



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
ESCUELA NACIONAL DE ESTUDIOS SUPERIORES UNIDAD MORELIA

**Factores que determinan la estructura y composición entre
asociaciones de encinos (*Quercus*: Fagaceae) en un paisaje
fragmentado en la Cuenca del Lago de Cuitzeo Michoacán.**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

RAFAEL AGUILAR ROMERO

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MORELIA, MICH. ENERO 2019



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LIC. IVONNE RAMÍREZ WENCE

Directora General de Administración Escolar, UNAM
Presente

Por medio de la presente me permito informar a usted que en la reunión ordinaria del Subcomité de Biología Experimental y Biomedicina del Posgrado en Ciencias Biológicas, celebrada el día 01 de octubre de 2018, se aprobó el siguiente jurado para el examen de **DOCTOR EN CIENCIAS** del alumno **AGUILAR ROMERO RAFAEL** con número de cuenta 512027168, con la tesis titulada: "**Factores que determinan la estructura y composición entre asociaciones de encinos (*Quercus: Fagaceae*) en un paisaje Fragmentado**", bajo la dirección del **Dr. Alberto Ken Oyama Nakagawa**:

Presidente: Dr. Armando Horacio Paz Hernández
Vocal: Dr. Adrián Ghilardi
Secretario: Dr. Antonio González Rodríguez
Suplente: Dr. Alejandro Velázquez Montes
Suplente: Dra. Susana Valencia Avalos

Sin otro particular, quedo de usted.

ATENTAMENTE

"POR MI RAZA HABLARÁ EL ESPÍRITU"

Cd. Universitaria, Cd. Mx., a 05 de octubre de 2018.

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA



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RESUMEN

Explicar que factores determinan la distribución de las plantas es un tema relevante en la ecología. En diferentes estudios se han identificado que la distribución de las especies de plantas está determinada por factores ambientales. En el caso de los encinos (*Quercus* spp.) se ha planteado que las diferencias en su distribución a nivel de paisaje se debe a la especialización en una porción del gradiente ambiental, lo que sugiere una diversidad funcional que favorece la repartición del hábitat entre especies relativamente cercanas. El presente trabajo explora cuáles son los factores que determinan la distribución de las especies y los mecanismos que promueven la coexistencia de especies de encinos a nivel de paisaje. Se evaluó i) si las especies de encinos difieren en su distribución y si está relacionada con el ambiente y ii) si existe diferenciación funcional entre las especies de encinos que explican su distribución en el ambiente.

Para llevar a cabo el trabajo se censaron 78 fragmentos de encinares en la Cuenca de Cuitzeo en Michoacán. A lo largo de esta cuenca se detectó un gradiente de aridez y nueve especies de encinos, cuatro de la sección *Lobatae* y cinco de la sección *Quercus*, en las que se cuantificaron atributos biofísicos y fisiológicos. Además, se exploró la disyuntiva entre la tolerancia a la sequía y la capacidad de las especies para adquirir recursos (agua). Las especies mostraron diferencias notables en su distribución: se detectaron tres grupos de especies a través de un análisis de Escalamiento Multidimensional No-métrico (NMDS). Se observó una relación entre la distribución de las especies de encinos con la temperatura y la precipitación. Se detectaron asociaciones entre pares de especies, siendo las más frecuentes entre especies de las diferentes secciones *Quercus* y *Lobatae*. Por último, se detectaron diferencias entre los atributos de las especies de ambas secciones, aunque una gran parte de la variación se explicó a nivel interespecífico, más que entre secciones. Se identificaron dos ejes de covariación: 1) una disyuntiva entre especies con tejidos densos y especies con tejido suaves (eje costos en la construcción de tejidos), y 2) una disyuntiva entre resistencia a la cavitación del xilema y escape a la sequía vía su caducifoleidad.

Se concluye que el patrón de distribución de las especies de encinos está determinado por factores ambientales, lo que sugiere que existe una repartición del hábitat lo cual deriva en una menor competencia por los recursos. Las estrategias de uso de agua de las especies están relacionadas con el ambiente: las especies de zonas áridas tienen hábitos caducifolios y tienen una mejor eficiencia en el uso del agua, mientras que las especies de zonas con mayor humedad son de hábitos brevi-decuidos y su xilema es más resistente a la formación de embolismos.

ABSTRACT

Elucidating the factors determining plant distribution is still on discussion. It has been stated that the distribution is mostly determined by environmental factors, but evidence on whether this or other processes are the determinants remains inconclusive. In the case of oaks (*Quercus spp.*), it has been suggested that their differential distribution at landscape level is due to their specialization to a portion of environmental gradients, which suggests that a functional differentiation favors the partition of the habitat between relatively close species. The present study sought to elucidate the mechanisms that determine the coexistence of the species of oaks at the landscape level. It was evaluated i) if the species of oaks differ in their distribution and if it is related to the environment and ii) if there is functional differentiation among the species of oaks that explain their distribution in the environment. To carry out the work, 78 oak fragments were counted in the Cuitzeo Basin in Michoacán, Mexico, which has an arid gradient and nine oak species have been recorded. Biophysical and physiological attributes were quantified in four species of oaks in the *Lobatae* section and in five in the *Quercus* section, and the trade-offs between tolerance to drought against the ability of the species to acquire was explored resources (water). The species showed notable differences in their distribution. Three groups of oak species were detected through an NMDS (Non-metric Multidimensional Scaling) analysis. A relationship was observed between the distribution of oak species with temperature and precipitation. Associations between pairs of species were detected, being the most frequent among species from the different *Quercus* and *Lobatae* sections. On the other hand, when exploring the attributes, differences were detected between the species of both sections, although a large part of the variation was explained at the species level rather than at the section level. Two axes of covariation were identified: 1) between species with dense tissues versus soft tissue species (the axis of cost of tissue construction), and 2) a trade-off between resistance to cavitation of the xylem against deciduous trees. It is concluded that the distribution pattern of the species of oaks is determined by environmental factors, which suggests that there is habitat distribution and thus avoid competing for resources. The water use strategies of the oaks are related to the environment: the oak species distributed in drier zones tend to be more

deciduous and have a greater efficiency in the use of water while the species occurring in a more humid areas are less deciduous and their xylem is more resistant to embolisms.

CAPÍTULO I

INTRODUCCIÓN GENERAL

1.1 Introducción

Los ecosistemas templados en México ocupan cerca de 33 millones de hectáreas que representan el 16% del país y el 5.5% corresponde a los bosques de encinos (Flores et al. 1971; Toledo y Ordoñez 1993; Rzedowski 1998; Challenger y Soberón 2008). De esa superficie de bosques solo 1 385 032 de hectáreas han sido decretadas como áreas protegidas (Torres-Miranda et al. 2011). Tanto al interior como alrededor de esas áreas boscosas se localizan asentamientos humanos que representan el 20% de la población de México, las cuáles dependen de los servicios ecosistémicos que esos bosques proveen, particularmente la regulación y calidad del agua (INEGI 2005a; Balvanera et al. 2009; Vörösmarty et al. 2010). En México, los bosques templados o bosques de pino-encino se distribuyen principalmente en zonas montañosas en climas semihúmedos (Rzedowski 1998). En los bosques templados se encuentran 43 especies de *Pinus* de las 110 descritas a nivel mundial (Farjon 1996; Farjon y Styles 1997) y en el caso de las especies de *Quercus* se encuentran 161 especies de las 531 descritas a nivel mundial (Govaerts y Frodin 1998; Valencia 2004; Challenger y Soberón 2008).

Estos ecosistemas han sufrido pérdidas de aproximadamente 25% en su cobertura debido al cambio de uso de suelo destinado para la agricultura y la ganadería (Mas et al. 2004). Diversos autores señalan que estos bosques serán muy vulnerables al cambio climático. Para México se ha predicho que se perderá el 13% debido al efecto del cambio climático (Villers-Ruiz y Trejo-Vázquez 1997). Trabajos más puntuales evalúan la vulnerabilidad de 34 especies de encinos y pinos bajo modelos de circulación global proyectados al 2050 (HHGGA50Mex y HHGSDX50Mex), encontrando que bajo estos dos escenarios (pesimista y conservador) todas las especies disminuirán su área de distribución (Gómez-Mendoza y Arriaga 2007).

La vulnerabilidad de las especies de *Quercus* ante el cambio climático es específica para cada especie y dependerá de sus afinidades climáticas. Sin embargo, la sensibilidad de las especies de *Quercus* al cambio climático incluye a las especies de distribución amplia y restringida (Gómez-Mendoza y Arriaga 2007). Un gran número de especies de *Quercus* en México presentan amplios intervalos de distribución geográfica, la gran mayoría se desarrollan en climas húmedos y cálidos; una menor proporción de especies se restringen a ambientes húmedos y fríos (Valencia 2004; Gómez-Mendoza y

Arriaga 2007). Con base en esto se predice que las especies más vulnerables al cambio climático serán aquellas que se desarrollan en zonas húmedas y frías, y las menos vulnerables serán las que se desarrollan en zonas semiáridas y subhúmedas (Gómez-Mendoza y Arriaga 2007). Sin embargo, los efectos del cambio climático han sido poco documentados en los bosques de encinos en México.

En el caso particular de las especies de encinos (*Quercus*) descritas para México, se han reportado patrones generales de diferenciación en la distribución de especies a nivel de sección. Se menciona que las especies pertenecientes a la sección *Lobatae* (encinos rojos), se distribuyen preferentemente en zonas templado-húmedas y subhúmedas. En cambio, las especies de la sección *Quercus* (encinos blancos) son más tolerantes a condiciones áridas y secas aunque también pueden encontrarse en zonas húmedas por lo que su área de distribución es más amplia (Zavala-Chávez 1998; Torres-Miranda et al. 2011). Sin embargo, en trabajos realizados a lo largo de gradientes ambientales, se han observado patrones de distribución diferencial entre especies independientemente de la sección a la que pertenecen (Cavender-Bares et al. 2004; Olvera-Vargas et al. 2010).

En general, se han propuesto diferentes modelos para clasificar las estrategias ecológicas de las plantas que se han desarrollado en función de la variación de sus rasgos funcionales a lo largo de diferentes ejes de especialización. El primer modelo fue planteado por Grime (1977), quien sugiere que las especies pueden distribuirse, crecer y establecerse a lo largo de tres ejes de variación. El primero definido por su capacidad competitiva (C), el segundo por su tolerancia al estrés (S) y el tercero por la respuesta a las perturbaciones y/o su capacidad ruderal (R). Estos ejes estarían determinados por un conjunto de rasgos ecológicos, morfológicos y fisiológicos que determinarían el éxito de las plantas. Sin embargo, no es claro sobre cuáles rasgos funcionales se considerarían y/o cuantificarían. A partir del esquema (CSR) propuesto por Grime, surge un segundo modelo propuesto por Westoby (1998), desarrollando otro modelo denominado (LHS), en el cual el área específica foliar de la hoja representa el eje (L) y refleja la variación en la respuesta de la captación de recursos y crecimiento de una determinada especie, mientras que el eje (R) se podía diferenciar en dos ejes diferentes en función de su altura (H) y del peso de la semilla (S). Este modelo es muy puntual con los rasgos funcionales que se

deben cuantificar, para la exploración de diferentes grupos funcionales o taxonómicos. Finalmente, en relación a las estrategias en el uso de recursos se ha planteado un eje de especialización conocido como “espectro de economía” (Díaz et al. 2004; Wright et al. 2004; Salguero-Gómez 2016), el cual se basa en la disyuntiva entre invertir recursos en la construcción de tejidos para perdurar y la capacidad de resistir a diferentes tipos de estrés ambiental (Freschet et al. 2010; de la Riva et al. 2014). De esta manera, en un extremo de este eje encontramos especies de crecimiento lento con un uso más conservador de los recursos, que les permiten ser competitivas en ambientes con poca disponibilidad de recursos (hábitats cálidos y secos) (Hobbie 1992; Aerts 1995), mientras que en el otro extremo se localizan especies con una mayor capacidad de explotar recursos lo cual se relaciona con tasas de mayor crecimiento y elevadas tasas de renovación de tejidos (órganos), esto les permiten ser dominantes en zonas con mayor disponibilidad recursos (hábitats fríos y húmedos) (Reich et al. 1998; Villar et al. 2006; Pooter y Garnier 2007). En las últimas décadas, los estudios sobre ecología funcional se han centrado en explicar la variación en el desempeño y la distribución de las especies bajo diferentes ambientes (Pineda-García 2013). Estos estudios se han realizado mediante la cuantificación de atributos morfológicos, de fácil medición y poco costosos ya que se pueden replicar para un gran número de especies (Cornelissen et al. 2003; Salgado-Negret. 2015; Salgado-Negret y Paz 2015). La ventaja de estos atributos es que han sido relacionados con una o varias funciones en la fisiología de la planta y que pueden influir en el desempeño de las especies (Cornelissen et al. 2003; Salgado-Negret. 2015; Salgado-Negret y Paz 2015). Mediante la cuantificación de un conjunto de atributos fisiológicos, morfológicos y fenológicos de los distintos órganos de la planta (raíz, tallo y hojas), es que ha sido posible relacionar ciertas funciones de la planta y establecer estrategias de uso de recursos (Freschet et al. 2010). Sin embargo, estos atributos pueden variar entre las diferentes especies e influir de manera directa o indirectamente en la adecuación maximizando su crecimiento o supervivencia (Arckerly et al. 2000; Westoby et al. 2002). El estudio de los atributos funcionales en las especies nos permite profundizar en procesos evolutivos y nos ayuda a entender como las especies pueden coexistir y repartirse los recursos en una misma región (Peñuelas y Filella 2001; Cavender-Bares et al. 2004; Badeck et al. 2004; Reusch y Wood, 2007).

