UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

ECOLOGÍA

(PROYECTO)

ADAPTABILIDAD ANATÓMICA A LA SEQUÍA DE *QUERCUS MEAVEI* Y *QUERCUS DELGADOANA*: ESPECIES RELICTO-ENDÉMICOS DEL BOSQUE MESÓFILO DE MONTAÑA

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

ADAPTATION POTENTIAL OF NEOTROPICAL MONTANE OAKS TO DROUGHT EVENTS: WOOD ANATOMY SENSITIVITY IN *QUERCUS DELGADOANA* AND *QUERCUS MEAVEI*

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

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Ciudad Universitaria, CDMX, febrero 2025

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
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A mis padres Olivia y Raúl

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Dos ratoncillos cayeron en un cubo de nata;

el primer ratón enseguida se rindió y se ahogó,

el segundo ratón decidió pelear y se esforzó tanto

que finalmente transformó la nata en mantequilla y

consiguió escapar. Damas y caballeros, desde este

momento yo soy ese segundo ratón.

Christopher Walken

ÍNDICE

RESUMEN

Actualmente, los bosques enfrentan un aumento e intensidad de eventos de sequía a escala mundial. Estas tendencias climáticas han propiciado mayor vulnerabilidad para los bosques mesófilos de montaña (BMM) en México. En el presente estudio se evaluó la adaptabilidad anatómica de la madera de dos especies de encinos relicto-endémicos y amenazados (*Quecus delgadoana* y *Q. meavei*), que se distribuyen y coexisten bajo diferentes condiciones microclimáticas de manera fragmentada en el BMM de la Sierra Madre Oriental, Hidalgo.

Mediante, el uso de técnicas dendro-anatómicas se analizaron las estrategias de las especies ante eventos de sequía y no sequía para evaluar la capacidad plástica del ancho de anillos y características anatómicas de los vasos (diámetro hidráulico [D_H], densidad de vasos [V_D,], índice de agrupación de vasos [I_G] e índice de vulnerabilidad *VI*]) Asimismo, se evaluó la asociación con variables climáticas como la temperatura ($T_{\text{máx}}$), la precipitación (Prec), y la evapotranspiración (EvT).

Se obtuvo que, las dos especies de encinos difirieron en la arquitectura funcional y ecológica del ancho de anillo y de los caracteres de los vasos, estas diferencias anatómicas de la madera se explican mediante las variables ambientales específicas. *Quercus meavei* fue más vulnerable hidráulicamente debido a la combinación de sus vasos más estrechos, que limitan el transporte de agua en condiciones de sequía, y en consecuencia a una alta presión negativa en su xilema, incrementa el riesgo de interrupciones en el flujo hídrico. Esta vulnerabilidad se ve agravada por su distribución en microhábitats donde las condiciones de humedad pueden ser insuficientes durante

eventos de sequía prolongados. Por el contrario, *Q. delgadoana* mostró una mayor capacidad para mantener o recuperar el ancho de sus anillos de crecimiento bajo condiciones de sequía. Esto refleja una mayor resistencia, recuperación y resiliencia, ya que el mantenimiento del crecimiento radial sugiere que esta especie puede tolerar y recuperarse más eficazmente del estrés hídrico durante eventos de sequía. El ancho del anillo de los árboles, los rasgos funcionales y ecológicos de los vasos mostraron aclimatación anatómica de la madera en las especies de encinos, estos rasgos son cruciales para comprender cómo están respondiendo a un déficit hídrico, evitando el desarrollo de cavitación o embolismo de los vasos inducidos por la sequía.

Las características bióticas y abióticas, son los principales factores evolutivos que impulsan la variación adaptativa y plasticidad en la arquitectura hidráulica de la anatomía de la madera de las especies de encinos. Conocer como las características anatómicas de la madera han sido influenciadas por el clima típico del BMM en comunidades vegetales específicas y/o analizar como la persistencia de especies relicto-endémicas se han aclimatado a los eventos climáticos extremos pronosticados para el futuro, son interrogantes que exigen su comprensión.

Este estudio proporciona conocimiento sobre el funcionamiento de sistemas hidráulicos que determinan la anatomía de la madera con respecto a la respuesta a la variación climática y la sequía en ambas especies de estudio. Esta información es útil para predecir las repuestas de especies arbóreas pertenecientes al BMM a futuros eventos de sequía.

ABSTRACT

Forests are currently facing increase and intensification of drought events on a global scale. These climate trends have increased the vulnerability of tropical montane cloud forests (TMCF). The present study, the anatomical variability of the wood of (*Quercus delgadoana* and *Q. meavei*), was evaluated. Both species of oaks are endemic and threatened and are distributed in a fragmented manner in TMCF of the Sierra Madre Oriental, Hidalgo, under different microclimatic conditions.

Therefore, using dendro-wood anatomical techniques, the strategies of woody species were analysed using ring width capacity and the anatomical characteristics of the vessels (Hydraulic diameter [D_H], Vessel density [V_D], Vessel grouping index [V_G] and Vulnerability index [VI]) during historical drought and non-drought events recorded at the study site, associated with the effect of temperature ($T_{\text{máx}}$), precipitation (Prec) and evapotranspiration (EvT).

Both species of oak differed in the functional and ecological architecture of their vessels; these anatomical differences of the wood are explained by specific environmental requirements. *Quercus meavei* was more hydraulically vulnerable and *Q. delgadoana* showed wide tree rings with greater resistance, recovery and resilience to drought events. The width of the ring and ecological functions of the vessels revealed anatomical plasticity among the oak species, crucial to understand how they are responding to the development of cavitation or vessels embolism induced by drought.

The specific climate and local environment are the primary evolutionary triggers that drove the adaptive variation and plasticity in the hydraulic architecture of xylem vessels depending on the oaks. How the anatomical characteristics of wood have been influenced by the climate of specific communities of relict-endemic forests and the persistence of tree species are open questions that require an understanding of the responses of the remaining trees to extreme climatic events. Our results support the evidence for hydraulic mechanisms that determine the specific anatomical function of wood in response to climate variability and tree species acclimation to drought.

INTRODUCCIÓN

La inmersión frecuente y persistente de niebla, asociada con elevaciones altitudinales superiores a los 600 y hasta los 3000 m s.n.m. favorecen la distribución de los bosques mesófilos de montaña (BMM) (Bruijnzeel, 2001; Oliveira et al., 2014; Gotsch et al., 2016), los cuales representan un ecosistema importante dado su alto nivel de endemismos en flora, micobiota y fauna (Hu y Riveros-Iregui, 2016; Salinas et al., 2021). No obstante, este tipo de vegetación se encuentra amenazado globalmente a causa de la perturbación antropogénica, deforestación, erosión de suelo y/o disminución de la inmersión de humedad (Challenger 1998; Foster, 2001; Ponce-Reyes et al., 2012).

Estudios recientes sobre proyecciones climáticas indican afectaciones negativas en la dinámica autoecológica de las especies que habitan este tipo de vegetación (Allen et al., 2010; Mátyás y Sun, 2014; Choat et al., 2018), como menor disponibilidad de agua, aumento de temperatura e intensificación de eventos de sequía, alterando el ciclo hidrológico (Gutiérrez-García et al., 2022). Pompa-García et al. (2014) indica que los ecosistemas forestales son sensibles a las variaciones climáticas, modificando a nivel de xilema la capacidad plástica adaptativa de los vasos en las diferentes especies arbóreas, propiciando mayor vulnerabilidad (Nadkarni y Solano, 2002; Ponce-Reyes et al., 2012; Toïgo et al., 2015; Rodríguez-Ramírez y Luna-Vega, 2020).

La variabilidad climática histórica es importante en relación con los cambios en las precipitaciones, ya que los fenómenos extremos como las sequías prolongadas tienen repercusiones negativas en el crecimiento y la supervivencia de los árboles (Fuhrer et al., 2006; Lindner et al., 2010; Pompa-García y Castagneri et al., 2017; Camareno et al., 2019). Se atribuye como principal responsable de eventos de mortalidad masiva de árboles a nivel mundial al incremento de frecuencia e intensidad de eventos de sequía (Ogle et al., 2000; Foster, 2001; Fonti et al., 2010).

No obstante, aún no se conoce a profundidad la asociación de los factores ambientales y fisiológicos que desencadenan los mecanismos eco fisiológicos asociados a los rasgos

anatómicos que hacen más susceptibles a unos árboles que a otros y así predecir la respuesta de estos a la sequía extrema (Anderegg, 2015; Pellizzari et al., 2016; Acosta-Hernández, et al., 2017; De Micco et al., 2019).

En este contexto, el uso técnicas dendro-anatómicas permiten evaluar cómo los árboles reflejan en sus caracteres anatómicos los efectos climáticos (Venegas-González et al., 2015) que han quedado registrados en sus anillos de crecimiento anuales y las estructuras anatómicas presentes en los mismos (Corcuera et al., 2004; Fonti et al., 2010; Venegas-González et al., 2015; Rodríguez-Ramírez et al., 2018).

Las características anatómicas de la madera han sido poco estudiadas. Sin embargo, representan una fuente adicional de información ecológica (Fonti y García-González, 2004; Camareno et al., 2018; Puchi et al., 2021). A partir del análisis de la estructura anatómica de los anillos de los árboles y la plasticidad de los vasos del xilema se puede evaluar la variación del crecimiento radial en especies arbóreas y la plasticidad de los vasos con respecto al estrés por sequía (Fonti y García-González, 2004; De Mico et al., 2019; De Andrés et al., 2021; Puchi et al., 2021; Fontes et al., 2022).

La plasticidad anatómica puede ser un mecanismo potencial para reducir un déficit hídrico y evitar el riesgo de mortalidad cuando los árboles se exponen a extremas condiciones climáticas (Pritzków et al., 2009; Anderegg y Meinzer, 2015; Choat et al., 2018). El conocimiento de la plasticidad anatómica permite obtener información sobre la resiliencia y la capacidad de recuperación a eventos climáticos extremos (Lloret et al., 2011; Márquez et al., 2018).

Uno de los mecanismos adaptativos más importantes en los árboles ante este escenario es la arquitectura de xilema, el cual ha estableciendo un balance eficiente entre el caudal hidráulico óptimo y la resistencia a embolias (Hacke et al., 2001; Fonti et al., 2010; Fonti y Jansen, 2012; Venturas et al., 2017).

Por ello, a través del análisis cuantitativo de los rasgos anatómicos de los vasos como el diámetro, densidad, número, disposición o agrupación entre otros, se puede evaluar las fallas hidráulicas en los vasos del xilema (Scholz et al., 2014; Rodríguez-Ramírez y Luna-Vega, 2020). Lo cual nos permitirá inferir las respuestas fisiológicas de corto y largo plazo que reflejen adaptaciones funcionales para vincular la estructura del xilema y el ambiente (De Andrés et al., 2021; Fontes et al., 2022).

Por otro lado, alrededor del 60% de algunas especies leñosas en el BMM se encuentran en alguna categoría de amenaza en México (González-Espinosa et al., 2011; 2012), ya que han enfrentado una reducción crítica en sus poblaciones (Lindner *et al*., 2010; Foster, 2001). Especies pertenecientes a la familia Fagaceae, concretamente los géneros *Quercus* y *Fagus*, se encuentran entre los elementos boreales más importantes y distintivos del BMM (González-Espinosa et al., 2012; Gual-Diaz, 2014).

