Journal of Arid Environments 109 (2014) 15–22

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Climatic drivers of tree growth in a swamp forest island in the semiarid coast of Chile

M.P. Peña [a], [b], [*], J. Barichivich [c], [d], A. Maldonado [e]

[a] Laboratorio de Dendrocronología y Cambio Global, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, Campus Isla Teja, Casilla 567, Valdivia, Chile
[b] Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja, Casilla 567, Valdivia, Chile
[c] Climatic Research Unit, School of Environmental Sciences, University of East Anglia, Norwich, UK
[d] Laboratoire des Sciences du Climat et de l'Environnement, CEA-CNRS-UVSQ, L'Orme des Merisiers, 91191 Gif-sur-Yvette, France
[e] Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Universidad de La Serena, Raúl Bitrán s/n, La Serena, Chile

ARTICLE INFO

Article history:
Received 29 May 2013
Received in revised form
30 April 2014
Accepted 15 May 2014
Available online

Keywords:
Dendrochronology
Drought
ENSO
Groundwater
Swamp forest

ABSTRACT

Isolated patches of swamp forests surrounded by xerophytic vegetation occur along the semiarid coast of Chile. Supported by shallow groundwater, these unique ecosystems have endured a long-term aridity trend during the Holocene and historical land use change. In this study, we investigated the patterns and climate drivers of annual tree growth in a coastal swamp dominated by the hygrophilous tree *Myrceugenia exsucca*. A tree-ring width chronology spanning the period 1864–2007 was developed and compared with long-term precipitation, temperature and soil moisture dynamics. There is a general lack of significant climate response during the earlier part of the 20th century, but a time-dependent positive growth response to temperature and moisture variability took place following partial drainage of the forest (1930s). Furthermore, a shift from a concurrent to a lagged growth response to moisture occurred around 1980, coinciding with increased frequency of ENSO-related moisture extremes. These results suggest that the ecological functioning of swamp forests in this region is very resilient to short-term climate variability, but even slight drainage disturbance can trigger very dynamic growth responses to climate variability. The degree of anthropogenic disturbance of these ecosystems will likely influence their response to projected increases in regional aridity during the coming decades.

1. Introduction

Isolated patches of swamp forest surrounded by xerophytic vegetation occur through the narrow Pacific coastal plains of the semiarid coast of north-central Chile (30°S–36°30′S), near the southern edge of the Atacama Desert. These forests represent the northernmost extent of the discontinuous swamp forest ecosystems in Chile (30°S–41°S), which are restricted to floodplains and low lying areas prone to permanent or temporary flooding (Varela, 1981; San Martín et al., 1988). Anthropogenic disturbance associated with drainage and widespread clearance of forest for agriculture in the fertile Chilean lowlands has largely reduced the extent of swamp forests during the last two centuries (Villagrán, 1982; Villa-Martínez and Villagrán, 1997; Maldonado and Villagrán, 2006). Regardless of their location, the structure and composition of the remaining swamp forests are relatively similar. Typically, the canopy is completely closed and dominated by evergreen flood-tolerant tree species from the Myrtaceae family, including *Myrceugenia exsucca* (DC) Berg., *Luma chequen* (Molina) A. Gray and *Blepharocalyx cruckshanksii* (Hook. Et Arn.) Niedenzu.

The swamp forests of the semiarid coast of Chile are regarded as environmental archives of millennial-scale vegetation and aridity fluctuations over central Chile during the Holocene. Pollen analysis of the sediments deposited in these swamps indicates that most of them were established between 5000 and 9900 years ago, when wetter past climatic conditions raised the local groundwater level and stimulated the formation of swamp-like habitats (Villagrán and Varela, 1990; Villa-Martínez and Villagrán, 1997; Maldonado and Villagrán, 2002). In the present, these forests are restricted to small areas of permanent flooding by groundwater seepage and near-surface flow along creeks. Therefore, their functioning and survival are thought to be strongly connected to rainfall patterns

---

[*] Corresponding author. Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja, Casilla 567, Valdivia, Chile. Tel.: +56 63 2221347; fax: +56 63 2221599.
E-mail address: mppena@gmail.com (M.P. Peña).

http://dx.doi.org/10.1016/j.jaridenv.2014.05.003

and groundwater dynamics from seasonal to millennial time scales (Maldonado and Villagrán, 2006). Nevertheless, these connections have not been demonstrated empirically and our understanding of the ecological functioning and climate responses of these northern swamp forest ecosystems is still poor (Correa-Araneda et al., 2011).

Precipitation has declined steadily during the last 130 years in north-central Chile (LeQuesne et al., 2006; Vuille and Milana, 2007). Further drying is expected to occur during the coming decades with ongoing climate change (Fuenzalida et al., 2007). This observed and projected increase in aridity is of concern for the survival of the swamp forests and for ecosystem structure and function in the surrounding drylands as well. Here, we investigate the relationship between interannual climate variability and tree-ring growth in a semi-desert swamp forest, called 'Palo Colorado' (Maldonado and Villagrán, 2006). We combined a local tree-ring record with gridded precipitation and temperature estimates, local observations of groundwater level and model-based estimates of soil moisture to assess how climate variability affects the ecological dynamics of the swamp. This study is the first of its kind and provides new empirical insights into the functioning and likely responses of these unique swamp forest ecosystems to increased aridity in the coming decades.

2. Regional climate and study site

The semiarid region of north-central Chile (27°–32°S), which is bounded by the Pacific Ocean to the west and the Andes to the east, is known as the 'Norte Chico'. It represents a steep biome transition between the Mediterranean-type ecosystems of central Chile and the hyper-arid Atacama Desert to the north (Fig. 1a). The seasonal dynamics of the subtropical eastern Pacific anticyclone and the permanent blocking effect of the Andes result in a Mediterranean-type rainfall regime (Miller, 1976). Almost all annual precipitation (about 200 mm) occurs during the austral winter between May and August (see Fig. 3). The rainy season is then followed by a continuous dry period during the rest of the year. The El Niño Southern Oscillation (ENSO) is the main driver of interannual climate variability in the region (Aceituno, 1988, Garreaud et al., 2009). Warm El Niño events weaken the eastern Pacific anticyclone and produce higher than average precipitation and temperature anomalies throughout the region, whilst cold La Niña events result in drier and colder than normal conditions (Montecinos and Aceituno, 2003).