Los patrones de distribución de las plantas y el ensamble de especies en las comunidades son determinados por las adaptaciones a la disponibilidad de recursos y a la heterogeneidad ambiental (Tilman, 1982; Tokeshi, 1999; Ackerly, 2003; Cavender-Bares *et al.* 2004; Ackerly *et al.* 2006; Kelly *et al.* 2008; Mills, 2009; Pérez-Ramos *et al.* 2012; de la Riva *et al.* 2014). Por esta razón, se plantea que las especies han desarrollado adaptaciones que les permiten establecerse y sobrevivir a diferentes niveles de recursos. (Pérez-Ramos *et al.* 2012; de la Riva *et al.* 2014; López-Iglesias *et al.* 2014; Reich 2014). La disponibilidad de agua es un factor clave para las plantas en diversos ambientes como se ha reportado para zonas templadas, áridas y tropicales (Sack 2004; Padilla y Pugnaire 2007; Engelbrecht *et al.* 2007). La disponibilidad de agua determina la sobrevivencia, el establecimiento y la distribución de las especies (Engelbrecht *et al.* 2007). En general, se ha encontrado que las plantas han desarrollado diversas estrategias para tolerar la sequía (Joffre *et al.* 1999; Chaves *et al.* 2002; Valladares, 2008). En función de estas estrategias, se definen dos grupos de plantas: i) las especies **tolerantes a la sequía** son aquellas que presentan rasgos que les permiten seguir funcionando a niveles de baja disponibilidad de agua y ii) las especies capaces de **escapar a la sequía** son aquellas que generalmente pierden sus órganos aéreos (hojas) durante la temporada de secas (Ogaya y Peñuelas 2003). Se ha reportado que las especies que se distribuyen en sitios con baja disponibilidad de agua presentan disyuntivas entre ganar carbono y perder agua (Cowan y Farquhar, 1997). Es decir, cuando las plantas cierran los estomas evitan la pérdida de agua y a su vez interrumpen la captura de carbono repercutiendo en el crecimiento y la productividad del bosque (Zweifel *et al.* 2007; Quero *et al.* 2006; Valladares y Sánchez-Gómez, 2006). En consecuencia, se esperaría que las especies adaptadas a la sequía presenten bajas tasas de crecimiento (Férrnandez y Reynolds, 2000). Uno de los mecanismos de mayor relevancia, para entender la respuesta de las plantas ante escenarios de sequía es el funcionamiento del sistema hidráulico. El sistema está conformado por un tejido denominado xilema, el cual es responsable de suministrar mediante una red de conductos el agua al interior de la planta para satisfacer las diferentes funciones incluidas la fotosíntesis, el crecimiento y la reproducción. Las disrupciones en la red hidráulica como consecuencia del estrés hídrico han sido identificadas como mecanismos claves para entender la tolerancia de los árboles a la

sequía (McDowell et al. 2008; Kursar et al. 2009; Adams et al. 2017). En el xilema, la estabilidad del agua líquida disminuye a medida que baja el potencial hídrico y cuando este llega a ser muy negativo, el agua tiende a evaporarse en el interior de los conductos del xilema, produciéndose burbujas de aire (embolismo) que obstruyen los conductos (Zimmermann, 1983; Martínez-Vilalta y Piñol 2003). Estos embolismos bloquean el flujo de agua y reducen el suministro de agua al dosel y a los tejidos regenerativos (meristemos apicales y cambiales) (Brodrribb y Cochard 2009; Rodríguez-Domínguez et al. 2018). Generalmente, ante condiciones de sequías prolongadas se genera mayor tensión en el xilema y existe una mayor probabilidad de que se generen embolismos a través de la red de conductos causando bloqueos en el sistema hidráulico (Brodrribb y Cochard 2009; Rodríguez-Domínguez et al. 2018).

En particular, las especies de encinos se distribuyen en diferentes partes del mundo, se les puede encontrar en Norte América, en zonas propensas a sequía como el Mediterráneo y California, y finalmente en zonas tropicales con estacionalidades muy marcadas (Renninger et al. 2013). De manera general, se ha documentado que las especies de encinos están adaptadas a diversos ambientes ya que presentan estrategias contrastantes. Por un lado, evitan la sequía mediante sistemas radicales profundos (o despojándose de sus hojas) o bien la toleran mediante un mayor control estomático (Abrams, 1990; Ehleringer y Phillips 1996; Cavender-Bares y Bazzaz 2000; de la Riva et al. 2014; López-Iglesias et al. 2014). Los diferentes mecanismos que explican sus patrones de distribución han sido detectados en diferentes órganos de la planta: ciertas especies pueden desarrollar sistemas radiculares muy profundos que les permiten acceder a una fuente más estable de agua y seguir operando su maquinaria durante la sequía (Abrams, 1990; Ehleringer y Phillips 1996, Cavender-Bares y Bazzaz 2000; Renninger et al. 2014; López-Iglesias et al. 2014). Por otro lado, a nivel de rasgos foliares se han encontrado disyuntivas entre especies brevi-decíduas o decíduas y perennifolias. Las especies brevi-decíduas presentan valores altos de área foliar específica, clorofila y nitrógeno, un síndrome considerado para especies de rápido crecimiento. Las especies perennifolias muestran características consideradas en especies de crecimiento lento ya que presentan hojas densas y gruesas, valores altos de contenido de materia seca, raíces

más profundas y esclerofilia en las hojas (Abrams, 1990; de la Riva et al. 2014; López-Iglesias et al. 2014). Por otro lado, el grado de especialización en sus respuestas adaptativas y el uso diferencial de recursos ha contribuido a la divergencia de nichos entre especies, lo cual ha promovido una alta diversidad en las comunidades de encinos (Cavender-Bares et al. 2004). Sin embargo, esta información ha sido generada para especies de Estados Unidos y Europa y es todavía muy poca la información generada para especies de México.

En México uno de los grupos de árboles más importantes son los encinos debido a su gran diversidad de especies. En particular, se han descrito 161 especies, de las cuales 109 son endémicas al país; 76 corresponden a encinos rojos (sección *Lobatae*), 81 a encinos blancos (sección *Quercus*) y 4 especies de encinos intermedios (sección *Protobalanus*) (Valencia, 2004). Los encinos rojos son más abundantes en las zonas templadas húmedas y sub-húmedas de los ecosistemas montanos del país, a diferencia de los encinos blancos, que a pesar de estar presentes en zonas húmedas, pueden tolerar condiciones áridas y secas, por lo que su área de distribución se vuelve más amplia (Zavala-Chávez 1998; Torres-Miranda et al. 2011). Sin embargo, aún es poca la información que se tiene acerca de cómo cambia la distribución de los encinos a escala de paisaje y, menos aún, cómo difieren en sus estrategias de uso de recursos. De esta manera, el presente trabajo plantea entender cómo se distribuyen las especies a nivel de paisaje, qué factores ambientales determinan la distribución y qué mecanismos les permite diferenciarse para establecerse en sus diferentes hábitats. Entender la biología y las estrategias de las especies para explotar los recursos es de vital importancia para proponer planes de manejo, conservación y restauración de los bosques templados en el centro del país.

1.2 Descripción del área de estudio

Este estudio fue realizado en la Cuenca del Lago de Cuitzeo, que cuenta con una superficie de 4,026 km². Se localiza sobre la Faja Volcánica Transmexicana, al norte del estado de Michoacán y al sur del estado de Guanajuato. El clima es templado con lluvias en verano, presentándose un gradiente de humedad y descenso de temperatura que va de

norte a sur. La temperatura media anual es de 17° C, y la precipitación promedio anual es menor a 800 mm. La topografía y los suelos se derivan de materiales provenientes de actividades volcánicas (lavas y piroclastos) (López et al. 2006; Mendoza et al. 2006; Chávez-Vergara et al. 2013). El tipo de vegetación predominante en la zona son los bosques de encinos (Fig.1), aunque en la actualidad estos han sufrido un alto grado de fragmentación creado por el cambio de uso de suelo (López et al. 2006). Los bosques que en algún momento fueron bosques continuos se han reducido a pequeños fragmentos de diferentes tamaños debido al crecimiento de asentamientos humanos, la expansión de zonas agrícolas y a la tala de bosques para la producción de carbón vegetal (López et al. 2006; Aguilar-Romero et al. 2012; Herrera-Arroyo et al. 2013).

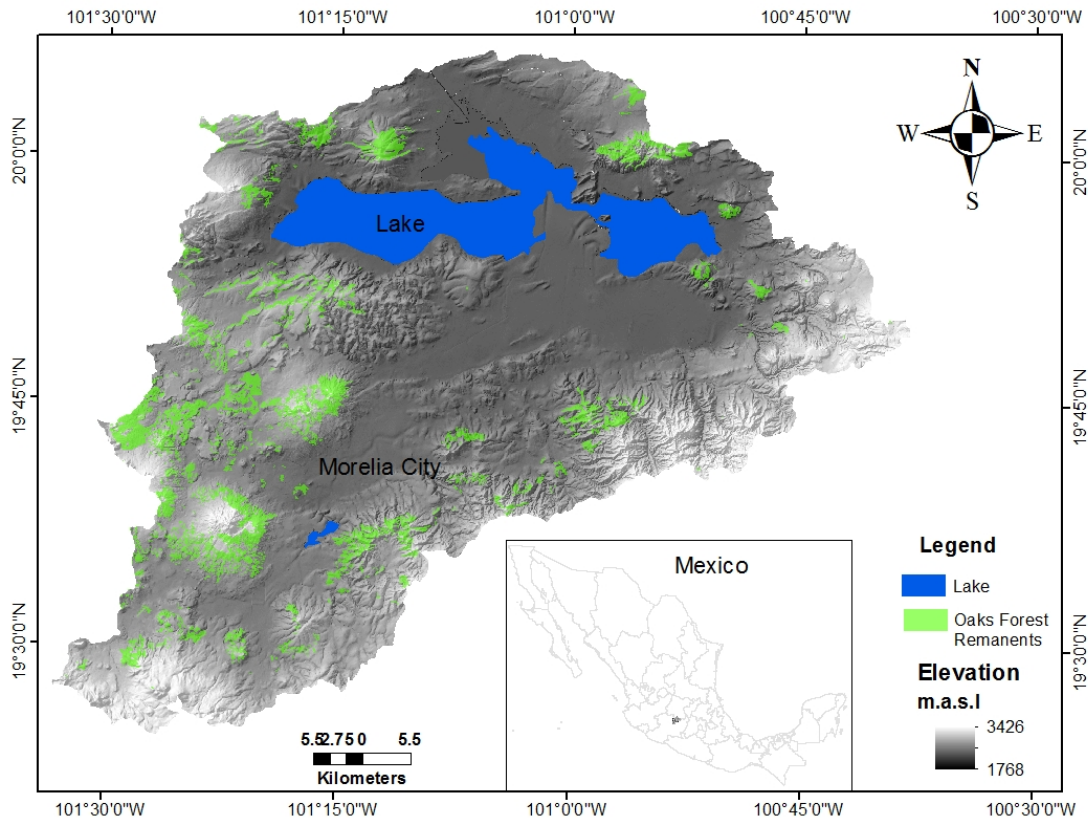


Figura 1. Cuenca del lago de Cuitzeo y los bosques de encinos (*Quercus*) remanentes.

1.3 Preguntas generales

Preguntas capítulo II

- 1.- ¿Existe una distribución diferencial de las especies de *Quercus* dentro de la Cuenca de Cuitzeo?
- 2.- ¿Qué factores determinan la distribución de las especies?
- 3.- ¿Existen asociaciones entre pares de especies?

Preguntas capítulo III

- 1.-¿Existen diferencias entre las especies en sus atributos funcionales?
- 2.-¿Cuáles son las estrategias de uso de agua de las especies?
- 3.-¿Existe una relación entre el uso de recurso y el ambiente de las especies?

1.4 Objetivo general

Determinar los patrones de distribución espacial y la diferenciación ecológica de las especies de encinos en la Cuenca de Cuitzeo, Michoacán.

1.5 Objetivos particulares

Analizar qué factores determinan la distribución y la coexistencia de especies.

1.6 Estructura de la tesis

Para cumplir con los objetivos de esta tesis se desarrollaron dos capítulos que abordan cada uno de los objetivos particulares (**Capítulo II y III**), además de presentar una introducción general en el **Capítulo I**, la discusión general en el **Capítulo IV** y finalmente las conclusiones generales en el **Capítulo V**.

Capítulo II. Patterns of distribution of nine *Quercus* species along an environmental gradient in a fragmented landscape in central Mexico.

En este capítulo se presenta un estudio que tuvo como objetivo identificar los factores que determinan la distribución de las especies de *Quercus* en la Cuenca del Lago de Cuitzeo Michoacán. De manera particular, se exploraron i) los patrones de distribución de

las especies de *Quercus* en una escala de paisaje; ii) los factores climáticos, edáficos y topográficos que determinan su distribución; y iii) el grado de asociación de las especies dentro de los fragmentos. Para esto se censaron 78 parcelas en los encinares en la Cuenca de Cuitzeo, registrando nueve especies de encinos. Las especies mostraron claras diferencias en su distribución; tres grupos de especies de *Quercus* que difieren significativamente en su arreglo espacial fueron detectados con un análisis NMDS (Escalamiento Multidimensional No-métrico). Así mismo, se observó una relación entre la distribución de las especies de encinos, y la temperatura y la precipitación. En este capítulo fue posible identificar que ciertas especies tienen más afinidad a zonas húmedas y frías, en contraste con otro conjunto de especies que son más frecuentes en zonas más áridas. Así mismo, se identificaron asociaciones entre pares de especies de *Quercus*, encontrando que las más frecuentes son entre especies de las secciones *Quercus* y *Lobatae*. Determinar los factores que operan en la distribución de las especies de *Quercus* y el grado de asociación entre especies pertenecientes a diferentes secciones a escala de paisaje, representa información relevante para entender los requerimientos ambientales y las sinergias positivas que pueden presentarse entre especies de las diferentes secciones. Dicha información sirve de parte aguas para establecer planes de restauración y conservación de los bosques de *Quercus* en el centro de México.

Capítulo III. Differentiation in the water-use strategies among oak species from central Mexico.

En este capítulo se presenta un estudio que tuvo como objetivo identificar cuáles son los mecanismos que les permiten a las especies de *Quercus* distribuirse de manera diferencial a través de un gradiente de aridez. Para responder al objetivo se midieron atributos fisiológicos y biofísicos en nueve especies de encinos (cuatro pertenecientes a la sección *Lobatae* y cinco a la sección *Quercus*), a lo largo de un gradiente de aridez en la Cuenca del Lago de Cuitzeo, Michoacán. A su vez se exploró si las disyuntivas funcionales guían la diferenciación entre especies, particularmente en su tolerancia a la sequía y su capacidad de adquisición de agua. Se determinó si las estrategias de uso de agua estaban relacionadas con alguna porción del ambiente que ocupan. Se realizó un análisis para evaluar las diferencias entre especies y secciones (*Lobatae* y *Quercus*),

detectándose una mayor diferenciación a nivel de especie que entre secciones. Se detectaron estrategias entre especies con tejidos densos y especies con tejidos suaves. Así también, se detectaron disyuntivas funcionales entre especies que resisten la cavitación y especies que escapan a la sequía vía su caducifoleidad. Las estrategias estuvieron relacionadas con el ambiente ya que se encontró que las especies de zonas áridas presentan un patrón de caducidad y son más eficientes en el uso de agua. En contraste, las especies de zonas húmedas presentan menor caducidad y un xilema más resistente a sufrir embolismos. Esto demuestra que los filtros ambientales segregan las especies para repartirse en el espacio.

CAPÍTULO II

Patterns of distribution along environmental gradients of nine *Quercus* species in central Mexico.