El género *Quercus* posee una alta diversidad, además de una amplia distribución geográfica en México (Manos, 1999; Valencia, 2004; Gual-Díaz, 2014). De las 450 especies estimadas a nivel mundial, entre 130 y 150 de estas se encuentran en el territorio nacional (Nixon, 1998). Específicamente, las latifoliadas en climas templados producen anillos de crecimiento anuales con una evidente respuesta climática (Stahle et al., 2000; Haneca et al., 2009). En el caso de México, los estudios dendrocronológicos en el género *Quercus* son limitados (Ortega-Arroyo et al., 2021; Villanueva-Díaz et al., 2021), ya que la mayoría de investigación dendrocronológica se ha enfocado en coníferas (Acosta-Hernández et al., 2017).

A pesar de que existen diversos estudios de anatomía descriptiva de la madera en el género *Quercus* (Ruíz-Aquino et al., 2017), son escasos aquellos donde se analiza la relación entre variables anatómicas y el clima (Arenas-Navarro et al., 2023).

Particularmente, las Fagaceaes *Quercus delgadoana* S. Valencia, Nixon et L. M. Kelly y *Quercus meavei* S. Valencia, Sabás et O.J.Soto han sido poco estudiadas. Estas especies son consideradas endémicas y en peligro de extinción, se distribuyen de manera fragmentada en

los BMM de la Sierra Madre Oriental, en los estados de San Luis Potosí, Querétaro, Hidalgo, Puebla y Veracruz (Valencia-Ávalos *et al*., 2011). En estos bosques las especies dominantes son *Fagus mexicana* Martínez, y las co-dominantes *Pinus patula* Schltdl. et Cham, *Magnolia schiedeana* Schltdl, *Liquidambar styraciflua* L., *Quercus corrugata* Hooker, *Carpinus caroliniana* Walter, entre otras especies (Rodríguez-Ramírez et al., 2013; Rodríguez-Ramírez y Luna-Vega, 2020).

Ambas especies de encinos coexisten en el BMM bajo diferentes condiciones microclimáticas; *Quercus delgadoana* posee individuos de aproximadamente 25 m de altura, habitando en pendientes pronunciadas con elevaciones de 1,840 a 1,900 m s.n.m. en condiciones de humedad relativamente bajas aproximadamente del 60% (Valencia et al., 2011). En contraste, *Quercus meavei* alcanza hasta 30 m de altura, se ubica en zonas con elevaciones de 1,750 a 1,850 m s.n.m. cerca de pequeños arroyos con alta humedad 90% (Valencia et al., 2016).

Quercus delgadoana se encuentran en La Lista Roja del BMM, La Lista Roja de Encinos 2020 y la IUCN señalándola como una especie en la categoría “EN” (“EN” = en peligro de extinción por sus siglas en inglés) (González-Espinosa et al., 2011; Carrero et al. 2020; IUCN, 2022). Por el contrario, *Quercus meavei* se ubica en la categoría VU (Vulnerable) en La Lista Roja de Encinos 2020 y la IUCN (Carrero et al. 2020; IUCN, 2022). Sin embargo, *Q, meavei* no se encuentra considerada en La Lista Roja del BMM mexicano.

Cabe destacar que ambas especies tienen diferente fenología y microhábitats, por ello es necesario investigar su capacidad de adaptación y resiliencia a los eventos climáticos extremos proyectados en el cambio climático presente y futuro. Esta información resulta ser relevante en la planificación y conservación de ambas especies de encino amenazadas.

Adaptation potential of Neotropical montane oaks to drought events: wood anatomy sensitivity in *Quercus delgadoana* and *Quercus meavei*

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RESEARCH PAPER

Adaptation potential of Neotropical montane oaks to drought events: wood anatomy sensitivity in *Quercus delgadoana* and *Quercus meavei*

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Abstract

1. Climate and local water availability are major evolutionary drivers of adaptive variation and plasticity in the hydraulic architecture of Tropical montane cloud forest tree species. Xylem vessel variability is key to understanding the adaptation potential of wood anatomy of trees to drought. How wood anatomical features have been influenced by the typical Tropical montane cloud forest climate and how tree species persist in these environments remain open questions, particularly in the context of predicted extreme climate events in the future.

2. Here, we evaluated the effects of changes in temperature, precipitation, and evapotranspiration during drought events on ring-width and anatomical vessel traits (hydraulic diameter, vessel density, vessel grouping index, and vulnerability index) for two relict endemic and threatened oak species (*Quercus delgadoana* and *Q. meavei*) from a Mexican Tropical montane cloud forest.

3. The study species differed in their functional and ecological vessel anatomical traits, and their wood anatomical differences are related to specific environmental requirements. However, the Ring Width Indices (RWI) calculated for these species indicate that both have high resistance and recovery, and thus high resilience to drought events.

4. Ring-width and vessel functional traits show differences in the variability of xylem traits associated with the hydraulic efficiency of these oak species, which is crucial to understanding how they avoid drought-induced embolism and cavitation in vessel conduits. Our results provide evidence of the existence of specific hydraulic mechanisms that determine functional wood anatomy related to climatic variation and the responses to drought in the study species. Further research assessing the wood anatomical adaptation to different climatic variables and identifying the xylem functional traits that underlie these adaptations, along with the mechanism allowing tree species persistence in these environments, is essential to gain insight into the responses of Tropical montane cloud forests to future drought events.

KEYWORDS

oak wood, relict species, resilience to drought, threatened oak species, vessel variability, xylem cavitation resistance

1. INTRODUCTION

In the Tropical montane cloud forests (TMCFs; *sensu* Hamilton et al. 1993a) of Mexico, current trends of change in precipitation and the increasing frequency of extreme droughts are projected to modify physiological and phenological processes in trees occurring in relict ecological communities, impacting ecosystem resilience (Barros et al., 2022; González-Espinosa et al., 2011; Habel & Assmann, 2019; Rodríguez-Ramírez et al., 2020). Reduced rainfall and rising temperatures, known as global-change-type droughts (Breshiers et al. 2005; Bruijnzeel et al., 2011), cause of mass tree mortality. These climate-induced events are expected to have profound consequences for species' geographical ranges and local community composition (Gordon, 2008; Rahman et al., 2018).

Many TMCF tree species are drought-sensitive since they cannot readily adapt to drastic environmental changes (Hu & Riveros-Iregui, 2016; Schröter et al., 2005). Anthropogenic activities such as logging, agriculture, and grazing have been proposed to be the main disturbance agents, with noteworthy impacts on TMCFs (Toledo-Aceves et al., 2011; Gual-Díaz & Rendón-Correa, 2014; Williams-Linera, 2012). Nevertheless, current studies show that changes in precipitation and temperature are becoming the most critical factors compromising the maintenance of tropical montane humid ecosystems (Báez et al., 2022; Rahbek et al., 2019). For instance, recent studies using dendroecological techniques have documented the negative impacts of extreme droughts on the radial growth of Mexican TMCF tree species (Astudillo-Sánchez et al., 2019; Campelo et al., 2009; Gutiérrez-García & Ricker, 2019; Rodríguez-Ramírez et al., 2018; Rodríguez-Ramírez & Luna-Vega, 2020), based on the wood anatomical features of tree rings, and xylem and tracheid vessel variability (Rodríguez-Ramírez et al., 2020). Hence, variation in xylem vessel variability linked to hydraulic architecture functionality has received much attention as an essential component of plant resilience to drought, and might determine tree survival in the long-term (Fontes et al., 2022; Fonti et al., 2010; Rita et al., 2015a). Further studies on wood anatomical variability are required to fully understand how TMCF tree species will be affected by climate change.

Dendro-wood anatomical studies in the TMCF are scarce and there is a need for an in-depth examination of the hydraulic adaptive response and resilience to climatic effects in relict threatened tree species (Rodríguez-Ramírez et al., 2021) to better understand the wood-anatomical strategies adopted by them (Brienen et al., 2016; Scholz et al. 2014). The interplay of inter-ring variability and vessel anatomy will allow retrospective inferences on tree-resilience to drought periods through wood anatomical variability (García-González & Fonti, 2006; Granato-Souza et al., 2018; Oliveira et al., 2014).

In this study, we hypothesised that two oak species from the TMCF with contrasting habitat preferences regarding moisture conditions respond differently to drought events, and that these differential responses are related to differences in the variability of their wood anatomy. Therefore, we aimed to: (1) identify the most relevant climatic factors that influence radial growth in the study species; (2) examine the effects of droughts on tree growth; (3) assess the resistance, recovery, and resilience of these species to drought events; and (4) evaluate vessel trait variability (hydraulic diameter, vessel density, vessel grouping, and hydraulic vulnerability) in tree-rings formed during historical drought events, as well as local climatic effects on vessel traits in these two oak species.

2. MATERIAL AND METHODS

2.1 Study area

The study forest is located in the Medio Monte Natural Protected Area, Hidalgo State, eastern Mexico (20° 24′ 50″ N, 98° 15′ 4.31″ W; Figure 1A, B). The climate is humid temperate (Cwb; Peel et al., 2007), with temperatures ranging from 14.5 to 24.4 °C and total annual rainfall ranging from 824 to 2458 mm (Rodríguez-Ramírez et al., 2018) (Figure 1C). The soil type is Humic (Th) (FAO-UNESCO, 1998), with a light sandy-clayey-loamy texture and pH ranging from 4 to 6 (Peters, 1995). In the study TMCF, the upper canopy is dominated by *Fagus mexicana* Martínez, whereas the mid-canopy is composed mainly of *Pinus patula* Schltdl. & Cham., *Magnolia schiedeana* Schltdl., *Quercus trinitatis* Trel., *Q. meavei*, and *Q. delgadoana* (Rodríguez-Ramírez et al., 2020; Valencia-Ávalos et al., 2011).

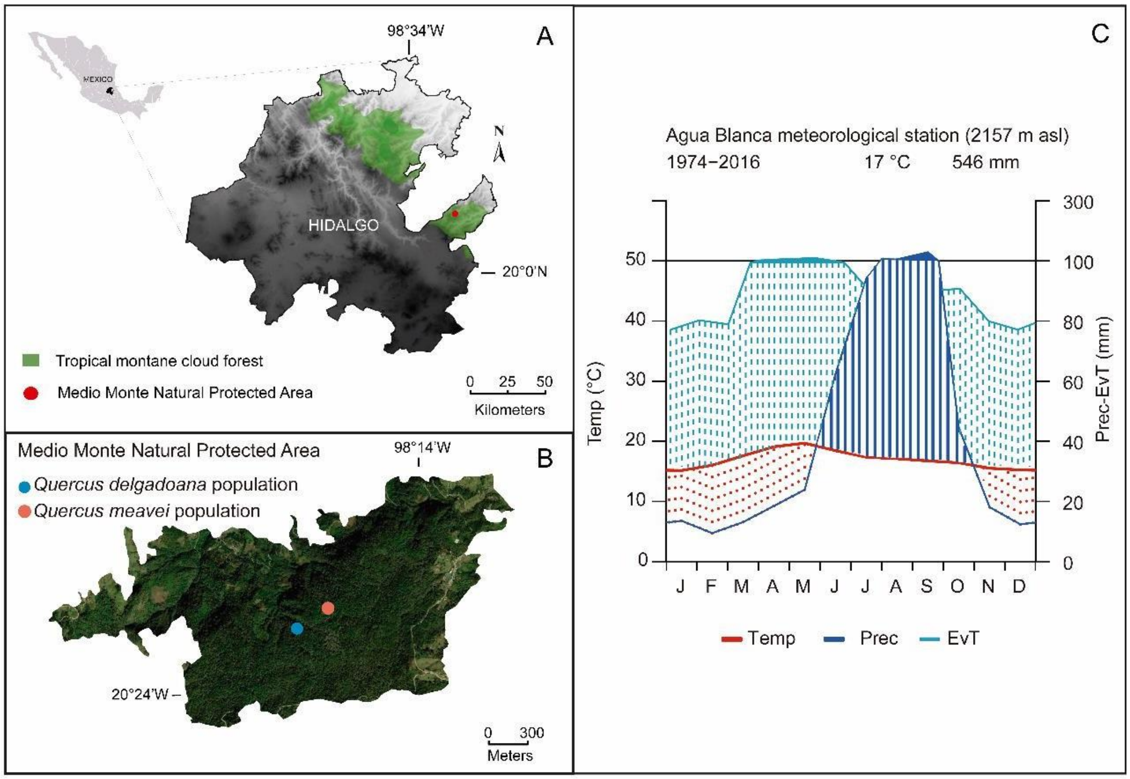

Figure 1. Study site location and climatic conditions. (A) The range of Tropical montane cloud forest in Hidalgo state, Mexico. (B) Map of the Medio Monte Natural Protected Area showing the locations of the populations of the two studied oaks. (C) Walter-Lieth climate diagram for the Agua Blanca meteorological station (20.3° N; 98.4° W; 2157 m asl) for the 1974-2016 period. Dotted shading indicates months with high or low values of climatic variables. Evt, evapotranspiration; Prec, precipitation; and Temp, temperature.