The *Palo Colorado* swamp forest (32°05′S; 71°29′W) is a small forest patch (2.5 ha) dominated by flood-tolerant Myrtaceous trees and surrounded by semi-desert scrub vegetation (Maldonado and Villagrán, 2006). The forest is located in a permanently inundated area next to a small ravine that runs through the coastal plain from the adjacent coastal hills. This forest was established about 10,000 years ago under wetter climatic conditions, and provides the longest palynological record of any swamp forest in the semiarid region of Chile (Maldonado and Villagrán, 2006). Since the flooded soil is unsuitable for agriculture, the forest has been relatively well protected from the intense anthropogenic disturbance that affects the surrounding semiarid scrub vegetation. However, some drainage work was carried out during the second half of the 1930s. The dense forest canopy is dominated by *M. exsucca* trees that can reach up to 10 m in height and 40 cm in diameter (Fig. 1b). Most mature *M. exsucca* trees develop buttresses at the stem base, similar to other trees growing in swamps such as the tupelo gum and bald cypress (Pallardy and Kozlowski, 2007). Other hygrophilous trees

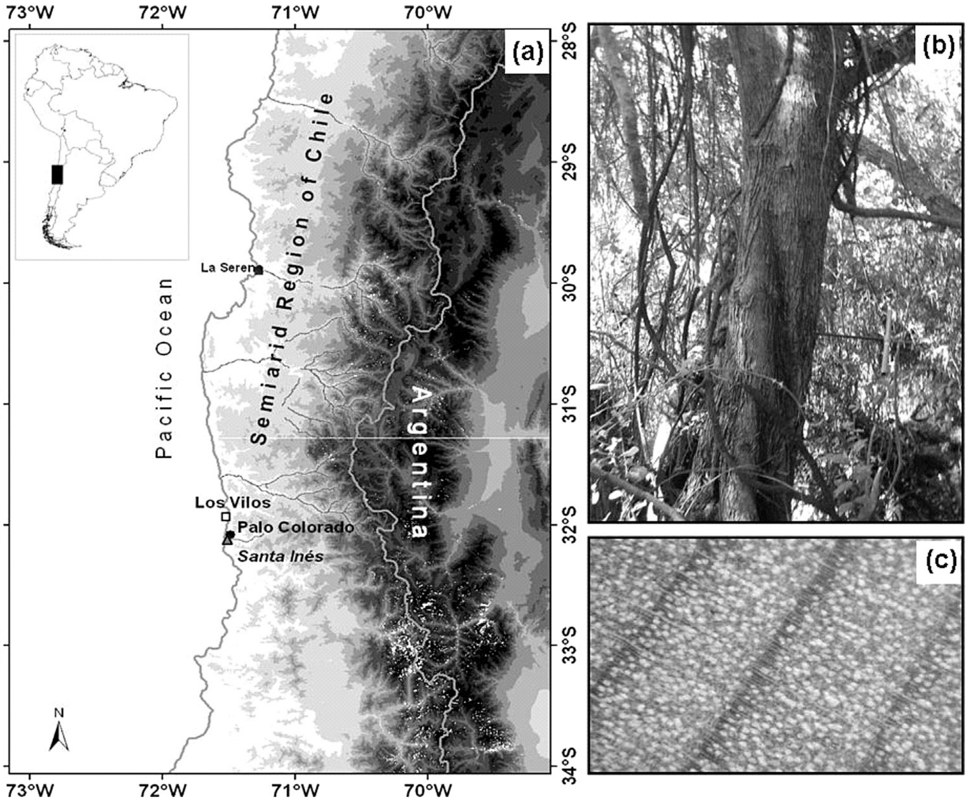

Fig. 1. Location map of the study site in the semiarid region of north-central Chile and growth features of *M. exsucca*. (a) Topographic map showing the location of the Palo Colorado swamp forest. Black shading denotes elevations above 4000 m a.s.l. (b) Mature individual of *M. exsucca* growing in the swamp. (c) Annual growth rings of *M. exsucca* (the bark is towards the right).

such as *L. chequen*, *Escallonia pulverulenta*, *Maytenus boaria* Molina and *Schinus latifolius* (Gill. Ex Lindl.) Engler dominate the canopy at the edge of the swamp, where sun-light is more abundant.

3. Methods

3.1. Sampling and tree-ring chronology development

A total of 120 increment cores were extracted from 60 mature *M. exsucca* trees, with two samples taken from each tree. Trees without buttressing were preferentially sampled, or alternatively cores were extracted above the buttress to reduce eccentric growth patterns. We used standard dendrochronological procedures to process the samples and develop tree-ring width chronologies (Fritts, 1976). Annual growth rings were dated to the year in which growth starts during the austral spring, and measured to an accuracy of 0.001 mm. Visual crossdating and ring-width measurements were checked using the quality-control program COFECHA (Holmes, 1983).

The age/size related trend in the tree-ring width measurements was modelled by using a negative exponential function or a linear regression with negative slope, and removed from the measurement series by division using the CRUST program (Melvin and Briffa, in press; available at: http://www.cru.uea.ac.uk/cru/software/crust/), a new software for tree-ring standardization developed at the Climatic Research Unit (CRU). The detrended growth series were averaged together into a mean chronology, representing common interannual to decadal growth variations in the forest stand. It is important to bear in mind that together with the short lifespan of most of the sampled trees, this curve-fitting detrending procedure acts as a high-pass filter on the individual series (Cook et al., 1995) and most of the multidecadal and longer-term growth variability is lost in the resulting chronologies. Therefore, our focus is primarily on interannual to decadal time scales.

The Expressed Population Signal statistic (EPS; Wigley et al., 1984) was used to assess the strength of the common growth signal in the mean chronology over time. This statistic measures the magnitude of the common variability between trees over a given period, taking into account sample replication. The EPS was computed using 20-year sliding windows with 10 years of overlap. There is no formal significance test for this statistic but a threshold of 0.85 (85% of variance in common and 15% of noise) is commonly accepted for a significant common signal.

