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VULNERABILIDAD DE GRUPOS FUNCIONALES FRENTE AL CAMBIO CLIMÁTICO:
REGIÓN DE LAS GRANDES MONTAÑAS, VERACRUZ, MÉXICO.

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Vulnerability of functinal groups to climate change:
Region of the Great Mountains, Veracruz, Mexico

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Resumen

La vulnerabilidad se define como el grado en que se puede dañar o perjudicar un sistema, dependiendo no sólo de la sensibilidad del sistema, sino también de su capacidad para adaptarse a las nuevas condiciones. Por su parte, la vulnerabilidad ecofisiológica es el grado de susceptibilidad o la incapacidad de un organismo para adaptar sus funciones fisiológicas a cambios ecológicos y ambientales. Uno de los principales cambios ambientales que afectan la distribución, establecimiento y supervivencia de las especies es el cambio climático. El cambio climático es una de las fuerzas que moldean a los sistemas naturales, representando una fuerte amenaza para la biodiversidad, al exacerbar los efectos negativos provocados por la actividad humana (deforestación, sobreexplotación de recursos y contaminación, entre otros), los cuales pueden tener consecuencias impactantes en los patrones y procesos globales, así como en el funcionamiento y la estabilidad de los ecosistemas. El cambio climático actual ya ha afectado a la biodiversidad de la Tierra, y es probable que la tasa de cambio se acelere en el futuro, donde los cambios en temperatura, precipitación, y frecuencia e intensidad de los eventos extremos, pueden influir directamente en el funcionamiento del ecosistema. Principalmente, los cambios en la disponibilidad y la escasez de agua son críticos para las especies.

El bosque mesófilo de montaña (BMM) de la Región de las Grandes Montañas en el estado de Veracruz, México, es considerado el ecosistema terrestre más amenazado a nivel nacional debido a los cambios de uso del suelo y los efectos del cambio climático global, a pesar de su alto valor estratégico para el desarrollo sostenible, el papel que desempeña en el mantenimiento del ciclo hidrológico, y como reserva de biodiversidad endémica. Para evaluar la vulnerabilidad frente al cambio climático en esta región, analizamos: *i*) en términos ecofisiológicos dos rasgos fisiológicos (conductancia estomática y potencial hídrico foliar), cuatro variables climáticas (temperatura del aire, radiación fotosintéticamente activa, déficit de presión de vapor, disponibilidad de agua), y la distribución geográfica potencial de diferentes especies arbóreas de este bosque, y *ii*) en términos socio-económicos, el impacto de los cambios en las tendencias de temperatura y precipitación sobre los principales cultivos de la región.

Para nuestro análisis ecofisiológicos utilizamos el método de las funciones envolventes, debido a su capacidad para analizar las variables que afectan directamente a las especies; midiendo el efecto de las variables climáticas sobre la conductancia estomática. Esto nos proporcionó un análisis efectivo de la diversidad de respuestas ecofisiológicas. El uso de este método ayudó a predecir los valores extremos que las especies podrían tolerar, y también brindó información sobre la sensibilidad de las especies. La sensibilidad de las especies nos permitió desarrollar un índice comparativo de vulnerabilidad. También propusimos este método como una herramienta para formar grupos funcionales. La formación de estos grupos puede ayudarnos a entender cómo se comportan los individuos y responden a los cambios en su entorno, y nos permite abordar de manera más sencilla el estudio de la vulnerabilidad, al poder estudiar un mayor número de especies.

También evaluamos de manera paralela la vulnerabilidad frente a la sequía con un análisis de rasgos de sequía duros y suaves, y desarrollamos una serie de modelos para predecir el potencial osmótico a turgencia completa. La efectividad de dichos modelos fue evaluada con el criterio de información de Akaike.

Encontramos que la región de las Grandes Montañas es altamente vulnerable frente al cambio climático, encontrado cambios en las tendencias de temperatura y precipitación. La vulnerabilidad de la región se da en términos ambientales, ecofisiológicos y socio-económicos. También encontramos que la vulnerabilidad de las especies es diferencial, encontrando especies y grupos funcionales más vulnerables, en particular a cambios en el estado hídrico de las especies.

Abstract

Vulnerability is defined as the degree to which a system may be damaged or harmed, depending not only on the system's sensitivity, but also on the ability to adapt to new conditions. Ecophysiological vulnerability is the degree of susceptibility or inability of an organism to adapt their physiological functions to ecological and environmental changes. One of the major environmental changes that affect species' distribution, establishment and survival is climate change. Climate change is one of the forces that shape natural systems, representing a major threat to biodiversity, by exacerbating negative effects caused by human activity (such as deforestation, overexploitation of resources, and pollution), which may have strong impact on global patterns and processes as well as on the ecosystems' functioning and stability. Current climate change has already affected the biodiversity on Earth, and it is likely that the rate of change will accelerate in the future, where changes in temperature, precipitation, and frequency and intensity of extreme events, can directly influence the ecosystem functioning. Mainly, changes in the availability and water scarcity are critical for species.

The cloud forest of the Region of the Great Mountains in the state of Veracruz, Mexico, is considered the most endangered terrestial ecosystem at national level because of changes in land use and the effects of global climate change, despite its strategic value for sustainable development, the role it plays in maintaining the water cycle, and as a reservoir of endemic biodiversity. To assess vulnerability to climate change in this region we analyzed: *i*) in ecophysiological terms two physiological traits (stomatal conductance and leaf water potential), four climatic variables (air temperature, photosynthetically active radiation, vapor pressure deficit, water availability), and the potential geographical distribution of different tree species, and *ii*) in socio-economic terms, the impact of changes in temperature and precipitation trends on the major crops of the region.

