Drought effects on vessel plasticity of two endemic Magnolia species in the tropical montane cloud forests of eastern Mexico

Ernesto Chanes Rodríguez-Ramírez¹, J. Antonio Vázquez-García², Othón Alcántara-Ayala¹
and Isolda Luna-Vega¹*

¹Laboratorio de Biogeografía y Sistemática, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico.

²Laboratorio de Ecosistemática, Instituto de Botánica, Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, km 15.5 carr. Guadalajara-Nogales, Camino Ing. Ramón Padilla Sánchez 2100, Nextipac, 45221, Zapopan, Jalisco, Mexico.

¹*Corresponding author: luna.isolda@gmail.com, isolda_luna-vega@ciencias.unam.mx
Abstract: The distribution of Mexican Magnolia species occur under restricted climatic conditions. As many other tree species from the tropical montane cloud forests (TMCF), Magnolia species appear to be sensitive to drought. Through the use of dendrochronological techniques, this study aims to determine the climate influence on the vessel traits of M. vovidesii and M. schiedeana which are endangered tree species that are endemic to the Sierra Madre Oriental in eastern Mexico. Because most of the tree species in TMCFs are sensitive to climate fluctuations, it is necessary to investigate the differences in the climatic adaptability of the vessel architecture of these trees. This could allow us to further understand the potential peril of climate change on TMCFs. We compared vessel frequency, length and diameter in drought and non-drought years in two Mexican Magnolia species. We used tree-rings width and vessel traits to assess the drought effects on Magnolias' diffuse-porous wood back to the year 1929. We obtained independent chronologies for M. vovidesii with a span of 75 years (1941–2016), while for M. schiedeana we obtained a span of 319 years (1697–2016). We found that temperature and precipitation are strongly associated with differences in tree-ring width (TRW) between drought and non-drought years. Our results showed anatomical differences in vessel trait response between these two Magnolia species to climatic variation. We suggest that our approach of combining dendroclimatic and anatomical techniques is a powerful tool to analyse anatomic wood plasticity to climatic variation in Magnolia species.

Keywords: adaptive forestry; dendroecology; diffuse-porous wood; drought years; vessel traits; wood anatomy.
1. Introduction

Tropical montane cloud forests (TMCFs) represent an example of forest ecosystems where direct anthropogenic disturbance and climate change quickly affect the feedback between forests and the hydrological cycle [1,2]. These ecosystems are influenced by climate change mainly through the carbon cycle [3,4] and play an important role in the regulation of atmospheric flows, humidity and rainfall recycling, which directly influences local, regional and continental climates [5–7]. Climate fluctuations show that worldwide TMCFs have experienced a warming trend and an increase in elevation of the 0°C isotherm during the second half of the 20th century [1,8].

Dendroclimatology is a useful tool that provides past climatic information about the development and ecology of tree species [9–12]. Several studies have confirmed the relationship between climatic seasonality and seasonal growth rings development as a response from tree species. Such a relationship that can be observed in tropical ecosystems with the use of dendrochronology [11,13,14]. Climate signals such as precipitation (e.g., rain, mist, fog and cloud water), temperature and/or droughts regulate the growth of TMCFs’ tree species [15,16]. Dendroecology allows us to identify climatic processes across time and can be used to reconstruct past local and regional climates [9,16,17]. In this context, one of the most important advances in dendrochronological studies has been the additional focus on anatomical features such as vessel traits and/or tree–ring anatomy [13,18,19]. For TMCFs’ trees, water conduction through the xylem vessels is relevant to understand the effects of stress caused by climatic changes such as those provided by drought years. In particular, plasticity adjustments of the vessel dimensions could be closely related to temperature and precipitation [20,21]. Most of the tree species inhabiting the TMCFs develop reliable and anatomically characteristic annual growth rings.
Growth provides trees with the ability to perform anatomical adjustments and since these modifications are, year after year, recorded in growth rings the radial variation of the wood structure along tree–rings can cause hydric and physiological stress [24–27]. This stress usually manifests itself in changes in the anatomy and morphology of the plants (e.g., size, thickness and venation architecture of the leaves, the structure of the xylem vessels, among others), allowing them to survive in unfavorable conditions [22,27].