3.2. Tree growth and climate variability

In order to identify the main climatic drivers of tree growth, the tree-ring width chronology was correlated with gridded monthly precipitation and temperature from the nearest 0.5° grid box of the CRUTS 3.20 dataset (Harris et al., in press), and also with gridded monthly soil moisture data simulated by the Climate Prediction Center (CPC) Leaky-Bucket model (Fan and van den Dool, 2004) for the period 1948–2007 (available at: http://www.cpc.ncep.noaa.gov/soilmst/leaky_glb.htm). Leaky-Bucket is a simple, single-layer hydrological model driven by observed monthly precipitation and temperature data. It estimates soil moisture, evaporation and runoff in a standard soil column of 1.6 m over the global land surface at a spatial resolution of 0.5°. The model is run with constant parameters, estimated using observed runoff data in eastern Oklahoma, US. In order to evaluate the reliability of simulated soil moisture data as a proxy for the local water-table level in the swamp, we extracted monthly CPC soil moisture estimates for the nearest grid box to Palo Colorado and compared these data with a 11-year record (1989–1999) of in situ groundwater level measured in a monitoring well (Santa Ines) located 6 km away from the swamp (Fig. 3).

All correlations with monthly climate (1901–2007) and soil moisture (1948–2007) data were computed on running windows of 20 years with the *bootRes* R package (Zang and Biondi, 2013). A window overlap of 10 years was used for temperature and precipitation and 5 years for the shorter soil moisture data. This allowed identification changes in correlation and tree-growth responses over time with a robust significance testing based on bootstrapping. Significance was tested at the 90% level.

To provide a regional context for the growth patterns observed in the swamp, the tree-ring chronology of *M. exsucca* was compared with a tree-ring chronology of an evergreen montane tree (*Kageneckia angustifolia* D. Don) published earlier by Barichivich et al. (2009). This chronology spans the period 1842–2004 and has been shown to capture well the regional patterns of vegetation growth in the water-limited interior drylands. It is located in the Andean foothills at about 140 km north-west of Palo Colorado.

4. Results

4.1. Tree-ring chronology

Tree-rings of *M. exsucca* are clearly identifiable (Fig. 1c), indicating a marked annual seasonality of tree growth in the swamp. The latewood cells appear as a darker band that defines the annual termination of the growth ring at the macroscopic level (Fig. 1c). Despite the clear tree-ring anatomy, crossdating was very challenging due to absent rings associated with stem buttresses. In addition, in some cases it was not possible to identify ring boundaries in the recent portion of the samples because of mechanical damage, growth suppressions or poor contrast in anatomical features. As a result, only 32 samples out of 120 were successfully crossdated and measured. The annual ring widths varied from less than a tenth of a millimetre in slow growing trees to about 9 mm in fast growing trees or periods of rapid growth (Fig. 2a). The oldest sampled and successfully crossdated tree had a minimum age of 97 years, but most of the trees had ages between 40 and 60 years. This resulted in a tree-ring chronology spanning

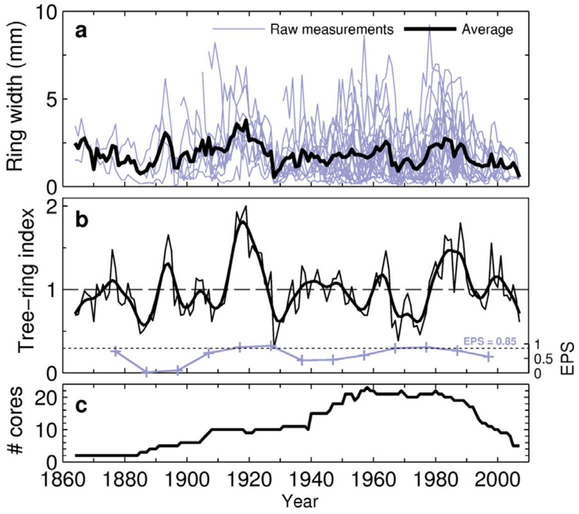

Fig. 2. *M. exsucca* tree-ring width chronology. (a) Raw ring-width data. (b) Average standard tree-ring chronology spanning the period 1864–2007 and the EPS statistic (light grey) computed in 20-year windows with an overlap of 10 years. The commonly accepted 0.85 EPS threshold (i.e., 85% common signal and 15% noise) is indicated by the dotted horizontal line. (c) The associated sample size of the average chronology for each year.

144 years from 1864 to 2007 (Fig. 2b), and represent the first well replicated tree-ring chronology of the endemic tree species of the Myrtaceae family from the semiarid coast of Chile. The average intercorrelation between the samples was 0.41, a relatively modest value compared with species in the drylands. This suggests an important degree of spatial heterogeneity in growth patterns across the swamp.

The tree-ring chronology indicates that the growth of *M. exsucca* in this swamp has a pattern of strong decadal variability, with periods of high growth rates around 1920 and 1980 (Fig. 2b). Periods of reduced growth occurred during the latter half of the 1930s and most of the 1960s and 1970s. The growth patterns are more uncertain prior to 1900, when the chronology is made up of less than 6 samples (Fig. 2c). The EPS indicates a high degree of common signal in the tree-ring chronology since around 1900 but a sustained weakening of this signal occurred between the 1930s and 1950s (Fig. 2b).

4.2. Correlation of tree growth with climate and moisture variability

Monthly model-based soil moisture data show a remarkable temporal agreement with in situ groundwater levels (Fig. 3a). The level of the water-table and soil moisture peaks at the end of the rainy season (June–September), after all the annual soil water recharge has occurred. This is followed by a continuous decline as a result of increased evapotranspiration and no further recharge, reaching a minimum at the end of the dry season in late autumn. This strong agreement demonstrates that the model-simulated soil moisture data are a good proxy for seasonal and interannual water level fluctuations in the swamp.

Correlation analysis with monthly temperature, precipitation and soil moisture indicates that tree growth in the swamp has a very complex and time-varying response to climate variability during the current and previous growing seasons (Fig. 4). There is a general lack of consistent climate response prior to the 1950s, followed by a period of significant ($P < 0.1$) and positive growth response to temperature and to a lesser extent to precipitation. The temperature response was significant during the rainy season of the previous year (from June to September), during most of the previous growing season from October to April and during the rainy and growing seasons from July to December of the current year. The emergence of this growth response to thermal variability around 1950 is illustrated in Fig. 5a by comparing tree growth with temperature averaged from July to October of the previous year. This figure shows that growth patterns since 1950 closely track interannual and decadal variations in temperature most of the time ($r = 0.37$ for the period 1951–2007, $P < 0.01$).