For our analysis we used the method of envelopes functions because of its ability to analyze variables that directly affect the species, measuring the effect of climatic variables on stomatal conductance. This method provided an effective analysis of diverse ecophysiological responses. Using

this method helped to predict extreme values that the species could tolerate, and also provided information on species' sensitivity. Species' sensitivity allowed us to develop a comparative vulnerability index. We also proposed this method as a tool to form functional groups. Formation of functional groups can help to understand how individuals behave and respond to changes in their environment, and allows us to study more easily vulnerability.

Also, we evaluated vulnerability to drought with an analysis of hard and soft drought traits, and we developed a series of models to predict osmotic potential at full turgor. Effectiveness of these models was evaluated with the Akaike information criterion.

We found that the region of the Great Mountains is highly vulnerable to climate change, finding changes in temperature and precipitation trends. Vulnerability in the region is given in environmental, ecophysiological and socio-economic terms. We also found that vulnerability of the species is differential, finding species and functional groups more vulnerable, particularly to changes in water status.

Índice

Capítulo 1

Introducción

Antecedentes

De acuerdo al Panel Intergubernamental de Cambio Climático (IPCC - Intergovernmental Panel on Climate Change, Fischlin et al. 2007) los impactos del cambio climático sobre la biodiversidad ya están siendo observados en un amplio intervalo de ecosistemas. En términos generales, los cambios actuales y futuros provocados por el calentamiento global actúan sobre diferentes aspectos de los sistemas naturales, tales como: 1) interacciones funcionales entre especies; 2) distribución espacial y temporal de especies; 3) diversidad genética, y 4) procesos ecosistémicos, entre otros (eg. Bermeo-Estrella 2010). Los ecosistemas de América Latina no son la excepción, por ejemplo, el aumento en la frecuencia e intensidad del fenómeno de El Niño, junto con el retroceso de los glaciares, el aumento de temperatura y los cambios en los patrones de precipitación, afectarán de diversas formas a las áreas naturales protegidas y a los ecosistemas, así como a las especies que éstos albergan (Magrin et al. 2007).

Se espera que el cambio climático afecte el funcionamiento, la estructura y la distribución de los ecosistemas, las especies constituyentes y sus recursos genéticos (Robledo y Forner 2005). Los estudios relacionados con el impacto del cambio climático y la vulnerabilidad de los ecosistemas en México hasta ahora han sido muy generales (Villers y Trejo 2004). Respecto al ámbito nacional se han utilizado algunos modelos de sensibilidad, así como Modelos de Circulación General en los cuales se considera el CO_2 en la atmósfera (Gay 2000). Estudios recientes sobre cambio climático regional y global señalan con alto grado de confiabilidad que de manera particular los incrementos de temperatura pueden afectar tanto a los sistemas físicos como a los sistemas biológicos del planeta en distintos niveles (eg. McCarthy et al. 2001).

Vulnerabilidad y Cambio Climático

Vulnerabilidad

La vulnerabilidad se define como el grado por el cual un sistema es susceptible o incapaz de enfrentarse a los efectos adversos del cambio climático; asimismo, la vulnerabilidad es función de la sensibilidad del sistema y de su capacidad de adaptación (IPCC 2001):

Vulnerabilidad = [Sensibilidad] - [Adaptabilidad Autónoma + Adaptabilidad Planeada]

Donde la sensibilidad se define como acultad de un ser vivo de percibir estímulos externos e internos a través de los sentidos, la adaptación autónoma es la que puede tener lugar sin la intervención de alguien que tome la decisión, y la adaptación planeada es la que se efectúa en función de acciones y medidas informadas y estratégicas (IPCC 2001).

La vulnerabilidad también puede referirse al grado en el que el servicio de un ecosistema es sensible a cambios, más el grado en el que el sector del que depende este servicio es incapaz de adaptarse a los cambios (Metzger et al. 2006). De manera más puntual, después de asociar las variables ambientales con las respuestas fisiológicas, la vulnerabilidad ecofisiológica se define como el grado de susceptibilidad o la incapacidad de un organismo para adaptar sus funciones fisiológicas a los cambios ecológicos y ambientales (Esperón-Rodríguez y Barradas 2014a).

El cambio climático en México

El cambio climático es una de las fuerzas que moldean a los sistemas naturales, representando una fuerte amenaza para la biodiversidad; al exacerbar los efectos negativos provocados por la actividad humana (deforestación, sobreexplotación de recursos y contaminación, entre otros), los cuales pueden tener consecuencias impactantes en los patrones y procesos globales, así como en el funcionamiento y la estabilidad de los ecosistemas (Parmesan y Yohe 2003).

Como se mencionó anteriormente, los cambios provocados por el cambio climático actúan sobre las interacciones funcionales inter- e intra-específicas, las distribuciones de las especies, la diversidad genética y los procesos ecosistémicos. La capacidad de adaptación de los ecosistemas frente a estos cambios depende significativamente del potencial de migración y de dispersión de las especies y las poblaciones, su diversidad, su plasticidad genética y su tolerancia a los cambios en el clima; factores también afectados por las actividades antropogénicas (Kappelle et al. 1999).