The genus *Magnolia* L. belongs to one of the most ancient families of angiosperms (Cretaceous ≈50 to 65 Ma BP; [28]) and has a complex biogeographic and climatic history [29]. In Mexico, *Magnolia* includes 36 species spread into three well supported clades that are considered by several authors as three separate genera: *Metamagnolia* Sima & Lu, *Magnolia* and *Talauma* Juss. [30,31], treated as sections: *Macrophylla* Figlar & Noot., *Magnolia* and *Talauma* Juss. [75]. An outstanding 94% of these species are endemic to Mexico, with a restricted distribution which life forms compose the low and medium strata (7–25 m high) but can also form a part of the canopy and emergent trees (25–45 m high). These species coexist with dominant tree species that form the canopy of a wide range of ecosystems, from the *Pinus–Liquidambar* forest, tropical montane cloud forest, pine–oak tropical subdeciduous forest to the tropical rain forest.

*Magnolia vovidesii* A. Vázquez, Domínguez-Yescas & L. Carvajal and *M. schiedeana* Schltdl. are considered endemic tree species found along the fragmented TMCF range of the Sierra Madre Oriental in eastern Mexico [29]. *M. vovidesii* belongs to sect. *Macrophylla*. It is a deciduous and short–lived woody species (e.g. longevity of *M. macrophylla* ca. 50–150 years), mid–successional and shade–tolerant species inhabiting in the *Cupressus, Pinus* or *Liquidambar* forests of Central Veracruz.
On the other hand, *M. schiedeana* belongs to sect. *Magnolia*. It is mostly an evergreen and short- to long-lived woody species (e.g., longevity of *M. grandiflora* of 318 ± 20 years), it commonly grows under the canopy of *Quercus, Liquidambar, Meliosma, Fagus* and *Podocarpus* [27–29], and is often associated with *Ternstroemia, Oreopanax* and *Styrax*. It also occurs in secondary conditions with *Alnus* and *Clethra*. This species has a greater morphological variability and a wider distribution, occurring in Hidalgo, Puebla and Veracruz [71,74], ranging from the eastern United States to Mexico and Central America as well as the North of Cuba, it reaches its southern distributional limit at Panamá.

Both species are classified as endangered species under the Red List of Magnoliaceae [56] and the Red List of Mexican cloud forest trees [27–29]. Because both species have very different morphologies and life strategies, it is imperative to research their ability to adapt and resilience to future climate change for conservation planning.

Diffuse–porous wood is an anatomical adaptation that grants a high performance in hydraulic conductance during drought events in TMCFs [32]. Magnolia’s wood is mainly characterized as a diffuse–porous wood where xylem vessels maintain the same diameter and are evenly distributed within a growth ring [33,34]. We studied the drought effect on the annual tree–rings width (TRW) of individual trees in two populations of Mexican *Magnolia* species (*M. vovidesii* and *M. schiedeana*; see descriptions in Dieringer and Espinosa [35] and Vázquez-Garcia et al. [36]). Until now, the effects of drought events on vessel plasticity of *Magnolia* species have not been analyzed. By using dendroclimatic tools, the aim of this study was to determine the influence of past climatic fluctuations, such as years with prevalent drought (here thereafter, drought years) on vessel plasticity of two Mexican magnolias (*M. vovidesii* and *M. schiedeana*) with different morphologies and
life strategies. Furthermore, evidence of plasticity changes to the vessel’s anatomy during drought years could be used as ecological proxies.