We selected two oak species occurring in this forest but differing in their habitat preferences: (1) *Quercus delgadoana* (endangered according to IUCN; www.iucnredlist.org; Figure 2A), which grows to heights of ~25 m and is more frequent on steep slopes (> 25º) at relatively higher elevations (1840–1900 m asl) and lower air humidity conditions (~60%); and (2) *Q. meavei* (vulnerable; www.iucnredlist.org; Figure 2B), which attains heights of up to 30 m (Valencia-Ávalos et al., 2016) and is more frequent at lower elevations (1750–1840 m asl), particularly in protected ravines near small streams where high air moisture (≥ 90%) conditions prevail. Both species are narrow endemics and co-occur in the naturally fragmented TMCF of the Sierra Madre Oriental in eastern Mexico (Carrero et al., 2020).

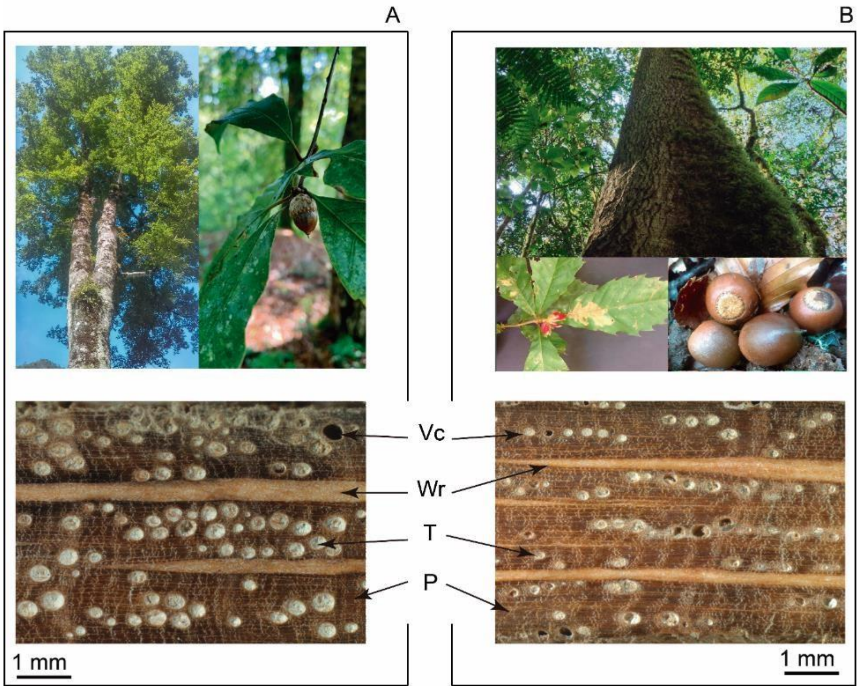

Figure 2. Images of the study species and their wood anatomy. (A) Adult tree, leaves, and acorn (top) and digital image of a wood core (bottom) of *Quercus delgadoana* (classified as endangered species). (B) Adult tree, leaves, and acorns (top) and digital image of a wood core (bottom) of *Quercus meavei* (classified as a vulnerable species). Vc, Vessel conduits; Wr, Wood ray; T, Tyloses; P, Parenchyma.

2.2 Sampling techniques and chronology development

We collected wood cores from 20 trees from each oak species with a diameter at breast height (DBH; 1.3 m) ≥ 40 cm. We collected two cores per tree at breast height with an increment borer of 5 mm inner diameter (Häglof®, Langsele, Sweden) (Stokes & Smiley, 1996). We filled borer holes with wood plugs treated with a mixture of 80% ethanol and 20% purified water, which have proved effective against a broad spectrum of bacteria, fungi, and viruses (Thiercelin et al., 1972). Wood cores were air-dried at room temperature, glued onto wooden supports, and sanded with successive coarse-grit sandpapers (400, 600, 1000, 1200, and 2000) until the cellular structure of the xylem became recognizable at a maximum of ×100 magnification (Speer, 2010; Stokes & Smiley, 1996). We removed wood dust inside the lumina with heat using a hair dryer (Rodríguez-Ramírez et al., 2018). Wood cores are stored at the Biogeography and Systematics Laboratory, Faculty of Science, Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico.

We measured ring widths to the closest 0.001 mm using a stereoscopic microscope (Olympus® SZ61, Olympus Corporation, Center Valley, PA, USA) with the TSAP-Win v.4.67c program and a Velmex tree-ring measuring stage (Velmex, Inc., Bloomfield, NY, USA). We statistically verified the dating accuracy through the COFECHA software (Holmes, 1983). To minimize the non-climatic variance linked to local climatic variations and thus maximize drought evidence, we removed non-climatic trends from each tree-ring series using a cubic spline with a 50% response over 10-yr periods (Gareca et al., 2010; Rodríguez-Ramírez et al., 2020).

We standardized raw ring-width series with autoregressive modelling to remove serial correlation using the ARSTAN program to calculate the mean value of detrended Ring-Width Indices (RWI; a standardized index for annual radial growth; Cook & Holmes, 1996). We assessed the quality of the chronologies with EPS (Expressed Population Signal) as a measure of the total signal present in the chronology, considering values > 0.85 (Briffa, 1999) and the mean correlation coefficient among tree-ring series (R-bar; Wigley et al., 1984). Additionally, we evaluated the signal-to-noise ratio (SNR), which expresses the strength of the observed common signal among the trees in a chronology.

2.3 Climate-growth correlations

We retrieved climatic data from the CLICOM database of the National Meteorological Service (http://clicom-mex.cicese.mx/). We extracted the mean monthly maximum temperature (T_{max}), total monthly precipitation (Prec), and total monthly evapotranspiration (EvT) data for a nearby weather station (Agua Blanca, 20.3°N, 98.4°W; 2157 m asl), which kept records from 1974 to 2016. We used Spearman's correlation coefficients (r_S; because the climatic variables tend to change simultaneously; Pouteau et al., 2018) as a similarity measure to assess growth sensitivity to climate in the study species. We used the standard chronology and monthly climate data for T_{max}, Prec, and EvT for a period spanning from the previous growth year (Jun (-1)) to the current growth year (Sep). We conducted this analysis with SigmaStat v.4 (Jandel Scientific, 2016).

2.4 Identification of historical drought events

To select tree rings formed during drought events for subsequent digitization (Rodríguez-Ramírez & Luna-Vega, 2020), we used specific historical drought years (1976, 1983, 1991, 1999, and 2012; directly from the Agua Blanca weather station). The drought events indicated by these data were confirmed using the information provided by the Mexican Drought Atlas (Stahle et al., 2016). The chronologies were compared with the monthly values of the Palmer Drought Severity Index (PDSI) to estimate drought intensity. The association of narrow ring formation with historical drought years allowed distinguishing specific drought events (through the calculation of *z*-scores; Eq. 1) in the RWI for both species (1976, 1983, 1991, 1999 and 2012).

We calculated the *z*-score for each oak chronology as:

$$z_t = (x_t - x)/s \qquad \text{(Eq. 1)}$$

where *z* is the standardised value of the drought year, x_t is the reconstructed drought ranking, *x* is the mean of the reconstructed chronology, and *s* is the standard deviation of the reconstructed chronology. By plotting the *z*-score and the ≤ 5th percentile, we identified the historical drought years estimated to have been significantly mild or harsh (Jones & Hulme, 1996).

2.5 Effect of drought events on tree growth

We performed a Superposed Epoch Analysis (SEA; Mooney et al., 1993) to explore the effects of the five historical drought years on RWI related to the growth of the two oak study species. SEA links RWI time series with a set of drought events. For each drought event, a 5-yr window was considered including 2 years before and 2 years after the year of the event. The 5-yr windows for all the events were superimposed and averaged to obtain the mean pattern of RWI linked to drought events. The mean RWI pattern for the selected years was assessed statistically for significance (95% confidence interval) by performing 1000 Monte Carlo simulations (Mooney et al., 1993) using random years from the RWI record. We performed these analyses in R with the *dplr* package (Bunn, 2008).

Next, to determine historical drought effects on RWI for each oak species, we assessed three sensitivity indicators, namely resistance (*Rt*; Eq. 2), recovery (*Rc*; Eq. 3) and resilience (*Rs*; Eq. 4) based on Lloret et al. (2011), as follows:

$$Resistance\ (Rt) = \frac{Ring\ width_t}{Ring\ width_{t-2}}, \qquad (2)$$

$$Recovery\ (Rc) = \frac{Ring\ width_{t+2}}{Ring\ width_t}, \qquad (3)$$

$$Resilience\ (Rs) = \frac{Ring\ width_{t+2}}{Ring\ width_{t-2}}, \qquad (4)$$

where *Ring* $width_t$ is the growth width of the annual ring in year *t*, *Ring* $width_{t-2}$ is the mean ring width for the 2 years previous to year *t*, and *Ring* $width_{t+2}$ is the mean ring width for the 2 years following year *t* (Anderegg & Meinzer, 2015). We calculated the indices at the individual tree level for each year during the 1930-2012 period. Finally, we performed an ANOVA and *post-hoc* Tukey's test to compare the means of these indicators between year type (drought vs. non-drought) and species. These analyses were conducted using BoxPlotR: a web tool for box-plot creation (http://shiny.chemgrid.org/boxplotr/).

2.7 Tree-ring digitalization and measurement of xylem anatomical traits

To assess drought effects on vessel anatomical variability, we randomly selected 10 cores for each oak species to obtain digital wood core images for vessel traits measurements. We previously prepared the wood cores using the finest grit (2500, Wetordry™). We produced the digital wood core images by using a stereoscopic microscope (Leica Z16 APOA) with a 13 to 51 μm depth of field. Digital wood core images were taken with a digital camera (Leica DFC 490) and saved in TIFF format with a 1.3 µm per pixel resolution (Rodríguez-Ramírez et al., 2018). Within each digital wood core image, we identified the area occupied by each growth ring between two wood rays (~16.5 µm wide × 54.4 µm long). We located the growth ring limits using Adobe Illustrator CC v. 23.0.5 (www.adobe.com; Rodríguez-Ramírez & Luna-Vega, 2020).

For each oak species, we calculated the following vessel traits: hydraulic diameter (D_H), vessel density (V_D), vessel grouping index (V_G), and vulnerability index (VI). We measured vessel traits in digital wood core images for the tree-rings previously identified for three different moments: before, during, and after each drought event (Rodríguez-Ramírez et al. 2020). Vessel traits (D_H, V_D, V_G, and VI) were calculated for each digital tree ring area using ImageJ-Fiji4 (Schneider et al., 2012).