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Patterns of distribution of nine *Quercus* species along an environmental gradient in a fragmented landscape in central Mexico

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VERSIÓN PRELIMINAR

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Abstract

Elucidating the factors determining plant distribution is still on discussion. It has been stated that the distribution is mostly determined by environmental factors, but the evidence on whether this or other processes are the determinants remains inconclusive. In the present study, we hypothesized that oak species differ in their distribution, which might be mostly influenced by the environment. Particularly, we explored: i) the patterns of distribution of *Quercus* species at a landscape scale; ii) the climatic, soil and topographic factors that might determine their distribution, and iii) the degree of association between the species within fragments. The study included the analysis of 78 oak forest fragments at the Cuitzeo lake Basin in Michoacán state, Mexico in which nine oak species were registered. The species showed clear differences in their distribution; three groups of oak species that differ significantly in their spatial arrangement were detected with a NMDS (Non-metric Multidimensional Scaling) analysis. We observed a relationship between oak species distribution with temperature and precipitation. In particular, *Q. candicans*, *Q. crassipes* and *Q. rugosa* were frequently distributed at sites with higher rainfall and lower temperature; in contrast, *Q. deserticola*, *Q. gentryi* and *Q. glaucooides* were at more arid areas. We found associations between pairs of oak species; the most recurrent one was between species from the *Quercus* and the *Lobatae* sections. Overall, the pattern of distribution among oak species was determined by environmental factors, which suggests that they partition their habitat to avoid competition for resources.

Key words: coexistence, ecological niche, habitat fragmentation, patterns of distribution, oaks.

Patrones de distribución de nueve especies de *Quercus* a lo largo de un gradiente ambiental en un paisaje fragmentado del centro de México

Resumen

Elucidar los factores que determinan la distribución de las plantas todavía se encuentra en debate. Se ha dicho que la distribución es principalmente determinada por factores ambientales, pero la evidencia de si estos u otros procesos son los más determinantes aún no es concluyente. En el presente estudio, se predijo que las especies de *Quercus* difieren en su distribución, y está principalmente determinada por el ambiente. En particular, se exploró: i) los patrones de distribución de especies de *Quercus* en una escala de paisaje; ii) si los factores climáticos, edáficos y topográficos determinan su distribución; y iii) el grado de asociación entre especies dentro de los fragmentos. En este estudio se censaron 78 fragmentos de encinares en la Cuenca de Cuitzeo en el estado de Michoacán, México, en los cuales se registraron nueve especies de encinos. Las especies mostraron claras diferencias en su distribución; tres grupos de especies de *Quercus* que difieren significativamente en su arreglo espacial fueron detectados con un análisis NMDS (Escalamiento Multidimensional No-métrico). Así mismo, se observó una relación entre la distribución de las especies de encinos, y la temperatura y la precipitación. En particular, *Q. candicans*, *Q. crassipes* y *Q. rugosa* frecuentemente se distribuyen en sitios con mayor precipitación y menor temperatura; en contraste, *Q. deserticola*, *Q. gentryi* y *Q. glaucooides* estuvieron en zonas más áridas. Se detectaron asociaciones entre pares de especies de *Quercus*; las más frecuentes fueron entre especies de las secciones *Quercus* y *Lobatae*. En general, el patrón de distribución entre especies de encinos está determinado por factores ambientales, lo cual sugiere que las especies se reparten el hábitat para evitar competir por recursos.

Palabras clave: coexistencia, encinos, fragmentación del hábitat, nicho ecológico, patrones de distribución.

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A recurrent issue in plant ecology is to elucidate the key factors that influence species distribution and assemblages of communities (Tilman, 1982; Huston, 1994; Scott *et al.* 2002). Previous studies had proposed that plant species distribution within communities is mainly driven by stochastic processes (Brokaw and Busing, 2000; Hubbell, 2001; Tilman, 2002; Huston, 2002; Tuomisto *et al.* 2003). In contrast, other studies had proposed that plant spatial distribution and assemblages of species within a community are determined by the adaptation of species to the available resources and heterogeneity of the environment (Tilman, 1982; Tokeshi, 1999; Ackerly, 2003; Cavender-Bares *et al.* 2004; Ackerly *et al.* 2006; Kelly *et al.* 2008; Mills, 2009; Pérez-Ramos *et al.* 2012; de la Riva *et al.* 2014). However, the analyses of environmental factors determining plant species distribution and plant community composition at different spatial scales are still a recurrent theme in community ecology.

Mexico with the complexity of its orography has promoted habitat partitioning and species diversification (Rzedowski, 1978; Villaseñor, 2003; 2004). Particularly, Mexico is considered the center of diversification of several plant groups including the genus *Quercus* L. (oaks) (Villaseñor, 2004; Nixon, 2006). Most of oak species are endemic to the country with a particular pattern of distribution (Nixon, 1993; Abrams, 2003; Valencia-A., 2004; Nixon, 2006; Torres-Miranda *et al.* 2011; Torres-Miranda, 2014). At a continental scale, white oaks (section *Quercus*) occur in drier and warmer environments than red oaks (section *Lobatae*), which are distributed in more humid and colder sites (Zavala-Chávez., 1998; Abrams, 2003; Valencia-A., 2004; Mills, 2009; Torres-Miranda, 2009; Torrez-Meza *et al.* 2009; Rodríguez-Trejo and Myers 2010). Furthermore, closely-related oak species tend to diverge in their habitat preferences to avoid competition, as well as in response to environmental factors (Torrez-Meza *et al.* 2009; Olvera-Vargas *et al.* 2010; Pérez-Ramos *et al.* 2012; de la Riva *et al.* 2014). Particularly, nutrient availability and fire regime, topography, soil and altitude frequency have influenced oak distribution (Abrams, 1990; 2003; Cavender-Bares *et al.* 2004; Meave *et al.* 2006; Olvera-Vargas *et al.* 2010; Rodríguez-Trejo and Myers 2010; de la Riva *et al.* 2014). However, it is still unknown if these patterns of oak distribution hold at regional scales.

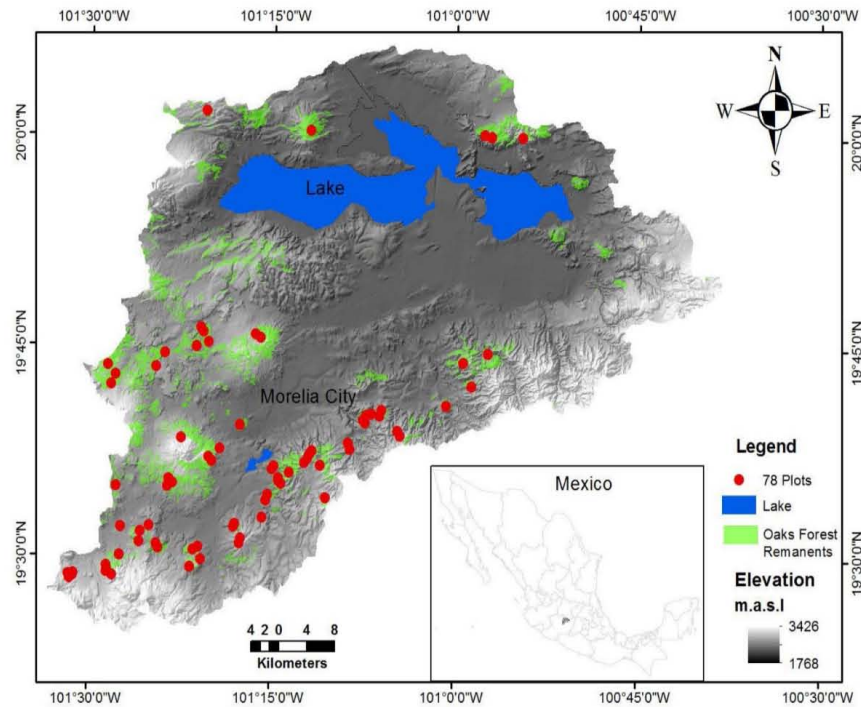
On the other side within communities, it is thought that species coexistence is promoted if they have a contrasting resource use strategy, are temporally separated at some point of their life stage, (Nakashizuka, 2001; Silvertown, 2004; Cavender-Bares and Pahlisch 2009) or develop positive synergic effects between each other (Kaye *et al.* 2000; Gartner and Cardon 2004; Chávez-Vergara *et al.* 2014; 2015). Recently, it was detected that the association of two oak species produce higher nutrient availability, which resulted advantageous for one of the species (Chávez-Vergara *et al.* 2014; 2015). Although, this exhibited the benefits of species coexistence, the evidence supporting the frequency of the associations between oak species is still scant.

In this study, we analyzed the structure of oak communities at a landscape scale in a basin located in Central Mexico. We studied 78 plots distributed in different oak fragments within the Cuitzeo basin (> 4,000 km²) in Michoacán state, Mexico. In the Cuitzeo basin, it has been reported that precipitation increases and temperature decreases from north to south of the basin (Mendoza *et al.* 2006; Leal-Nares *et al.* 2010). The aim of the study was to detect whether oak species have a defined pattern of distribution, and if the environment influences such pattern. We were also interested to determine associations between pairs of species based on the oak species environmental affinities. Particularly, the objectives of this study were to: i) know the patterns of spatial distribution of oak species at a landscape scale; ii) determine the environmental factors affecting oak species distribution, and iii) know the degree of association between pairs of oak species.

Methods

Study area. The Cuitzeo basin has 4,026 km² and it is located at 19° 30'-20° 05'N and 100° 35'-101° 30'W in the Trans-Mexican Volcanic belt between the States of Michoacán and Guanajuato (Figure 1). Climate at the basin is temperate with a marked rainy season during summer months (June to September), but it has been detected that precipitation increases while temperature decreases from south to north and with altitude (Mendoza *et al.* 2006). The mean annual temperature ranges from 14 to 20 °C, and the average annual precipitation ranged from 646 to 1,402 mm (Leal-Nares *et al.* 2010). The soils and the topography of the study area are product of

Figure 1. Cuitzeo lake basin and the distribution of the 78 plots in oak fragments.



the volcanic activity from Quaternary (Mendoza *et al.* 2006; Chávez-Vergara *et al.* 2014). The dominant soils are vertisols, luvisols, leptosols, acrisols and andosols (Mendoza *et al.* 2006). The oak forests (*Quercus*) are the predominant vegetation type; however, as a consequence of land-use change, they are very fragmented (Mendoza *et al.* 2006). The development of urban areas, the expansion of agriculture and the production of oak charcoal are the principal threats for these forests (Mendoza *et al.* 2006; Aguilar *et al.* 2012; Herrera-Arroyo *et al.* 2013).

A total of 78 oak forest fragments were selected within the Cuitzeo basin. A plot of 100×20 m (15.6 ha) was established within each forest fragment, in which all oak trees with a ≥ 5 cm of diameter at breast height (dbh) were identified and its height and dbh was measured. For each site, the altitude, inclination and orientation of the slope were obtained with a digital elevation model framed on GIS ArcView ver. 3.3 (ESRI, 1999).

Nutrients and carbon content in litter and soil. Four transects of 1×100 m of length were established within each plot to quantify nutrient and carbon contents in both the surface litter and soil beneath it. In each transect, a soil sample was taken from the first 20 cm with a soil-core sampler every 20 m. The 20 soil samples extracted at each plot were evenly mixed and kept in a plastic bag. Five samples of litter were randomly collected at each plot with a polyvinyl chloride (PVC) ring with a diameter of 160 mm. Soil and litter samples were transported into the laboratory in a cooler, and stored in bags and placed in darkness at 4°C until analysis (Chavez-Vergara *et al.* 2014). In the laboratory, total forms of C, N and P were analyzed for both, soil and litter samples. The litter samples were oven-dried at 70°C for 72 hours. Thus, samples were grounded with a mill (Retsch MM400) and sieved through a 40 mesh. Similarly, soil samples were oven-dried and grounded with a pestle and agate mortar. Total N and P were determined following acid digestion in a mixture of concentrate H_2SO_4 and K_2SO_4 plus CuSO_4 , the latter as a catalyst; N was determined by a micro-Kjeldahl method (Bremner, 1996) and P by the molybdate colorimetric method following ascorbic acid reduction (Murphy and Riley 1962). The extraction was measured by colorimetry in an autoanalyzer (3Bran-Luebbe; Nordestedt, Alemania). Carbon analysis was done in a total carbon analyzer (UIC mod 5012; Chicago, USA) and determined by colorimetric detection (Huffman, 1977).

Climatic variables. First, to characterize the climate of each plot, nineteen bioclimatic variables derived from monthly precipitation and temperature values (period 1910-2009) were extracted at 30 arc seconds and downscaled using a digital elevation model at 30 m of resolution for the study area by Cuervo-Robayo *et al.* (2014) and Correa-Ayram *et al.* (in press), respectively. Nineteen climatic variables were finally extracted for each plot, using GIS ArcView ver. 3.3 (ESRI, 1999).

Statistical Analysis. Differences in composition between of oak forest fragments across the landscape were explored with a Non-metric Multidimensional Scaling Analysis (NMDS). For this analysis, we included all the presence data of the nine oak species from the 78 plots. Matrices of dissimilarity between plots were developed with the Bray-Curtis index (Faith *et al.* 1987). Differences in species composition between sites were evaluated with an analysis of similarities (ANOSIM). The ANOSIM included 999 random permutations to explore if dissimilarities between sites were statistical significant (following Warwick *et al.* 1990).

A Canonical Correspondence Analysis (CCA) was conducted to determine the relationship between oak species distribution and the environmental variables. First, the 19 variables extracted for each plot to characterize its climate were used to construct the CCA. However, to avoid errors associated with overrepresentation of the climatic variables, the collinearity between pair of characteristics was explored with Pearson paired-correlations (Marquínez *et al.* 2003). When a coefficient of determination ≥ 0.90 was detected between pair of variables, the climatic variable that had the least biological meaning was discarded (Thuiller *et al.* 2003). We only included the following climatic variables in the CCA: maximum temperature in the warmest month (MTWM), maximum temperature in the coldest month (MTCM), annual precipitation (AP), seasonality of the precipitation (SP), and precipitation at the driest quarter of the year (PDQ) (Table 1). At the same time the CCA included the soil and litter nutrient content and the topographic variables (Table 1). Overall, three environmental matrices were included in the CCA analysis; each one included climatic, soil and topographic variables (Table 1), and the species abundance matrix. All the environmental characteristics were log-transformed to satisfy normality. In the CCA analysis, we performed 999 permutations to evaluate the degree of significance of the CCA model, axes and variables ($P = 0.001$) (Table 3). Both CCA and NMDS were implemented in R with the vegan package (Oksanen *et al.*, 2010).

Table 1. Environmental variables used in CCA analysis.