2. **Materials and Methods**

2.1. **Study sites**

This study was conducted in two TMCFs located in the Sierra Madre Oriental: (1) El Batda, Huayacocotla, Veracruz (20°33’N, 98°24’W; 1829–1894 m. a.s.l) and Medio Monte, San Bartolo Tutotepec, Hidalgo (20°24’N, 98°14’W; 1840–1876 m. a.s.l) (Figure 1A–C). In these two sites, *Magnolia* populations typically occur on steep slopes or ravines. The two sites share a temperate climate (Cb) sensu García [37], characterized by mild temperatures (14.5–24.4°C). Humidity levels are found in the range of 60–90% [38]. The soil of the sites is Humic (Th) andosols [39] with light sandy-clay loam texture.

El Batda is located on slightly rugged terrain and is characterized by trees that reach up to 25 m in height. The forest is dominated by *Liquidambar styraciflua* L., *Pinus patula* Schltdl. & Cham., *P. greggii* Engelm. ex Parl, and several oak species such as *Quercus meavei* Valencia-A., Sabás & Soto, *Q. delgadoana* S. Valencia, Nixon & L. M. Kelly. and *Q. trinitatis* Trel. The mid-canopy of the forest is mainly composed of *Magnolia vovidesii*, *Clethra mexicana* DC., *Befaria aestuans* L. and *Podocarpus matudae* Lundell, whereas the low–canopy consists mainly of several tree fern species (*Cyathea fulva* (M. Martens & Galeotti) Fée, *Cyathea bicornata* Liebm., *Dicksonia sellowiana* var. *arachneosa* Sodiro and *Alsophila firma* (Baker) D.S. Conant).

Medio Monte’s TMCF’s canopy stratum is characterized by trees that reach between 30–45 m in height. The forest is dominated by several oak species such as *Quercus delgadoana*, *Q. trinitatis* and *Q. meavei*, as well as *Magnolia schiedeana*, *Pinus patula*,...
Liquidambar styraciflua and rarely Ulmus mexicana (Liebm.) Planch., this last one as an emergent tree (≥ 80 m). In some places, Fagus grandifolia subsp. mexicana (Martínez) A.E. Murray is part of the canopy stratum. The mid–canopy of the forest is mainly composed of Befaria aestuans, Clethra mexicana, while the low–canopy consists mainly of Cyathea fulva, Dicksonia sellowiana var. arachneosa and Alsophila firma.

2.2. Sampling, processing and anatomical measurements

For each site, we extracted two wood cores from 20 individual magnolia trees with a diameter at breast height (DBH) ≥ 20 cm, at breast height (1.3 m) with the use of a Häglof borer. Wood cores were air–dried at room temperature, glued onto wooden supports, and sanded with successive coarse–grit sandpapers 100 and 360 and four finer–grit sandpapers (400, 600, 1000 and 1200) until the xylem’s cellular structure was distinguishable with at most a 100 x amplification [9]. Tyloses and wood dust inside vessel lumina were removed with heat by using a hair–dryer. In order to obtain a high contrast between xylem vessels of diffuse–porous and background wood, the vessels were filled with white chalk [20,40,41].

We measured TRW series using a stereoscopic microscope (Olympus SZ61) to the nearest 0.001 mm for each tree–ring, with the TSAP-Win v. 4.67c program and Velmex tree–ring measuring system (Velmex, Inc., Bloomfield NY, USA). Additionally, we verified the cross–dating with the software COFECHA [42,43]. We used the Northern Hemisphere criteria [44–46] to date our tree–ring series and assigned every ring the year in which growth started. False tree–rings were detected through re–examination and comparison between wood cores and a cross–section from fallen trees to correct the chronologies from each site [15,47].
2.3. Analysis of chronologies

Growth–related trends were removed using a cubic spline with 50% response of 10–year periods, flexible enough to maximize high–frequency climatic information and minimize the non–climatic variance, such as the age–size related trends and the effects of the stand dynamics [10, 15, 48]. We achieved chronologic quality according to standard dendrochronological procedures [10]. Autoregressive modeling was performed on each standardized series to remove temporal autocorrelation [49] in order to maximize the climatic signal using the ARSTAN computer program [50]. To produce a standardized chronology, the resulting indexed series were averaged using a bi–weight mean to decrease the influence of outliers [51]. Temporal autocorrelation in chronologies is common because of the residual impact of growing conditions from previous years [52].