Hydraulic diameter (D_H; in µm; Eq. 5) is related to fundamental environmental conditions and maximizes climatic signals (García-González et al., 2016). This trait was calculated as:

$$D_H \frac{\sum_{n=1}^{N} D_n^5}{\sum_{n=1}^{N} D_n^4}, \qquad (5)$$

where D is the vessel diameter (raised to the 4th and the 5th power), and N is the number of conduits within tree-ring containing n vessels (Souto-Herrero et al., 2017).

To estimate vessel density (V_D; number per mm^2), we counted the number of vessels in each selected image of each wood core and expressed this figure as 'number per mm^2' in the area between two wood rays per tree-ring (Rodríguez-Ramírez & Luna-Vega, 2020).

To assess the vessel grouping index (V_G; the total number of vessels divided by the total number of vessels groups; Eq. 6), we first added the number of isolated vessels to the number of vessel groups (Scholz et al., 2013a), which produced $N_{vessels}$, and then used the formula:

$$V_G = \frac{N_{vessels}}{N\ groups}, \qquad (6)$$

Carlquist's vulnerability index (VI; with values ranging from 1.0 to 3.0; Eq.7) *sensu* Hoeber *et al*. (2014) is commonly used to reveal species adaptations to either xeric (values close to 1.0) or mesic conditions (values close to 3.0). Species with narrow and abundant vessels show low vulnerability, in agreement with the often-observed trade-off between vessel size and cavitation resistance. VI was calculated by dividing the mean vessel diameter by vessel density, as follows Carlquist (2020):

$$VI = \frac{D}{V_D}, \tag{7}$$

where vessel diameter (D, μm) and vessel density (V_D, number per mm^2) provide a raw signal of the plant's ability to withstand drought-induced cavitation or embolism.

Differences in vessel trait values between drought years (DY) and non-drought years (NDY) for each study species were assessed through two-way ANOVA and *post-hoc* Tukey pairwise comparisons of all pairs of species-year type combinations, with the *lme4* (Bates et al., 2015), and *ggplot2* (Wickham et al., 2021) R-packages.

2.8 Local climate effects on xylem hydraulic variability

We examined climatic effects on vessel traits through generalised linear mixed modelling (GLMM) with Gamma distributions (Ver Hoef & Boveng, 2007) for each species separately; the response variables were the vessel traits (D_H, V_D, V_G, and VI), whereas T_{max}, Prec, and EvT were the explanatory factors (fixed effects); given the possible lack of independence between sampled individuals, we included the individual tree as random factor.

We tested normality (Wilcoxon–Mann–Whitney test; Dehaene et al., 2021), collinearity, and homogeneity of the variance (χ^2 test; Garson and Moser, 1995) for the residuals of response variables. For each species, we selected the vessel traits values corresponding to the recorded drought years (1976, 1983, 1991, 1999, and 2012), as well as for the two consecutive years before each drought event (*i.e.*, 1974–1975, 1981–1982, 1989–1990, and 2010–2011). We evaluated the effects and significance of each explanatory variable through multi-model inference, by first fitting 10 models for each response variable, and the best model for each of them was selected using the sample corrected Akaike Information Criterion (AICc; Hurvich & Tsai, 1989); the best model was defined as that having ΔAICc = 0. We ran all GLMM analyses in R with the *glm2* (Donoghoe, 2018), *lm4* (Bates et al., 2015), *MuMIn* (Bartoń, 2022), and *ggplot2* (Wickham et al., 2021) packages.

3. RESULTS

3.1 Wood anatomical features and tree-ring chronologies

The wood of the two study species is brown with no visible difference between sapwood and heartwood, with pronounced grain, straight or straight grain and a coarse texture. Both oak species show a semi-ring-porous anatomy with large diameter early wood from five to 10 vessels per mm^2. A band of marginal apotracheal and paratracheal parenchyma facilitates growth ring demarcation. We observed tyloses in the interior of vessel conduits (Figure 2).

We detected a consistent relationship with the drier conditions revealed by the PDSI record for the region that influenced each oak's chronology (Figure 3A). The independent chronologies spanned up to 96 years for *Quercus delgadoana* (1923–2019; DBH range, 20 –88 cm; Figure 3B), and 111 years for *Q. meavei* (1908–2019; DBH range, 20-45 cm; Figure 3C); we used the chronologies from 1930 to 2012 (Figure 3) to assess the effect of historical drought years in eastern Mexico on RWI and vessel traits.

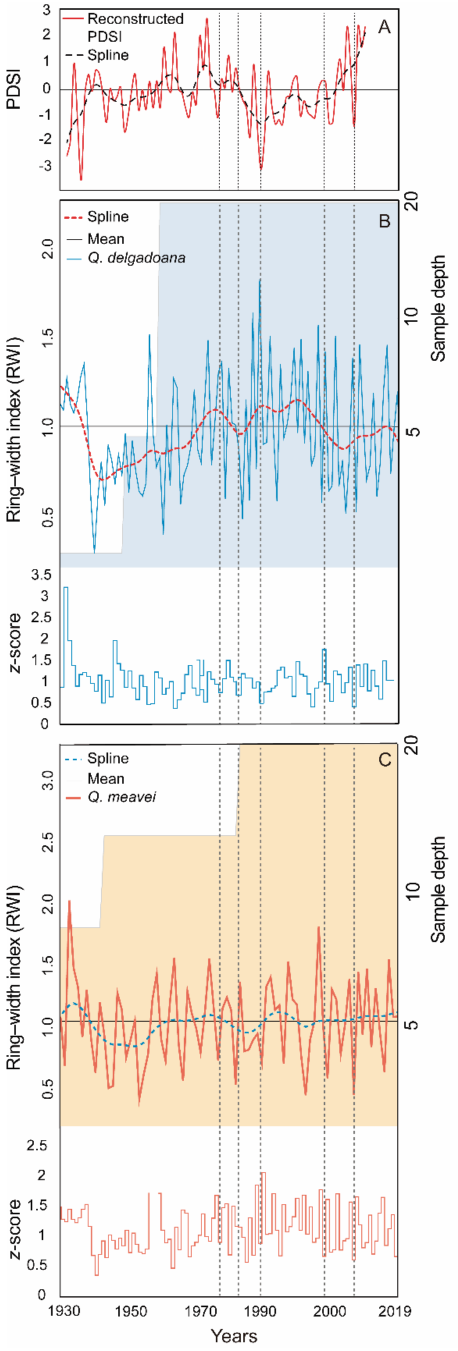

Figure 3. (A) Reconstructed Palmer Drought Severity Index (PDSI; 1929–2012 period; Stahle et al., 2016) responses of the regional chronologies of the two study oaks. (B) Ring-width chronology for *Quercus delgadoana*. (C) Ring-width chronology for *Quercus meavei*. For both chronologies, *z*-scores (≤ 5th percentile) are shown as vertical dotted lines to represent the historical drought years selected for the analysis.

The association of narrow ring formation with historical drought years allowed us to distinguish specific drought events (z-score ≤ 5th percentile) in the RWI; for both species we detected four drought events, two of them shared between the two species: 1976, 1983, 1991 and 2012 for *Quercus delgadoana* (Figure 3B); and 1976, 1991, 1999 and 2012 for *Q. meavei* (Figure 3C).

For all chronologies, evident growth synchrony was detected; chronologies showed inter-series correlations ranging from 0.631 (*Q. delgadoana*) to 0.701 (*Q. meavei*), with R-bar > 0.5 and SNR > 4.5, suggesting a common climatic forcing influencing the growth of individual trees. We detected high EPS values (≥ 0.85), indicating an appropriate replication and a robust common signal among the radial growth of oak trees in the study forest. Mean sensitivity and R-bar values were higher for the more mesic (*Q. meavei*) for the less mesic (*Q. delgadoana*) species (Table 1), which implies that for the former species, year-to-year variability in radial growth linked with inter-annual fluctuations in local climatic conditions is more noteworthy, and that a common growth signal is stronger among individual trees.

Table 1. Growth-ring statistics of *Quercus delgadoana* and *Q. meavei* in a tropical montane cloud forest of the Sierra Madre Oriental, Mexico.

Statistics	**Oak species of study**	
	Quercus delgadoana	*Quercus meavei*
Sampled trees	20	20
Crossdated trees[a]	28	30
Master series (years)	1920–2019	1908–2019
Crossdated rings[a]	2068	2848
Series intercorrelation[a]	0.63	0.70
Mean sensitivity[a]	0.45	0.54
Common interval[a]	1945–2019	1965–2019
EPS[b]	0.85	0.87
R-bar[b]	0.63	0.55
Signal to–noise–ratio (SNR)[c]	4.64	5.19

[a] Values obtained with COFECHA (Holmes, 1999b)
[b] R–package *dplR* (Bunn, 2008)
[c] Values calculated with ARSTAN (Cook & Holmes, 1999)

3.2 Local climate correlations

For both species, growth correlated positively with the mean maximum monthly temperature in current April to May ($r_s \geq 0.5$); by contrast, it correlated negatively for *Quercus meavei* during current June ($r_s = -0.5$; Figure 4A). Though *Q. delgadoana* showed negative correlations with monthly precipitation (Prec) in the previous August, a noteworthy positive relationship ($r_s \geq 0.5$) was found for the previous October and current June (Figure 4B). In turn, *Q. meavei* exhibited positive correlations with current June and August ($r_s = 0.5$; Figure 4B). The two species showed significant positive relationships ($r_s \geq 0.5$) between tree growth and monthly evapotranspiration (EvT) from previous July to September; however, both also exhibited negative important correlations with EvT of current May to July, the period corresponding to the dry season ($r_s \leq 0.5$; Figure 4C).

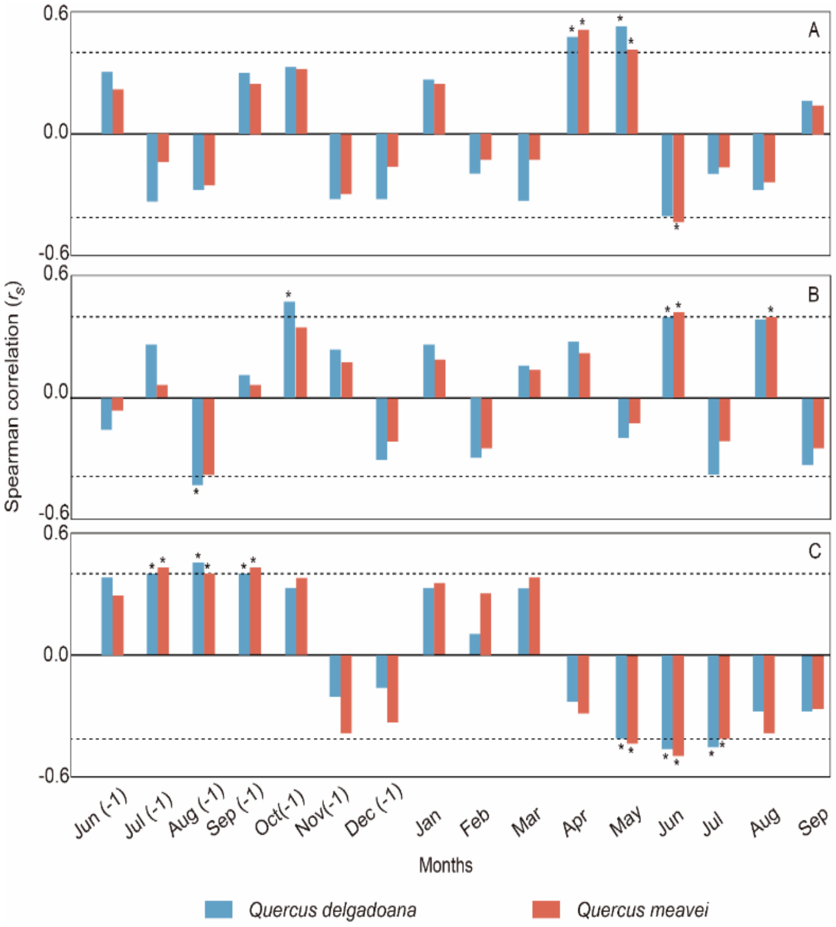

Figure 4. Correlations between chronologies of the two study species and climatic variables for each drought year (June-1 to current September) from 1941 onward. (A) Correlation with mean monthly maximum temperature (T_{max}). (B) Correlation with total monthly precipitation (Prec). (C) Correlation with total monthly evapotranspiration (EvT). Horizontal dashed lines represent 95% confidence intervals for the correlation coefficients.