Para México, que constituye una región con una diversidad biológica extraordinaria y es considerado como un país megadiverso (Sarukhán y Dirzo 2001), la afectación que se pueda causar en las comunidades vegetales relacionada con el cambio climático, así como por otros factores como la reducción en la superficie de ecosistemas naturales, la transformación a otros usos de suelo, los cambios en la composición de especies, por mencionar algunos, cobra una mayor importancia cuando se considera que la pérdida de estos ecosistemas conlleva una gran disminución de la biodiversidad mundial (Villers y Trejo 2004).

Los escenarios de cambio en los patrones climáticos proyectados para las décadas futuras (2025, 2050) exceden la habilidad de muchas especies para adaptarse mediante estrategias como la migración, cambios en el comportamiento o modificaciones genéticas; por lo que dicho cambio climático puede resultar en la reducción de las áreas de distribución de muchas especies, en la disminución de algunas poblaciones e incluso en la extinción de aquellas especies que resulten más sensibles a los cambios (Smith 1997).

Adger y colaboradores (2007) mencionan que el proceso adaptativo supone ajustes para reducir la vulnerabilidad y fortalecer la capacidad de recuperación tras los cambios observados y esperados en el clima. Pero estos, para producirse, necesitan ir acompañados de la percepción de la vulnerabilidad climática.

Sistema suelo-planta-atmósfera

Las plantas son capaces de absorber agua del suelo gracias al flujo que se establece en el sistema suelo-planta-atmósfera. En este sistema, el agua se mueve debido a diferencias en su estado termodinámico, es decir, se difunde de un sitio de mayor a menor concentración de solutos, de modo que su movimiento se produce por el gradiente de potencial hídrico (Ψ) que se encuentra a lo largo de la planta, la planta sólo puede absorber agua cuando la energía potencial del agua es menor en las raíces que en el suelo. Esto tiene como consecuencia que lo potenciales hídricos de la plantas siempre sean negativos (Salisbury y Ross 1994).

De manera general, la continuidad suelo-planta-atmósfera se genera por la diferencia de presión de succión que existe entre la planta y la atmósfera (ya que ésta última, por lo general, no se encuentra saturada por vapor de agua), el agua fluye de un menor a un mayor potencial de succión. El potencial de succión del suelo en condiciones normales de agua varía entre -0.1 y -1 MPa; en las hojas va de -0.2 a -5 MPa; mientras que en la atmósfera oscila entre -10 y -200 MPa, lo cual explica el ascenso de la columna de agua y la dirección del sistema. Este flujo también se produce cuando existe una diferencia entre el potencial químico del agua pura y del agua de cualquier parte del sistema de la planta en las mismas condiciones de presión y de temperatura (Milthorpe y Moorby 1974). La pérdida de agua de las hojas a través de la transpiración origina un potencial en la hoja más bajo que el potencial hídrico del xilema, este es a su vez más bajo que el de la raíz, y éste último menor que el del suelo (Kramer y Boyer 1995).

La mayoría de las plantas superiores obtienen sus requerimientos de agua a partir de la humedad presente en el suelo. El agua disponible en el sustrato puede encontrarse de diferentes formas: agua gravitacional, higroscópica y capilar. La forma capilar es la más importante, ya que puede ser aprovechada por las plantas. La cantidad de agua que se encuentra en realidad disponible para el crecimiento de la planta, así como su velocidad de movimiento, depende de las características del sustrato (eg. porosidad, densidad, estructura, granulometría, homogeneidad) y su textura (Lambers et al.1998).

La mayor resistencia al flujo de agua en la planta se localiza en la raíz y en la hoja, el resto son pequeñas. El agua entra a la raíz impulsada por un gradiente de potencial hídrico que se establece en el suelo (Bannister 1979). A pesar de la corta distancia que hay entre el suelo y el xilema de la raíz (menos de 1 mm), es muy alta la resistencia que hay frente al flujo de agua. El agua debe atravesar la epidermis, el tejido cortical, la endodermis (donde se localiza la mayor resistencia, debido a que el flujo se da sólo a nivel simplasto) y el periciclo. Una vez que el agua alcanza el xilema es conducida a las hojas por el tallo, a través de los conductos de los vasos (angiospermas) o por medio de traqueidas (gimnospermas), donde la resistencia al flujo es pequeña. El agua en las hojas es cedida (transpiración) a la atmósfera casi en su totalidad a través de los estomas de las hojas. Este es el segmento del continuo suelo-planta-atmósfera donde la caída en el potencial hídrico es más grande, y donde se ejerce el mayor control del flujo de agua en el sistema (Davies 1986).

La resistencia de la hoja a la pérdida del vapor de agua puede ser subdividida en dos: una interna y otra externa. La resistencia interna se encuentra determinada por la resistencia al movimiento a través de los espacios de aire intercelulares del mesófilo y por la resistencia estomática. Por su parte, la resistencia externa se encuentra determinada por la resistencia de la capa limitante o limítrofe (Jarvis 1976, Bannister 1979, Davies 1986, Jones 1992).