2.4. Climatic–growth relationships

For each site, we compared variation in the chronologies to the mean minimum and mean maximum temperatures ($T_{\text{min}}$ and $T_{\text{max}}$) and monthly precipitation (P) directly from nearby weather stations (Huayacocotla, Veracruz; 20.5 N, -98.5 W; and Tenango de Doria, Hidalgo; 20.3 N, -98.2 W). More specifically, the CLICOM (http://clicom-mex.cicese.mx/) database was only used for the periods comprising the years of 1961–2015 (Huayacocotla) and 1941–2015 (Tenango de Doria), which were complemented with data from INIFAP weather stations (http://clima.inifap.gob.mx/) for the years 2016–2017 (Figure 1B).

Climate–growth relationships were computed as Pearson’s correlation coefficients between the chronologies and climate records ($T_{\text{max}}$, $T_{\text{min}}$, and P). The significance level of
the correlations followed the bootstrap technique [53]; for this, we performed 10,000 iterations for each coefficient and implemented the correction proposed by Mason and Mimmack [54] to obtain the percentile bootstrap confidence intervals.

2.5. Drought effects on vessel traits

To assess whether or not drought years have an effect on the plasticity of vessel traits (frequency, length and diameter) of the Magnolia species studied, we selected a subset of 15–18 wood cores to take tree–ring digital images for drought years. We obtained recorded drought events from Climate Data (http://sala.lab.asu.edu/research/drought-net/) [55] (e.g., 1929–30, 1940, 1963, 1970, 1972, 1976, 1983, 1991, 1997, 2012 and 2015–16). We also followed this procedure for two consecutive years before and two years after El Niño Southern Oscillation events (ENSO). Wood core digital images were captured using a stereoscopic microscope (Leica Z16 APOA) with a 12.9 to 50.3 μm field of depth. Images were taken with a digital camera (Leica DFC 490) and saved as TIFF format with a 1.3 μm resolution. From both Magnolia species studied, a total of 216 digital images were taken (108 for each one).

For each wood core digital image, we quantified and manually measured all the vessel features using the software ImageJ [56] by means of the VesselJ plugging (García-González, not published). The correct recognition of all vessels was often hindered by the detection of dust spots or other undesired objects, which were manually excluded, retaining only the objects larger than 10,000 μm², and that had a width smaller than twice their length. Vessel outlines were improved by applying morphological operations (erode–dilate 2 × 2 one pass, and calculation of the convex hull).
We performed a multiple comparison Tukey test to assess whether the values of vessel traits (frequency, length, and diameter) present a significant difference between drought years (DY) and non-drought years (NDY) for the *Magnolia* species studied. These analyses were performed in R (version 3.5.1) using the R-package `ggplot2` (https://cran.r-project.org/web/packages/ggplot2/ggplot2.pdf [57]).

### 3. Results

#### 3.1. Tree-ring width chronologies

The cross-dated chronology of *Magnolia vovidesii* we gathered shows a span of 75 years (1941–2016), while for *M. schiedeana* we obtained a span of 319 years (1697–2016). The chronologies also showed a distinct inter-annual variation pattern for the *Magnolia* species studied, except for those tree-rings developed in strong drought years such as 1929–30, 1940, 1963, 1970, 1972, 1976 (Figure 2), 1983, 1991, 1997, 2012 and 2015–16. Correlations among chronologies were strongly significant in all cases. In Medio Monte, mean TRW varied between 0.032 and 2.12 mm for *M. schiedeana*, while in El Batda the mean TRW range was 0.456 and 3.02 mm for *M. vovidesii* (Table 1). Signal-to-noise ratio (SNR) and the mean between-trees correlation was high in the *Magnolia* species studied, suggesting a strong common signal is expressed as climate effect on growth rates (Table 1). Mean sensitivity of *Magnolia schiedeana* was higher compared to *M. vovidesii* in the chronologies studied. There is a larger relative change between consecutive rings for non-drought years (NDY) than that for drought years (DY) between *Magnolia* species studied (Figure 2, Table 1).