3.3 Drought influence on RWIs

An increase in temperature associated with drought events seems to have reduced ring width in both oak species. The SEA confirmed the significant relationship ($P < 0.05$) between historical drought events and RWI in both species in the following year (Figure 5).

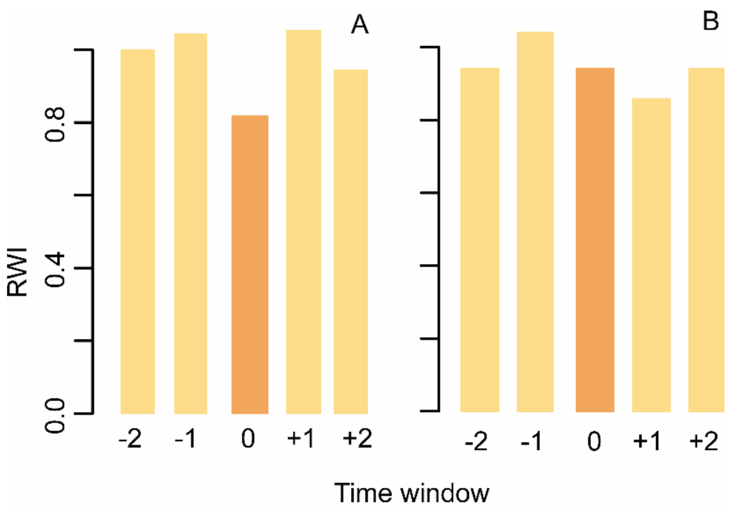

Figure 5. Results of the Superposed Epoch Analysis (SEA) showing the significant influence of drought events on the RWI of (A) *Quercus delgadoana*, and (B) *Q. meavei*. On the *x*-axis, 0 indicates the drought event, and -1 and -2 and +1 and +2 indicate the time window spanning one and two years before and after the drought events (yellow bars), respectively. The orange bars represent the 95% confidence intervals calculated through 1000 Monte Carlo iterations. The common period of the two Neotropical oak species spans from 1930 to 2012.

The analyses of the resistance (*Rt*) of RWI to drought for the two species revealed their high resistance to the drought event (*Rt* range= 0.5 to 2; Figure 6A), with *Q. meavei* being significantly less resistant; however, *Quercus meavei* displayed a higher ability to return to tree-ring width values after a drought (*Rc*) compared with *Q. delgadoana* (Figure 6B). Finally, both oaks showed a similarly high ability to absorb the drought effect and return to its previous tree ring features, i.e., a high resilience (*Rs*), (Figure 6C).

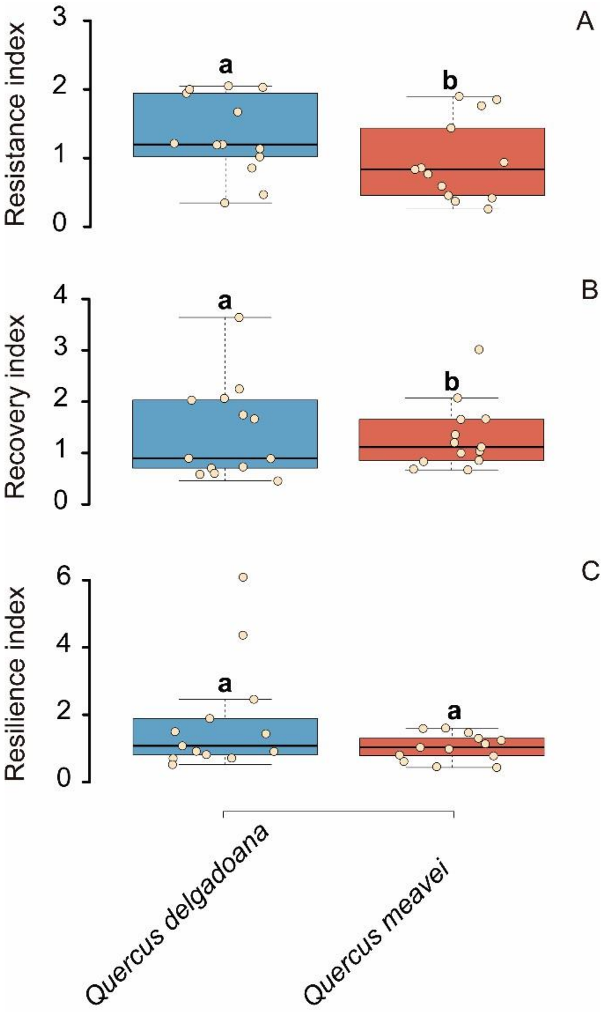

Figure 6. Box plots showing the ranges of variation of the RWI for the two study oak species. (A) Resistance index; (B) Recovery index; (C) Resilience index. Box plots with different letters are significantly different as tested using a *post-hoc* Tukey test ($P < 0.05$).

3.4 Xylem vessel trait adaptation in the study oak species

Wood anatomical differences in tree-ring width between DY and NDY in both species are indicative of the existence of an acclimate potential in these trees to extreme climatic events. A hydric deficit that occurs during drought event triggers the formation of narrow rings and the variation in vessel traits. Noteworthy, differences between DY and NDY largely accounted for the observed variance in D_H, V_D, V_G, and VI (Table S1). Associated with higher annual precipitation (i.e., non-drought years), D_H, V_D, and VI values for *Quercus delgadoana* tended to be larger (but not significantly so) than those for *Q. meavei*.; D_H ranges were larger in *Q. delgadoana* for both year types (DY, 10–400 µm; NDY, 80–580 µm) than in *Q. meavei* (DY, 30–280 µm; NDY, 200–420 µm) (Figure 7A). We observed a similar pattern of variation for V_D in DY and NDY between the two species (Figure 7B), and again, no significant differences in the V_G values were found between oaks although they differ between year types (ranges for *Q. delgadoana*, 1-6 for DY and 1–4 in NDY; ranges for *Q. meavei*, 1–3 for DY and 0.5–2 in NDY; Figure 7C). Finally, the VI values were more or less similar (but with significant differences) between species (from 1 to 6) during DY; however, it is noteworthy that the VI was highly plastic in *Q. delgadoana* (from 0.3 to 0.8), whereas the variation in this index was much more constrained for *Q. meavei*, particularly during NDYs (from 0.9 to 1.4) (Figure 7D).

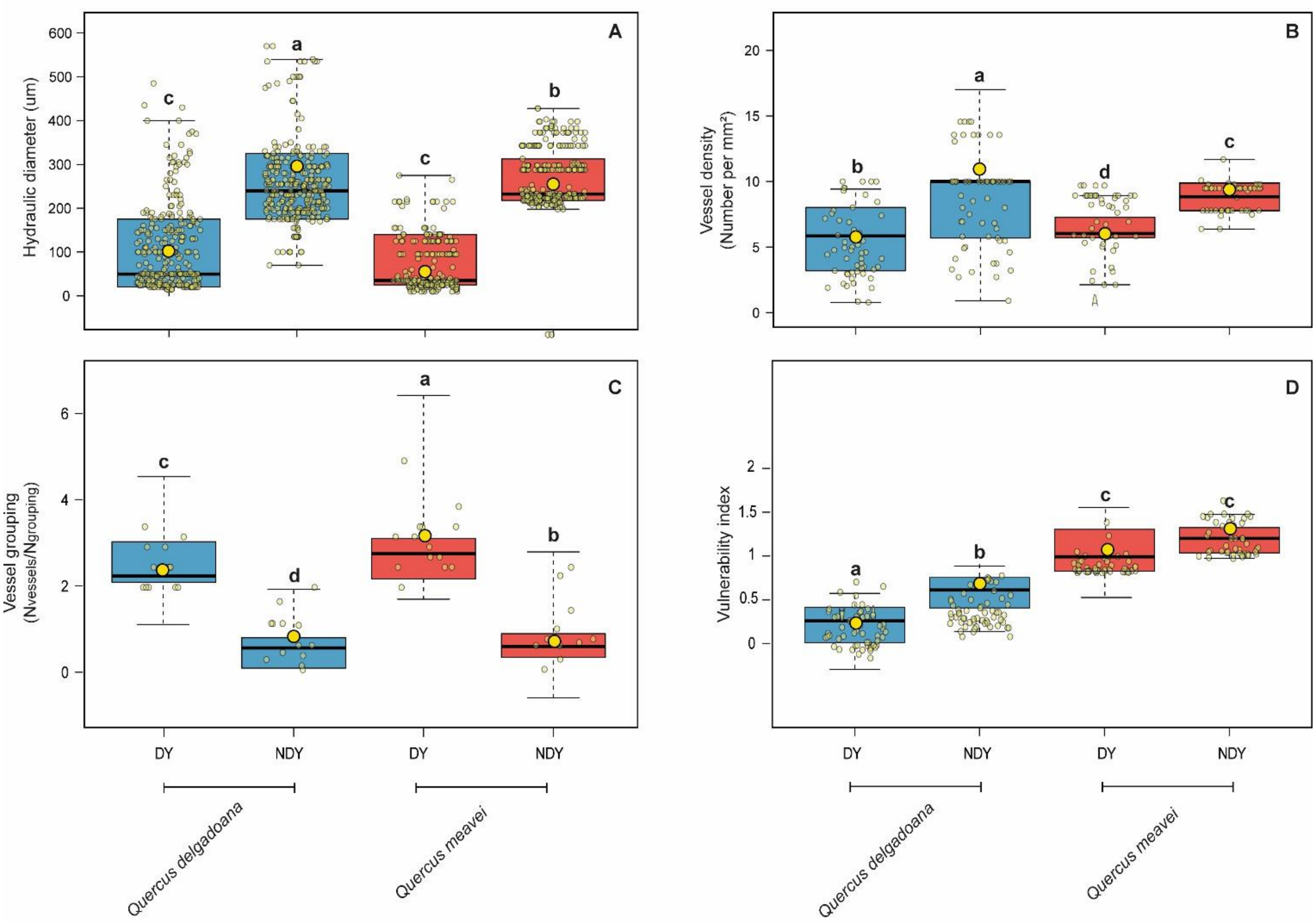

Figure 7. Jitter-plots overlays of box plots showing vessel trait variations between drought years (DY) and non-drought years (NDY) for the two study oak species. (A) Hydraulic diameter; (B) Vessel density; (C) Vessel grouping; and (D) Vulnerability index. Box plots with different letters are significantly different as tested using a *post-hoc* Tukey test.

3.5 Climatic effect on xylem hydraulic adaptation

The GLMM analysis showed a differential influence of climate factors on vessel traits in the two study oaks. For *Quercus delgadoana*, EvT had a negative effect on D_H ($\beta = -0.004$, $P = 0.024$); EvT ($\beta = 0.004$, $P = 0.049$) and T_{max} ($\beta = 0.960$, $P = 0.006$) had positive effects on V_G, but V_D and VI were not significantly influenced by climate factors (Figure 8, Table S2). In turn, for *Q. meavei*, T_{max} affected D_H negatively ($\beta = -0.837$, $P = 0.017$), whereas climate factors did not significantly affect V_D, V_G, and VI (Figure 8; Table S2).

