over an extended time period, and showed strong reduction (37%) in growth during the 13 El Niño-years included in our dataset. Whether reductions in growth are due to drought, as in our study, or to higher temperatures (cf. Devall *et al.*, 1995; Fichtler *et al.*, 2004; Trouet *et al.*, 2006) or a combination of both factors will depend probably on local climate conditions (e.g., total annual precipitation, length of dry season, etc.). In large parts of the tropics, El Niño's lead to drier and warmer conditions (Lyon, 2004; Malhi & Wright, 2004) and will thus negatively affect growth (Zuidema & Boot, 2002; Clark *et al.*, 2003).

The detection of relatively strong El Niño-signals in the tropical zone of Mexico warrants further dendrochronological explorations in this area. The correlations

between growth and ENSO indices that we obtained are among the highest reported for the tropics (Jacoby & D'Arrigo, 1990; Enquist & Leffler, 2001; Trouet *et al.*, 2001; Fichtler *et al.*, 2004; Schöngart *et al.*, 2004, 2006) and it is estimated that a large portion of species (48% from 21 sampled species) in this area produces annual rings (Brienen *et al.*, 2009). Currently, only two ENSO reconstructions are based on data from the tropics (Jacoby & D'Arrigo, 1990; Schöngart *et al.*, 2004), while most are from northern Mexico and southwestern USA (cf. Cook, 1992; Stahle *et al.*, 1998; Martijena, 2003), where the effect of ENSO is weaker and opposite (Trenberth & Caron, 2000; Caso *et al.*, 2007). Hence, if suitable, long-lived species with tree rings are found, an important gap in dendroclimatological reconstructions of ENSO signals may be filled, leading to more reliable predictions of climate change impacts on tree growth.

Responses to changing climate

Global climate change is thought to lead to a redistribution of rainfall in the tropics with decreasing rainfall in dry subtropical regions at the margins of the convection zones (Chou *et al.*, 2006; Held & Soden, 2006; Seager *et al.*, 2009). Hence, rainfall in Central America will very likely decrease in future. In spite of the generally low agreement of local rainfall predictions, two independent studies including more than 20 climate models show a high level of correspondence on the trend of gradual drying in our study region, with rainfall reductions of 9–18% (Neelin *et al.*, 2006; IPCC, 2007). We estimated that such reductions would lead to strong growth declines of 12–21%, depending on the emission scenario used. These numbers do not take into account possible negative effects of the predicted temperature rise of 3 °C. It is difficult to predict however, how such a temperature rise might directly affect growth of our species as we did not observe such high temperatures during the study period. Indirect, such a rise in temperature will impose extra drought stress by reducing soil water availability. On the other hand, rising [CO₂] may stimulate growth through increases in photosynthesis (Lloyd & Farquhar, 2008) and improved water use efficiency (Hietz *et al.*, 2005) thus partially offsetting the negative effects of drought stress. However, these effects may be small when water availability is strongly limited. A complicating factor in predicting future growth responses is the possible increase in frequency of extreme climatic events (IPCC, 2007).

M. acantholoba forms mono-dominant stands in secondary forests throughout Central America (Lebrija-Trejos *et al.*, 2008). The strong reduction of *Mimosa* growth that we project for the end of the century, may therefore have direct consequences for the rate of

carbon sequestration in *Mimosa*-dominated secondary forests. If other dry forest tree species respond in similar ways to rainfall fluctuations (Bullock, 1997; Fichtler *et al.*, 2004; Trouet *et al.*, 2006; Gebrekirstos *et al.*, 2008), carbon sequestration will further decrease. On the other hand, if drought-induced reduction of growth is smaller in other species, shifts in competitive strength among pioneer species may occur, leading to changes the course of secondary succession (Lebrija-Trejos *et al.*, in press). At present, our knowledge on climate–growth and climate–survival relationships of tropical dry forest trees is insufficient to make inferences about the community-wide responses of these ecosystems to climatic changes. Such insights are direly needed, as tropical dry forests are regionally important in storing carbon (Jaramillo *et al.*, 2003; Read & Lawrence, 2003), covering as much as 42% of global (sub)tropical forested area (Murphy & Lugo, 1986), and half of Central America area (Murphy & Lugo, 1986). Studies directed to assess the role of secondary forests as carbon sinks are important as such forests are becoming the predominant vegetation cover in Neotropical dry landscapes (FAO, 2005; Wright, 2005).

Acknowledgements

We thank the people of Nizanda for help during sampling, Diego Pérez-Salícup for the use of the VELMEX measurement table, and Manuel Gloor, Oliver Phillips and three anonymous reviewers for their comments on an earlier version of the manuscript. RJWB acknowledges the Dirección General de Asuntos del Personal Académico of UNAM for the received postdoctoral grant and ELT acknowledges CONACYT, Mexico (Reg.No. 168169).

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