Variable	Acronym	Units
Climate		
Isothermality	I	°C
Maximum temperature in the warmest month	MTWM	°C
Maximum temperature in the coldest month	MTCM	°C
Annual precipitation	AP	mm
Precipitation at the rainiest month	PRM	mm
Seasonality of the precipitation	SP	mm
Precipitation at the driest quarter of the year	PDQ	mm
Precipitation at the warmest quarter of the year	PWQ	mm
Carbon and Nutrients in Litter		
Total Carbon	CL	mg/g
Total Nitrogen	NL	mg/g
Total Phosphorous	PL	mg/g
Carbon and Nutrients in Soil		
Total Carbon	CS	mg/g
Total Nitrogen	NS	mg/g
Total Phosphorous	PS	mg/g
Topography		
Altitude	A	masl
Orientation	O	o
Slope	S	%

Table 2. List of species recorded at the 78 plots of the oak forests in the Cuitzeo lake basin, Michoacán, Mexico.

Species	Section	Number of Individuals	Number of Sites
<i>Quercus castanea</i> Née	<i>Lobatae</i>	2147	58
<i>Q. deserticola</i> Trel.	<i>Quercus</i>	1720	33
<i>Q. laeta</i> Liebm.	<i>Quercus</i>	841	33
<i>Q. rugosa</i> Née	<i>Quercus</i>	724	16
<i>Q. magnoliifolia</i> Née	<i>Quercus</i>	412	18
<i>Q. candicans</i> Née	<i>Lobatae</i>	186	9
<i>Q. crassipes</i> Bonpl.	<i>Lobatae</i>	77	9
<i>Q. glaucoides</i> M. Martens & Galeotti	<i>Quercus</i>	67	2
<i>Q. gentryi</i> C.H. Mull.	<i>Lobatae</i>	46	2

To detect associations or niche overlap between pair of oak species, we performed a Discriminant Analysis. The analysis included de abundance matrix and the environmental matrices from the CCA. However, to avoid overestimation of species distribution, this analysis included only the plots that had ≥ 10 individuals for each species. We calculated the centroid of each species at the multivariate space, and then we traced an ellipse on the data points representing the distribution of the species. When over positioning between the ellipses of two species was detected, we calculated the area of overlap with the Jaccard index. The index evaluates the degree of similarity between paired of data, and the value oscillates from zero to one (one equals to complete similarity between species niche). Discriminant analysis and species ellipses overlap were implemented in R with the ellipse package (Oksanen *et al.*, 2010).

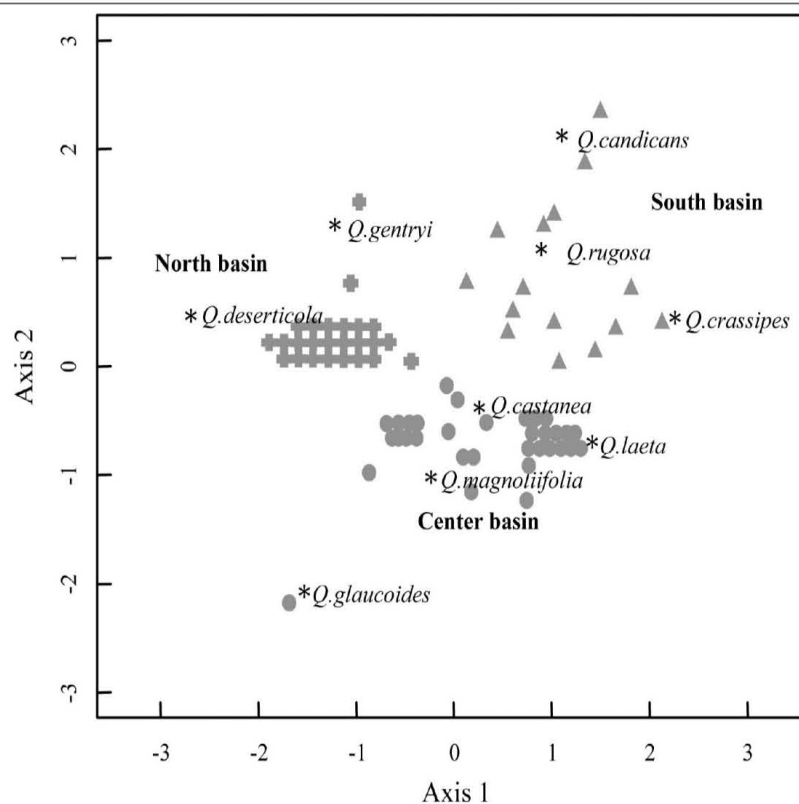
Results

Oak forests community composition. A total of 6, 248 trees (≥ 5 cm of dbh) belonging to nine species of *Quercus* were recorded in the 78 fragments (Table 2). The most abundant species were *Q. castanea*, *Q. deserticola*, *Q. laeta*, *Q. rugosa* and *Q. magnoliifolia*; *Q. gentryi* and *Q. glaucoides* were found only in one and two fragments, respectively.

Species distribution at the landscape. The NDMS analysis exhibited that the two axis solution was the most parsimonious solution in explaining the variation of the fragments composition. Overall, the analysis showed variation in the composition between the 78 oak forest fragments, and therefore that *Quercus* species differed in their distribution pattern within the landscape ($P < 0.01$; Stress = 0.06; $R^2 = 0.98$) (Figure 2). At the two dimension-space, we detected three groups (ANOSIM $R = 0.83$, $P < 0.001$): *Q. rugosa*, *Q. candicans* and *Q. crassipes* define one group located at the south of the basin; a second group was composed by four species which were more frequent at the center of the basin, *Q. castanea*, *Q. laeta*, *Q. magnoliifolia* and *Q. glaucoides*; and *Q. deserticola* and *Q. gentryi* conformed a third group located in the northern part of the basin.

Relationship between species distribution and environmental variability. The canonical correspondence analysis (CCA) explained a total of 35 % of the variation of the plot environmental variables and species distribution data ($P < 0.001$). The first two principal axes explained 59 % of the total variation (CCA1 = 0.35 and CCA2 = 0.24) (Figure 3). The variables that had a significant correlation with each axis were I, MTWM, MTCM, AP, SP and PDQ (Table 3). In general, the analysis demonstrated that the species distribution was related with a gradient of water availability and with variation in the temperature. Particularly, the sites with higher seasonality in the precipitation and higher temperature during the colder months were at the positive side of the first axis. In contrast, the sites with higher annual precipitation and with larger variation of the daily temperature were found at the other side of the first axis. The second axis was also related with the annual precipitation and with the temperature of the warmest month. The warmest sites were at the positive side of the axis, while the more humid sites were at the negative part of the axis.

Figure 2. Non-metric multi-dimensional scaling (NMDS) that includes the species abundance data collected in the 78 plots of oak forests at the Cuitzeo lake basin. ($P < 0.01$; Stress 0.06, $R^2 = 0.98$). The asterisks, triangles, circles and crossings indicate the relative position of the species and plots at the multi-variate space, respectively.

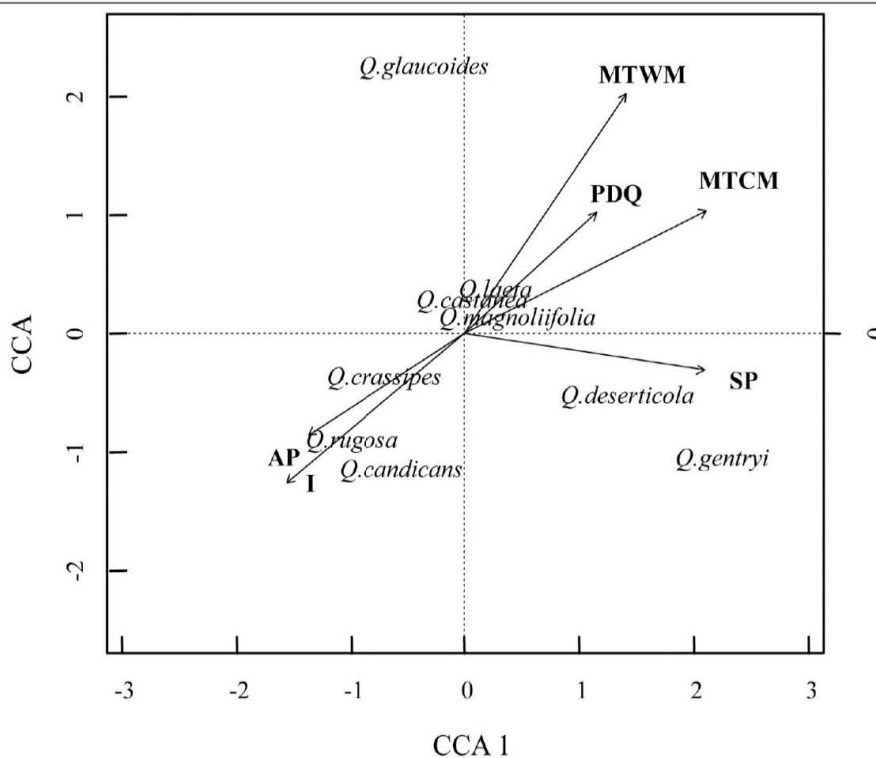


Overall, the CCA showed that *Quercus deserticola* and *Q. gentryi* were located at sites with a marked dry season. In contrast, *Q. crassipes*, *Q. candicans* and *Q. rugosa* were placed at sites with higher daily variation in the temperature and with higher annual precipitation, while *Q. glaucooides* was located at sites with higher maximum temperatures during the warmest months. Interestingly, *Q. castanea*, *Q. magnoliifolia* and *Q. laeta* were located at the center of the CCA

Table 3. Canonical correspondence analysis. The two axes that explained the highest proportion of the variation (CCA1 = 0.44; CCA2 = 0.30), the coefficient of correlation and the statistical analysis for each environmental variable are shown. The asterisk denotes significance (P) of each axis: *** = 0.001. In bold are the variables that were significant. Acronyms follow Table 1.

Eigenvalues	CCA1 ***	CCA2 ***	GL	Chisq	F	P
I	0.44	0.3				
	-0.56	-0.47	1	0.21	5.81	0.001
MTWM	0.50	0.72	1	0.13	3.50	0.002
MTCM	0.75	0.37	1	0.17	4.88	0.001
AP	-0.49	-0.30	1	1.10	2.85	0.009
PRM	0.41	0.36	1	0.12	3.36	0.001
SP	0.74	-0.11	1	0.10	2.90	0.01
PDQ	-0.21	-0.22	1	0.08	2.29	0.02
PWQ	-0.55	-0.45	1	0.06	1.70	0.098
PS	-0.35	-0.52	1	0.04	1.01	0.38
NS	-0.04	0.08	1	0.06	1.55	0.142
NL	0.00	-0.14	1	0.04	1.14	0.312
PL	-0.07	-0.13	1	0.04	1.04	0.344
A	-0.11	0.20	1	0.01	0.34	0.933
O	0.14	0.16	1	0.04	1.09	0.339
P	-0.41	-0.20	1	0.01	0.37	0.909

Figure 3. Canonical correspondence analysis. The analysis included presence/abundance, climate, soil and topography matrices for the 78 plots distributed at the oak forests of the Cuitzeo lake basin. The vectors indicate the variables that had a significant correlation with each axis (Table 3). The length and direction of the vectors indicate the strength and sign of the correlation, respectively.



space, which suggests that the environmental characteristics evaluated in this analysis were not related with their distribution.

Association between species. The first two axes of the discriminant analysis explained 68 % of the variation (LD1 = 0.42 and LD2 = 0.26). The variables that defined the species niche were MTWM and MTCM for each axis, respectively (Table 4). In general, we detected six associations between species belonging to different sections (*Lobatae* and *Quercus*): *Quercus castanea* – *Q. deserticola*, *Q. castanea* – *Q. laeta*, *Q. castanea* – *Q. magnoliifolia*, *Q. candicans*

Table 4. Discriminant Analysis. The table shows the two axes that explained the highest proportion of the variation (LD1 = 0.42; LD2 = 0.26) and coefficients of linear discrimination for each variable. In bold are the variables with the higher coefficient of discrimination. Acronyms follow Table 1.

Discriminant coefficient	LD1	LD2
I	-0.64	-0.19
MTWM	1.22	-2.30
MTCM	-1.43	1.47
AP	0.06	0.14
PRM	-1.12	0.37
SP	-0.61	0.07
PDQ	0.94	-1.09
PWQ	-0.03	0.44
SP	0.35	0.42
SN	0.06	0.16
MN	0.11	0.39
MP	-0.04	-0.29
A	-0.13	-0.16
O	-0.03	-0.04
P	0.19	-0.04

Table 5. Niche climatic overlap index between pair of oak species. The symbols denote associations between sections: *, *Lobatae-Quercus*; +, *Quercus-Quercus*; and x: *Lobatae-Lobatae*. Species acronyms: *Q. cas*: *Q. castanea*; *Q. des*: *Q. deserticola*; *Q. can*: *Q. candicans*; *Q. rug*: *Q. rugosa*; *Q. lae*: *Q. laeta*; *Q. cra*: *Q. crassipes*; *Q. mag*: *Q. magnoliifolia*; *Q. gla*: *Q. glaucoides*; *Q. gen*: *Q. gentryi*.

	<i>Q.cas</i>	<i>Q.des</i>	<i>Q.can</i>	<i>Q.rug</i>	<i>Q.lae</i>	<i>Q.cra</i>	<i>Q.mag</i>	<i>Q.gla</i>	<i>Q.gen</i>
<i>Q.cas</i>	0.99								
<i>Q.des</i>	0.28*	0.99							
<i>Q.can</i>	0.06	0.1	0.99						
<i>Q.rug</i>	0.19	0.06	0.29*	0.99					
<i>Q.lae</i>	0.8*	0.28+	0.08	0.2	0.99				
<i>Q.cra</i>	0.35x	0.12	0.17	0.37*	0.42*	0.99			
<i>Q.mag</i>	0.57*	0.36+	0.1	0.09	0.61+	0	0.99		
<i>Q.gla</i>	0	0	0	0	0	0	0	0.99	
<i>Q.gen</i>	0	0	0	0	0	0	0	0	0.99

— *Q. rugosa*, *Q. crassipes* — *Q. rugosa* and *Q. crassipes* — *Q. laeta*. We also detected three associations between species within the *Quercus* section (*Q. deserticola* — *Q. laeta*, *Q. deserticola* — *Q. magnoliifolia* and *Q. laeta* — *Q. magnoliifolia*) and one association between species from the *Lobatae* section (*Q. castanea* — *Q. crassipes*) (Table 5).

Discussion

In this study, we detected that oak species distribution differs at the landscape level. Particularly, water availability and both rain and temperature seasonality were the most determining factors for the distribution pattern of oak species. However, the distribution of some oak species was not related neither with climatic nor edaphic factors. Overall, this suggests that at the study area oak species are segregated along the landscape, which might limit competition between them and therefore, facilitating their coexistence. Nevertheless, not all the variation was explained by the environmental gradients, implying that other factors, such as species interactions, might be influencing their distribution. However, we observed that some species are frequently associated between them, and this pattern of coexistence is more common between the more distantly related species.