El ambiente y la temperatura a largo del gradiente altitudinal

La región de las Grandes Montañas en el estado de Veracruz tiene como una característica principal el presentar una topografía muy pronunciada en un gradiente altitudinal (García-García y Montañés 1991; Barradas et al. 2004). El clima en esta región es el resultado de una interacción compleja de los sistemas sinópticos que predominan (sistemas tropicales en verano y de latitudes medias en invierno, por el desplazamiento del anticiclón de Las Azores-Bermudas), de la topografía-orografía, de la interacción vegetación-atmósfera y de la gran cercanía al litoral del Golfo de México (Barradas et al. 2004). Así, las variables climáticas definen las áreas de distribución, los límites de supervivencia y los pisos altitudinales de la vegetación, e influyen en la distribución de las especies y de las comunidades (Prentice et al. 1992).

En cuanto a la temperatura atmosférica, ésta es el indicador de la cantidad de energía calorífica acumulada en el aire (eg. Fernández-Avilés y García-Centeno 2009). La altitud influye en variables ambientales, como es en el caso de la temperatura, presentándose una gran variación en ésta (Friend et al. 1989). Sin embargo, el estudiar los sistemas tropicales conlleva la ventaja de que la temperatura del aire disminuye al aumentar la altitud, sin confundirse con los efectos del cambio estacional (Hikosaka et al. 2002). En general, en un gradiente altitudinal se presenta el efecto de continentalidad, por el cual se registra un descenso de 1ºC por cada 100 m de altitud con aire seco y un descenso de 0.6ºC con aire húmedo, lo que es el resultado de la expansión adiabática del aire a medida que la presión atmosférica disminuye al aumentar la altitud (Harper 1977).

La respuesta estomática a la temperatura ha sido un tema de gran controversia. Aunque, en general, los experimentos muestran que al incrementar la temperatura se abren los estomas (eg. Hovenden y Brodribb 2000), las temperaturas elevadas provocan su cierre, que hace posible que exista un intervalo y un valor óptimo de temperatura, en que la apertura de los estomas se presenta (Jones 1992), lo que de acuerdo a Mansfield (1971) dependerá de las características de cada planta.

Conductividad estomática (g_s)

Los estomas, localizados principalmente en las hojas, son una parte importante de las plantas, ya que la planta transpira la mayor parte del agua a través de los estomas. los cuales se localizan en la superficie foliar, y se comunican con los espacios intercelulares del mesófilo de la hoja, que permiten la salida del vapor de las hojas hacia la atmósfera. El comportamiento de la hojas a nivel estomático consiste en el incremento o disminución en la transpiración, la cual optimiza la proporción fotosintética. El movimiento estomático es uno de los principales mecanismos que controlan el estado hídrico de las plantas, y juega un papel importante en la fotosíntesis y la productividad vegetal; este movimiento es proporcional a la conductividad estomática (Jones 1992). Es a través de los estomas que se controla el flujo de agua entre las plantas y la atmósfera; además, se realiza la toma de dióxido de carbono (CO_2) para la fotosíntesis, de tal manera que la apertura y cierre de los estomas controlan el intercambio gaseoso, el cual es indispensable para el adecuado funcionamiento metabólico de las plantas. En los estomas ocurre la principal resistencia a la pérdida de agua de la planta hacia la atmósfera. El inverso de la resistencia estomática es la conductividad, la cual es determinada por la apertura y la densidad de los poros estomáticos (Jones 1992).

La mayoría de las medidas significativas del funcionamiento estomático se realizan mediante la medición de la resistencia o conductividad que presentan los estomas al paso del vapor de agua (Jones 1992). La g_S, inverso de la resistencia (r_S), es directamente proporcional al diámetro de la apertura estomática, y representa la facilidad de paso del vapor de agua a través del estoma (Pearcy et al. 1991). Los movimientos estomáticos dan lugar, como respuesta directa, a aumentos o disminuciones del contenido osmótico de las células de cierre u oclusivas, al hacer que aumente su volumen (se abran) o se tornen flácidas (se cierren) (Landa-Ochoa 2008).

Hovenden y Brodribb (2000) realizaron un estudio donde concluyeron que la g_S también puede estar relacionada con la altitud de origen de la planta; es decir, la respuesta fisiológica en las plantas se podría ser un carácter heredable. Los estudios realizados en diversas especies de plantas demuestran que la respuesta estomática aumenta en sitios húmedos, cerrando sus estomas a medio día como respuesta al déficit de saturación, pero las mismas especies no muestran la misma sensibilidad en un sitio seco, lo que se puede interpretar como una respuesta adaptable con un cierre estomático, posiblemente para reducir la pérdida de agua (Korner et al. 1986). Es importante mencionar que también existente variación en el tamaño y en la frecuencia estomática entre diferentes especies, la edad de la hoja, la posición de la misma, las condiciones de crecimiento, los cambios estacionales, entre otros, éstas son variables que afectan la conductividad estomática (Hale y Orcutt 1987).

El efecto individual de cada uno de los factores ambientales (temperatura, radiación, humedad, etcétera) sobre la g_S ha sido estudiado en experimentos bajo condiciones controladas; sin embargo, el comportamiento estomático en los ambientes naturales es más complejo, debido a la interacción de los diferentes factores físicos (Jarvis 1976).

OBJETIVOS

General: El objetivo principal de este proyecto es abordar el estudio de la vulnerabilidad del ecosistema de las Grandes Montañas del estado de Veracruz, México, ante el cambio climático, a partir del análisis, evaluación y vinculación de distintas variables fisiológicas y sus respuestas con respecto a parámetros ambientales que se ven afectados con el cambio climático, incrementando la vulnerabilidad de dicho ecosistema.