Contrary to our expectation, the correlation between tree growth and precipitation in the swamp is less consistent than with temperature (Fig. 4). Significant but unstable correlations occur with precipitation during the peak (July–August) of the previous and current year rainy seasons. Correlations during the rainy season of the current growing year were significant and positive from around the 1930s until the 1970s, indicating a concurrent growth response to rainfall anomalies during this earlier period. This is followed by a shift to a lagged growth response to rainfall variability during the most recent decades, as correlations during the current year turned negative and those during the previous year became positive and significant. Fig. 5b illustrates the relationship between tree growth and precipitation variability during the peak of the rainy season (July–August) of the previous year ($r = 0.31$ for the period 1951–2007, $P < 0.05$). The increased correspondence of growth and previous year rainfall anomalies from about 1980 depicts a 1-year lag in the growth response. For instance, heavy precipitation associated with a strong El Niño event in 1987–88 (the highest positive precipitation anomaly in Fig. 5b) is linked to increased tree growth during the following year.

Correlations of tree growth with monthly soil moisture dynamics (1948–2007) during the current and previous year are consistent with the evidence for a shift towards a lagged growth response to moisture anomalies from 1980 (Fig. 4). Correlations are significant ($P < 0.1$) only from June to December of the current growing year and shift from positive to negative around 1980. The temporal lag in the growth response is much clearer than with precipitation. Frequent, ENSO-related wet anomalies during recent decades are always associated with increased tree growth during the following year (Fig. 5c). A clear example of this delayed growth response occurred during the strong El Niño event in 1997.

Taken together, these correlation patterns suggest that tree growth in the swamp became more sensitive to climate variability during the second half of the 20th century, when a very dynamic positive growth response to temperature and moisture variability during the current and previous year has taken place.

4.3. Tree-growth patterns in the swamp and drylands

Tree growth patterns in the swamp differ substantially from growth patterns in the montane drylands on a yearly basis (Fig. 6a and b), but agree well on decadal to interdecadal time scales (Fig. 6c). The lack of overall agreement ($r = 0.15$ for 1864–2004; $P > 0.1$) in year-to-year variability is primarily associated with differences in magnitude and timing of growth responses to moisture anomalies in these contrasting environments. Tree growth in the more stable swamp environment has stronger temporal persistence and reduced interannual variability as a result of slowly

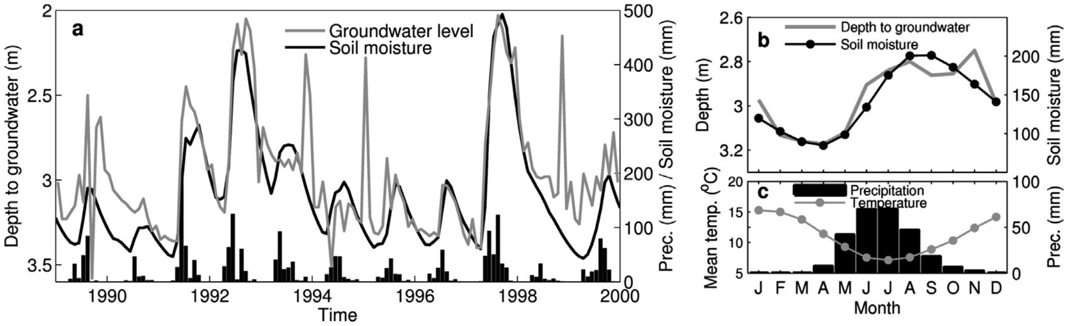

Fig. 3. Comparison of monthly and seasonal variability of the water-table level measured in the Santa Ines well since 1989 with monthly gridded soil moisture estimated by the CPC Leaky-Bucket hydrological model, and precipitation for the nearest grid box to Palo Colorado. (a) Monthly variability and (b–c) climatologies.

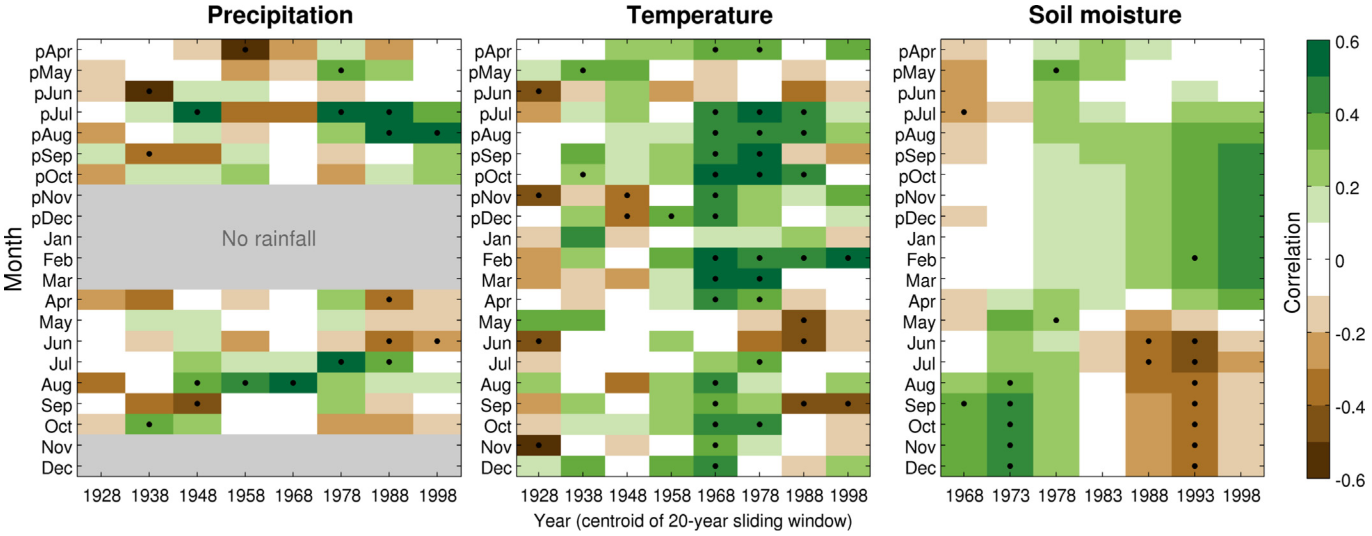

Fig. 4. Temporal patterns of correlation between the annual growth of *M. exsucca* and monthly precipitation, temperature and soil moisture from April of the previous growing year (p) to December of the current growing year. Correlations are shown for 20-year running windows. An overlap of 10 years between consecutive windows is used for precipitation and temperature and 5 years for soil moisture. The stippling denotes significant correlations ($P < 0.1$).

varying growing conditions, whereas rapidly changing moisture conditions in the drylands result in highly variable and concurrent growth anomalies. The shift to a lagged growth response to moisture anomalies in the swamp during recent decades further decreases the overall correlation with growth patterns in the drylands (Fig. 6b). Thus, these differences in growth dynamics reduce the synchrony of interannual growth anomalies (Fig. 6a–b) but do not affect the consistency of longer term growth variability as shown in Fig. 6c.