Previous studies have established the climatic affinity of oak species (Kappelle and Van-Uffelen 2006; Nixon, 2006); for example *Quercus glaucoides* and *Q. magnoliifolia* in Mexico are more frequently observed at warmer and drier sites (Rzedowski, 1978; Fernández-Nava *et al.*, 1998). Cuitzeo basin has a very complex topography, nevertheless, we observed that temperature and precipitation were guiding the species distribution, both factors vary strongly from north to south of the basin. In particular, we detected that the northern part of the basin has a marked dry season, receive less amount of precipitation and is warmer. In contrast, the southern part has a higher precipitation and lower temperature. This gradient of temperature and precipitation plays an important role determining oak species distribution at the landscape scale. Particularly, *Q. deserticola*, *Q. glaucoides* and *Q. gentryi* are more frequent at warmer and drier sites. In contrast, *Q. candicans*, *Q. rugosa*, *Q. crassipes* occur at sites that receive a higher amount of precipitation and lower temperatures. Interestingly, *Q. castanea*, *Q. magnoliifolia* and *Q. laeta* were located at the center of the CCA analysis, suggesting a clear relationship between the environmental variables included in the analysis and its distribution. Our study supports the findings from previous works where it has been reported that oak species distribution are affected by the variation of precipitation or soil moisture gradients (Cavender-Bares *et al.*, 2004; Olvera-Vargas *et al.*, 2010; de la Riva *et al.*, 2014). Overall, this suggests that the pattern of distribution of the oak species might reflect functional adaptations to survive under water stress or to efficiently exploit high levels of water availability. However, the CCA analysis was only able to explain a fraction of the variation indicating that other factors might influence the species distribution.

The niche overlap analysis also confirmed the oak species partitioning of the environmental gradient and that the pattern of distribution was independent of the taxonomic section. We also detected associations between pair of species; the most frequent association occurred between distantly related species belonging to *Quercus* and *Lobatae* sections. The finding that two species share the same climatic niche suggests that they are functional equivalent. Nevertheless, a recent study had detected strong functional differentiation among these nine oak species (Aguilar-Romero personal communication). Two hypotheses could explain the association among oak species. The first one indicates that coexistence could be promoted by being temporally separated in their growth stages (i.e. acorn maturity and seedling establishment at different moments of the year) (Cavender-Bares and Pahlisch 2009; Olvera-Vargas *et al.* 2010; Pérez-López *et al.* 2013) or by exploiting different areas of the soil water-table depth (López-Barrera *et al.* 2006; Pérez-López *et al.* 2013). Another hypothesis is that one of the species could get advantage from the presence of the other by positive synergic effects, which could promote the establishment and survival of both species in the same site (Chávez-Vergara and García-Oliva 2013). It has been shown that when more than two species inhabit the same area, the community of microorganisms increments its abundance and activity promoting higher soil nutrient availability (Gartner and Cardon, 2004). Therein, a recent study found that *Quercus deserticola* benefits *Q. castanea* by incorporating nutrients to the soil and facilitating the decomposition of litter (Chávez-Vergara and García-Oliva 2013; Chávez-Vergara *et al.* 2014; 2015). Overall, this complementarity effects might promote coexistence. Nonetheless, further research needs to be conducted to determine the generality of this mechanism among oak species.

Conclusions

Our study exhibits a non-random pattern of oak species distribution at the landscape level. The species distribution was mainly determined by the environmental heterogeneity within the basin. Particularly, we detected that species restricted to the south of the basin experience higher water availability and lower temperatures, at the other extreme species at the north, receive lower precipitation with a marked dry season and higher temperatures. Overall, the study suggests that oak species differ in their resource use strategy and in their tolerance to water stress, and that species segregate along the environmental gradient to avoid competition among them. However, part of the variation in the pattern of oak species distribution was not explained by the environmental heterogeneity. At the same time, we detected associations of species, being the most recurrent between species from different taxonomic sections, which suggests positive synergic interactions allowing coexistence of species.

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CAPÍTULO III

Differentiation in the water-use strategies among oak species from central Mexico.

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Research paper

Differentiation in the water-use strategies among oak species from central Mexico

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Oak species (Fagaceae: *Quercus*) differ in their distribution at the landscape scale, specializing to a certain portion of environmental gradients. This suggests that functional differentiation favors habitat partitioning among closely related species. To elucidate the mechanisms of species coexistence in oak forests, we explored patterns of interspecific variation in functional traits involved in water-use strategies. We tested the hypothesis that oak species segregate along key trade-offs between xylem hydraulic efficiency and safety, and between hydraulic safety and drought avoidance capacity, leading to species niche partitioning across a gradient of aridity. To do so, we quantified biophysical and physiological traits in four red and five white oak species (sections *Lobatae* and *Quercus*, respectively) across an aridity gradient in central Mexico. We also explored the trade-offs guiding species differentiation, particularly between the drought tolerance versus water acquisition capacity, and determined whether the water-use strategy was associated with the portion of the environmental gradient that the species occupy. In a trait-by-trait analysis, we detected differences between white and red oak species. However, a larger part of the variation was explained at the species rather than at the section level. We detected two primary axes of trait covariation. The first exhibited differences between species with dense tissues and species with soft tissues (the tissue construction cost axis); however, the oak sections did not constitute separate groups, while the second suggested a trade-off between xylem resistance to cavitation and tree deciduousness. As expected, the water-use strategies of the species were related to the environment; oak species from arid areas had more deciduousness and a higher instantaneous water-use efficiency. In contrast, their humid counterparts had less deciduousness and had a xylem that was more resistant to embolisms. Altogether, these results suggest that aridity filters closely related species, resulting in habitat partitioning and niche divergence.

Keywords: aridity gradients, biophysical traits, functional trade-offs, *Quercus*, water-use strategy.

Introduction

Differences in the distribution of plant species at a local scale suggest niche partitioning and ecological specialization to a certain range of resources and conditions (Tilman 1982, Chapin et al. 1993, Reich 2014). This means that plant species must develop adaptations that allow them to successfully establish and survive under a given level of resources (Pérez-Ramos et al. 2012,

de la Riva et al. 2014, Reich 2014). It has been stated that there is a continuum of plant strategies for surviving under different levels of resources, reflecting a fundamental trade-off (Reich 2014). At one extreme of this continuum are the species that inhabit areas with low level of resources, which tend to develop a more resource-conservative and stress-tolerant strategy (Grime 1977, 2001, Chapin et al. 1993, Aerts 1999, Reich et al. 2003, Angert et al. 2009, Pineda-García et al. 2015). At the other

extreme, species that are specialized to resource-rich environments have evolved a high capacity for resource acquisition and growth (Grime 1977, Reich et al. 1999, Ackerly 2004, Wright et al. 2005, Pineda-García et al. 2015). This trade-off could provide a plausible mechanism to explain the habitat partitioning and species co-occurrence along resource gradients in a given community.

In the case of water, species with an acquisitive strategy tend to have traits that confer plants a greater capacity for water absorption, conduction and use. In contrast, drought tolerant species have traits that enable them to operate under a water deficit. Particularly at the xylem level, drought-tolerant species are very resistant to embolisms but have a low efficiency for water conduction, while acquisitive species have a highly conductive tissue but are more vulnerable to cavitation under drought stress. Overall, this reflects an efficiency–safety trade-off at the xylem level, the generality of which is still under discussion (Tyree and Zymmermann 2002, Tyree et al. 2003, Choat et al. 2005). In addition, xylem adaptations to variations in water availability have evolved in coordination with other plant responses, such as leaf water-use efficiency (WUE) and deciduousness (Santiago et al. 2004, Meinzer et al. 2008, Pineda-García et al. 2011, 2015, Méndez-Alonzo et al. 2012). For instance, deciduous species that avoid water stress have a xylem that is highly vulnerable to embolism, usually with an elevated hydraulic capacitance (Meinzer et al. 2009, Méndez-Alonzo et al. 2012, McCulloh et al. 2014, Pineda-García et al. 2015). Conversely, evergreen species have a resistant xylem and can therefore tolerate soil drought, overall suggesting a trade-off between drought tolerance and drought avoidance (Méndez-Alonzo et al. 2012, Pineda-García et al. 2015). Ecological and anatomical studies suggest that wood density can be an indirect indicator of the mentioned trade-offs given the evidence that drought survival and xylem traits (fiber content, capacitance, vessel density, lumen diameters) correlate with wood density (Cavender-Bares and Holbrook 2001, Jacobsen et al. 2007, Pratt et al. 2007, Meinzer et al. 2008, Hacke et al. 2009, Poorter et al. 2010, Méndez-Alonzo et al. 2012, among others). Additionally, a coordinated variation between branch and leaf tissue densities suggests that mechanisms of drought tolerance may operate together at both levels (Pineda-García et al. 2015). There is evidence indicating that these functional strategies to address water availability segregate along gradients of drought risk (Cavender-Bares et al. 2004a, Kursar et al. 2009, Savage and Cavender-Bares 2013). However, the known phylogenetic conservatism of some physiological and morphological traits suggests potential for important constraints on niche partitioning, especially among closely related species (Reich et al. 2003, Cavender-Bares et al. 2004b, Ackerly et al. 2006, Cavender-Bares et al. 2006, Ricklefs 2010, Willis et al. 2010). Whether the trade-offs between ways to resist drought and exploit water are general mechanisms of niche differentiation and species sorting along gradients of drought risk is still unclear. Additionally, further investigation is needed to

determine whether trait conservatism constrains the species distribution and differentiation along this trade-off.

Oak species (genus *Quercus*) are a very diverse group of woody plants in North America, especially in Mexico, which is a major center of secondary diversification (Rzedowski 1978, Manos et al. 1999, Villaseñor 2003, 2004, Nixon 2006). Within the genus *Quercus*, it has been suggested that species belonging to the *Lobatae* (red oaks) and the *Quercus* (white oaks) sections have contrasting patterns of distribution. Particularly, it is thought that white oak species are in general more drought tolerant than red oaks, which is reflected in their spatial distribution in different environmental scenarios (Nixon 1993, Zavala 1998, Poulos 2009, Torres-Miranda 2009, 2014, Renninger et al. 2013). Thus, habitat partitioning by oak species may be restricted by phylogenetic relatedness given conserved adaptations. However, this hypothesis has not been rigorously examined among Mexican oak species, particularly regarding their water-use strategy. Therefore, we compared the drought tolerance between white and red oak species occurring along an environmental gradient at a local scale. We aimed to test whether drought resistance of species is constrained along the trade-off between the capacity to tolerate, and the ability to avoid, drought through the use of water reserves and foliar area reduction, and if strategies segregate across a gradient of aridity. To do so, we characterized, in adult trees, the water-use in leaves, the plant water status, the vulnerability of xylem to cavitation and the plant leaf phenology as a response to drought. Furthermore, we measured biophysical traits related to the water use strategy of plants, such as stem and leaf density. Finally, we explored whether the species water-use strategy was related to the environment experienced in their habitat. In particular, we evaluated the following questions: (i) Is water-use strategy highly conserved among red and white oak species? (ii) Do the drought tolerance–water exploitation and drought tolerance–drought avoidance trade-offs guide the patterns of functional differentiation among species? (iii) Is the water-use strategy related to the environment of the species' habitat?

Materials and methods

Study area

The study was conducted at the Lake Cuitzeo basin, which has an extension of 4026 km². It is located in central Mexico at the north and south of the Michoacán and Guanajuato states, respectively, and is part of the Trans-Mexican Volcanic Belt morphotectonic province (Ferrusquía-Villafranca 1993). The climate is temperate with a mean annual temperature of 17 °C, average annual precipitation >800 mm and a marked precipitation seasonality. At the basin, the precipitation increases and the temperature decreases from north to south (Mendoza et al. 2006, Aguilar-Romero et al. 2016). The soils and the topography of the study area are all derived from volcanic activity produced during the Quaternary (Mendoza et al. 2006, Chávez-Vergara et al. 2014). Oak forests

are the predominant type of natural vegetation (Mendoza et al. 2006, Aguilar-Romero et al. 2012, Herrera-Arroyo et al. 2013). The following nine oak species differ in their distribution along an aridity gradient at the basin: *Quercus candicans*, *Q. castanea*, *Q. crassipes*, *Q. gentryi*, *Q. deserticola*, *Q. glaucooides*, *Q. magnoliifolia*, *Q. laeta* and *Q. rugosa*. The former four species belong to the *Lobatae* section and the latter five to the *Quercus* section (Aguilar-Romero et al. 2016). Different leaf habits have been reported for numerous oak species from distinct regions (Damesin et al. 1998, Cavender-Bares et al. 2004a, Baldocchi et al. 2010). Particularly, our studied oak species also differ in their leaf habit (McVaugh 1974, González-Villareal 1986, Bello-González and Labat-Noel 1987, Romero-Rangel et al. 2014, 2015).

Based on extensive surveys of oak populations across the studied landscape (Aguilar-Romero et al. 2016), we were able to locate for each species one site within the area where the species presented its maximum recruitment and adult abundance. Thus for each species we proceeded to measure functional traits at the area where they thrive (Figure 1).

Morphological and physiological traits

In each site, we quantified morphological and physiological traits to characterize the water-use strategy of the study species. To analyze the morphological traits, we randomly selected

10 individuals of each species. For each tree, we collected 10 mature sun-exposed leaves with no visible damage, five branch samples from terminal twigs and three terminal twigs with leaves on them. The plant samples were wrapped in humid paper towels, stored in plastic bags and transported in coolers to the lab. The leaf samples were left in the paper towels for 12 h, and the fresh weight was then determined using an analytical balance. The stem samples were left submerged in distilled water for 12 h, and their fresh weight without bark was then obtained. The stem volume was obtained by the water displacement method (following Pineda-García et al. 2011). The stem and leaf samples were oven-dried at 70 °C for 72 h, and their dry weight was then determined. We calculated the leaf dry matter content (LDMC) as the ratio of the leaf dry weight to leaf humid weight and the stem density (SD) as the ratio of the stem volume to dry weight. The saturated sapwood water content (SWC) was calculated as $\{[(\text{fresh weight} - \text{dry weight}) / \text{dry weight}] \times 100\}$. For the terminal twigs, we measured the sapwood diameter without bark using a digital caliper. All the leaves supported by the twig were scanned and their area determined using digital image with the WinFOLIA software (Regent Instruments Inc., Ville de Quebec, QC, Canada). Thereafter we calculated the Huber value (Hv) as the twig sapwood cross-sectional area/leaf area.

