



The influence of climate on the masting behavior of Mexican beech: growth rings and xylem anatomy

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Received: 23 November 2017 / Accepted: 21 August 2018 / Published online: 31 August 2018
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Abstract

Key message The Mexican beech undergoes masting events, on average, every 5.5 years. These events depend directly on precipitation.

Abstract Climate change has considerably impacted the protective functions of tropical montane cloud forests, possibly influencing the synchronicity of phenological processes and the distribution and physiology of plants. In particular, climatic fluctuations cause changes in the distribution of tree species. Mexican beech (*Fagus grandifolia* subsp. *mexicana*) is considered an endangered species, due to its restricted distribution and its being a Miocene relict, limited to tropical montane cloud forests in the mountains of the Sierra Madre Oriental in eastern Mexico. We analyzed the influence of temperature and precipitation in prompting changes to tree-ring width, as well as vessel frequency and diameter, of Mexican beech in eastern Mexico. We used growth rings and xylem vessels traits to infer the historical masting events of Mexican beech over the last 128 years. We obtained independent chronologies for Mexican beech in each of the studied sites, dating back 152–178 years. Precipitation was strongly associated with differences in tree-ring width between masting and non-masting years. Our study highlights the use of dendroecological research to detect climate-induced modifications in the vessel frequency and diameter of tree species inhabiting tropical montane cloud forests. This association also explained differences in vessel frequency and diameter recorded before, during, and after masting events. Our results revealed that Mexican beech undergoes masting events every 5.5 years on average, and that these events directly depend on minimum annual precipitation. In conclusion, our results advance our understanding on the plasticity of growth rings and vessels traits (frequency and diameter) in response to fluctuation in precipitation.

Keywords Climate variables · Dendromastecology · *Fagus grandifolia* subsp. *mexicana* · Tropical montane cloud forest · Xylem vessels · Masting

Introduction

Climate change is likely to have serious impacts on the protective functions of tropical montane cloud forests worldwide (Webster 1995). Climatic fluctuations significantly

influence the phenology, distribution and physiology of plants (Speer 2010; Ming-Lee et al. 2015). Although cycles of climate change extend over centuries and millennia (e.g., climatic variations), current global warming is expected to generate similar climatic fluctuations over the following decades. The rapid rate of change is expected to have a direct effect on the capacity of forest species to adapt to future climatic conditions (Helama et al. 2004; Tinoco-Rueda et al. 2009; Schoene and Bernier 2012; Rehm et al. 2015). More specifically, ongoing precipitation and temperature variations might have a severe impact on tropical montane cloud forests by influencing the phenology and distribution of several plant species in these communities.

Apart from deforestation, current climate change represents the greatest threat to tropical montane cloud forests, due to changes in the patterns of precipitation and cloud

Communicated by A. Bräuning.

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immersion (e.g., fog, mist and cloud water), which are associated with rising temperatures, habitat fragmentation, and increasing green-house gas emissions (Price et al. 2011; Ponce-Reyes et al. 2012). Reduced cloud immersion and increased evapotranspiration, resulting from global warming, directly influence several ecological and phenological processes in tropical montane cloud forests plant species, such as masting events (Price et al. 2011; Esperón-Rodríguez and Barradas 2015; FAO 2015).

Masting behavior occurs in many tree species in temperate regions (Harper 1977), serving as an adaptive strategy to climatic variation and/or as a strategy to avoid seed predation (Kelly 1994; Pearse et al. 2016). Several studies have shown that temperature, precipitation, and phenological events in masting years directly affect growth-ring width and vessel traits (García-González and Fonti 2008; Fonti et al. 2010; Speer 2010; González-González et al. 2013).

In recent decades (since 2001), dendroecological research has provided important tools for describing historical–ecological events and phenological variation in forest species (Schweingruber 1996; Speer 2010; D'Arrigo et al. 2014; Hacket-Pain et al. 2015; Amoroso et al. 2017). Such events are inferred from variation in tree-ring width and vessel traits, which, in turn, are used to reconstruct the forest history of relict and endemic tree species (Gareca et al. 2010; Génova and Moya 2012; Rita et al. 2015). Several authors have analyzed various environmental factors (e.g., maximum and minimum temperature and precipitation) associated with the timing of mass flowering in beech trees (Övergaard et al. 2007; Kon and Noda 2007; Sawada et al. 2008; Latte et al. 2015). Most of these authors suggest that flowering mostly occurs after years with benign environmental conditions, such as high temperatures during the summer months. These environmental conditions promote high rates of carbon assimilation by trees, leading to enhanced flower bud development and beechnut production. Several authors have studied different factors that trigger flowering and, in consequence, beechnut production. Masting events typically occur after 2 years with high temperature and low precipitation during the summer months, preceded by a year with low summer temperature and high precipitation (Matyas 1965; Norton and Kelly 1988; Piovensan and Adams 2005; Övergaard et al. 2007; Burns 2012; Etemad and Sefidi 2017).

Temperature represents one of the most important environmental factors affecting the growth of *Fagus* worldwide (Fang and Lechowicz 2006). In addition, several authors have suggested that high summer temperatures (June–July), in a particular year, are strongly associated with the onset of masting in *Fagus* during the following year (Ehni 1981; Suzuki et al. 2005; Kon and Noda 2007; Bradshaw et al. 2010; Hacket-Pain et al. 2015). For instance, Bayramzadeh et al. (2008) and Noyer et al. (2017) reported that vessels of *Fagus* trees develop structural modifications in

response to climatic and phenological events. These climatic events (e.g., high temperature and precipitation) are detected through temporal variations in tree-ring width in angiosperms and gymnosperms, partly due to the increased recovery-times of trees after such events (Speer 2010; Bryukhanova and Fonti 2013).

Fagus grandifolia subsp. *mexicana* (Mexican beech) is a Miocene relict species that is endemic to the tropical montane cloud forests of eastern Mexico. This species occurs at elevations of 1450–1987 m and is considered as endangered under Mexican law (Télliz-Valdés et al. 2006; SEMARNAT 2010; González-Espinosa et al. 2011). Reports suggest that Mexican beech diverged from *Fagus grandifolia* Ehrh, which inhabits the USA and Canada, approximately 7 million years ago (Manos and Stanford 2001; Denk and Grimm 2009). Mexican beech exhibits synchronous masting, which might be the result of autoecological reproductive strategies or a product of environmental changes, such as persistent droughts (Kelly 1994; Piovensan and Adams 2005).