Particulares:

- Determinar grupos funcionales que puedan ser indicadores de la vulnerabilidad del ecosistema, y que así permitan valorar las pérdidas o ganancias de biodiversidad de cada lugar.
- Evaluar la vulnerabilidad eco-fisiológica de las especies con respecto a cambios de temperatura y precipitación en escenarios de cambio climático.
- Evaluar la vulnerabilidad potencial de las especies con respecto a la respuesta de la conductancia estomática frente a cambios de temperatura, radiación fotosintéticamente activa, déficit de presión de vapor y potencial hídrico
- Analizar las tendencias de temperatura y precipitación de la región y proponer escenarios de cambio climático.
- Analizar la vulnerabilidad socio-económica de la región bajo el escenario del cambio climático.
- Proponer un índice de vulnerabilidad frente al cambio climático.
- Elaborar escenarios de cambio climático con prospecciones para los años 2025, 2050, 2075 y 2100.

HIPÓTESIS

Los posibles cambios en la biodiversidad podrían ser consecuencia del emergente cambio climático; cuyos elementos son, en la mayoría de los casos, susceptibles a ser evaluados cuantitativamente y, a partir de sus interrelaciones, proponer un índice de vulnerabilidad.

Capítulo 2

Caracterización de grupos funcionales de plantas con base en rasgos ecofisiológicos y en respuestas al clima en la región central de Veracruz, México

Characterization of plants functional groups based on ecophysiological traits and climate responses in the central region of Veracruz, Mexico

Manuel Esperón-Rodríguez & Víctor L. Barradas

(Sometido)

RESUMEN: La formación de grupos funcionales es común para entender y estudiar la biodiversidad. Un grupo funcional es un conjunto de organismos que presentan respuestas y efectos similares en el funcionamiento de los ecosistemas. La formación de estos grupos puede ayudarnos a entender cómo se comportan los individuos y responden a los cambios en su entorno. Esta formación puede variar y ser tan arbitraria y selectiva como lo requiera la investigación que se desarrolle. En este trabajo se seleccionaron tres rasgos fisiológicos (conductancia estomática, potencial hídrico y transpiración), y tres variables climáticas (radiación fotosintéticamente activa, temperatura del aire y déficit de presión de vapor) para formar estos grupos con cuatro especies arbóreas de la región central de Veracruz: *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite*. Se utilizaron tres métodos para caracterizar la formación de los grupos: 1) uno general; 2) la función envolvente, y 3) un método gráfico. Hubo diferencias estadísticas significativas en la formación de los grupos dependiendo de los métodos. Se concluye que los métodos de la función envolvente y del gráfico son mejores y más confiables, ya que el primer método es sensible a las diferencias y que la formación de un grupo funcional puede variar dependiendo del parámetro que se utiliza para analizar las respuestas de las especies.

Palabras clave: conductancia estomática, déficit de presión de vapor, potencial hídrico, radiación fotosintéticamente activa, temperatura del aire, transpiración

ABSTRACT: To understand and study biodiversity is common the formation of functional groups. A functional group is a set of organisms sharing similar environmental responses and similar effects on the ecosystem functioning. Formation of functional groups can help us to understand how individuals behave and respond to changes in their environment. Formation of functional groups can vary, and can be as arbitrary and selective as the work in progress requires. In this work we selected three physiological traits (stomatal conductance, leaf water potential and transpiration), and three climate variables (photosynthetically active radiation, air temperature and vapor pressure difference) to form functional groups using four tree species from the central region of Veracruz: Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua, and Pinus ayacahuite. We used three methods to analyze the groups' formation: 1) a general method; 2) a method using the envelope function, and 3) a graphic one. Statistical differences were found when forming functional groups among methods. We concluded that the envelope function and the graphic methods are better and more reliable, because the general method is more sensitive to differences, it is also concluded that the functional group formation might vary depending on the used parameter to analyze the species responses.

Key words: air temperature, leaf water potential, photosynthetically active radiation, stomatal conductance, transpiration, vapor pressure deficit

2.1 INTRODUCTION

Biodiversity is the integration of biological variability on Earth, and includes variation at all scales of biological organization, from genes and species to ecosystems (Walker, 1992; Gaston and Spicer, 2004). And it is because of the magnitude of the scales studied by the biodiversity that it is extremely difficult to know how precisely many species exist (Purvis and Hector, 2000). Due to the high number of species estimated (ca. 13.5 million of species, Gaston and Spicer, 2004) the approach to the biodiversity studies is by means of the analysis and formation of functional groups.

A functional group is a group of species sharing similar morphological and physiological attributes, behave or have similar life-histories, and also use the same resources and play similar roles in the ecosystem (Golluscio and Sala, 1993; Chapin III *et al.*, 2002). These groups function similar regardless their evolutionary lineage or biogeographic distribution (Reich *et al.*, 1997; Duckworth *et al.*, 2000). For plants, formation of functional groups is based on the environment interactions among species to produce consistent patterns of physiological, morphological and life-history responses (Shugart, 1997). Also, functional groups can be identified by their effects on the properties of biotic communities and ecosystems as well as their responses to changes in the environment, caused for example, by natural disturbances/disasters or by man (e.g. Duckworth *et al.*, 2000; Hooper *et al.*, 2002; Lavorel and Garnier, 2002). Functional groups formation is made artificially, and can be accomplished in many different ways and based on different parameters. The concept of functional group may be lax because there is not a functional classification for species (Gitay and Noble, 1997). The formation and classification of functional groups depends on the purpose of each study (Petchey and Gaston, 2006).