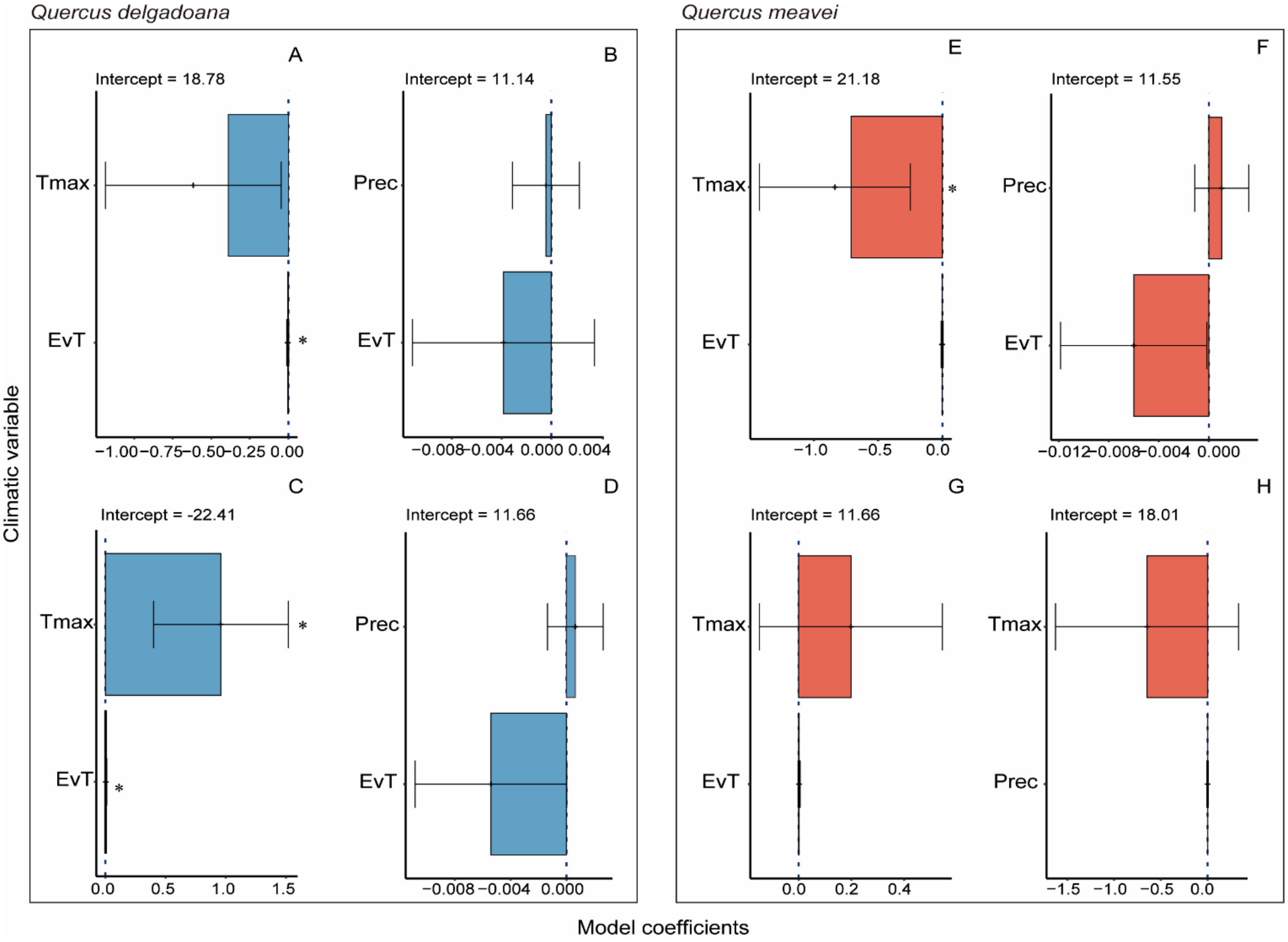

Figure 8. Model coefficients of the best GLMMs constructed to examine the effects of T_{max}, EvT, and Prec on vessel trait variation in the two study oak species. (A–D) *Quercus delgadoana*, (E-H) *Quercus meavei*. Response variables: (A, E) Hydraulic diameter; (B, F) Vessel density; (C, G) Vessel grouping; and (D, H) Vulnerability index. Dotted lines represent the trends of the data. Asterisks show model coefficients that are significantly different from 0 ($P < 0.05$).

4. DISCUSSION

In this study, we show that climatic variations in the TMCF directly influence the anatomical features of the xylem vessels in the two oak species. Although the diffuse porosity suggests mesic wood adaptations in both species, it was noticeable that the tree-rings in both of them revealed high resistance, recovery, and resilience to drought,-despite the differences in habitat preferences (wetter in-*Quercus meavei* and less moist in *Q. delgadoana*) between the two species. Interestingly, the differences in wood anatomical adaptation potential between these oak species do not suggest a different probability to persist to drought periods in this forest between them. A further important finding of our study is that only temperature and evapotranspiration rates have contrasting effects on specific vessel hydraulic functional properties of the study species.

4.1 Growth ring sensitivity to drought events

Our results demonstrate that at least some climate factors do influence growth-ring variation in the study species. The mean sensitivity and inter series-correlations not only revealed a large inter-annual growth ring variation but also a strong common signal among individual series in each oak chronology. Relative to other tree chronologies from Mexican TMCF, the mean R-bar statistics calculated for the study species (*Quercus delgadoana*, 0.55; *Q. meavei*, 0.63) were relatively high compared to *Magnolia schiedeana* (R-bar = 0.40–0.46; Rodríguez-Ramírez et al., 2020), *Pinus pseudostrobus* Lindl. (R-bar = 0.40; Gutiérrez-García et al., 2020), *Symplocos coccinea* Bonpl. and *S. speciosa* Hemsley (R-bar = 0.39 and 0.37, respectively; Rodríguez-Ramírez et al., unpublished data). Likewise, the expressed population signal (EPS) values (0.85 for *Q. delgadoana* and 0.87 for *Q. meavei*) suggest that the two study species can readily respond to limiting factors operating locally such as temperature and moisture rates, confirming that chronologies are useful for the study of climate-growth relationships (Fritts, 2012).

4.2 Climate and tree-growth relationships

Correlations with climatic variables (T_{max}, Prec, and EvT) showed that the annual growth of both study species is mainly driven by T_{max} from April to May (dry warm season), confirming earlier reports by Rodríguez-Ramírez et al. (2018), who detected a strong positive relationship between RWI and T_{max} (in the same months) for *Fagus mexicana*, and by Rodríguez-Ramírez et al. (2020a, b), who found a significant relationship between RWI and T_{max} (in May) for *Magnolia schiedeana*. Unexpectedly, Prec was statistically important for both species during current June only. Unlike other TMCF tree species (Rodríguez-Ramírez et al., 2018; Rodríguez-Ramírez et al., 2020a, b), we found a negative association between radial growth and Prec in the previous year [Aug (-1), Oct (-1) for *Q. delgadoana*)], and a positive one during current June for both species (as well as in August for *Q. meavei* only). The explanation for these results may be related to the high moisture and precipitation levels typical of TMCF of which our study species form part. Although in the study forest yearly precipitation values as low as 824 mm have been recorded (Rodríguez-Ramírez et al., 2018), it is very likely that horizontal precipitation (i.e., water entering the system as drizzle, fog and mist) compensates for this low precipitation, modulating the growth sensitivity of both oak species during the dry season, as suggested by Fang & Lechowicz (2006), and Long et al. (2022). Moreover, annual growth in both study species is also strongly influenced by EvT ($r_s \geq 0.5$) under drought-stressed conditions, when temperature peaks [i.e., the midsummer period; from Jun (-1) to Aug (-1)], whereas the EvT from current May to current July seems to exert a negative effect on radial growth. Increasing temperatures result in high evapotranspiration levels (Singh et al., 2021), which led to previous suggestions that oaks from moist forests are considered sensitive and vulnerable tree to climate change (Jiménez-García & Peterson 2019; Brizuela-Torres et al., 2023). Nevertheless, future studies will have to pay attention to reductions in horizontal precipitation, given their potential effects on the responses of TMCF trees to droughts, which are usually only recorded as decreased precipitation.

4.3 Growth ring vulnerability to drought

The RWI-drought sensitivity in both study species provided additional evidence for the specific effects of climate variation. Interestingly, the three growth sensitivity indicators (*Rt*, *Rc*, and *Rs*) showed specific variation in the study species. Overall, for resistance (*Rt*), which quantifies the negative effect of drought events on growth, *Quercus meavei* showed lower values, most likely because this species grows mostly near water streams, which guarantees some water provision even in dry years. By contrast, *Quercus delgadoana* showed higher *Rc* and *Rs* values, suggesting that this species is somewhat better able to persist even at marginal sites of its range under sub-optimal soil conditions compared with the *Quercus meavei* (Valencia-Ávalos et al., 2016).

In interpreting the resilience results for the two study species, it must be noted that the fact that the growth sensitivity indicators used here are relative values of growth ratios (before, during, and after drought events) implies that they are strongly influenced by growth in the period just preceding the onset of the hydric stress (Lourenço et al., 2022). In theory, a high resistance index could be determined simply by poor growth before the drought events, providing evidence of ‘ecological stress memory’ (Mu et al., 2022) proving tree growth resistance to a climate-stresses occurred in previous years. A similar argument holds for the resistance index (Figure 7; Poorter et al., 2021). Even so, our approach based on growth sensitivity indicators assessment, also used in other studies, has proved useful for assessing tree growth responses to drought events through within- or between-species comparisons (Bose et al., 2020).

4.4 Vessel trait variation in drought and non-drought years

The observed differences in wood anatomical variability between the two oak species have important implications (Figure 7), as they suggest specific adaptations reflected as a differential hydraulic functional reduction in vessel traits during DYs compared to NDYs. Between-species differences in the magnitude of wood anatomical adaptability may play a key role in the acclimation potential and competitive abilities of co-occurring species (Carlquist, 2020; Gea-Izquierdo et al., 2012; Rita et al., 2015). Wood variability is crucial to identify TMCF tree adaptability to climate variation (Rodríguez-Ramírez et al., 2020a). *Quercus meavei* exhibited somewhat lower vessel traits values, including D_H, $V_{D,}$ and VI, but higher values for V_G, than its drought-adapted counterpart, with a noteworthy low intraspecific variation in V_D (Figure 7), suggesting a slightly higher adaptation potential to drought events. In turn, *Q. meavei* was identified as a species with higher resistance to drought-induced embolism and or cavitation, thus avoiding the blockage of the hydraulic pathway (Scholz et al., 2014). This finding suggests that the two study species, each one being related to a particular micro-habitat of the forest where they occur, have contrasting hydraulic adaptation potentials (Anderegg & Meinzer, 2015). Species from moist environments often display an acquisitive resource strategy that leads to increased hydric adaptation abilities (diffuse porosity), suggesting a more efficient hydraulic function (Choat et al., 2007; Fontes et al., 2022). These results imply that at least some TMCF tree species that live at the edge of their hydraulic safety margins (ring porosity) may have the ability to adapt (Fonti et al., 2010; Fonti & Jansen 2012) under the projected climatic conditions (Ponce-Reyes et al., 2012). This result is consistent with the established pattern of xylem anatomical strategies of TMCF tree species (Rodríguez-Ramírez et al., 2020b), such as reduced vessel diameter, and increased intervascular wall thickness and vessel density, all of which are traits that can assist species in coping with increased drought stress and preventing embolism (Choat et al., 2012).