We measured the CO₂ assimilation rate with a portable infrared gas analyzer (LICOR 6400XL, Lincoln, NE, USA). The

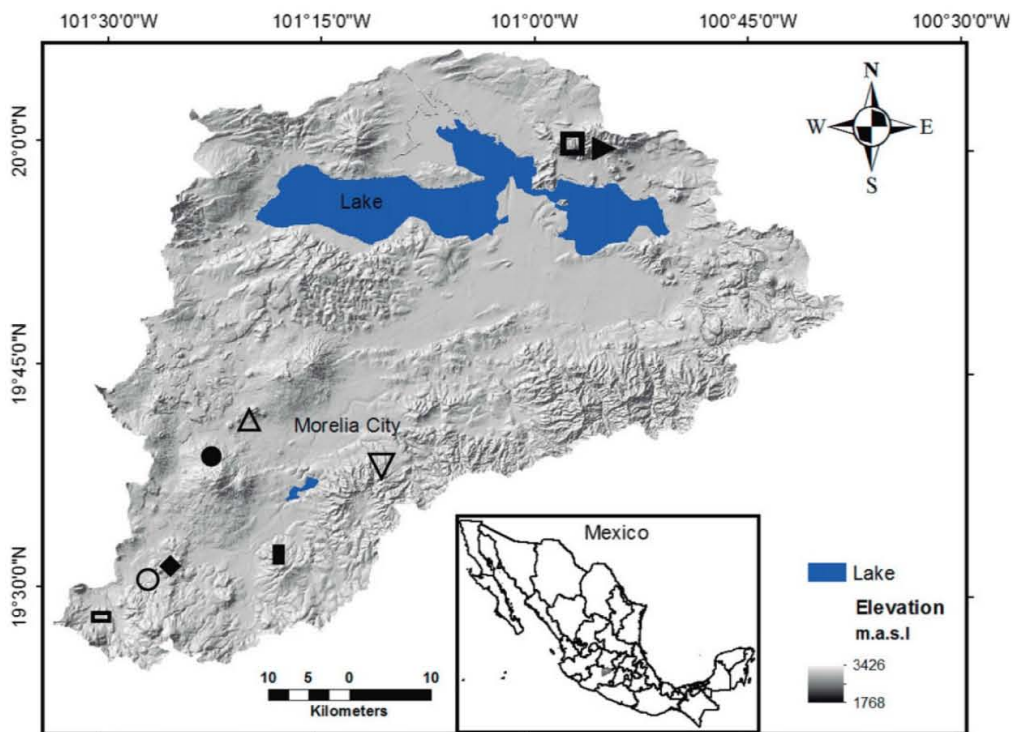


Figure 1. Distribution of the populations of nine oak species at the Lake Cuitzeo basin, Michoacán, México. In the map are shown the sites of data collection for each of the nine oak species. Symbols: *Q. glaucooides*, open up-pointing triangle; *Q. deserticola*, open square; *Q. magnoliifolia*, open down-pointing triangle; *Q. crassipes*, filled diamond; *Q. castanea*, filled rectangle; *Q. gentryi*, filled right-pointing triangle; *Q. laeta*, open circle; *Q. candicans*, filled circle; and *Q. rugosa*, open rectangle. Open symbols indicate *Quercus* section species and filled symbols represent *Lobatae* section species.

measurements were taken in eight fully expanded sun-exposed leaves in five trees per species between 9:00 and 12:00 h. Photosynthetically active radiation was kept at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a light lamp, and the CO_2 was maintained at $\sim 400 \mu\text{mol mol}^{-1}$. We calculated the instantaneous WUE as the ratio of the CO_2 assimilation rate to the transpiration rate.

The midday plant water potential (Ψ_{midday}) was measured between 13:00 and 15:00 h with a Scholander pressure chamber (1000, PMS Instrument Co., Albany, OR, USA). The determinations were performed in terminal branches that had been enclosed in plastic bags after the predawn to allow the stabilization of the water potential (Begg and Turner 1970). Given that these oak species in general have a very short petiole, the plant water potential was measured in three terminal leaf-bearing twigs in six trees per species during the middle of the dry season (April 2014), when the plant experiences the highest water stress before they drop their leaves ($\Psi_{\text{soil}} < -5 \text{ MPa}$ across species sites).

Vulnerability to cavitation was measured in terminal, leaf-bearing shoots. The branch samples to quantify the xylem vulnerability to cavitation were collected during the first month of the rainy season, when the probability of xylem cavitation is low given that the soil water availability has been reestablished (Mota-Guerrero 2015). Ten to 20 full sun-exposed branches from at least six trees for each species of $\sim 1.5 \text{ m}$ in length were pruned at predawn, to avoid excessive cavitation, and immediately recut under water to remove potential vessel blockage. The branches were transported to the lab under water and covered with black plastic bags. Vulnerability curves were determined by the bench drying technique (Cochard 1992). The shoots were hung upside-down to dry in the sun, until a desired level of dehydration was reached. For each level of dehydration, two to three stem segments per shoot were selected for the hydraulic conductivity measurements. The segments were covered in black plastic bags for a 30 min period of stabilization, and the plant water potential was then estimated for two twig samples of each segment with a Scholander pressure chamber (PMS Instrument Co.). The stems were recut under water into smaller segments with a mean length ($\pm \text{SE}$) of 110.09 mm (± 0.71) and with a mean diameter of 5.60 mm (± 0.06) across species. The leaves were removed, and all scars were sealed with glue. The segments were connected to a plastic tubing manifold, holding up to five samples, which was attached to a pressurized reservoir ($\sim 3 \text{ kPa}$) filled with a degassed and filtered ($0.2 \mu\text{m}$) 10 mM KCl solution. With the stems attached to the reservoir and after a 15 min period of stabilization, we quantified the native water flow (mass per 15 s ; g s^{-1}) passing through the stem section. Three consecutive measurements were taken to assure that the water flow had reached a steady state. The native hydraulic conductivity was calculated as the ratio between the water flow (F) passing through the stem section and the pressure gradient (dP/dx) (Tyree and Ewers 1991). The maximum conductivity (k_{smax})

of each stem was then obtained after flushing out emboli by applying a 100 kPa pressure head for 10 min , and then re-measuring the water flow. For each stem, we quantified the percentage loss of hydraulic conductivity (PLC) as: $\text{PLC} = 100 \times ((k_{\text{smax}} - k_s) / k_{\text{smax}})$. The sample sizes ranged from 25 to 140 stem sections depending on the species.

Leaf area in response to drought

We aimed to quantify to what extent individuals of each species reduced leaf area in response to seasonal drought. To do so, in five trees per species, we counted the number of leaves present in three sun-exposed terminal twigs, both at the onset (31 August 2013) and at the middle part (25 April 2014) of the dry season. We selected adult trees making an effort to control for tree size, resulting in a range in diameter at breast height between 8.6 and 18.4 cm , with a mean ($\pm \text{SE}$) of 13.9 cm ($\pm 1.10 \text{ cm}$) for all species. For each tree, we calculated the proportion of leaves present at the middle of the dry season, relative to those present at the beginning of this period. This variable, hereafter named as leaf number change (LNC), reflects the balance between leaf loss and production as the dry season proceeded; values > 1 indicate leaf are increase, while values < 1 indicate leaf are reduction.

Environmental variables

First, to characterize the climate at each site where species have their maximum abundance, two bioclimatic variables derived from monthly precipitation and temperature values were extracted from high-resolution monthly climate surfaces of the study area (Cuervo-Robayo et al. 2014) using GIS ArcView ver. 3.3 (ESRI 1999). Both bioclimatic variables were modeled using integrated data from 1910 to 2009. Therefore, based on temperature and annual precipitation we derived the De Martonne aridity index (Maliva and Missimer 2012) for each site as follows:

$$A_m = \frac{P}{T + 10}$$

where P is the annual precipitation; and T the mean annual temperature.

Statistical analysis

The general hypothesis that red (*Lobatae*) and white (*Quercus*) oak species differ in their water-use strategy was tested by both a trait-by-trait and a multiple trait analysis. To determine the trait-by-trait conservatism in the resistance to drought between white and red oak species, we used a nested analysis of variance (ANOVA) and calculated how variance in the measured traits was partitioned among and within sections (*Lobatae* and *Quercus*), and the direction of the differentiation between them. A post hoc Student's t -test ($\alpha=0.05$) was performed to explore the differences between the species. For the xylem hydraulic

vulnerability, we plotted the percentage loss of maximum conductivity against the plant water potential, fitted a four-parameter Weibull model, and derived the Ψ at which the xylem lost PLC 50 (Lopez et al. 2005, Pineda-García et al. 2013). For the Ψ_{plant} at PLC 50 we obtained a single value per species, and therefore we explored only the differences between sections with a one-way ANOVA. To detect the existence of a trade-off between drought tolerance and drought avoidance, and water exploitation capacity we performed a principal components analysis (PCA) on the multiple traits evaluated for each species (Hv, LNC, positivized PLC 50, wood density (Wd), LDMC, positivized Ψ_{midday} , SWC and WUE), and looked for negative correlations of traits within each of the two principal components. We decided to perform two separate analyses, the first including the eight traits evaluated, and the second excluding the LDMC, because the nested ANOVA indicated that this trait is highly phylogenetically conserved. This last analysis allowed us to explore patterns of covariation among traits that are more likely related to adaptations to current environments. Then, to test for differences in the multivariate water-use strategies between red and white oak species, a *t*-test was performed on the species scores of the two principal component axes. Finally, to test whether aridity filters drought-tolerant or drought-avoiding species, we performed correlations between the aridity index and the species scores of the two principal components (as indicators of species strategies).

Results

Functional differentiation between and within sections

The nested ANOVA showed that only three (LDMC, Hv and SWC) out of the eight analyzed traits differed significantly between the red and white oak sections, with LDMC being the only trait with a strong phylogenetic signal (section explained more than 30% of the total variation) (Table 1; Figure 2). In particular, the *Lobatae* section (red oak species) exhibited a higher LDMC, higher Hv and lower SWC than the *Q.* section. The analysis also demonstrated that two traits, WUE and SD, differed among species but not between the two sections of the genus (Table 1; Figure 2). Particularly, *Q. glaucoides*, a species from dry habitats, had the highest instantaneous water-use efficiency (Figure 2). *Quercus crassipes* and *Q. rugosa*, which inhabit areas with higher water availability, had the higher SD. Finally, we did not detect differences at either the section or the species level in the midday plant water potential (Ψ_{midday}), indicating a high variation among individuals (Table 1). In the case of the plant water potential at PLC 50 (cases for which one value per species was available), we did not observe differences between sections (Table 1; see Figure S1 available as Supplementary Data at *Tree Physiology* Online). For the LNC, we detected two contrasting leaf phenological responses among the species. Species

in the first group, including *Q. castanea*, *Q. candicans*, *Q. laeta* and *Q. rugosa*, dropped some but not all of their leaves in the middle of the dry season, and produced new leaves at the end of the dry season (from now on we will refer to these species as brevi-deciduous). The second group includes species that dropped all their leaves and remained leafless until the beginning of the rainy season (deciduous).

Multiple trait covariation

Both PCAs looking for trade-offs yielded similar results when including and excluding LDMC, the most conserved trait within the two oak sections (Figure 3; see Figure S2 available as Supplementary Data at *Tree Physiology* Online). In this analysis, the first axis explained 38.9% of the variation, and represents a tissue construction axis; species with soft tissues and with a greater capacity for water storage in the stem were located at the negative end of the axis (Figure 3). Conversely, species with dense stems and a higher Hv were located at the positive side of the axis. The second PCA axis synthesized the variation (30.1%) in the tolerance to low plant water potential, at the stem level, leaf deciduousness and leaf WUE. Brevi-deciduous species, which drop a fraction of their leaves at the beginning of the dry season but produce new leaves immediately after and bear them at the end of the dry season, and have a xylem resistant to embolism, are at the negative end of the axis. Deciduous species, which are leafless by the end of the dry season and exhibit higher leaf WUE and xylem with low tolerance to water stress, are at the positive side of the axis (Figure 3). Overall, PCA axis 2 (PC2) indicated a trade-off between drought tolerance and drought avoidance. The red and white sections did not differ in their multivariate water-use strategy (PC1: $t = -1.83$, $P = 0.1$; PC2: $t = 0.08$, $P = 0.93$).

Relationship between the environment and the water-use strategy of species

PC1 scores of species were not correlated with the level of aridity of the sites where species thrive ($r = 0.32$, $P = 0.4$). In contrast, we detected a relationship between PC2 scores (indicative of the drought tolerance vs drought avoidance trade-off) and the aridity index ($r = -0.80$, $P = 0.008$). Particularly, deciduous species with a higher WUE and higher tolerance to low Ψ_{midday} were distributed in more arid areas (Figure 4). In contrast, species that retain their leaves during the dry season and that are more resistant to embolism are found in less arid areas (Figure 4).

Discussion

It has been proposed that red and white oaks have different strategies to deal with drought, suggesting conserved ancient adaptations. Our study partially supports this idea since we detected section differences in morphological and physiological traits,

Table 1. Functional variation among nine oak species. Differences were explored through a nested ANOVA, nesting species within the two taxonomic sections included (*Lobatae* and *Quercus*).

	<i>F</i>	<i>P</i>	<i>r</i> ²
WUE			
Section	1.81	0.19	0.02
Species	5.42	0.0003	0.50
LDMC			
Section	79.56	<0.0001	0.32
Species	12.19	<0.0001	0.35
Hv			
Section	27.33	<0.0001	0.17
Species	8.16	<0.0001	0.35
Ψ_{midday}			
Section	2.38	0.13	0.04
Species	0.93	0.49	0.12
Wd			
Section	3.78	0.06	0.03
Species	5.65	<0.0001	0.32
SWC			
Section	11.02	0.0014	0.08
Species	6.33	<0.0001	0.32
LNC			
Section	13.4	0.0004	0.06
Species	13.1	<0.0001	0.72
PLC 50			
Section	1.54	0.25	0.18

Functional traits: WUE, water-use efficiency; LDMC, leaf dry matter content; Hv, Huber value; Ψ_{midday} , midday plant water potential at the dry season; Wd, wood density; SWC, stem water content; LNC, leaf number change; PLC 50, plant water potential at 50% loss of stem hydraulic conductivity.

Significant differences are shown in bold/italics ($P \leq 0.05$).

reflecting some degree of trait conservatism. Nevertheless, a larger variation, aside from the section level, was detected among the nine oak species. It has been hypothesized that closely related species are less likely to compete with each other, given the differences in their resource and conditions requirements, and overall niche divergence (Cavender-Bares et al. 2004a, Olvera-Vargas et al. 2010, Torres-Miranda 2014). This idea has been supported in previous studies documenting the differences in the distribution of closely related species at both regional and larger geographic scales (Cavender-Bares et al. 2004a, Torres-Miranda 2009, 2014, Olvera-Vargas et al. 2010, Savage and Cavender-Bares 2013, de la Riva et al. 2014, Aguilar-Romero et al. 2016). Likewise, in our study we provided evidence that the variation in water-use strategies among oak species is related to the species distribution along a gradient of aridity and that such a pattern is also expressed at small spatial scales, particularly at the landscape level. Overall, two axes of trait covariation defined the patterns of species differentiation, which were related to the environmental gradients.