Plant species are often classified into functional groups based on morphological and physiological traits to simplify data analysis and interpretation (Lauenroth *et al.*, 1978). Formation of functional groups can range from very general, such as the division of autotrophic and heterotrophic (Martínez-Ramos, 2008), based on adaptive response to the environment (Hobbs, 1997) or based on life forms, such as shrub, herbaceous and trees.

Due to the tree importance in the montane cloud forest, we selected four tree species from the central region of Veracruz, to analyze the formation of functional groups using three physiological traits: stomatal conductance (g_S), leaf water potential (Ψ), and transpiration (E); and three climate variables: air temperature (T_A), photosynthetically active radiation (PAR), and vapor pressure deficit (VPD). By creating functional groups we tried to obtain a set of species having the same role in the ecosystem (Pla *et al.*, 2012); therefore, by studying a low number of species, we can extrapolate our results, with the respective advantages implied. Also, forming functional groups related to physiological responses can provide a better understanding of the vegetal associations, it can explain the local distributions of the species, and can help to find more vulnerable groups to climate changes and/or environmental disturbances (Gratani, 2014).

Our aim was to analyze and evaluate the formation and the characterization of functional groups comparing three different methods: 1) the general method, using the data obtained directly from the individuals; 2) the envelope function method, using the data obtained from the envelope curves generated by this method, and 3) the graphic method, using the predicted curves from the envelope function method.

2.2 Materials and Methods

Study Area

The region of the Great Mountains within the central mountain region of Veracruz, Mexico (19º54’08’’ N, 96º57’19’’ W) (**Figure 2.1**) is part of Neovolcanic Ridge and the Sierra Madre Oriental. Abrupt topography is the main characteristic of this region with a pronounced altitudinal gradient, from the sea level up to 5500 m asl, in a distance of 100 km, and with vegetation types that goes from tropical montane cloud forest to semi-arid and arid communities (Gómez-Pompa, 1978; Barradas, 1983). Average annual temperatures range between 10 and 29 ºC, and annual precipitation ranges from 600 to 1200 mm, with a maximum of 3000 mm in wetter regions.

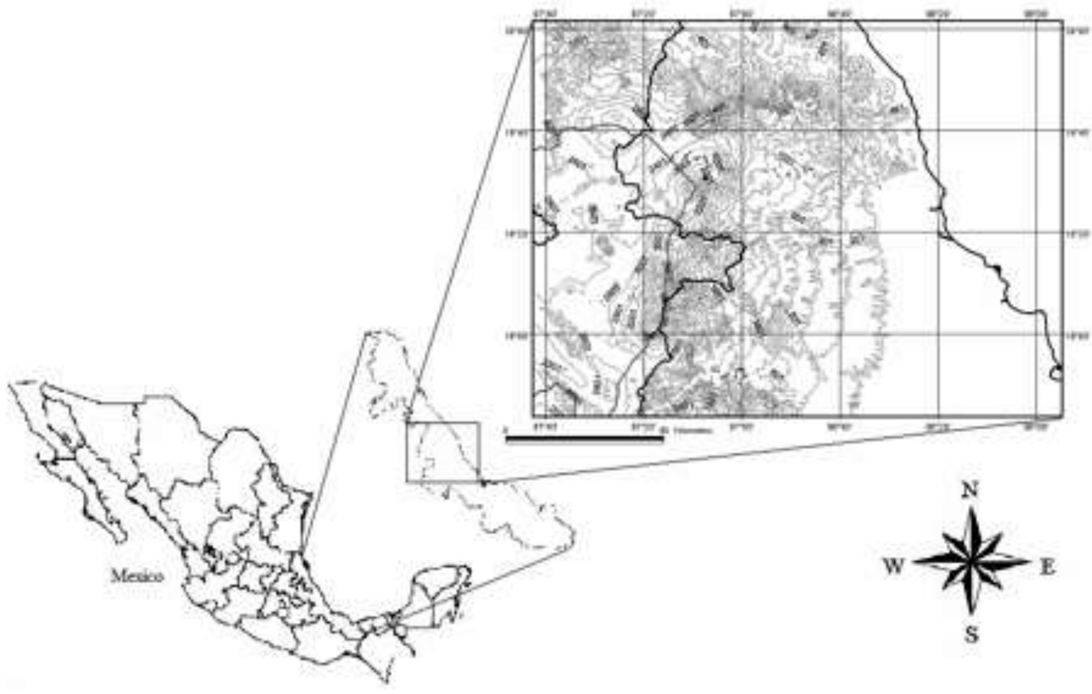

Figure 2.1. Location of the region of the Great Mountains in the state of Veracruz, Mexico.

Plant material

To illustrate the formation of functional groups we selected four tree species from different altitudinal ranges: *Alnus acuminata* Kunth, *Quercus xalapensis* Bonpl., *Liquidambar styraciflua* L., and *Pinus ayacahuite* Ehren (**Table 2.1**). Fifteen individuals of each species from 45 to 90 cm height were kept at the greenhouse. Individuals were transplanted in a mixture of peat moss after having been sterilized by autoclaving for 90 minutes. Individuals were kept at the humid greenhouse of the Institute of Ecology, UNAM under well-watered and field conditions.

Table 2.1. Altitudinal distribution, precipitation range, optimal temperature (T_O), and optimal thermal range (T_R) for stomatal function for *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite*.