4.5 Xylem traits reflect the climate and climatic variability

Despite the long-standing recognition of the importance of climatic variation for TMCF tree species (Rahman et al., 2018), assessing drought effects on xylem functional hydraulic variability is relatively new. Knowledge about how climate factors on xylem variability are related to the resilience of TMCF tree species will provide insight into their future potential responses to climate change (Rodriguez-Ramirez et al., 2020a, b). Our results show that D_H was influenced by EvT in *Q. delgadoana* and by T_{max} in *Q. meavei*, both factors resulting in narrow vessels when limiting (Figures 8A, E), showing functional adaptations in xylem properties (Fontes et al., 2022) similar to those of other TMCF tree species (Rodríguez-Ramírez et al., 2020a, b). A high number of narrow vessels is safer in terms of resistance to embolism compared to fewer wider vessels (e.g., Abrantes et al., 2012). Interestingly, V_G was significantly influenced by T_{max} and EvT in *Q. delgadoana* only (Figure 8C), which could imply a higher resilience in this species to droughts, preventing air seeping through the hydraulic pathway and thus providing a considerable degree of hydraulic safety in environments with reduced moisture (Scholz et al. 2013b).

High elevation exerts a strong influence on the climatic stress tolerance of several TMCF tree species, which is mediated by the specific leaf morphology in trees growing under those conditions (Velázquez-Rosas et al., 2002; Toledo-Aceves et al., 2022). In particular, the leaves of *Q. delgadoana* have entire leaf margins, an adaptation to water-limited environments and higher temperatures; by contrast, *Q. meavei*, with toothed leaf margins, is better adapted to high moisture environments. Therefore, these two morphological features will probably play a key role in xylem functional plasticity in the face of climate variation (Fonti & Jansen, 2012). These results should be taken with caution, however, since our study did not include the entire geographical ranges of the two study species, and differences in forest structure across these ranges could be associated with particular environmental features, ultimately influencing the wood anatomical variability and resilience in the event of droughts (Arenas-Navarro et al. 2021).

5. CONCLUSIONS

In this paper, we examined how temperature, precipitation, and evapotranspiration influence tree-ring width and xylem hydraulic architecture in two relict and endemic Neotropical oak species. Based on our results, we reject the hypothesis that the two oak species respond differently to drought events according to their wood anatomy adaptation potential to hydric deficit. Nevertheless, we demonstrated the usefulness of wood anatomical features as proxies of climate and moisture environmental conditions. In fact, we posit that xylem vessel functional traits represent climatic signals better than growth-ring width. A second conclusion derived from this study is that most of the wood anatomical variability can be explained by a few climate variables. The assessment of drought effects on particular xylem anatomical features must give special consideration to those traits conferring resilience upon the growth of these species.

Based on our results for wood anatomical variability, as reflected by vessel trait differences between drought and non-drought years, we suggest that future climatic variation may not necessarily be as detrimental to the growth resilience of TMCF oak species as anticipated. Notwithstanding, this possibility needs to be revised in the light of reductions of horizontal precipitation (Long et al., 2022), along with the presence of illegal logging, another factor currently threatening the persistence of TMCF tree species (Ames-Martínez et al. 2022).

Our study advances our understanding of the wood anatomical adaptations to drought periods and identifies those xylem functional traits that underlie these adaptations, as well as the persistence mechanisms of oak species inhabiting the endangered TMCFs across a range of habitats with different micro-environments. This knowledge is essential to make better and more robust predictions of the responses to climate change of this highly diverse but vulnerable ecosystem and its biota.

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DISCUSIÓN GENERAL

El presente estudio proporciona el primer análisis sobre la evaluación de los rasgos anatómicos de los vasos de la madera en *Quercus delgadoana* y *Q meavei*. Ambas especies son susceptibles a variaciones climáticas, influenciadas principalmente por el clima local y el déficit hídrico, ya que estos factores determinan la anatomía funcional de la madera desencadenando respuestas de variabilidad adaptativa y plasticidad en la arquitectura del xilema.

De acuerdo con los resultados en ambas especies de encinos, se detectaron anillos estrechos durante los años históricos de sequía vinculados al índice de ancho de anillo (RWI) mediante el Índice de Severidad de Sequía de Palmer (PDSI), lo cual concuerda con los resultados de encinos europeos como *Q. robur*, *Q. petraea* y *Q. suber* (Degtyarev y Sklyar, 2015; Olivera et al., 2016; Mendes et al., 2019) indicando que el ancho de anillo disminuyó fuertemente durante los años de sequía, mostrando que el crecimiento radial del árbol es sensible al clima y sus fluctuaciones interanuales. Con respecto a la obtención de los estadísticos; R-bar en *Q. delgadoana*, 0.55 y *Q. meavei*, 0.63 fue relativamente alto, esto podría significar una fuerte señal común encontrada dentro de las cronologías (Pederson et al., 2004; Souto-Herrero et al., 2017;2018; Cook y Pederson, 2011), en comparación con otras especies pertenecientes al bosque mesófilo de montaña como *Magnolia schiedeana* (R-bar = 0.40–0.46; Rodríguez-Ramírez et al., 2020), *Symplocos coccinea* (R-bar = 0.39), *S. speciosa* (R-bar = 0.37); Rodríguez-Ramírez et al., 2023) y de bosques templados como *Pinus pseudostrobus* (R-bar = 0,40) (Gutiérrez-García et al., 2020), entre otras. Adicionalmente, según García-Suárez et al. (2009) y Jump et al. (2017) sugieren que los factores climáticos controlan la variabilidad del crecimiento de los árboles a gran escala, independientemente de la distribución de la población y las condiciones ambientales locales.

Se observó que el valor de la señal poblacional (EPS) de *Q. delgadoana* (0.85) y *Q. meavei* (0.87) tiene un valor de EPS por encima del umbral general aplicado de (0.85) debido a ello especies como los encinos poseen alto potencial dendrocronológico (Wigley et al.,1984; Briffa et al., 2009; Campelo et al., 2010). Lo que junto con la sensibilidad media y la correlación entre series mostrada en las especies revela que los anillos de crecimiento están sincronizados y confirman una correlación significativa con los registros

climáticos durante la formación del ancho del anillo (Fritts, 1976; Manzanilla-Quiñones et al., 2021; Villanueva-Díaz et al., 2021).

Se examinó la correlación entre el ancho de los anillos de los árboles y las señales climáticas mensuales como precipitación, temperatura y evapotranspiración, dichos factores influyen en el crecimiento de especies arbóreas pertenecientes al BMM (Rodríguez-Ramírez et al., 2021; Brizuela-Torres et al., 2023). En las dos especies de *Quercus* se registró una correlación positiva con la $T_{máx}$ en abril y mayo (estación cálida seca), lo que concuerda con Rodríguez-Ramírez et al. (2018; 2020), quienes demostraron una fuerte relación positiva entre el índice de ancho de anillo (RWI) y la $T_{máx}$ para *Fagus mexicana* y *Magnolia schiedeana*. Esto se debe a que en el mes de abril hay alta precipitación estacional favoreciendo el crecimiento radial por su influencia directa en la disponibilidad de humedad del suelo, compensando así la pérdida de agua por el proceso de evapotranspiración (Li et al., 2006; Rodríguez-Ramírez et al., 2019). Aunado a que, este período comprende alta actividad cambial, debido a la baja disponibilidad de humedad lo cual influye negativamente en el crecimiento de los árboles y en consecuencia hay disminución en el transporte de fotosintatos en la zona cambial (Gutiérrez-García et al., 2020). Por el contrario, se observó una correlación negativa en $T_{máx}$ para *Q. meavei* durante junio actual, porque generalmente las especies arbóreas que se desarrollan cerca de sus límites de distribución natural y en altitudes elevadas tienen un factor limitante como la temperatura que afecta el crecimiento anual (Rodríguez-Ramírez et al., 2020).

En este sentido, *Q. delgadoana* presentó una correlación negativa en Prec de agosto anterior lo cual también ocurrió con la precipitación mensual registrada en la conífera *Abies hickelii* y con *Fagus mexicana* durante agosto (-1). Igualmente, Rodríguez-Ramírez et al. (2020) y Gutiérrez-García et al. (2020) revelaron que la precipitación mensual en octubre (-1) de *Magnolia vovidesii* se debe a causa de la estación seca y fría. En contraste, durante junio y octubre anterior ambos encinos presentaron una correlación positiva en Prec, este hecho se registró en otro relicto del bosque de niebla en Hidalgo donde se distribuyen las especies *Magnolia vovidesii* y *M. schiedeana* demostrando una influencia positiva en

la tasa de crecimiento del índice del ancho de anillo (Rodríguez-Ramírez et al. 2020). Asimismo, durante agosto-octubre (estación de otoño-invierno), *Q. meavei* tuvo una correlación positiva en Prec, probablemente a que la precipitación durante octubre estación fría es de baja intensidad lo que favorece la infiltración de agua en el subsuelo, producto de la escasa evapotranspiración (Seiler y Gat, 2007; Gutiérrez-García et al., 2020).

En este sentido, *Q. delgadoana* y *Q. meavei* están fuertemente influenciadas por una correlación positiva de EvT durante la estación de verano largo y fresco de (julio a septiembre) donde los niveles de humedad oscilan entre el 60 y 85% siendo representados por la precipitación oculta (*i, e.*, niebla, neblina y/o llovizna) (Peters 1995; Jarvis y Mulligan, 2011). Además, durante septiembre se ha indicado que la humedad es más alta y las lloviznas son constantes, favoreciendo las tasas máximas de crecimiento radial pero disminuyen durante el inicio de invierno (Rodríguez-Ramírez y Luna-Vega, 2020; Rodríguez-Ramírez et al., 2023). Por otro lado, se registró una correlación negativa de mayo a julio actual (verano seco), teniendo un efecto negativo en el crecimiento, causado por las alteraciones en los patrones de temperatura donde se incrementa y propicia una disminución de niebla que reduce la radiación solar entrante debido al cambio climático (Bruijnzeel., 2001; Rodríguez-Ramírez et al., 2018; Aparecido et al., 2018).

Con relación al Análisis de Época Superpuesta (SEA), se demostró un aumento de temperatura vinculado a los eventos de sequía propiciando una reducción en el ancho de anillo. Se menciona que, los anillos de los árboles son marcadores precisos para determinar el efecto de la intensidad de las condiciones ambientales (Orwing y Abrams, 1997; Toigo et al., 2015; Liang et al., 2019; Rao et al., 2019). Estas especies muestran estrategias diferentes para hacer frente a la intensidad de los eventos de sequía, *Q. meavei* tuvo un efecto negativo para resistencia (Rt), probablemente a causa de habitar microhábitats cercanos a pequeños cuerpos de agua Anfodillo y Olson. (2021); Bohner y Diez. (2005); Guarín y Taylor. (2021) mencionan que en teoría los factores locales como la altura de los árboles y el entorno competitivo influyen en árboles altos provocando mayor vulnerabilidad al estrés hídrico, ya que el agua debe moverse por una superficie más larga, además al encontrarse en ambientes competitivamente densos pueden estar

sujetos a mayor competencia por el agua, dando como resultado efectos drásticos de sequía en sitios mésicos.

Con respecto a lo anterior, los siguientes autores (Gazol et al., 2017; Steckel et al., 2020) mencionan que la importancia de las condiciones microclimáticas del sitio influyen en la resistencia de especies arbóreas. Asimismo, (Muñoz-Gálvez et al., 2021) reveló que *Q. pyrenaica* tuvo baja resistencia a la sequía en rodales mixtos y densos con condiciones hídricas limitadas, mientras que para *Q. delgadoana* la recuperación frente a estos episodios fue alta y podría deberse a la creciente capacidad de esta especie para tolerar y continuar desarrollándose en condiciones de humedad subóptimas y altamente perturbadas (Valencia-Ávalos et al., 2016).