The most extensive and least disturbed Mexican beech forests are located in the state of Hidalgo, in eastern Mexico (Rodríguez-Ramírez et al. 2013). These forests are characterized by the presence of masting events at every 2- to 8-year intervals (Ehni 1981; Pérez-Rodríguez 1999). It was found that Mexican beech is susceptible to climatic variations, such as those associated with higher elevations, drought, and seasonal frosts (Ehni 1981; Rodríguez-Ramírez et al. 2016, 2018). Natural disturbances, such as strong winds, hurricanes, and storms, regulate the development of Mexican beech forests (Peters 1992), causing suppression and release events in tree-ring width (Peters 1995).

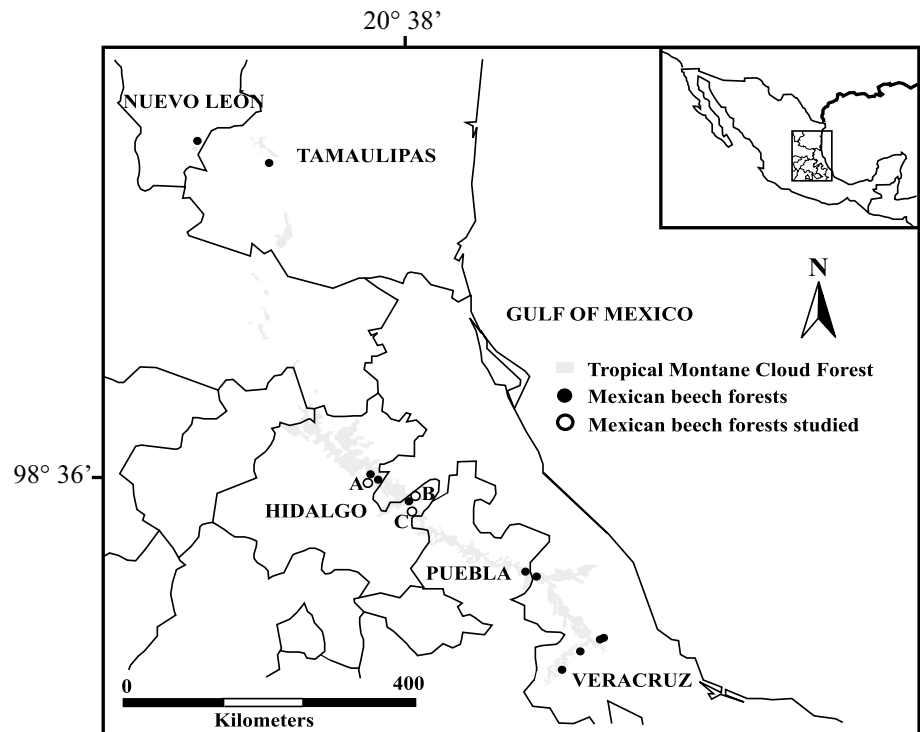
The relationship between tree-ring width and vessel traits in masting events of Mexican beech trees and the climatic factors that trigger these processes remain largely unknown (Rodríguez-Ramírez et al. 2018). Because of this, our main aim is to reconstruct historical masting events of Mexican beech trees using dendroecological methods. The objectives of this study are: (1) to identify how precipitation and temperature are associated with masting events, and (2) to identify if any differences exist in tree-ring widths and vessel traits (e.g., diameter and frequency) between masting and non-masting years occurring between the years 1980 and 2012.

Materials and methods

Study area

We selected three fragments of Mexican beech forests located in the Sierra Madre Oriental, which stretches in a north–south direction throughout eastern Mexico (Fig. 1). Temperate climate (Cb sensu García 1988)

Fig. 1 Geographical location of the three study sites of *Fagus grandifolia* subsp. *mexicana* (Mexican beech) in the tropical montane cloud forests of the Sierra Madre Oriental, Mexico. **A** La Mojonera; **B** Medio Monte; **C** El Gosco



was characterized by mild temperatures (14.5–24.4 °C), including a dry cool season from November to January, a dry warm season from early February to May, cool summers (June–July) and a wet cool season from August to October. Humidity levels are in the range of 60–85% (Peters 1995; Williams-Linera et al. 2002). The soils of the sites are vitric (Tv) and humic (Th) andosols (FAO-UNESCO 1988) with light sandy-clay loam texture and pH values of 4 to 6 (Peters 1995).

The Mexican beech forests are characterized by dominant tree species with Holarctic affinities, such as Mexican beech (*F. grandifolia* subsp. *mexicana*), Martínez spruce (*Picea martinezii* T. F. Patterson), Mesoamerican yew (*Taxus globosa* Schltdl.), Magnolia (*Magnolia schiedeana* Schltdl.), Patula pine (*Pinus patula* Schltdl. & Cham.), Aztec pine (*Pinus teocote* Schltdl. & Cham.), several oak species (*Quercus meavei* Valencia-A., Sabás & Soto, *Q. delgadoana* S. Valencia, Nixon & L. M. Kelly and *Q. trinitatis* Trel.), sweetgum (*Liquidambar styraciflua* L.), and Mexican *Clethra* (*Clethra mexicana* DC.). These species are intermingled with evergreen tree species with Neotropical affinities, such as Zapotillo (*Sideroxylon portoricense* subsp. *minutiflorum* (Pittier) T.D. Penn.), Tarflower (*Befaria aestuans* L.), sweetwood (*Nectandra* spp.), wild avocado (*Persea* spp.), and Sabino (*Podocarpus matudae* Lundell) (Gual-Díaz and Rendón-Correa 2014; Rzedowski 2015).