Species	**Altitudinal distribution (m asl)**	**Precipitation range (mm)**	**T_O (ºC)**	**T_R (ºC)**
Alnus acuminata	1300 - 2800	1000 - 3000	29.7 (0.5)	22.17-37.17
Quercus xalapensis	400 - 2700	1400 - 2300	28.2 (0.4)	20.65-37.39
Liquidambar styraciflua	400 - 1800	1000 - 1500	27.5 (0.3)	19.55-36.19
Pinus ayacahuite	2000 – 3500	800 - 1500	26.2 (0.2)	18.26-34.56

Stomatal conductance, leaf water potential and transpiration

Stomatal conductance (g_S) and transpiration (E), were measured in all individuals of each species on at least four fully expanded leaves per plant, with a steady-state diffusion porometer (LI-1600, LI-COR, Lincoln, Nebraska, USA). Leaf water potential (Ψ) was measured in all individuals of each species on four fully expanded leaves per plant, with a pressure chamber (PMS, Corvallis, Oregon, USA) (Scholander *et al.*, 1964). Physiological measures were made daily from October 22 to December 7, 2012, at 7 and from 10 to 18 hours (h, local time) at 2 h intervals, in well-irrigated individuals.

Climatological measurements

Air temperature (T_A), photosynthetically active radiation (PAR) and relative humidity (RH) were determined next to each measured leaf with a quantum sensor (LI-190SB, LI-COR Ltd., Lincoln, Nebraska, USA), a fine wire thermocouple, and a humicap sensor (Vaisala, Helsinki, Finland). Leaf temperature (T_L) was also measured. Thermocouples were mounted in the porometer. The air vapor pressure deficit (*VPD*) was calculated from T_A, T_L and RH measurements. Climate measurements were made daily from October 22 to December 7, 2012, at 7 and from 10 to 18 hours (h, local time) at 2 h intervals.

The envelope function method

The effect that each climate variable has on the stomatal conductance (g_S) is determined from simple methods that are referred as envelope functions. This method consists of selecting data of the probable upper limit of the function, represented by a cloud of points in each of the diagrams produced by plotting stomatal conductance as a function of any variable (edaphic and climatic) and normalized to the maximum g_S ($g_{SMAX} = 1$). This method has three theoretical assumptions: 1) the envelope function represents the optimal stomatal response to the selected parameter (i.e. PAR), 2) the points below the selected function are the result of a change in any of the other variables (*VPD* and T_A) and 3) that there are not synergistic interactions among variables (Jarvis, 1976; Fanjul and Barradas, 1985; Jones, 1992; Ramos-Vázquez and Barradas, 1998; Barradas *et al.,* 2004).

The relationship of g_S in terms of air temperature (T_A) is given by the envelope values that fit a quadratic equation.

$$g_S = A + B\,T_A + C\,T_A^{\,2} \quad (1)$$

where A, B and C are parameters of the parabola, being possible to determine the optimum temperature (T_O) at which g_{SMAX} occurs, and the cardinal temperatures (minimum and maximum).

Envelope values of stomatal conductance (g_S) as a function of photosynthetically active radiation (PAR) are consistent with a hyperbolic function:

$$g_S = [a\mathrm{PAR}/(b + \mathrm{PAR})] \quad (2)$$

where a is the asymptotic value of g_S or g_{SMAX} and b is g_S sensitivity to changes in PAR. While the g_S function in relation to vapor pressure deficit (*VPD*) generates a simple linear equation.

$$g_S = a + bVPD \quad (3)$$

where b is g_S sensitivity to the *VPD*, and a is the zero drift.

Similarly, the stomatal response to water potential is also a simple linear equation:

$$g_S = a + b\Psi \quad (4)$$

where b is g_S sensitivity to the Ψ, and a is the zero drift.

We also analyzed the relation between the g_S and transpiration (E) by a simple linear equation:

$$g_S = a + bE \quad (5)$$

where b is g_S sensitivity to E, and a is the zero drift.

Statistical analysis

We analyzed our data to find significant differences between the three methods using one-way analysis of variance (ANOVA). All data were tested for homogeneity of variances using Levene's Test. The non-parametric statistical test of Kruskal-Wallis was used when data were not normally distributed, or when variances were unequal for the groups being compared. Statistical significance was considered to be $P < 0.05$ in all cases.

2.3 Results

Alnus acuminata registered the highest values of g_S, T_A, and E. Concerning Ψ and PAR the highest values corresponded to *P. ayacahuite*, whilst *Q. xalapensis* recorded the highest *VPD* (**Table 2.2**). Regarding g_S, we found significant differences when comparing the four species (Kruskal-Wallis H = 231.591, $P < 0.001$), and we formed three functional groups: 1) *Q. xalapensis* and *L. styraciflua*, 2) *A. acuminata*, and 3) *P. ayacahuite*. When analyzing Ψ, we found significant differences (Kruskal-Wallis H = 240.852, $P < 0.001$), forming three functional groups: 1) *A. acuminata*, 2) *Q. xalapensis* and *P. ayacahuite*, and 3) *L. Styraciflua*.