Studies analyzing distribution of oak species at regional scales have suggested that white oaks (*Quercus* section) are more resistant to drought (Abrams 1990, 2003, Nixon 1993,

Zavala 1998, Poulos 2009, Renninger et al. 2013, Aranda et al. 2014). Based on this evidence, we predicted that the studied species belonging to the white oak section would show traits related to a higher drought resistance than the species from the red oak section. Our results do not support this hypothesis since physiological components of water-use strategy did not differ between sections, and morphology, denser tissues (branches and leaves) and higher Hv in red oaks (section *Lobatae*) suggest a higher resistance to water stress than in white oaks. In contrast, the strong variation in most of physiological and morphological traits among the nine species studied, independently of section, indicated trait divergence between closely related species.

In our study, we found evidence to support the hypothesis that oak drought resistance was constrained along the trade-off between the capacity to tolerate drought and the ability to avoid it through an efficient water use and leaf area reduction. Interestingly, we detected that biophysical traits related to the plant hydraulics, such as Wd and xylem water content, were independent of the oaks' physiological response to drought. Particularly, the PCA permitted us to determine the patterns of covariation among traits, detect trade-offs and to define the resource-use strategy of the oak species. We were able to identify two mayor axes of variation that were persistent even after removing LDMC, which was the most conserved trait at the section level of the traits analyzed. The first axis was primarily driven by the negative association between the xylem density and stem water storage capacity. It was previously determined that denser wood results from thicker vessel cell walls and/or from a higher proportion of fibers with reinforced walls (Abrams 1990, Cavender-Bares and Holbrook 2001, Jacobsen et al. 2007, Pratt et al. 2007, Pineda-García et al. 2011). Conversely, species with soft wood had a higher content of water in the stem tissue, typically due to an elevated proportion of parenchyma or storing fibers and thus higher capacity to store reserves (water and/or non-structural carbohydrates), and vessels and fibers with a large lumen (Borchert and Pockman 2005, Choat et al. 2005, Jacobsen et al. 2007, Pratt et al. 2007, Méndez-Alonzo et al. 2012). The positive association between the density of the leaves and the stem suggests that mechanisms of plant persistence and robustness are shared by the different plant organs (Markesteijn et al. 2010, Pineda-García et al. 2011, Paz et al. 2015). Interestingly, dense-wooded species exhibited twigs with an elevated conductive section (larger Hv), suggesting a mechanism to compensate narrow-vessel restriction in water transport to the leaves.

In contrast, the second axis of differentiation was mostly defined by physiological traits. Species that are highly resistant to xylem cavitation were brevi-deciduous, as they barely reduced their leaf area at the middle of the dry season. On the other hand, formally deciduous species exhibited a lower dry-season plant water potential and high vulnerability to xylem cavitation

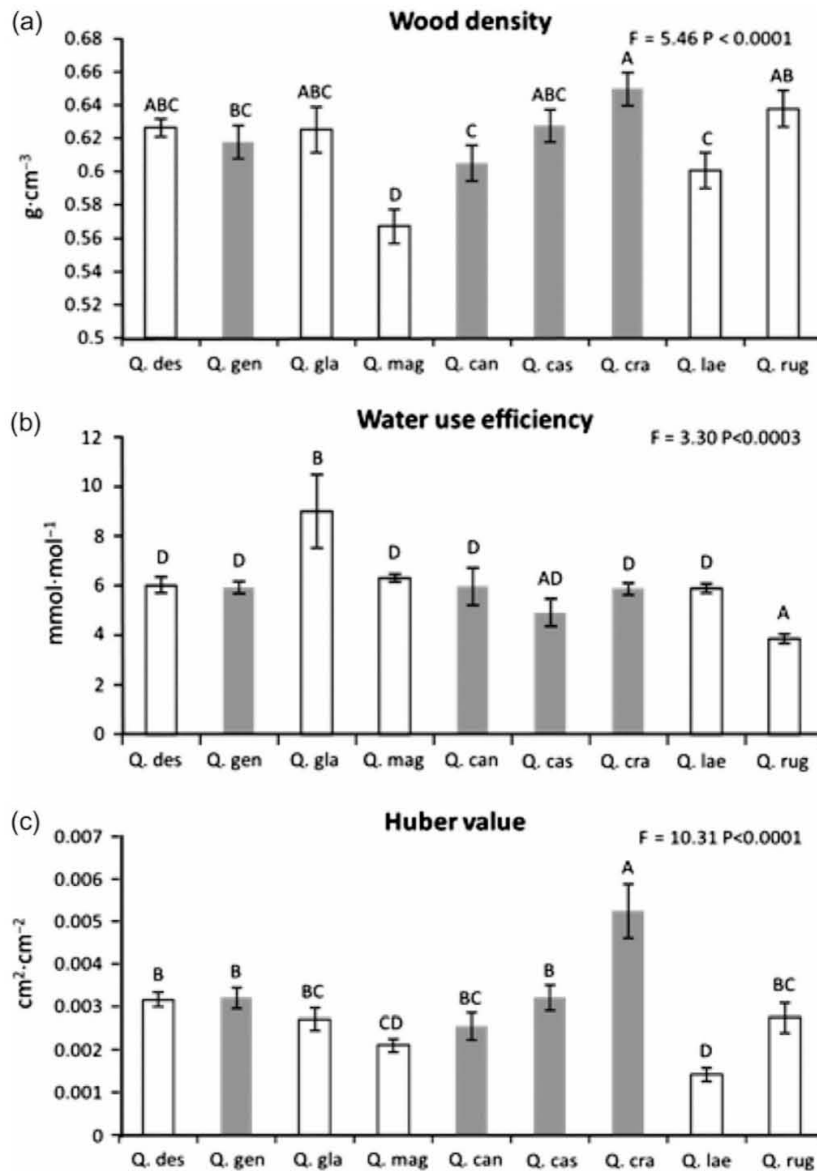


Figure 2. Functional differentiation between nine oak species that differ in their distribution along an aridity gradient at the Lake Cuitzeo Basin, Michoacán, México. Wood density (a); water-use efficiency (b); and Huber value (c). F and P values resulting from the nested ANOVA are shown (species nested within section). Q. des: *Q. deserticola*; Q. gen: *Q. gentryi*; Q. gla: *Q. glaucooides*; Q. mag: *Q. magnoliifolia*; Q. can: *Q. candicans*; Q. cas: *Q. castanea*; Q. cra: *Q. crassipes*; Q. lae: *Q. laeta*; and Q. rug: *Q. rugosa*. Open bars indicate *Quercus* section species and filled bars represent *Lobatae* section species.

and had higher intrinsic WUE, altogether indicating that deciduous species tend to work closer to their hydraulic safety limit. This is in line with previous evidence from tropical and other temperate trees showing that deciduous species are more vulnerable to cavitation and function closer to their hydraulic safety limit than brevi-deciduous and evergreen species (Ackerly 2004, Markesteijn et al. 2010). Likely, a shorter growth period in deciduous species has promoted mechanisms to maximize resource capture, while a quick leaf shedding may compensate for the sensitivity of the xylem to suffer hydraulic dysfunction (Sobrado 1996, Baldocchi et al. 2010,

Markesteijn et al. 2010, Pineda-García et al. 2011, Méndez-Alonzo et al. 2012). Additionally, in accordance with previous studies, we detected a coupling between stem water transport traits and water use and loss in photosynthesis (Santiago et al. 2004), and between leaf phenology and stem hydraulics (Borchert 1994, Holbrook 1995, Sobrado 1996, Pineda-García et al. 2011, 2015, Méndez-Alonzo et al. 2012). The fine-tuning between water transport and use in the leaves might be favored in plant communities where water availability is a major determinant of growth and mortality (Pineda-García et al. 2013, Zeballos et al. 2016).

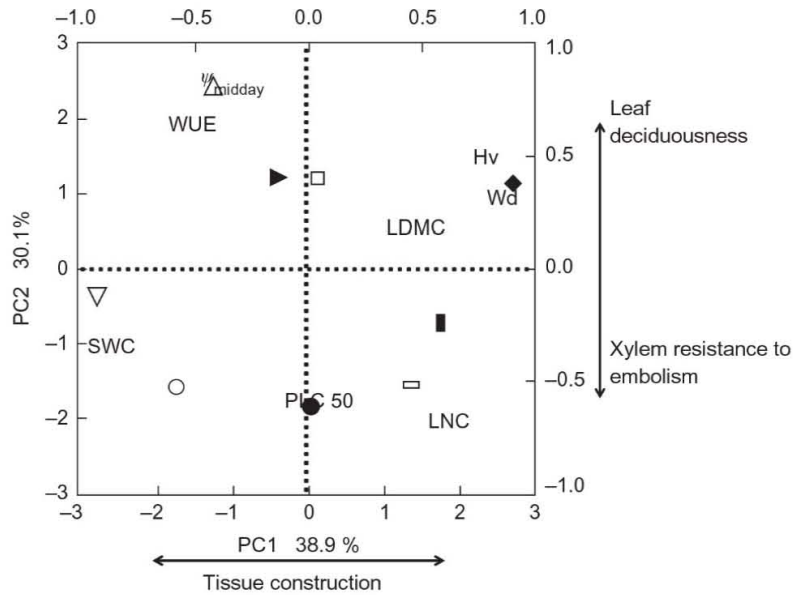


Figure 3. Principal component analysis showing the two axes of trait covariation: tissue construction cost and xylem resistance to embolism-leaf deciduousness. The analysis included the midday plant water potential measured during dry season (Ψ_{midday}), leaf number change (LNC), instantaneous water-use efficiency (WUE), stem water storage capacity (SWC), Huber value (Hv), wood density (Wd), leaf dry matter content (LDMC) and plant water potential at 50% loss of stem hydraulic conductivity (PLC 50). Symbols: *Q. glaucooides*, open up-pointing triangle; *Q. deserticola*, open square; *Q. magnoliifolia*, open down-pointing triangle; *Q. crassipes*, filled diamond; *Q. castanea*, filled rectangle; *Q. gentryi*, open right-pointing triangle; *Q. laeta*, open circle; *Q. candicans*, filled circle; and *Q. rugosa*, open rectangle.

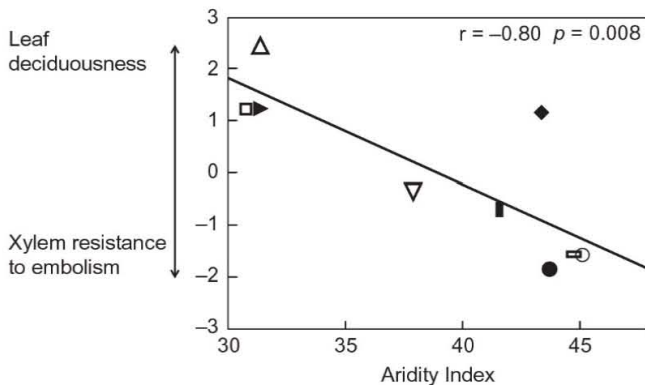


Figure 4. Relationship between the aridity gradient and the xylem resistance to embolism-leaf deciduousness trade-off among oak species as reflected by the species scores of the second PCA axis. Symbols: *Q. glaucooides*, open up-pointing triangle; *Q. deserticola*, open square; *Q. magnoliifolia*, open down-pointing triangle; *Q. crassipes*, filled diamond; *Q. castanea*, filled rectangle; *Q. gentryi*, open right-pointing triangle; *Q. laeta*, open circle; *Q. candicans*, filled circle; and *Q. rugosa*, open rectangle.

Interestingly, in our study the physiological traits and leaf phenology, but not the morphological traits, did vary with the climatic conditions experienced by the species, as indicated by the correlation between the index of aridity and the PCA axis 2, but not for the PCA axis 1. In particular, the species with a xylem vulnerable to embolism, leaves with higher WUE and a more deciduous habit were located at the relatively more arid sites. In contrast, the least deciduous species, with a xylem less

vulnerable to embolism, were located at more humid areas. Together these results suggest that species from arid sites restrict their growth and carbon gain to the favorable rainy season, and they tend to drop their leaves, reducing embolism and shoot die-off, during the dry season. Therefore, oak species from arid zones use a more opportunistic and drought-avoiding strategy. In principle, the dominance of species resistant to xylem cavitation in the more humid areas seem to be counter-intuitive and contradicts the findings from previous studies (Cochard et al. 2008, Costa-Saura et al. 2016). Although these areas receive a higher amount of annual precipitation, evergreen oak species suffer episodes of strong drought (Mendoza et al. 2006) during which they might be more susceptible to experiencing massive cavitation given that they retain most of their leaves year-round. Therefore, brevi-deciduous or evergreen oak species from humid areas might have evolved a mechanism to prevent embolism during possible water shortages, as detected in other species (Sobrado 1993, Maherali et al. 2004, Chen et al. 2009, Kröber et al. 2014).

The patterns of functional variation detected suggest that in an area with the same geological origin and with a large climatic variability, the physical environment filters species and promotes habitat partitioning, overall favoring niche and trait divergence among oak species (Cavender-Bares et al. 2004a, Willis et al. 2010). However, it is important to note that though we characterized the functional response of each species in the sites that reflect their optimum habitat, we recognize that they do not have

such a confined distribution, and some of them, such as *Q. castanea*, exhibit a wider distribution along the environmental gradient (Aguilar-Romero et al. 2016). This suggests that phenotypic plasticity or genetic divergence can be important mechanisms used by plants to thrive in different habitats, and these factors remain to be evaluated.

Conclusions

We compared morphological and physiological traits of white and red oak species to evaluate trait conservatism within a seasonally rainy landscape in central Mexico. We found that oak sections differ in some traits, but contrary to our predictions, red oak species had traits associated with a more drought-tolerant strategy. However, our study provides evidence of a strong functional differentiation among oak species, contributing to the understanding of patterns of habitat specialization and niche partitioning along a gradient of aridity. We detected two major axes of trait covariation; one defined by the construction cost of morphological traits and the other by stem hydraulics and the leaf physiology and phenology. Overall, the species with a deciduous habit and a xylem highly vulnerable to embolism were located in more arid areas, while the brevi-deciduous species with a more protected xylem were frequently observed in more humid areas.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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CAPÍTULO IV

DISCUSIÓN GENERAL

En este estudio, se identificó que las especies de encinos no se distribuyen de manera aleatoria en el paisaje, sino que muestran patrones de especialización a lo largo de un gradiente de disponibilidad de agua y estacionalidad en la temperatura. Esta distribución en el paisaje en diferentes hábitats está relacionada con sus atributos morfo-fisiológicos que les permiten establecerse y sobrevivir. Los encinos en el área de estudio presentaron dos distintos mecanismos para tolerar y evitar la sequía: i) una disyuntiva (“trade-off) funcional entre especies con tejidos densos y especies con tejido suaves (un eje definido por los costos en la construcción de tejidos) y ii) una disyuntiva entre la resistencia a la cavitación del xilema y el escape a la sequía vía su caducifoleidad. Estos mecanismos les permiten a las especies repartirse a través del paisaje y desarrollarse en diferentes ambientes, evitando competir por los recursos y promoviendo su coexistencia.