#### 3.2. Response to climate
Correlations with mean maximum temperature ($T_{\text{max}}$) were positive in previous Jan (-1) (see Figure 3) (i.e. late Winter and early Spring (January to February)) and during the dry cool season (Oct (-1) to Nov (-1)) before tree–ring development. A negative correlation occurred in previous Sep (-1), Dec (-1) for radial growth chronology, and current late Spring and Summer (March to June). This drought–sensitive growth dynamics that are supported in the literature for the genus Magnolia worldwide [36,58–60]. The observed correlations between previous dry–cool season from Oct (-1) to Jan (-1) monthly precipitation (P) and growth season were positive in all cases, and mainly during the long cool Summer (June to September) were linked to higher growth ring indices, particularly in El Batda site (Figure 3).

Regarding $T_{\text{min}}$ in early February to May, these were also negatively associated with the growing season in both study sites. El Batda showed the highest correlation value ($r =0.41$) from May (dry warm season) to July (long cool summer) (three months). Medio Monte presented low correlation values ($r =0.30$) for June and July and had 4–month droughts (January, February, June, and July) (Figure 3).

### 3.3. The effect of climate on vessel anatomy

We measured a total of 12,582 vessels traits (8,334 for Magnolia vovidesii and 4,248 for M. schiedeana) in 15–18 wood core digital images (see the climate effect on vessel traits section). On average, for each annual tree–ring the cores contained 9.44 vessels for $M. vovidesii$ and 4.81 for $M. schiedeana$. The vessels of $M. vovidesii$ are larger and more recurrent than those found in $M. schiedeana$. Regardless, vessel frequency, length and diameter distribution between DY and NDY (Figure 4) showed strong differences between the two Magnolia species. Vessel frequency was dissimilar between Magnolia species ($M.$
schiedeana, ranges from 1–3 for DY and 1–12 in NDY; and M. vovidesii, ranges from 1–14 for DY and 1–20 in NDY; Figure 4A). The vessel diameter ranges from 45 to 181 in M. vovidesii, and from 12 to 180 in M. schiedeana (Figure 4B). A similar range of variations has been found for vessel diameter in DY and NDY between Magnolia species (Figure 4C). This variability influences the annual variability of the further derived hydraulic features.

4. Discussion

Our findings reveal that the Magnolia species we studied annually generate TRWs that are suitable to assess tree radial growth rate, age and their plasticity regarding climate fluctuations. The dendroecological tools allowed us to evaluate the drought effects on vessel anatomy of diffuse–porous wood up–to the year of 1929. We found evident differences in the vessel hydraulic architecture when comparing DY to NDY and between the two Magnolia species studied (Figure 3 and Figure 4). We argue that such disparities in the present modifications to the vessel traits are due to species–specific physiological plasticity in response to DY. Several studies suggest that recent ENSO events (from 1929 to 2016) pushed the TMCFs’ tree species to their anatomical and physiological limits [11,24,61]. Our results demonstrate that the Magnolia’s vessel traits show a perceptible trend to become less in number and smaller in size during drought periods (Figure 3).

Our results suggest that droughts could not only affect Magnolia species’ resilient ability to adapt to long drought–periods but also restrict them from remaining as a part of the TMCFs’ structure. For instance, Magnolia schiedeana is a frequent element in Mexican beech forests [15,62], this could indicate a historical dependency to the specific microclimatic conditions given by this forest type that are essential to its establishment and
survival [58,59]. Strong vessel plasticity from *M. schiedeana*, given drought events (Figure 4), enhances the statement of its need for specific microclimatic. Rodríguez-Ramírez et al. [32] found that Mexican beech trees develop similar vessel trait adjustments, which may indicate that this forest type may be very sensitive to drought and thus susceptible to climate change [17,63,64]. On the other hand, *M. vovidesii* appears to show resilience to climatic variations such as strong DY, this is seen as a response to climatic variations such as strong DY (Figure 4). The relationship between vessel traits and drought events (Figure 4) reflects that both Magnolia species are capable to effectively allocate carbon during high hydric stress. These anatomical adjustments can allow Mexican trees of diverse functional types to continue growth during Fall, even if they are evergreen, semi–deciduous or deciduous trees [22,32,61,65,66].