Por otro lado, la recuperación (*Rc*) en *Quercus delgadoana* tuvo amplia capacidad de restablecerse a los valores de ancho de anillos antes de la sequía, debido a un menor impacto de sequía, que puede estar relacionado con especies de porosidad difusa las cuales cierran rápidamente sus estomas en tiempos de estrés hídrico favoreciendo así la recuperación parcialmente de la conductividad de los vasos de xilema (Cochard y Tyree,1990; Cochard et al., 2001). Semejante a lo ocurrido con algunas especies europeas que habitan un clima similar, *Fagus sylvatica* L. obtuvo un valor de recuperación de (0.001) seguido de *Quercus petraea* y finalmente *Q. robur* (.024) (Vanhellemont et al., 2019). En comparación, *Q. meavei* obtuvo un valor mayor (Rc = 0.8 - 2.0).

En contraste, la resiliencia (*Rs*) en *Quercus meavei* tuvo alta capacidad para absorber el efecto de la sequía y volver a su estado previo. No obstante, *Q. delgadoana* fue más sensible a las variaciones climáticas, este patrón se identificó en *Pinus halepensis*, dicha especie no se recuperó ante los episodios de sequía (Serra-Maluque et al., 2018, Gómez-Márquez et al., 2018; Mu et al., 2022) sugiriendo que las condiciones ambientales de años anteriores son un factor determinante en la capacidad de los árboles para superar los efectos negativos de la sequía sobre el crecimiento, suceso que se han denominado como "memoria de estrés ecológica", demostrando que la resistencia al crecimiento de los árboles a las variaciones climáticas ocurrió en años anteriores.

Derivado de la frecuencia y gravedad de los episodios de sequía que influyen negativamente en las especies de estudio, se observaron diferencias anatómicas entre ambas, el D_H fue mayor en *Quercus delgadoana* durante los años de sequía y no sequía. Swenson y Enquist (2007), Eilman et al. (2009), Issac-Renton et al., 2018) mencionaron que el aumento del diámetro hidráulico podría ser una adaptación para compensar la reducción del ancho de los anillos en condiciones de sequía. Referente a los resultados sobre la densidad de la madera fue ligeramente menor en años de sequía, pero mayor en años de no sequía (Swenson y Enquist, 2007; Markesteijn et al., 2011) sugieren que es un pronosticador moderadamente bueno de la resistencia a la embolia provocado por la sequía. Por el contrario, *Q. meavei* mostró bajos valores sobre los rasgos anatómicos de los vasos en D_H, V_D y VI. El diámetro hidráulico promedio de los vasos conductores tiende a ser más pequeños debido a que las heladas y las sequías, aumentando el riesgo de cavitación aunado a que los vasos de menor tamaño son más resistentes (Fonti et al., 2010; Lens et al., 2011; Hacke et al., 2017). Estos autores reportaron que la reducción en el tamaño medio de los vasos y la baja densidad, son rasgos de tolerancia a la sequía en encinos, lo que permite a las plantas adaptarse localmente a regiones más secas (Fontes et al., 2021), lo cual beneficiará el mantenimiento de la conductividad hidráulica incrementando la seguridad hidráulica del xilema es decir la diferencia entre el potencial hídrico negativo que experimentan las plantas en su ambiente, menos el potencial hídrico que conduce a una falla hidráulica significativa.

Sin embargo, *Q. meavei* mostró baja densidad de la madera en años de sequía posiblemente a causa de que especies latifoliadas se asocian a potenciales hídricos bajos de xilema (Hackee tal., 2001; Ackerly, 2004; Robert et al., 2017). Aunque curiosamente, los vasos más pequeños conjuntamente con una baja densidad de los mismos, podría estar vinculado a mayor resistencia a la cavitación. Ambos encinos mostraron valores más altos con respecto al índice de V_G durante los años de no sequía. Dicho patrón explicado por (Corcuera et al., 2004; Zang et al., 2011; Fontes et al., 2021) menciona que hay un mayor índice de agrupamiento de vasos en sitios fríos y/o secos. En cambio, durante los años de sequía *Quercus delgadoana* y *Q. meavei* evidenciaron bajos valores de V_G (Valladares et al., 2004; Hacke et al., 2001; 2015; Rodríguez-Ramírez et al., 2020) indican que, los vasos estrechos y abundantes pueden mejorar la conductividad cuando hay agua disponible, pero aumentan la propagación de la embolia cuando ocurre la cavitación. De acuerdo con los bajos valores obtenidos en el índice de vulnerabilidad, las dos especies

de estudio presentan alta susceptibilidad a la cavitación, este resultado muestra que, el progresivo aumento de los niveles de sequía influirá inevitablemente en altos niveles de formación de embolias en muchas especies de árboles que viven al borde de sus márgenes de seguridad hidráulica (Corcuera et al., 2004; Scholz et al., 2014). Lo cual eventualmente desencadenará la desecación total o parcial del árbol y/o la muerte progresiva.

Particularmente para *Q. meavei*, estudios previos mencionan que la arquitectura hidráulica del vaso es más vulnerable a la cavitación inducida por la sequía o las heladas en vasos más estrechos (Cochard y Tyree, 1990; Lo Gullo y Salleo,1993). No obstante, *Q. delgadoana* posee mayor resistencia a embolias o cavitación inducido por sequía VI (≥ 3.0). Choat (2013), Klein et al. (2018) y Rodríguez-Ramírez et al. (2022) explicaron que la capacidad adaptativa de los vasos podría estar relacionada a que opera cerca de sus márgenes de seguridad para evitar fallas hidráulicas, siendo menos vulnerables a cambios futuros en precipitación y temperatura evidenciándola capacidad anatómica de los vasos de xilema ante eventos climáticos (Choat et al., 2012; 2013).

Cada especie de estudio reflejó diferentes estrategias en las variaciones de los rasgos anatómicos de la madera sobre las respuestas estructurales del xilema en los árboles lo que sugiere una alta plasticidad adaptativa de manera individual ante el déficit hídrico y la prevención de embolias en los árboles pertenecientes al BMM y así responder a las variaciones climáticas de un año a otro (Bryukhanova y Fonti, 2013; Anderegg y Meinzer, 2015; Rita et al., 2016; Rodríguez-Ramírez et al., 2020). En relación con el efecto climático que influye sobre los rasgos anatómicos de la madera, estos son un determinante clave en la función hidráulica de las plantas leñosas (Fonti et al., 2010; Fonti y Jansen, 2012). En este sentido, *Quercus delgadoana* y *Q. meavei* registraron un efecto negativo en el diámetro hidráulico (D_H) influenciada por la EvT y $T_{máx}$, lo cual puede deberse a un transporte de agua deficiente entre los vasos del xilema y menor evapotranspiración. También, se sabe que el crecimiento radial en árboles de climas templados y boreales están condicionados principalmente por la temperatura cuya señal climática se registra en los caracteres anatómicos del xilema (Carrer et al., 2016; Castagneri et al., 2017; Swidrak et al., 2011).

Sin embargo, en ambas especies de estudio se observaron vasos estrechos. Por subsecuente, en ambientes fríos o secos el diámetro de los vasos es más estrecho, lo que aumenta la seguridad hidráulica (Sperry et al., 2008; Venegas-González et al., 2015; Olson et al., 2018). Los vasos más pequeños y agrupados son más resistentes lo cual demuestra el papel clave que juegan los diámetros de vasos estrechos como rasgos de tolerancia a la sequía en los encinos, permitiéndoles adaptarse mejor a regiones más secas. (Hacke et al., 2017; Castagneri et al., 2017; Fontes et al., 2022). Por otro lado, se observó en *Q. delgadoana* y Q. *meavei*, un efecto negativo por EvT en la densidad de los vasos (V_D). Estudios previos mencionan que la densidad de los vasos está mejor relacionada con la seguridad hidráulica, ya que una mayor densidad aumenta la capacidad de evitar la implosión de los vasos y, por lo tanto, está indirectamente relacionada con la capacidad de evitar las embolias inducidas por la sequía (Preston et al., 2006; Zanne et al., 2010; Jacobsen et al., 2012).

Nuestros hallazgos muestran una fuerte influencia positiva de la $T_{\text{máx}}$ y EvT sobre el V_G en *Q. delgadoana*, lo que parece implicar redes de vasos hidráulicos altamente agrupados y estrechos en comparación a vasos hidráulicos anchos y solitarios, favoreciendo la tensión del xilema y reduciendo así la formación de burbujas de aire (embolias), lo que podría indicar adaptaciones hídricas xéricas (Smith et al., 2013; Johnson et al., 2020). En este sentido, *Q. delgadoana* fue negativamente afectado por la EvT, lo cual concuerda con Lens et al. (2011), quienes mencionan que los conductos pequeños son más resistentes a la cavitación que los grandes, lo que resulta en una compensación entre xilema seguro. No obstante, *Q. delgadoana* tuvo un fuerte efecto de EvT observando altos valores en el índice de vulnerabilidad (VI) que puede estar relacionado al hábitat donde se desarrolla la especie en elevaciones altas (1840–2210 m s.n.m.) de modo que serán mejores competidores tanto en hábitats más secos (Valencia-Ávalos et al., 2011), en contraste con *Q. meavei* en donde habita elevaciones más bajas (1630-2250 s.n.m), en el cual prevalecen condiciones de alta humedad (Valencia-Ávalos et al., 2016). Dicha especie requiere alta eficiencia hidráulica, aunque sufre de baja seguridad hidráulica, por ello está restringida a hábitats que tienen alta disponibilidad de agua (Markesteijn et al., 2011).

En ambas especies de encinos, se observan estrategias adaptativas para hacer frente a variaciones climáticas extremas, que determinan la capacidad de las especies arbóreas para resistir a la sequía. Sin embargo, dichos resultados deben tomarse con cautela, debido a que no incluyó todos los rangos geográficos donde se distribuyen las especies, que podrían influir en las propiedades hidráulicas del xilema y por ende en la plasticidad anatómica de la madera e intervenir en la supervivencia o mortalidad de los árboles (Castagneri et al., 2017; Robert et al., 2017; Fontes et al., 2022).

CONCLUSIONES GENERALES

Este estudio contribuye al conocimiento dendro-anatómico de *Quercus delgadoana* y *Quercus meavei* especies relicto-endémicas pertenecientes al bosque mesófilo de montaña, en las cuales se evaluó el efecto de la temperatura, la precipitación y la evapotranspiración que influyen en el ancho sus anillos y en la arquitectura hidráulica de su xilema.

Los caracteres anatómicos de la madera son útiles como indicadores de las condiciones ambientales climáticas y de humedad. En ambas especies, los rasgos funcionales de los vasos de xilema son mejores predictores de las señales climáticas que el ancho de los anillos de crecimiento.

La mayor parte de la variabilidad anatómica de la madera se puede explicar por algunas variables climáticas.

La respuesta de los efectos de la sequía sobre los rasgos anatómicos del xilema deben considerar las características que aporten resiliencia al crecimiento de las especies de estudio.

El éxito del desarrollo y la competitividad de los árboles dependen de su capacidad para ajustar y optimizar su arquitectura hidráulica a su entono especifico.

Este estudio proporcionó un avance sobre el conocimiento de las adaptaciones anatómicas de la madera a los períodos de sequía e identifica los rasgos funcionales del xilema que subyacen a estas adaptaciones. Sin embargo, se requieren más estudios analizando otras especies
pertenecientes al BMM para establecer predicciones más robustas sobre las respuestas al cambio climático de este ecosistema diverso, pero altamente vulnerable.

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