Weak correlations between the swamp and dryland tree-ring chronologies during the first half of the 20th century (Fig. 6b) are consistent with the evidence for a poor climate response of the swamp forest during this period based on gridded meteorological data. However, strong correlations are observed in the earlier part of the swamp forest chronology around the year 1900, though admittedly this earlier part of the chronologies is less reliable (Fig. 2b) and this association may occur by chance. Prolonged

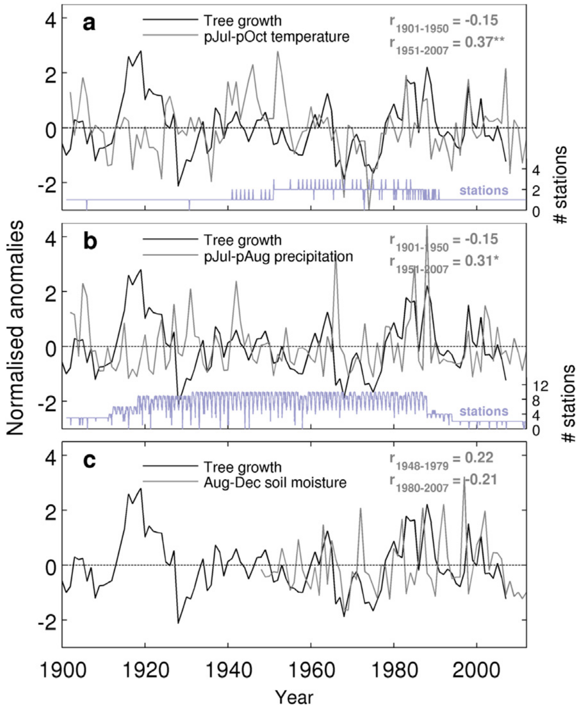

Fig. 5. Comparison of annual tree growth in the swamp with climate and soil moisture variations during the seasons with strongest correlations. (a) Mean temperature during July–October of the previous year, (b) precipitation during July–August of the previous year, and (c) soil moisture averaged over August–December of the current growing season. The monthly number of station records included in the CRUTS 3.20 precipitation and mean air temperature gridded fields in north-central Chile (located within a distance of 150 km north and south of Palo Colorado) is shown in the corresponding panels. These are the stations that contributed most to the gridded estimates at Palo Colorado. Correlations for different periods of interest and their significance (*: $P < 0.05$, **: $P < 0.01$) are indicated in the plots.

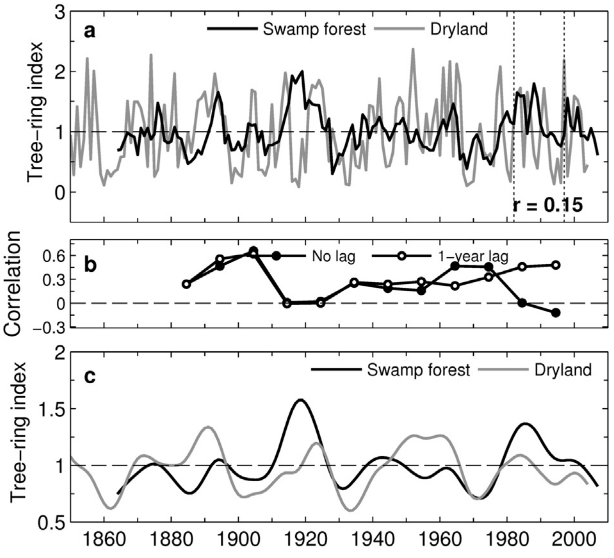

Fig. 6. Comparison of *M. exsucca* tree growth in the coastal swamp forest with the growth of the montane tree *Kageneckia angustifolia* in the interior Andean drylands. (a) Standard tree-ring chronologies; and (b) their 20-year running correlations with no lag and with 1-year lag. The strong El Niño events in 1982 and 1997 are indicated by vertical lines. (c) Comparison of decadal variability using 20-year low-pass filtered series.

periods of reduced growth in the swamp during the 1930s, 1960s and 1970s are consistent with reduced growth in the drylands and increased correlations between the chronologies (Fig. 6b). These periods are known to have been times of severe regional drought.

5. Discussion

The functioning and persistence of the swamp forest ecosystems in the semiarid coast of Chile are expected to be strongly associated with regional rainfall patterns and groundwater changes (Villagrán and Varela, 1990; Villa-Martínez and Villagrán, 1997; Maldonado and Villagrán, 2006). In this study, we show that annual tree growth in one of these swamps had a changing response to moisture and also to temperature variability over the course of the 20th century (Figs. 4 and 5). Temperature, rainfall and soil moisture variability were correlated with tree-growth patterns in the swamp only from around 1950, with no clear growth response to climate found in previous decades. This apparent lack of growth response to climatic variability prior to 1950 could be in part related to a decrease in the quality of the gridded records back in time, as the number of meteorological stations available for interpolation drops (Fig. 5). However, the same result is obtained when using station-based temperature and precipitation records instead of gridded estimates (Fig. S1). The gridded data are generally consistent with regional averages based on local stations ($r = 0.58$ for Jul–Oct temperature, 1930–2003, $P < 0.01$; $r = 0.98$ for Jul–Aug precipitation, 1901–2002, $P < 0.01$), though the gridded temperature estimates appear to be less reliable before 1950 (Fig. S2). The substantial weakening of the correlation between year-to-year variations of tree growth in the swamp and the drylands during the same period (Fig. 6b) provides independent evidence for the absence of a significant climate response. Therefore, it seems unlikely that the observed lack of growth response to climate variability during the earlier part of the 20th century is related to quality issues in the climate data.