Rivers et al. [58] and Vazquez-Morales et al. [36] mentioned that Magnolia species that inhabit disturbed fragments of the TMCF could be vulnerable to climate variations. Our study confirms that at the anatomical level, these types of analyses allow us to interpret the vulnerability of the Magnolia species. As such, we suggest that dendroecological and anatomic methods are useful to assess the effect of drought events on Magnolia species worldwide and to evaluate their vulnerability of certain trees to climatic stress [9,24,35,58,60,61]. On the hindsight, evaluating just these characteristics can not explain in its entirety the differences observed in TMCFs’ trees’ hydraulic conducting patterns and vessel functions [4,19,22].

In this study, Magnolia species’ TRWs showed the most significant correlation to $T_{\text{max}}$ and $T_{\text{min}}$ during March and June, negatively influencing the growth rates of *M. schiedeana* since tree ring growth starts in February. Maximum radial growth rates occur in September.
when humidity is higher, but rapidly decrease in November and December. We found a positive response between radial growth and monthly precipitation (P). Only during the months of –November, –December and January we found that the absence of a continuous rainfall unfavorable for growth in both *Magnolia* species. This result can be related to the end of the growth period in the TMCFs caused by a dry–cold season. An alternative explanation is that from November to January there is a lack water availability at mid–elevation stands. At higher stands (>1840 m. a.s.l) *Magnolia vovidesii* can also be found, usually coexisting with *Pinus patula, P. greggii, Liquidambar styraciflua* and several oak species, such as *Quercus meavei* and *Q. trinitatis*. In preserved areas, *M. vovidesii* has been suggested to be significantly more resistant than *M. schiedeana* to drought periods. Possibly, *M. schiedeana* has been affected by the microclimatic conditions of the Mexican beech forest structure (*Fagus grandifolia* subsp. *mexicana, Q. delgadoana, Q. meavei* and *Q. trinitatis*, and several tree fern species) and/or possible high genetic structure, affecting its climatic resilience [62]. We believe that there are specific climatic factors affecting TRWs’ growth rates allowing the individual trees to adapt to these climatic fluctuations. Opposed to this, from June to –September precipitation showed the opposite effect (Figure 3), precipitation had a positive impact on TRW’s growth rates in both species having an even greater benefit on growth rates of *M. vovidesii*.

Our analyses revealed that a great variability in vessel’s anatomy of diffuse–porous wood from the two *Magnolia* species studied is related to temperature and/or water availability. These anatomical adaptations result from a strong reduction in vessel frequency, length and diameter during DY compared to NDY, plastic adaptations that play an important role in water transport and safety [67]. We state that wood plasticity is
essential to identifying climate adaptability of trees in TMCFs. Our findings support that *M. schiedeana* is probably more sensitive to drought events than *M. vovidesii* due to poorer vessel structure when confronted against these types of climatic events (Figure 4). Our wood core digital images results demonstrate that most vessel traits show (i) high plasticity from DY to NDY, and (ii) that there are differences in the diffuse–porous wood anatomy and vessel plasticity of the different *Magnolia* species inhabiting the TMCFs (Figure 4). We deduce that drought induces increased hydraulic conductance with the consequence of high construction costs but reduced hydric transport efficiency and lower TRW growth rates (Figure 3 and 4) [13,24]. Within the growing season of a DY, drought events can potentially induce several xylem architecture modifications at the end of Summer when TMCF trees might merely respond by early ceasing tree–ring formation [15,22,24]. The features of the vessel traits, such as wall thickness, arrangement, frequency, diameter and length, among others, are not the only factors involved in the reduced efficiency of the hydraulic systems [20,68,69] but also prevailing climatic conditions. Adaptive responses to the loss of hydraulic conductivity result from the adjustments in the vessel anatomy of diffuse–porous wood that is required to adapt to new environmental requirements [18,21,69]. Similar responses have also been reported for different tree species such as *Fagus grandifolia* subsp. *mexicana* in Mexico [32], several oak species, such as *Quercus cerris* L., *Q. pubescens* Willd. Rita [70], *Q. canariensis* Willd [61] and *Q. pyrenaica* Steven in Spain [41], *Tectona grandis* L. f. and *Pinus caribaea* Morelet in Brazil [13], among others.