Sample collection and chronology development

At each site, 20 dominant Mexican beech trees were selected ($N=60$) based on the criteria established by Peters (1992) and Hokusima et al. (2013): (1) diameter at breast height (DBH) > 40 cm; (2) a height of 10–25 m; and (3) no evidence of scars or rot. For each tree, two cores were sampled at 1.3 m (breast height) with a Håglof® borer. We obtained a total of 120 wood cores from the three sites. At each site, we revised three complete cross-section discs from fallen trees as samples of growth patterns of Mexican beech in each locality and to detect ecological events (e.g., fire scars, defoliations, growth suppressions, and releases) affecting the forests (Fritts 1976). Sampled dominant Mexican beech trees were selected randomly within each site, ensuring that they encompassed the greatest possible variation in habitat characteristics (e.g., slopes ranging from 0.45° to 43.8° and distances of 30–500 m from water bodies).

The wood cores were dried at room temperature and were then mounted and polished with successively coarse grits (100 and 360) and fine grit sandpapers (400, 600, 3800, and 10,000) until the xylem cellular structure was visible in the transverse plane. Tree-ring series along the cores were dated by assigning calendar years to the rings through the identification of characteristic ring sequences (e.g., assigning to each ring the year in which growth started) as suggested by

Stokes and Smiley (1968) and Rozas et al. (2015). This dating was verified with software COFECHA (Holmes 1983; Grissino-Mayer 2001). We measured tree-ring widths using a stereoscopic microscope and a Velmex tree-ring measuring system with 0.001 mm accuracy using the software TSAP-Win v. 4.67c (Rinn 2003). The computer software COFECHA allowed the identification of missing tree rings and cross-dating errors. For the analyses, we excluded 60 wood cores that were in poor condition (e.g., cores with evidence of decay, cores that were not properly mounted, or cores of short length) following the recommendations of Rozas (2001).

To obtain the average of detrended tree-ring width indices (RWI), we standardized raw ring-width series with autoregressive modeling to remove serial correlation using the ARSTAN computer program (Cook and Holmes 1995). We removed the non-climatic trends from each tree-ring series using a cubic spline with a 50% response at 10-year periods. This approach was flexible enough to accentuate high-frequency climatic information and to reduce white noise from non-climatic variance related to ontogenetic trends and/or local disturbances (e.g., droughts, strong winds, hurricanes and storms). Through this, we enhanced inter-annual variability, possibly related to masting events and the production of narrow tree rings (Dittmar and Elling 2007; Gareca et al. 2010; Drobyshev et al. 2014; Rodríguez-Ramírez et al. 2018).

We performed autoregressive modelling of each standardized series to remove temporal autocorrelation (Box and Jenkins 1976) and maximize the climatic signal. To produce a standardized chronology, the resulting indexed series were averaged using a bi-weight mean to reduce the influence of outliers (Cook and Holmes 1995). Temporal autocorrelation in chronologies was prevalent, due to the residual impact of growing conditions from previous years (Speer et al. 2016).

Historical records of Mexican beech masting

We gathered data of past Mexican beech masting events registered for each studied site for the years 1980, 1990, 1992, 1997, 2004, and 2012 (Ehnis 1981; Pérez-Rodríguez 1999; Godínez-Ibarra et al. 2007; Rodríguez-Ramírez et al. 2013). There are no records on masting events for other Mexican beech populations along the distribution range of this species.

Digitalization of tree-ring width and vessels traits

For each site, we randomly selected five cores to obtain tree-ring digital images for the recorded masting years, as well as for the two consecutive years before and after masting events. The wood cores were prepared using the finest grit

sandpaper (10,000) and eliminating any dust with a hair drier. Since the ground tissue has very thick-walled fibers and parenchyma cells with dark deposits, the vessels lumen have a high contrast. In each digital image, we selected the area occupied by each tree-ring between two wood rays (an average of 7.5 mm width \times 9.1 mm length). The area varied with respect to tree-ring width before, during, and after masting events [e.g., the widest and narrowest rings were 6.6 mm width \times 8.3 mm length (ray to ray) and 2.5 mm width \times 1.6 mm length (minimum area of 54.7 and 4 mm², respectively; Fig. 2)]. These digital images were captured using a stereoscopic microscope (Axio Zoom.V16) with a 36 μ m field of depth and saved in TIFF format with a digital camera (AxioCam MRc 5, Zeiss) to a 1.3 μ m resolution. Figure 2 presents an example of a digitized core with marked radial tree-ring width and vessel traits (number of vessels/mm² and radial vessel diameter, μ m); this technique has been used successfully with other species (Venegas-González et al. 2015). In each area, we quantified and measured all the vessels present using the software ImageJ v. 1.5 with manual detection (Java-based Image Processing, National Institute of Health).

Reconstruction of masting events: dendromastecology

Mast year reconstruction used two sources of data. We first delimited the historical masting events in the tree-ring digital image of trees from Medio Monte according to the

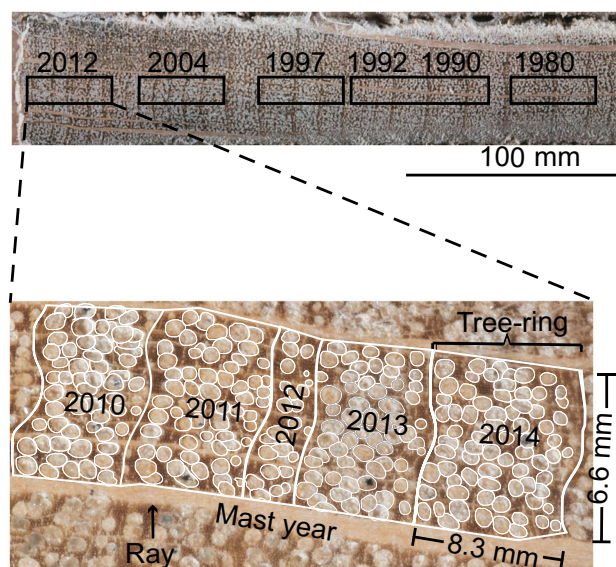


Fig. 2 Digitized images of a **a** representative wood-core of Mexican beech. **b** Micro-section of the representative wood-core showing annual tree rings (white lines) and vessels (white circles). Black rectangles represent historical masting years and ENSO event (year 2012)

historical records of Mexican beech masting. This region is considered as containing the most representative and best preserved Mexican beech forests studied (Rodríguez-Ramírez et al. 2013).