The shift towards increased climate sensitivity of the swamp forest in the early 1950s follows the beginning of the drainage activities in the forest around the year 1939. According to the landowner, cement channels were built around the forest to extract water for human consumption. Therefore, it is likely that this disturbance is the underlying cause for the increased correlation between climate variability and tree growth in the swamp over the recent decades. This implies that under natural growing conditions, such as the period prior to the drainage works, undisturbed swamp forests are generally very stable and highly resilient to short-term climate variations.

Even though the drainage disturbance may have turned the forest more vulnerable to environmental variability, tree growth appears to have responded more strongly and positively to temperature than to rainfall and moisture variability (Fig. 4). This positive growth response to temperature is a new finding of this study and could have not been anticipated from the limited ecological knowledge on the functioning of these swamp forests, which were believed to be controlled primarily by moisture variability (Maldonado and Villagrán, 2006). We hypothesize that the installation of drainage ditches around the forest did not result in excessive drying of the swamp but that the hydrological change was sufficient to significantly stimulate the decomposition rates of the thick layer of organic matter in the forest floor with warmer temperatures. Therefore, growth stimulation due to increased nitrogen mineralisation and nutrient availability caused by warmer conditions (Rustad et al., 2001) might explain the extended positive correlations found between temperature and tree growth (Fig. 4). This hypothesis is consistent with modelling and observational studies on the influence of water-table depth fluctuations on nutrient availability and plant productivity in riparian and wetland ecosystems (Holden et al., 2004; Hefting et al., 2004; Choi et al., 2007; Sulman et al., 2013). Furthermore, it is unlikely that such an extended positive growth response to temperature in this coastal environment is related to a dominant direct temperature limitation on cambial activity, as in some riparian species growing in the high Andean drylands (Roig et al., 1988; Schmelter, 1999).

Temporal changes in correlations between tree growth and model-based soil moisture and rainfall variability suggest a shift from a concurrent to a lagged growth response to moisture anomalies from around 1980 (Fig. 4). This coincides with an unusually high frequency of moisture extremes linked to more frequent and intense ENSO events after about 1976 (Trenberth and Hoar, 1997). Considering that El Niño events are essential to groundwater recharge in the region (Squeo et al., 2006), ENSO-induced wet extremes, such as during the rainy seasons of 1992–93 and 1997 are likely to result in unusually persistent flooding in the swamp during the entire subsequent growing season (Fig. 2a). Normal water levels return during the growing season of the following year, when the growth pulse occurs. Interactive effects of altered hydrology and biogeochemistry in the swamp after mild drainage, and nutrient and fine root dynamics during and following wet extremes are likely to be the main drivers of this delayed response of stem growth. However, we do not rule out the possibility of some systematic dating error in our tree-ring chronology since crossdating was difficult in many samples.

The nuances of the climate response of tree growth in the swamp result in poor correlations with vegetation growth (*Kageneckia*) in the interior montane drylands on a yearly basis (Fig. 6). However, the disagreement decreases on decadal and longer time scales because the influence of short term differences in the timing of growth responses to climate anomalies becomes smaller. Like in the swamp, tree growth in the montane drylands also has some degree of positive response to temperature (Barichivich et al., 2009). Therefore, common influences of both moisture and temperature variability contribute to the observed agreement between decadal growth patterns in the two environments. Prolonged growth reductions in the swamp and drylands coincide with severe drought during most of the 1960s and 1970s (Schneider, 1982; Barichivich et al., 2009), indicating a similar response to persistent climate anomalies.

Global climate models project a drying of the subtropical dry areas under increasing greenhouse gas (GHG) concentrations (Meehl et al., 2007). Therefore, regional aridity in north-central Chile is expected to continue increasing during the coming decades (Fuenzalida et al., 2007). This could pose a serious threat to the persistence of these millennial swamp forest ecosystems if they are not efficiently protected from anthropogenic disturbances that increase their vulnerability to climate changes.

Further research about the physiological responses of *M. exsucca* to flooding and drought conditions is needed. This tree species has morphological adaptations in the root system such as the formation of plank-buttressing, adventitious roots and aerenchyma tissue (González et al., 2003). These features are thought to facilitate the entry of oxygen into the root and the stem, and they are closely related to flooding duration. However, other physiological adaptations would be involved and these may vary seasonally according to habitat dynamics (Crawford, 2003). The effects of drought can be as important as flooding for tree survival and growth, particularly at the seedling stage (Parolin et al., 2010). A recent study in a swamp forest of the semiarid region of Chile highlights that *M. exsucca* seedlings are less resistant to drought conditions than the other dominant tree species of this ecosystem (Bascuñan-Godoy et al., 2013). These results become relevant under the projected climatic conditions for the semiarid region of Chile, which potentially could discontinue the present species composition of these swamp ecosystems.

6. Conclusion

The analysis of *M. exssuca* tree rings suggests that the ecological functioning of the swamp forests in this semiarid region is very resilient to short-term climate variability under natural growing conditions, but slight artificial drainage can trigger very dynamic growth responses to moisture and temperature variability. This indicates that well conserved, pristine swamps will be more resilient to the anticipated increase in regional aridity during the coming decades than swamps that have undergone artificial drainage or are affected by excessive groundwater abstraction. Further tree-ring studies in pristine swamps will help to validate the ecological patterns observed in the Palo Colorado swamp. In addition, ecophysiological studies looking at the links between temperature, nutrient dynamics and tree growth are needed to understand the complex ecological response to drainage found in this swamp.

Author contributions

M.P.P. and J.B. analyzed data and wrote the paper. All authors designed the research, discussed the results and commented on the manuscript.

Acknowledgements

The authors thank Juan Sparwater and Nina Sparwater for his good will and facilities when working in the Palo Colorado forest, Leticia González and José Reyes for fieldwork assistance, Duncan Christie and Daniel Sthale for providing useful comments on the manuscript, and the Dirección General de Aguas de Chile for facilitating the well static levels. We also thank two anonymous reviewers for their valuable comments. This work was carried out with the aid of grants from the Chilean Research Council (FONDECYT 11070016) and the Inter-American Institute for Global Change Research CRN II # 2047 supported by and the US National Science Foundation (GEO-0452325). M.P.P and J.B. were supported by scholarships from the Chilean Government for doctoral studies under the program Formación de Capital Humano Avanzado of CONICYT.

Appendix A. Supplementary material

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2014.05.003.