During DY, it is unlikely that drought–induced cavitation occurred within most vessels, this is because many vessels in the outermost annual ring of all diffuse–porous wood
species maintain their water transport functioning during the growing season

[13,25,27,64,71,72]. In a TMCF, drought could affect which tree species prevail over time, perhaps creating less favorable conditions for trees with relatively harder wood and coriaceous leaves such as *Magnolia schiedeana*, which present a higher vulnerability to drought conditions than the lusher species that contribute to canopy cover such as *M. vovidesii*.

We conclude that our results on specific vessel traits can provide information of the functional costs and benefits of the vessel hydraulic adjustment. This research contributes to a better understanding of the plasticity that occurs in xylem architecture as one of several strategies adopted by the TMCF trees (i.e. rainfall recycling and cooling [3,6,73]) when exposed to the several effects of climate change

Acknowledgments: We thank Doroteo San Juan for his support during fieldwork. Carlos Solís Hay for his critical observations and for improving the English style.


Funding: This study was conducted with support from the project DGAPA PAPIIT IN223218 project. The first author also thanks the financial support granted by the postdoctoral fellowship CONACYT 2018-2019.

Conflict of Interests: The authors declare no conflicts of interest.
References


D.V.; Tobella, A.B.; Ilstedt, U.; Teuling, A.J.; Gebrehiwot, S.G.; Sands, D.C.;


11. Schöngart, J.; Bräuning, A.; Barbosa, A.C.M.C.; Lisi, C.S.; Oliveira, J.M.


Fandohan, A.B.; Farwig, N.; Feeley, K.J.; Fischer, M.; Forshed, O.; Garcia, Q.S.;

Garkoti, S.C.; Gillespie, T.W.; Gillet, J.F.; Gonmadje, C.; Granzow-de la Cerda, I.;


Kessler, M.; Killeen, T.J.; Kooyman, R.M.; Laumonier, Y.; Laurance, S.G.;

Laurance, W.F.; Lawes, M.J.; Letcher, S. G.; Lindell, J.; Lovett, J.; Lozada, J.; Lu,


Martin, E.H.; Calderado Leal Matos, D.; Meave, J.A.; Melo, F.P.L.; Mendoza,

Z.H.A.; Metali, F.; Medjibe, V. P.; Metzger, J.P.; Metzker, T.; Mohandass, D.;

Munguia-Rosas, M.A.; Muñoz, R.; Nurtjahy, E.; de Oliveira, E.L.; Onrizal; Parolin,

P.; Parren, M.; Parthasarathy, N.; Paudel, E.; Perez, R.; Pérez-García, E.A.;

Pommer, U.; Poorter, L.; Qi, L.; Piedade, M.T.F.; Pinto, J.R.R.; Poulsen, A.D.;

Poulsen, J.R.; Powers, J.S.; Prasad, R.C.; Puyravaud, J.-P.; Rangel, O.; Reitsma, J.;

Rocha, D.S.B.; Rolim, S.; Rovero, F.; Rozak, A.; Ruokolainen, K.; Rutishauser, E.;