Finally, we compare variation in tree-ring width and vessel traits before, during and after masting year. We analyzed 10 randomly selected cores and captured tree-ring digital images, for the years ranging from 1847 to 2015 in Medio Monte to reconstruct historical masting events. The reason for restricting the analyses is because beech masting generally occurs in trees ≥ 40 years in age (Peters 1992; Drobyshev et al. 2010; Hukusima et al. 2013). Thus, we set 1886 as our initial year in the chronologies.

Earlier studies have suggested 2- to 8-year intervals between masting events (Rodríguez-Ramírez et al. 2013); therefore, we used this range of years to identify the tree-ring patterns around the recorded masting years. We used data on growth rings, before, during and after masting year to detect differences in tree-ring width and vessel traits.

Climate data

Several authors have suggested that mass flowering in beeches worldwide is triggered by two previous years with high summer temperature and low precipitation, preceded by a year with low summer temperature and high precipitation (Piovensan and Adams 2005; Kon and Noda 2007; Övergaard et al. 2007; Drobyshev et al. 2010; Ascoli et al. 2017).

To evaluate the association between temperature and precipitation with the masting data registered for Mexican beech trees, we gathered climate data for the period 1978–2011 (<http://clicom-mex.cicese.mx/>). These data included mean monthly values for minimum, average and maximum temperatures (T_{\min} , T_{avg} , and T_{\max}), as well as total annual precipitation (P_{rec}) of a single year with the lowest rainfall. We considered climatic data 2 years before each masting event (e.g., 1978, 1979, 1988, 1989, 1990, 1991, 1995, 1996, 2002, 2003, 2010, and 2011), which were corroborated using information from Climate-data.org (<http://es.climate-data.org/>).

Variation ranges of the tree-ring widths and vessel traits

We analyzed data on mean maximum temperatures and P_{rec} from climatic reconstructions for the State of Hidalgo (Cardoza-Martínez et al. 2013). To complete the missing information, we used the Drought-Net database (<http://www.drought-net.org/>) (Lemoine et al. 2016). This approach allowed the detection of narrow rings (≤ 1.00 mm) in the tree-ring digital images resulting from drought events, as suggested by Rozas et al. (2015).

We performed an Analyses of Variance (ANOVA) and Tukey multiple comparisons to assess if the values of tree-ring widths and vessel traits (frequency and diameter) differ significantly between drought years, non-masting years (NMY) and masting years (MY) in the studied forests. The analyses were performed using the R-library *vegan* in R (Version 2.14.0, <http://www.r-project.org>; Oksanen et al. 2016).

Influence of climate on tree-ring width and vessels traits

To test the relationship between climatic variables (T_{\max} , T_{\min} , T_{avg} and P_{rec}) and tree-ring width and vessels traits, we performed three non-metric multidimensional scaling (NMDS) analyses. This approach allowed for the detection of differences between tree-ring width developed in MY and NMY, and to identify which climatic variables influence tree-ring width and vessel traits.

NMDS ordination was based on Bray-Curtis distances and 20 randomizations to determine the most stable solution. In addition, Wisconsin double standardization and R^2 transformation were used as measures of ecological distance (Kenkel and Orlóci 1986). An advantage of this method is that the procedure is less dependent on data distribution than constrained methods, such as principal component analyses. The data were computed using the R-library *vegan* in the statistical software R.

To evaluate the NMDS, we used the stress-plot function and the Stress index to estimate R^2 values between the vectors and values of the ordination (R). The vectors for climatic factors (T_{\min} , T_{avg} , T_{\max} , and P_{rec}) and centroids were superimposed using the *envfit* function. We used the *ordisurf* function (within the *vegan* library) to draw the climatic variables in the space defined by two NMDS axes. *Ordisurf* fits smooth surfaces on the ordination using Generalized Additive Models (GAMs) with thin-plate splines (Wood 2000; Kindt and Coe 2005; Borcard et al. 2011). This approach allowed us to observe the relationship of climatic variables with tree-ring width and vessels traits. We used the Generalized Cross-Validation statistic (GCV score) to select the optimum model and minimize prediction error (Arlot and Celisse 2010).

Results

Dendromastecology of Mexican beech

The independent chronologies for Mexican beech extended up to 188 years for La Mojonera, 168 for Medio Monte, and 152 for El Gosco. A correlation between the three sites

Table 1 Growth-ring statistics for *Fagus grandifolia* subsp. *mexicana* (Mexican beech) at the three study sites in the Tropical Montane Cloud Forests of the Sierra Madre Oriental, Mexico

Statistics	La Mojonera	Medio Monte	El Gosco
Sampled trees	20	20	20
Crossdated series ^a	24	28	28
Master series (years)	1828–2015	1847–2015	1863–2015
Crossdated rings ^a	2198	3094	2700
Series intercorrelation ^a	0.67	0.68	0.71
Mean sensitivity ^a	0.39	0.33	0.36
Autocorrelation ^a	0.50	0.56	0.51
Mean/median age (years) ^b	93.29/89	110.5/119.5	96.5/92
Common interval	1942–2015	1899–2015	1949–2015
Signal to noise ratio ^c	27.10	16.21	21.72

^aValues obtained with COFECHA (Holmes 1999b)

^bValues statistically different using a Mann–Whitney test ($P=0.01$)

^cValues obtained with ARSTAN (Cook and Holmes 1999)

was detected, where the mean sensitivity to climatic variables was high and similar among sites (Table 1). Decreased radial growth was associated with several historical ENSO events (e.g., 1828–1830, 1850–1866, 1869–1890, 1905, 1913, 1918, 1929–1930, 1940, 1963, 1970, 1972, 1976, 1983, 1991, 1997, and 2012; Fig. 3a).