References

Aceituno, P., 1988. On the functioning of the southern oscillation in the South American sector. Part I: surface climate. Monthly Weather Review 116, 505–524.

Barichivich, J., Sauchyn, D.J., Lara, A., 2009. Climate signals in high elevation tree-rings from the semiarid Andes of north-central Chile: responses to regional and large-scale variability. Palaeogeography, Palaeoclimatology, Palaeoecology 281, 320–333.

Bascuñan-Godoy, L., Alcaino, C., Carvajal, D.E., Sanhueza, C., Montecinos, S., Maldonado, A., 2013. Different photoprotective responses under drought conditions of two predominant Chilean swamp forest species. Gayana Botánica 70, 279–286.

Choi, W.J., Chang, S.X., Bhatti, J.S., 2007. Drainage affects tree growth and C and N dynamics in a minerotrophic peatland. Ecology 88, 443–453.

Cook, E.R., Briffa, K.R., Meko, D.M., Graybill, D.A., Funkhouser, G., 1995. The 'segment length' curse in long tree-ring chronology development for palaeoclimatic studies. Holocene 5, 229–237.

Correa-Araneda, F., Urrutia, J., Figueroa, R., 2011. Estado del conocimiento y principales amenazas de los humedales boscosos de agua dulce de Chile. Revista Chilena de Historia Natural 84, 325–340.

Crawford, R.M.M., 2003. Seasonal differences in plant responses to flooding and anoxia. Canadian Journal of Botany 81, 1224–1246.

Fan, Y., van den Dool, H., 2004. Climate prediction center global monthly soil moisture data set at 0.5 degrees resolution for 1948 to present. Journal of Geophysical Research 109 (D10). Art. No. D10102.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, London.

Fuenzalida, H., Aceituno, P., Falvey, M., Garreaud, R., Rojas, M., Sánchez, R., 2007. Study on Climate Variability for Chile During the 21st Century (Technical Report prepared for the National Environmental Committee (CONAMA)). Department of Geophysics, Universidad de Chile, Santiago.

Garreaud, R., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day South American climate. Palaeogeography, Palaeoclimatology, Palaeoecology 281, 180–195.

González, M., Hauenstein, E., García, M., Peña-Cortés, F., Urrutia, O., 2003. Comentarios sobre bosques pantanosos, humedales importantes del centro-sur de chile. Gestion ambiental 13, 3–13.

Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2013. Updated high-resolution grids of monthly climatic observations. International Journal of Climatology 34, 623–642.

Hefting, M., Clement, J.C., Dowrick, D., Cosandey, A.C., Bernal, S., Cimpian, C., Tatur, A., Burt, T.P., Pinay, G., 2004. Water table elevation controls on soil nitrogen cycling in riparian wetlands along a European climatic gradient. Biogeochemistry 67, 113–134.

Holden, J., Chapman, P.J., Labadz, J.C., 2004. Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. Progress in Physical Geography 28, 95–123.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurements. Tree-Ring Bulletin 43, 69–75.

LeQuesne, C., Stahle, D., Cleaveland, M., Therrel, M., Aravena, J.C., Dunn, J., Barichivich, J., 2006. Ancient Cipres tree-ring chronologies used to reconstruct Central Chile precipitation variability from A.D: 1200–2000. J. Clim. 19, 5731–5744.

Maldonado, A., Villagrán, C., 2002. Paleoenvironmental changes in the semiarid coast of Chile (~32°S) during the last 6200 cal years inferred from a swamp-forest pollen record. Quaternary Research 58, 130–138.

Maldonado, A., Villagrán, C., 2006. Climate variability over the last 9900 cal yr BP from a swamp forest pollen record along the semiarid coast of Chile. Quaternary Research 66, 246–258.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.C., 2007. Global Climate Projections Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 747–845.

Melvin, T.M., Briffa, K.R., 2013. CRUST: Software for the implementation of regional chronology standardisation: part 1. Signal-free RCS. Dendrochronologia 32, 7–20.

Miller, A., 1976. The climate of Chile. In: Schwerdtfeger, W. (Ed.), World Survey of Climatology. Climates of Central and South America. Elsevier, Amsterdam, The Netherlands, pp. 113–131.

Montecinos, A., Aceituno, P., 2003. Seasonality of the ENSO related rainfall variability in central Chile and associated circulation anomalies. Journal of Climate 16, 281–296.

Pallardy, S.G., Kozlowski, T.T., 2007. Physiology of Woody Plants, first ed. Academic Press, New York.

Parolin, P., Lucas, C., Piedade, M.T.F., Wittmann, F., 2010. Drought responses of flood-tolerant trees in Amazonian floodplains. Annals of Botany 105, 129–139.

Roig, F.A., Villalba, R., Ripalta, A., 1988. Climatic factors in *Discaria trinervis* growth in Argentine Central Andes. Dendrochronologia 6, 61–70.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

San Martín, J., Troncoso, A., Ramírez, C., 1988. Estudio fitosociológico de los bosques pantanosos nativos de la cordillera de la costa en Chile central. Bosque 9, 17–33.

Schmelter, A., 1999. The temperature-growth relationship of Discaria trinervis in the central Andes of Argentina (33°35°S) and the influence of local site factors. Dendrochronologia 17, 87–98.

Schneider, Hans J., 1982. Drought, demography, and destitution: crisis in the Norte Chico. GeoJournal 6.2, 111–119.

Squeo, F.A., Aravena, R., Aguirre, E., Pollastri, A., Jorquera, C.B., Ehleringer, J.R., 2006. Groundwater dynamics in a coastal aquifer in north-central Chile: implications for groundwater recharge in an arid ecosystem. Journal of Arid Environments 67, 240–254.

Sulman, B.N., Desai, A.R., Mladenoff, D.J., 2013. Modeling soil and biomass carbon responses to declining water table in a wetland-rich landscape. Ecosystems 16, 491–507.

Trenberth, K.E., Hoar, T.J., 1997. El Niño and climate change. Geophysical Research Letters 24, 3057–3060.

Varela, J., 1981. Geología del Cuaternario del área de los Vilos-Ensenada El Negro (IV Región) y su relación con la existencia del bosque 'relicto' de Quebrada Quereo. In: Congreso Internacional de Zonas Áridas y Semiáridas, vol. 33, pp. 17–30. La Serena.