Sarker, S.K.; Schmitt, C.B.; Schoengart, J.; Schulze, M.; Sheil, D.; Sist, P.; Souza,

A.F.; Spironello, W.R.; Sposito, T.; Steinmetz, R.; Stevart, T.; Suganuma, M.S.;

Sukri, R.; Sultana, A.; Sukumar, R.; Sunderland, T.; Supriyadi; Suresh, H.S.;

Suzuki, E.; Tabarelli, M.; Tang, J.; Tanner, E.V.J.; Targhetta, N.; Theilade, I.;

Thomas, D.; Timberlake, J.; de Morisson Valeriano, M.; van Valkenburg, J.; Van


Table 1

Growth rings statistics for *Magnolia vovidesii* and *M. schiedeana* at the two study sites in the mountains of the Sierra Madre Oriental of eastern Mexico.

<table>
<thead>
<tr>
<th>Statistics</th>
<th>Magnolia vovidesii</th>
<th>Magnolia schiedeana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampled trees</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Cross-dated series</td>
<td>25</td>
<td>32</td>
</tr>
<tr>
<td>Master series (year)</td>
<td>1941–2016</td>
<td>1697–2016</td>
</tr>
<tr>
<td>Cross-dated rings</td>
<td>2545</td>
<td>2101</td>
</tr>
<tr>
<td>Series intercorrelation</td>
<td>0.501</td>
<td>0.785</td>
</tr>
<tr>
<td>Mean sensitivity</td>
<td>0.288</td>
<td>0.304</td>
</tr>
<tr>
<td>Autocorrelation</td>
<td>0.501</td>
<td>0.532</td>
</tr>
<tr>
<td>Mean/median age (years)</td>
<td>75/50</td>
<td>316/201</td>
</tr>
<tr>
<td>Common interval</td>
<td>1938-2016</td>
<td>1798-2016</td>
</tr>
<tr>
<td>Signal-to-noise</td>
<td>16.54</td>
<td>18.54</td>
</tr>
</tbody>
</table>

*Values obtained with COFECHA [42]*
*Values statistically different using Mann-Whitney test (P=0.05)*
*Values obtained with ARSTAN [50]*
Figure legends

Figure 1. Map showing the location (A) of the tree-ring sampling sites: El Batda and Medio Monte, located in eastern Mexico; (B) climatic diagrams of Huayacocotla, Veracruz (period 1961–2016; 20.5°N, -98.5°W; 2168 m. a.s.l.) and Tenango de Doria, Hidalgo (period 1941–2016; 20.3ºN, -98.2ºW; 1691 m. a.s.l.) weather stations; and (C) view of *Magnolia* species sampled.

Figure 2. Ring-width chronologies of *Magnolia vovidesii* and *M. schiedeana*. Micro–sections of the representative wood–core digital images showing annual tree rings and vessels. * Represents the drought year of 1976. A = *M. vovidesii*; and B = *M. schiedeana*

Figure 3. Correlations between chronologies against the mean maximum, mean minimum temperatures (T\text{max}, T\text{min}) and monthly precipitation (P) for each drought year (September to September) from the year 1941 onward. Lines indicate positive and negative correlations with a 95% confidence.

Figure 4. Violin plots showing differences in vessel traits between DY and NDY for both *Magnolia* species studied: For drought (DY) and non–drought (NDY) years: A = vessel frequency; B = vessel diameter; and C = vessel length.
Figure 1

(A) Map of Mexico showing the locations of El Batán and Medio Monte, with the Tropical Montane Cloud Forest highlighted. (B) Graphs showing temperature (T) and precipitation (P) data for Huayacocotla and Tenango de Doria weather stations. (C) Images of Magnolia species.
Figure 2

Magnolia virginiana

Magnolia schiedeana

(A)

(B)
Figure 3
Figure 4

A. Vessel frequency

B. Vessel diameter (mm)

C. Vessel longitude (μm)

Legend:
- Blue: Drought years
- Green: Non-drought years

Magnolia schillii

Magnolia wittkampii