The climatic reconstruction of Cardoza-Martínez et al. (2013) for the state of Hidalgo, together with data from Drought-Net, allowed us to recognize in the tree-ring digital images of trees from Medio Monte, 15 additional historical masting events for Mexican beech trees, to detect short 2-year periods (1955–1956, 1990–1992) between masting events (Fig. 3b). Notwithstanding, the dendrochronological reconstruction of historical masting events showed two 8-year periods (1926–1934, 2004–2012) between MY (Fig. 3b). Interestingly, these periods revealed precipitation values ranging from 1748 to 1798 mm, with a mean of ≥ 1750 mm (Fig. 3c). We estimated a mean of 5.5 years between MY recorded for Mexican beech in the state of Hidalgo. Likewise, we identify differences between tree-ring digital images and vessel traits formed during drought events, NMY and those associated with MY. ANOVA showed that statistically significant differences were present for vessel frequency and diameter in the Mexican beech forests studied (Table 2).

Vessel frequency and diameter were significantly higher in NMY and decreased in MY ($P < 0.05$). Both traits during the MY decreased one-fold or more compared to drought events and NMY, maintaining the negative scaling between these two variables ($rs_{MY} = -0.27$, $P < 0.05$). Notwithstanding, tree-ring widths did not differ significantly between NMY's, drought years and MY's (Fig. 4a); the

same pattern was maintained for the reconstructed MY events (Fig. 4b).

Linking climate variation with tree-ring width and vessel traits

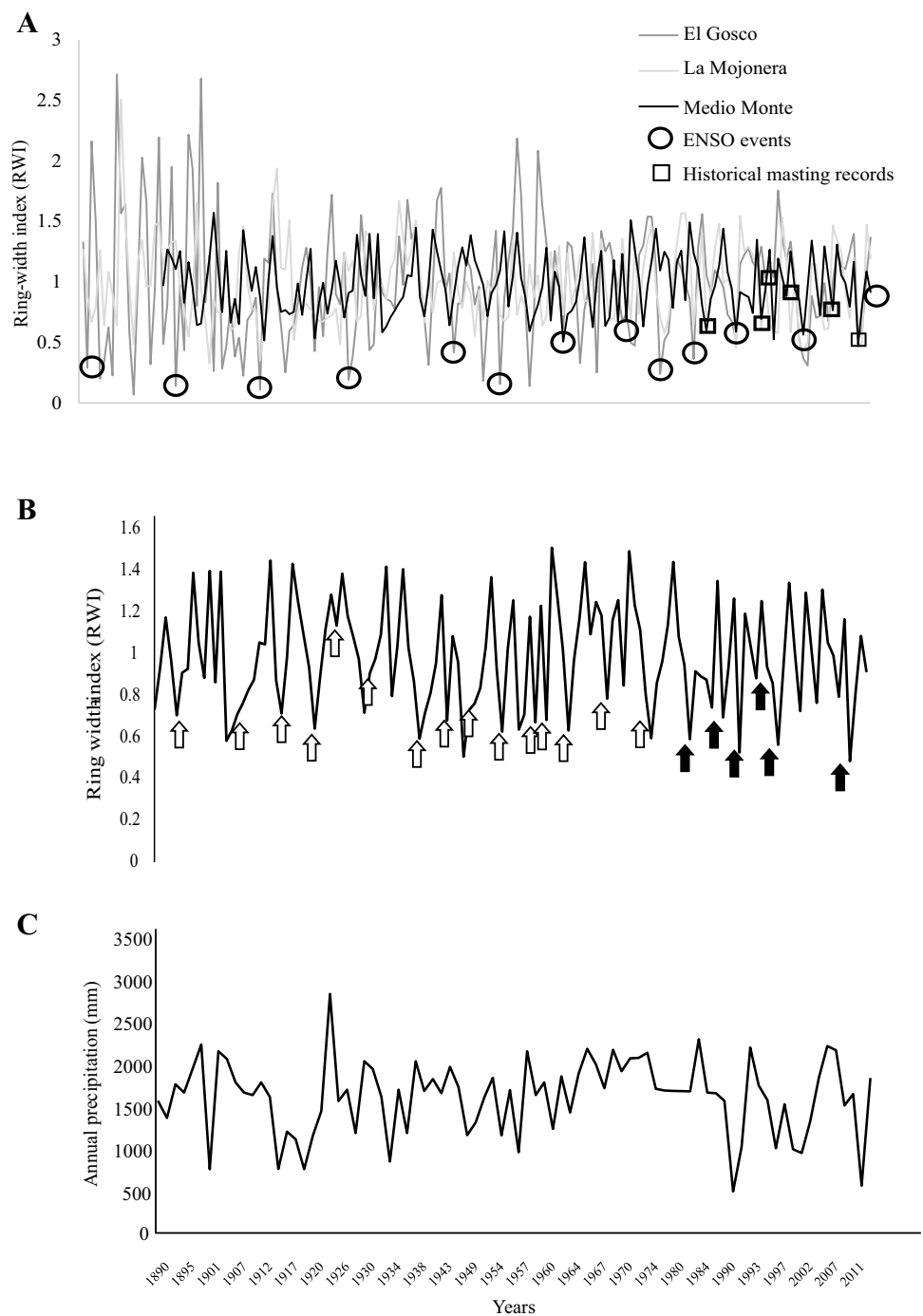
Ordination using NMDS showed that P_{rec} was significantly associated with tree-ring width at the three sites (Fig. 5a; GCV score: 0.044; stress: 0.104). In turn, P_{rec} had a considerable effect on vessel diameter and frequency (Fig. 5b, c; GCV score: 0.013, 0.044; stress: 0.120, 0.082). The NMDS2 values did not influence the T_{max} for tree-ring width (Fig. 5; Table 3). Notwithstanding, NMDS2 was slightly conspicuous for T_{max} with respect to vessel diameter and frequency (Fig. 5b, c).

Discussion

Tropical montane cloud forests drive important ecological, hydrological, and climatological processes (Price et al. 2011). If tropical montane cloud trees begin to experience drought conditions resulting in cavitation, forest die-off might occur, leading to substantial changes in the growth and regeneration capacity of many tree species. This study shows that the radial growth of Mexican beech has been affected by specific climatic events such as drought at each Mexican beech forest studied (Fig. 3; Table 1). Compared to the other two sites (La Mojonera and Medio Monte), the Mexican beech trees at El Gosco were younger and had lower rates of tree-ring width. This result reinforced the observation that the Mexican beech forest at El Gosco has been affected by anthropogenic and natural disturbances in the recent past (Rodríguez-Ramírez et al. 2013). Possibly, this effect might correspond to the phase of canopy closure, with the convergence of individual crowns and initiation of intra-tree competition. This effect was observed by *Podocarpus salignus* D. Don. in Chile (Rozas et al. 2016). Climatic variations at each site might influence the tree-ring width of beech trees (Gual-Díaz and Rendón-Correa 2014), which is reflected by the presence of narrow rings (Fig. 3).