Villagrán, C., 1982. Estructura florística e historia del bosque pantanoso de Quintero (Chile, V Región) y su relación con las comunidades relictuales de Chile Central y Norte Chico. Actas del III Congreso Geológico Chileno, 377–402.

Villagrán, C., Varela, J., 1990. Palynological evidence for increased aridity on the central Chilean coast during the Holocene. Quaternary Research 34, 198–207.

Villa-Martínez, R., Villagrán, 1997. Historia de la vegetación de los bosques pantanosos de la costa de Chile central durante el Holoceno medio y tardío. Revista Chilena de Historia Natural 70, 391–401.

Vuille, M., Milana, J.P., 2007. High-latitude forcing of regional aridification along the subtropical west coast of South America. Geophysical Research Letters 34, 1–6.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with application in dendroclimatology and hydrometeorology. Journal of Applied Meteorology 23, 201–213.

Zang, C., Biondi, F., 2013. Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. Dendrochronologia 1, 68–74.

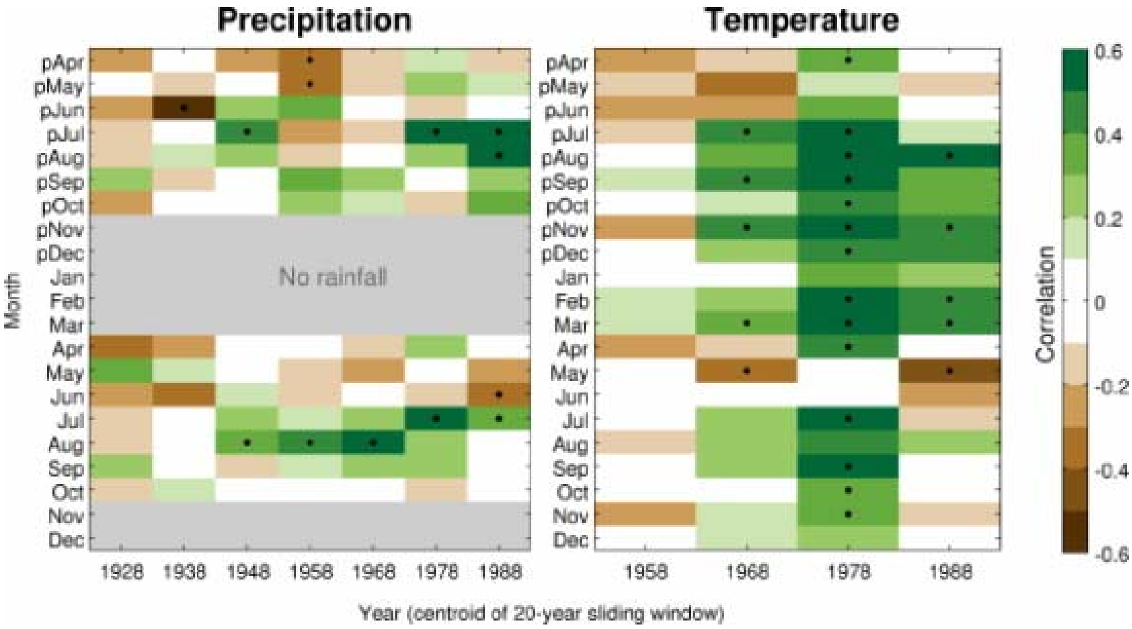

Fig. S1. Temporal patterns of correlation between the annual growth of *M. exsucca* and monthly precipitation and temperature based on regionally averaged station records rather than on gridded estimates. Correlations are shown from April of the previous growing year (p) to December of the current growing year using 20-year running windows with an overlap of 10 years between consecutive windows. The stippling denotes significant correlations ($P < 0.1$). The regional precipitation record covering the period 1901–2000 was developed by Barichivich et al. (2009) and corresponds to the average of 12 gauges located between 27° and 32°S. The mean air temperature record corresponds to the average of Punta Tortuga (29.92°S; 1930–1992) and La Serena (29.90°S; 1930–2003) stations, located in the semi-arid coast about 200 km north of Palo Colorado (32.08°S). Notice that the correlation patterns are very similar to those shown in Fig. 4 in the manuscript and thus support our results based on gridded data (CRUTS 3.20).

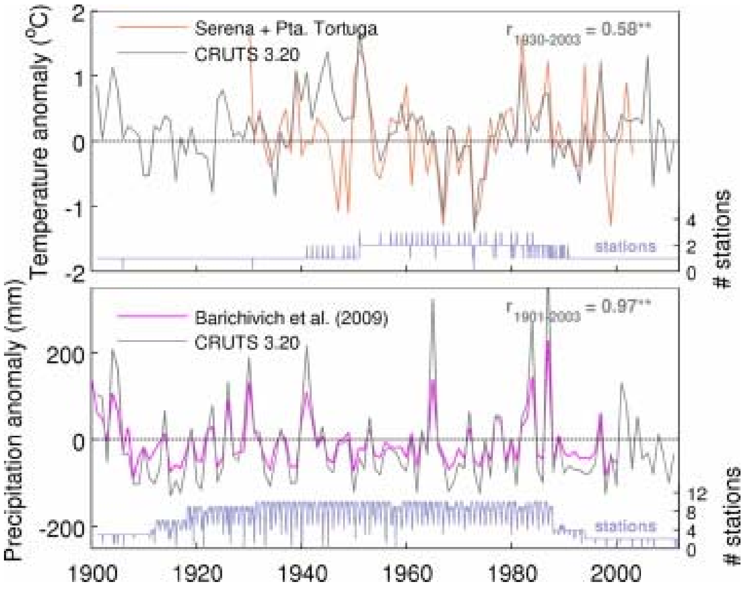

Fig. S2. Comparison between gridded (CRUTS 3.20, see Fig. 5) and station-based averages of mean air temperature during July–October and precipitation during July–August (see Fig. S1 for description). The monthly number of station records included in the CRUTS 3.20 gridded fields located within a distance of 150 km north and south of Palo Colorado is shown to assess the reliability of the gridded estimates. Correlations between the series and their significance (*: $p < 0.05$, **: $p < 0.01$) are indicated in each plot. Gridded estimates are generally highly consistent with regional series based on local station records, particularly for precipitation. The only discrepancy occurs between the temperature series during the period before 1950, when there is only one station included in the CRUTS 3.20 dataset within a distance of 150 km from the nearest grid box to Palo Colorado.