La disponibilidad de agua y la estacionalidad en la temperatura fueron los factores más importantes en determinar los patrones de distribución de los encinos en escala de paisaje. Sin embargo, la distribución de algunas especies no fue explicada por los factores climáticos y edáficos. Parte de esta variación no explicada sugiere que existen otros factores que están determinando la distribución de las especies. En general, las especies se agrupan y se distribuyen de manera diferencial a lo largo del paisaje. El área de estudio tiene una topografía muy compleja, la cual presenta patrones de precipitación y temperatura diferentes de norte a sur: en la parte norte se presenta una mayor estacionalidad en la temperatura y una disminución en la precipitación; en contraste, en la región sur aumenta la precipitación y disminuye la temperatura. Considerando lo anterior, se identificó que *Quercus deserticola*, *Q. glaucoides* y *Q. gentryi* se localizan en zonas cálidas y secas mientras que *Q. candicans*, *Q. rugosa* y *Q. crassipes* son más afines a zonas frías y húmedas. Por otro lado, las especies *Q. castanea*, *Q. magnoliifolia* y *Q. laeta* cuya ordenación en el análisis multivariado se localizaron en el centro del CCA, sugiere que los factores ambientales considerados en los análisis no determinan la distribución de estas especies. Estos resultados coinciden con lo reportado en estudios previos en especies de encinos en los que la variación a lo largo de gradientes de disponibilidad de recursos determinan la distribución de las especies (Cavender-Bares et al. 2004; Olvera-Vargas et al. 2010; de la Riva 2014).

La distribución diferencial de las especies a través del gradiente ambiental, es consistente con la hipótesis de que las especies filogenéticamente cercanas son menos competitivas entre sí, debido a las diferencias en sus requerimientos de recursos y condiciones promoviendo así la divergencia de nicho (Cavender-Bares et al. 2004; Olvera-Vargas et al. 2010; Torres-Miranda 2014). Esto concuerda con los resultados de este estudio en los que se detectaron ensambles entre especies pertenecientes a distintas secciones taxonómicas (*Quercus* y *Lobatae*). El análisis de traslape de nicho sugiere que las especies que comparten nichos similares presentan alta diferenciación funcional. Sin embargo, diferentes hipótesis han planteado este patrón de coexistencia entre especies de encinos que pertenecen a diferentes secciones, o con relación filogenética distante puede ser promovida por tres factores: 1) por una separación temporal o espacial en algún estadio ontogénico entre especies (e. g. la maduración de la bellota y el establecimiento de plántulas en diferentes estaciones del año o por la explotación de los recursos a diferentes profundidades del suelo) (Cavender-Bares y Pahlich 2009; Olvera-Vargas et al. 2010; Pérez-López et al. 2013); 2) por la sinergia positiva o facilitación de una especie en presencia de otra, la cual promueve el establecimiento y la sobrevivencia de ambas especies en el mismo sitio (Chávez-Vergara y García-Oliva 2013). Estudios previos muestran que cuando dos o más especies coexisten en una misma área, la comunidad de microorganismos incrementa su abundancia y favorece su actividad promoviendo una mayor disponibilidad de nutrientes (Gartner y Cardon, 2004). Trabajos recientes encontraron que *Q. castanea* se beneficia en presencia de *Q. deserticola* ya que esta última regresa follaje con una mayor calidad nutrimental promoviendo la fertilización del suelo (Chávez-Vergara y García-Oliva 2013; Chávez-Vergara et al. 2014; 2015) y 3) existe una mayor competencia por los recursos entre especies de la misma sección que entre especies de secciones taxonómicas distintas (Bourdeau, 1954; Wuencher y Kozlowski 1971; Racine 1971; Mohler, 1990; Cavender-Bares et al. 2001; Aguilar-Romero et al. 2016).

En general, las especies de estudio muestran distribuciones diferenciales y patrones de especialización a lo largo del gradiente de disponibilidad de agua y estacionalidad en la temperatura en el área de estudio. En estudios previos se ha

reportado que los patrones de distribución de las especies de la sección *Quercus* (encinos blancos) a escalas regionales tienen una mayor afinidad climática a zonas cálidas y secas sugiriendo mayor resistencia a la sequía (Abrams 1990, 2003; Nixon 1993; Chávez-Zavala 1998; Poulos 2009; Renninger et al 2013; Aranda et al. 2014), por lo que se probó si las especies de la sección *Quercus* (encinos blancos) presentan atributos más relacionados hacia una estrategia de resistencia a la sequía en comparación con especies de la sección *Lobatae* (encinos rojos) cuya afinidad climática se reporta en zonas más húmedas y frías (Chávez-Zavala 1998). Al explorar esta diferenciación a nivel de sección en atributos fisiológicos relacionados con estrategias en el uso de agua no se encontraron diferencias. Sin embargo, sí encontramos que las especies de la sección *Lobatae* presentaron atributos morfológicos (mayor densidad en tejidos tallos, hojas y valores altos de Huber) asociados con una estrategia de resistencia al estrés hídrico. En general, encontramos diferencias en los atributos fisiológicos y morfológicos entre las nueve especies independientemente de la sección taxonómica, lo que sugiere una divergencia entre los atributos funcionales de las especies estrechamente emparentadas.

Así mismo, al explorar cómo covarían en su conjunto los atributos morfológicos y fisiológicos detectamos dos patrones. Por un lado, en el análisis multivariado se detectó una asociación negativa entre la densidad de la madera y la capacidad de almacenamiento de agua. Es decir, las especies con valores altos de densidad presentan tejidos conformados por paredes con vasos más gruesos y con mayor cantidad de fibras que refuerzan sus paredes (Abrams 1990; Cavenders-Bares y Holbrook 2001; Jacobsen et al. 2007; Pratt et al. 2007; Pineda-García et al. 2011). Así mismo, presentaron una asociación positiva entre la densidad del tallo y las hojas sugiriendo mecanismos de persistencia y robustez en los distintos órganos de la planta (Markesteyn et al. 2010; Pineda-García et al. 2010; Paz et al. 2015). Además, estas especies presentan ramillas que exhiben una mayor conducción de agua a las hojas (Valor de Huber) sugiriendo mecanismos que compensan la restricción de tener vasos pequeños en el transporte de agua. En cambio, las especies con una mayor capacidad de almacenar agua en sus tallos, generalmente presentan una mayor proporción de parénquima y fibras asociadas al almacenamiento de reservas (Borchert y Pockman 2005; Choat et al. 2005; Jacobsen et al. 2007; Pratt et al. 2007; Méndez-Alonzo et al. 2012). El segundo patrón estuvo

determinado por atributos fisiológicos que definen la capacidad de tolerar y evitar la sequía. Es decir, las especies sub-caducifolias son más resistentes a la cavitación del xilema ya que se despojan de sus hojas a mitad de la estación seca. En cambio las especies de hábitos caducifolios son más vulnerables a la cavitación del xilema y presentan una mejor eficiencia en el uso de agua, estos atributos en su conjunto indican que las especies caducifolias trabajan con un menor margen de seguridad con respecto a su falla hidráulica. Esto sugiere que las especies de hábitos caducifolios presentan periodos cortos de crecimiento que promueven mecanismos que les permiten maximizar la captura de recursos y despojarse de sus hojas para prevenir falla hidráulica (Sobarado 1996; Baldocchi et al 2010; Markesteijn et al. 2010; Pineda-García et al. 2011; Méndez-Alonzo et al. 2012).

Estudios previos demuestran que especies tropicales y templadas con hábitos caducifolios son más vulnerables a la cavitación y que operan con un menor margen de seguridad respecto a la falla hidráulica contrario a las especies sub-caducifolias y perennifolias (Ackerly 2004; Markesteijn et al. 2010). Otros estudios encontraron una coordinación entre atributos relacionados con el transporte, uso y pérdida de agua durante la fotosíntesis (Santiago et al. 2004), entre la fenología (caducidad) y la hidráulica del tallo. Esta coordinación entre los distintos atributos favorece a las especies que se desarrollan en las comunidades donde la disponibilidad de agua es un factor limitante para su crecimiento (Pineda-García et al. 2013; Zeballos et al. 2016).

Por último, en este trabajo encontramos evidencia de que los atributos fisiológicos y fenológicos están relacionados con las condiciones ambientales que experimentan las especies. Es decir, las especies que son más vulnerables a la cavitación, tienen un mejor uso de agua y presentan hábitos caducifolios se desarrollan en sitios más áridos. Esto sugiere que estas especies restringen su crecimiento y ganancia de carbono a la estación de lluvias, mientras que en la estación de secas se despojan de sus hojas para evitar la cavitación. Además, estas especies presentan una estrategia más oportunista en la explotación de los recursos antes de la estación de secas. Por otro lado, las especies sub-caducifolias con un xilema menos vulnerable a la cavitación se desarrollan en sitios más húmedos. Sin embargo, las especies que se distribuyen en zonas húmedas reciben una mayor precipitación a lo largo del año y pueden llegar a experimentar episodios de sequía

(Mendoza et al. 2006), en los que podrían ser más vulnerables a la cavitación ya que retienen una mayor cantidad de follaje durante el año. Asimismo, las especies subcaducifolias y perennifolias pueden tener mecanismos que les permiten prevenir embolismos mediante el almacenamiento de agua en ciertos órganos de la planta (Sobrado et al 1993; Maherali et al. 2004; Chen et al. 2009; Kröber et al. 2014).

A nivel del paisaje se ha identificado un amplio gradiente ambiental, el cual sugiere que guía los patrones de variación funcional entre los encinos promoviendo la repartición de las especies en distintos hábitats (Cavender-Bares et al. 2004; Willis et al. 2010). Por último, es importante mencionar que se caracterizó la respuesta funcional de cada especie en su hábitat óptimo, reconociendo que no todas las especies tienen distribuciones restringidas y que algunas tienen distribuciones amplias a lo largo del gradiente ambiental (Aguilar-Romero et al. 2016). Esto sugiere que la plasticidad fenotípica y la divergencia genética pueden ser mecanismos importantes que pueden promover la adaptación de las especies en diferentes hábitats, sin embargo estos factores aún no se han considerado.

CAPÍTULO V

CONCLUSIONES

Con base en los resultados que se derivaron de los estudios realizados en la presente tesis, proponemos de manera general las siguientes conclusiones.

En el artículo del **Capítulo II** se propuso evaluar “Cuáles factores que determinan la distribución de las especies de *Quercus* en la Cuenca del Lago de Cuitzeo Michoacán”. Concretamente se buscó 1) identificar los patrones de distribución de las especies de *Quercus* en una escala de paisaje; 2) si los factores climáticos, edáficos y topográficos determinan su distribución; y 3) el grado de asociación de las especies dentro de los fragmentos.

1. Con base en los análisis de los patrones de distribución de las especies de encinos en la Cuenca del Lago de Cuitzeo.

- Las especies en el estudio mostraron patrones de distribución no-aleatorios a escala de paisaje.

2. Los factores que determinan la distribución de las especies.

- La distribución de las especies esta principalmente determinada por la heterogeneidad ambiental en la Cuenca.
- Las especies de las zonas sur de la cuenca experimentan una mayor disponibilidad de agua y bajas temperaturas, en cambio las localizadas al norte reciben una menor precipitación con una marcada estacionalidad y mayores temperaturas.
- Esto sugiere que las especies difieren en sus estrategias de uso de recursos y su tolerancia al estrés hídrico, segregándose a lo largo del gradiente ambiental para evitar competencia entre ellas.
- Sin embargo, gran parte de la variación en los patrones de distribución no fue explicada por la variación ambiental.

3. Grado de asociación entre especies dentro de los fragmentos.

- Finalmente se detectaron asociaciones entre especies, siendo las más frecuentes entre especies de diferente sección taxonómica, lo cual sugiere una interacción con sinergia positiva que promueve la coexistencia entre especies.

En el artículo del **Capítulo III** se propuso evaluar “Si existe diferenciación funcional entre las especies la cual explica su distribución en el paisaje”. Concretamente se evaluó 1) si existen diferencias entre las especies en sus atributos funcionales; 2) cuáles son las estrategias de uso de agua de las especies; y 3) si existe una relación entre el uso del recurso y el ambiente.

1. Existen diferencias entre las especies en sus atributos funcionales

- Al realizar la comparación entre atributos morfológicos y fisiológicos entre las especies de diferentes secciones taxonómicas para evaluar el conservadurismo de rasgos en una estación lluviosa en el centro de México. Se identificó que las secciones difieren en algunos rasgos, pero contrario a nuestra predicción las especies pertenecientes a los encinos rojos (sección *Labatae*), presentan rasgos asociados con estrategias de tolerancia a la sequía.
- Sin embargo, este estudio muestra evidencia de una fuerte diferenciación funcional entre especies, contribuyendo a entender los patrones de especialización y repartición de nicho a lo largo del gradiente de aridez.

2. Cuáles son las estrategias de uso de agua de las especies

- Al evaluar las estrategias funcionales se detectaron dos ejes de covariación de rasgos: uno está definido por los costos de construcción de rasgos morfológicos y el segundo por el sistema hidráulico, la fisiológica de la hoja y los patrones fenológicos.

3. Si existe una relación entre el uso del recurso y el ambiente.

- Al explorar si estas estrategias se relacionan con el ambiente se encontró que todas las especies de hábitos caducifolios y un xilema más vulnerable a la cavitación se localizan en las zonas más áridas, mientras que las especies brevideciduas con un xilema más resistente fueron localizadas en zonas más húmedas.

Conclusión general

El presente estudio muestra evidencia de que existe una repartición de nicho y un grado de especialización a una porción del gradiente ambiental que promueve la coexistencia entre las nueve especies de *Quercus* en el centro de México. Asimismo las especies muestran un menor grado de asociación entre especies de la misma sección taxonómica y una mayor entre especies de secciones taxonómicas distintas. Además, las especies muestran diferenciación funcional en sus atributos relacionados con la eficiencia de agua lo cual les permite especializarse en ambientes contrastantes específicamente en sitios con mayor precipitación y sitios con altas temperaturas. La futura ruta de investigación debería centrarse en explorar las estrategias funcionales de estas especies pero a nivel de plántulas para conocer la supervivencia en campo y bajo distintos escenarios de sequía.

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