Our results suggest that Mexican beech trees undergo masting events, on average, every 5.5 years and that these events might be directly dependent on P_{rec} . The results agree with those obtained by Drobyshev et al. (2014) for *Fagus sylvatica* from Europe. Climate change (e.g., high summer temperature, ENSO events) involving diminished precipitation might lead to the shortening of masting events (Fig. 3). Minimum annual precipitation plays a key role on tree-ring width of Mexican beech trees (Fig. 4; Table 2), rather than summer temperatures (Fig. 3), as for other species of *Fagus*

Fig. 3 **a** Ring-width chronologies for Mexican beech forests. Black circles represent ENSO events and gray squares historical masting. Gray areas indicate the period (1978–2015) including ring-width chronologies for masting years. **b** Ring-width chronologies and masting events for the Medio Monte site. Black arrows represent recorded masting years and white arrows represent reconstructed masting years; and **c** reconstruction of annual precipitation in eastern Mexico for the period 1890–2015 (modified from Cardoza-Martínez et al. 2013)



(Drobyshev et al. 2014; Hacket-Pain et al. 2015). These climatic fluctuations (temperature and precipitation) are congruent with the patterns observed in other deciduous tree species in montane forests, such as *Quercus ilex* Lour., *Olea europea* L., and *Ilex aquifolium* L. (Abrantes et al. 2013; Rossi et al. 2013; Rita et al. 2015).

Our results revealed no significant associations between tree-ring width and T_{\max} (Table 3; Fig. 5), which has been proposed as the main factor affecting growth in other

species of *Fagus* with northern distributions (Suzuki et al. 2005; Kon and Noda 2007; Bradshaw et al. 2010; Drobyshev et al. 2014; Hacket-Pain et al. 2015). The particular growth pattern of Mexican beech is the result of its southernmost distribution compared with other *Fagus* species worldwide. This phenomenon reflects the different plant associations and climatic conditions in which Mexican beech thrive (Fang and Lechowicz 2006; Rodríguez-Ramírez et al. 2016, 2018).

Table 2 Values (mean \pm SD and CV) for the Mexican beech forest studied

Sites	Tree-ring width (mm)		Vessel frequency (Vessel/ mm ²)		Radial vessel diameter (μ m)	
	Mean	CV	Mean	CV	Mean	CV
La Mojonera						
Drought year	0.81 \pm 0.80	1.32	110 \pm 103	10.3	85 \pm 9.4	2.54
NMY	1.1 \pm 1.12	0.8	250 \pm 232	18.3	90.2 \pm 10.1	5.87
MY	0.7 \pm 0.7	1.12	70 \pm 69	0.58	49 \pm 5.01	1.0
Medio Monte						
Drought year	0.80 \pm 0.91	2.28	100 \pm 112	1.9	91.4 \pm 9.1	4.32
NMY	1.13 \pm 1.45	3.84	120 \pm 132	2.35	82 \pm 8.7	4.56
MY	0.77 \pm 0.70	1.0	72 \pm 71	1.00	53 \pm 5.1	3.9
El Gosco						
Drought year	0.79 \pm 0.79	2.27	150 \pm 148	2.18	71 \pm 8.1	19.4
NMY	1.0 \pm 1.35	1.11	250 \pm 249	6.27	92 \pm 9.3	36.5
MY	0.81 \pm 0.80	1.23	71 \pm 72	1.00	48.9 \pm 4.3	1.56
	$F_{2,22} = 5.00$ $P \leq 0.0001$		$F_{2,22} = 7.18$ $P = 0.015$		$F_{2,22} = 2.37$ $P = 0.012$	

Bold values represent significant differences among variables as indicated by ANOVA and Tukey post hoc tests at $P < 0.05$

The observed differences in tree-ring width between MY and NMY in Mexican beech are indicative of the adaptive mechanisms of these trees to masting and climatic events (even ENSO events such as 2012, Figs. 2, 4; Table 2). The production of narrow rings in response to masting events, independent of climatic events (such as droughts), has also been reported in other *Fagus* species [e.g., *F. grandifolia* Ehrh in USA (Wason et al. 2017); *F. crenata* Blume in Japan (Sawada et al. 2008); and *F. sylvatica* L. in Europe (Hacket-Pain et al. 2015)]. Our results showed that tree-ring width within the MY had narrower variation than that of NMY or drought years. Therefore, instead of growth, resources are assigned to beechnut production during MY because of water deficits.

Our study revealed that vessel-related anatomical traits (frequency and diameter) adjust in response to drought events, NMY, and MY, corroborating the high plasticity mentioned for other *Fagus* species (Bayramzadeh et al. 2008; Pourtahmasi et al. 2011; Yin et al. 2016; Noyer et al. 2017). When a masting event occurs, Mexican beech develops fewer and narrower vessels, even narrower than in drought years (Fig. 4), maintaining their negative scaling. This finding is interesting because Mexican beech produces narrow vessels during MY to ensure hydraulic safety. Thus, vascular cambium modifications may be related with a trade-off between growth (narrow vessels during short periods of time) and beechnut production (Fig. 4). The plasticity in vessel frequency and diameter regulates water-transport efficiency, reflecting the ability of tropical montane cloud trees to adapt to climatic fluctuations as droughts and phenological events (Eller et al. 2017; von Arx et al. 2013;

Rodríguez-Ramírez et al. 2018). Further anatomical studies of *Fagus* species worldwide are needed to understand vessel plasticity during masting events.

Structural modifications were indicated in differences in vessels traits during MY. These modifications might be related to hormonal changes (Chan and Cain 1967; Aloni 1987; Tyree and Zimmermann 2002; Rita et al. 2015) and environmental conditions, such as temperature, precipitation, wind, and inter-annual differences (Kelly 1994; Pearse et al. 2016). Similar modifications have been observed in other beech trees species such as *Fagus orientalis* in Middle East (Eşen 2000; Pourtahmasi et al. 2011); *Fagus sylvatica* in Europe (Hacket-Pain et al. 2015); and *F. crenata* in Japan (Kabeya et al. 2017). In these species, individual trees structurally modify their vessels before masting (Speer 2001). However, other biotic and abiotic factors (e.g., volatile organic chemicals, pathogens, fires, pollution, environmental factors) are needed to generate specific structural changes, with carbon distribution contributing to the modification of vessels traits and the resulting development of narrow tree rings (Sass and Eckstein 1995; Anderegg and Meinzer 2015). Such narrow tree rings appear to be essential for the onset of masting events (Övergaard et al. 2007).

We used several dendroecological techniques to detect differences in tree-ring width between MY and NMY (Fig. 5), which allowed for the reconstruction of historical masting events that are not on record. Our results suggest that reduced annual precipitation (814–998 mm) directly influences tree-ring width and vessel traits. This reconstruction suggests that masting events, both over short (2 years)

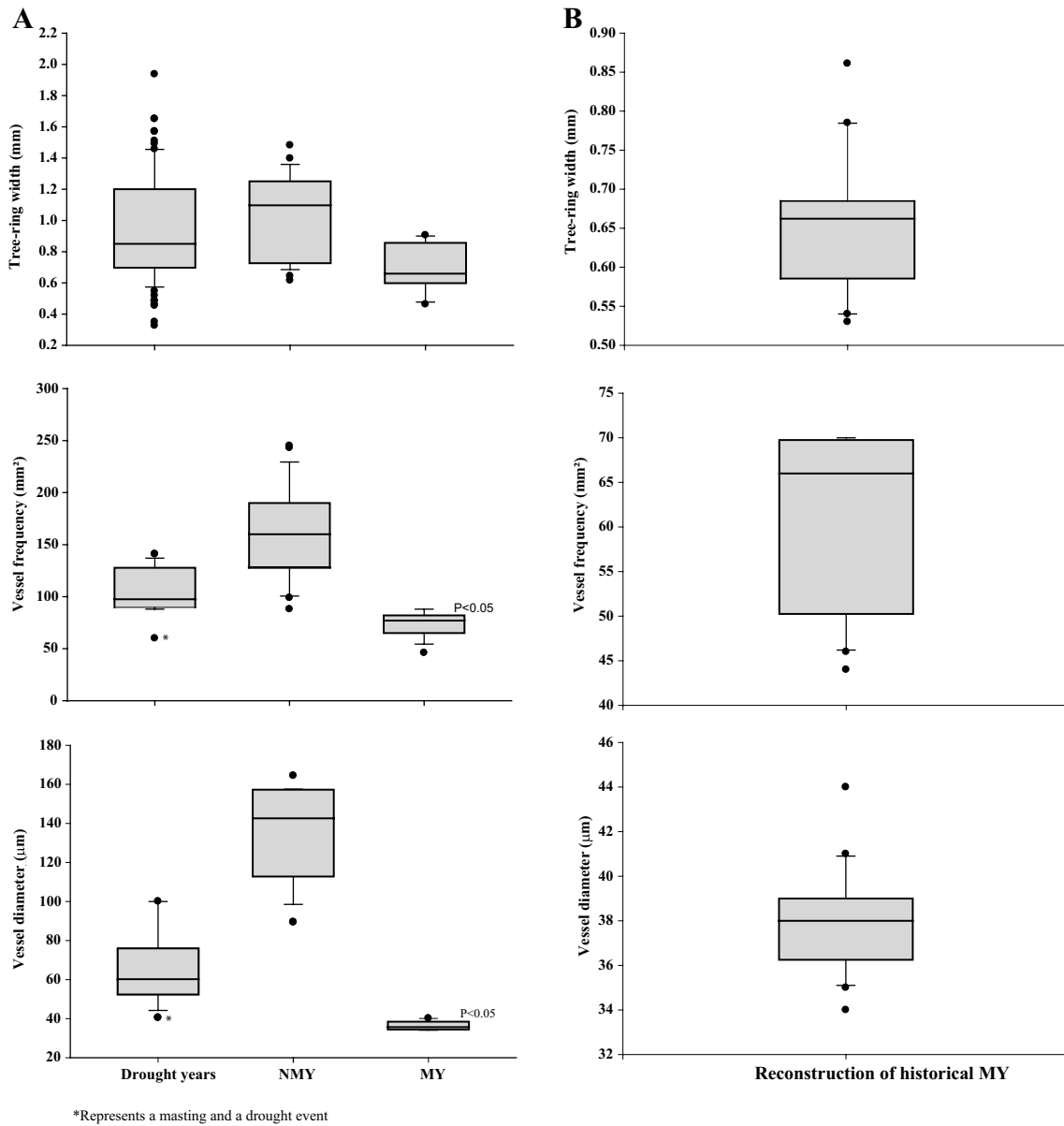


Fig. 4 Box plots showing the variation ranges of the tree-ring width, vessel frequency and diameter between drought years, NMY and MY. The upper and lower limits of the boxes represent the 75 and 25th percentiles, and whiskers represent the 90 and 10th percentile. Black

circles show outliers. The solid lines within each box indicate statistically significant differences ($P < 0.05$). **a** Historical masting years; and **b** reconstruction of historical masting events. *Shows masting and drought events

and long (8 years) time intervals, have occurred repeatedly in the past when the required precipitation is reached (Fig. 5) as suggested by Peters (1995).

This study advances our understanding on the reproductive strategies of Mexican beech in the face of climatic fluctuations, which appear to have a strong influence on phenological events, such as masting synchrony (Vacchiano et al. 2016). The observed relationship of P_{rec} with tree-ring width and vessels traits shows that this species has adapted to the southern part of its distribution range

by developing narrow rings and using its resources for beechnut production.

Finally, we suggest that further research should focus on how climatic phenomena (e.g., El Niño and La Niña effects) and deforestation affect the masting behavior of trees (Burns 2012; Fletcher 2015). More specifically, future studies should address the possible reduction in reproductive potential and survival of Mexican beech in the tropical montane cloud forests of the Sierra Madre Oriental.

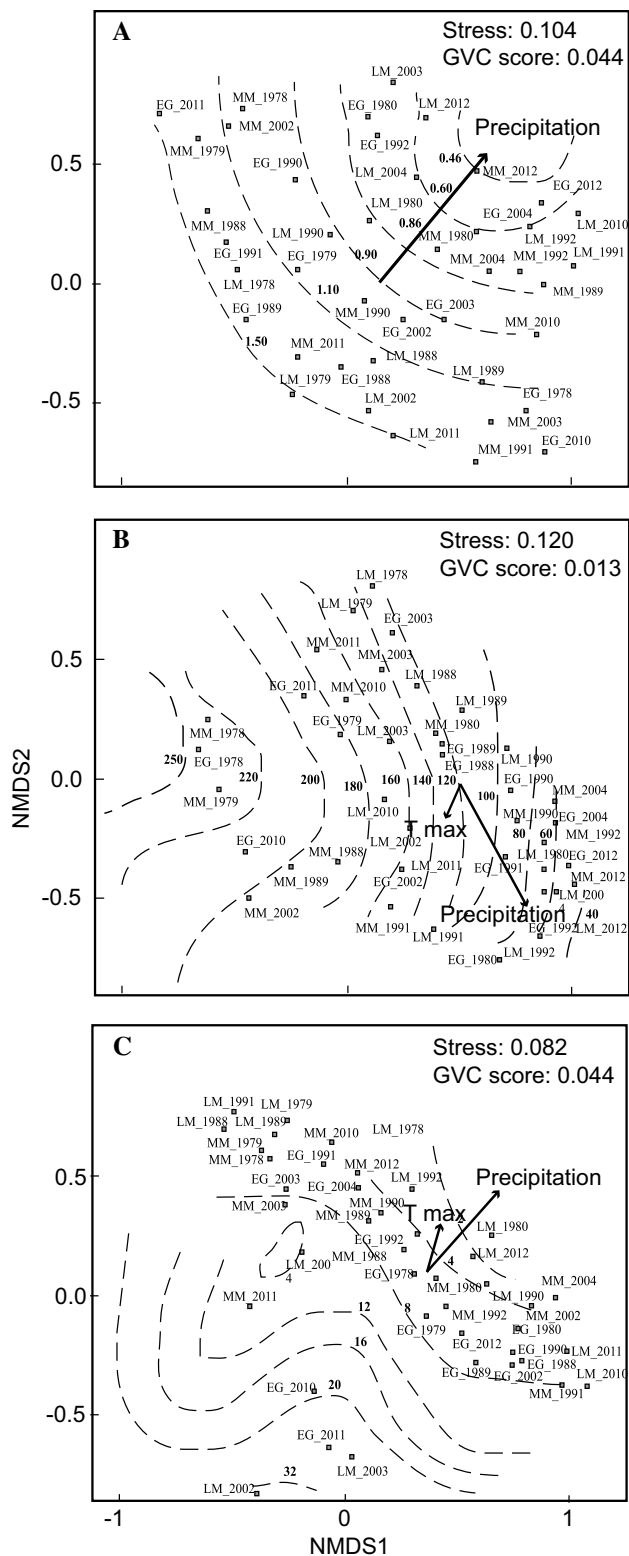


Fig. 5 Non-metric multidimensional scaling (NMDS) ordination, based on the relationship of climatic variables (T_{max} , T_{min} , T_{avg} and P_{rec}) on the tree-ring width and xylem vessels. **a** Tree-ring width, **b** vessel frequency; and **c** vessel diameter in Mexican beech. Labels represent growth rings for each year and site. LM, La Mojonera; MM, Medio Monte; EG, El Gosco. Variable values are indicated with bold numbers and dotted lines

Table 3 Climatic variables associated with ring width index (RWI), vessel frequency and diameter during masting years in Mexican beech. In bold are represented statistically significant variables (vectors)

Metrics	Vectors	NMDS1	NMDS2	R^2	Pr (> R)
RWI	T_{max}	0.756	-0.024	0.012	0.888
	T_{min}	-0.177	-0.984	0.137	0.266
	T_{avg}	0.978	0.209	0.104	0.371
	*Precipitation	0.610	-0.724	0.101	0.054
Vessel frequency	T_{max}	0.443	-0.896	0.258	0.077
	T_{min}	-0.147	-0.895	0.125	0.112
	T_{avg}	-0.124	-0.795	0.101	0.345
	*Precipitation	0.596	-0.700	0.128	0.062
Vessel diameter	T_{max}	0.396	-0.918	0.265	0.069
	T_{min}	-0.168	-0.887	0.139	0.245
	T_{avg}	0.885	0.210	0.124	0.198
	*Precipitation	0.588	-0.768	0.113	0.084

Signif. Codes: 0 '****' 0.001 '***' 0.01 '**' 0.05 '.' 0.1 ' ' 1

P values based on 1000 permutations

Author contribution statement ECHRR contributed in the research by designing the experiment, writing the paper and running the data analyses; TT helped writing the paper, designing the experiment and running the data analyses; ILV supervised and revised all the project stages, including the manuscript writing.

Acknowledgements We wish to thank Osvaldo Franco-Ramos and Lorenzo Vázquez-Selem for their help with tree-ring measurements and for lending the necessary equipment; Susana Guzmán Gómez and María del Carmen Loyola Blanco (Laboratorio de Microscopía y Fotografía de la Biodiversidad II, Instituto de Biología, UNAM) for technical assistance with the digital photographs; Othón Alcántara-Ayala and Rodrigo Ortega García for their support during field work; Ana Paola Martínez-Falcón for assistance with the statistical analyses; Santiago Ramírez-Barahona and Carlos Solís Hay for his critical observations. This research was financed by the project PAPIIT IN223218. The first author thanks the financial support granted by the postdoctoral fellowship DGAPA-UNAM 2015-2016.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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