After analyzing E, we also found significant differences when comparing the four species (Kruskal-Wallis H= 378.933, $P < 0.001$), and three functional groups were formed: 1) *Q. xalapensis* and *L. styraciflua*, 2) *A. acuminata*, and 3) *P. ayacahuite*. For PAR, we found significant differences when comparing the four species (Kruskal-Wallis H = 34.455, $P < 0.001$), where we formed two functional groups: 1) *Q. xalapensis, L. styraciflua*, and *A. acuminata*, and 2) *P. ayacahuite*. Finally, when we analyzed *VPD,* we did not find significant differences when comparing the four species (*F* = 2.20, *P* = 0.0858), and one functional group was formed: 1) *Q. xalapensis, L. styraciflua*, *A. acuminata*, and *P. ayacahuite* (**Table 2.3**).

Table 2.2. Stomatal conductance (g_S), water leaf potential (Ψ), transpiration (E), air temperature (T_A), vapor pressure difference (*VPD*) and photosynthetically active radiation (PAR) for *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite*. Averages are shown and ± standard error (n=870).

Species	**g_S (mmol m^{-2} s^{-1})**	**Ψ (Mpa)**	***E* (mmolH$_2$0 m^{-2} s^{-1})**	**T_A (°C)**	***VPD* (kPa)**	**PAR (µmol m^{-2} s^{-1})**
A. acuminata	433.963 ± 176.49	- 1.936 ± 0.98	17.755 ± 8.82	25.903 ± 3.81	2.263 ± 0.5	151.245 ± 63.62
Q. xalapensis	320.806 ± 125.53	-1.652 ± 0.44	13.128 ± 5.94	25.84 ± 3.71	2.279 ± 0.5	152.699 ± 62.74
L. styraciflua	329.658 ± 138.18	-1.723 ± 0.57	13.341 ± 6.13	25.839 ± 3.56	2.271 ± 0.48	144.93 ± 60.23
P.ayacahuite	377.5.49 ± 138.18	- 0.567 ± 0.37	14.069 ± 5.44	25.835 ± 3.53	2.209 ± 0.48	182.728 ± 84.99

Table 2.3. Functional groups formed according to stomatal conductance (g_S), leaf water potential (Ψ),transpiration (*E*), vapor pressure difference (*VPD*) and photosynthetically active radiation (PAR) from *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite* using Student-Newman-Keuls test.

Species	**Cases**	**Mean**	**Homogeneous groups**
		g_S	
Quercus xalapensis	824	309.533	X
Liquidambar styraciflua	827	317.999	X
Pinus ayacahuite	837	374.73	X
Alnus acuminata	833	428.113	X
		Ψ	
Quercus xalapensis	166	-1.93611	X
Liquidambar styraciflua	120	-1.72195	X
Pinus ayacahuite	149	-1.65262	X
Alnus acuminata	120	-0.526654	X
		E	
Quercus xalapensis	846	13.2008	X
Liquidambar styraciflua	846	13.4139	X
Alnus acuminata	846	17.8721	X
Pinus ayacahuite	846	20.5377	X
		VPD	
Pinus ayacahuite	836	2.25622	X
Alnus acuminata	831	2.30234	X
Quercus xalapensis	824	2.31653	X
Liquidambar styraciflua	827	2.3213	X
		PAR	
Liquidambar styraciflua	821	145.556	X
Alnus acuminata	831	151.289	X
Quercus xalapensis	823	153.095	X
Pinus ayacahuite	831	184.753	X

Assuming that the envelope function method allows us to predict the physiological response of the species, we developed the method based on the g_S response to T_A, PAR, *VPD*, Ψ, and *E* (**Table 2.4**), and from the predicted values of the envelope curves we formed functional groups.

When analyzing Ψ, significant differences were found (Kruskal-Wallis *H* = 201.125, *P* < 0.001) forming three functional groups: 1) *A. acuminata*, 2) *Q. xalapensis* and *P. ayacahuite*, and 3) *L. Styraciflua.* For T_A, we did not find significant differences when comparing the four species (*F* = 0.48,

$P = 0.6968$), and we formed one functional group: 1) *Q. xalapensis, L. styraciflua*, *A. acuminata*, and *P. ayacahuite* (Figure 2). Regarding PAR, we found significant differences when comparing the four species (Kruskal-Wallis $H = 17.1701$, $P < 0.001$), and we formed two functional groups: 1) *Q. xalapensis, L. styraciflua*, and *A. acuminata*, and 2) *P. ayacahuite*. As for *VPD*, we also found significant differences when comparing the four species (Kruskal-Wallis $H = 86.6859$, $P < 0.001$), and we observed three functional groups: 1) *Q. xalapensis* and *L. styraciflua*, 2) *A. acuminata*, and 3) *P. ayacahuite*. After analyzing *E*, we also found significant differences when comparing the four species ($F = 3.88$, $P = 0.0094$), and we found two possible functional groups: 1) *L. styraciflua*, *A. acuminata* and *Q. xalapensis*, and 2) *A. acuminata*, *Q. xalapensis* and *P. ayacahuite*. Finally, according to g_S average, we also found significant differences (Kruskal-Wallis $H=170.471$, $P < 0.001$), and we could form four different functional groups: 1) *Q. xalapensis,* 2) *L. styraciflua*, 3) *A. acuminata*, and 4) *P. ayacahuite* (**Table 2.5**).

Table 2.4. Calculated envelope functions for stomatal conductance (g_S) versus air temperature (T_A), photosynthetically active radiation (PAR), vapor pressure difference (*VPD*), transpiration (*E*) and leaf water potential (Ψ) for *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite* (r^2 is the coefficient of determination).

Parameter	Theoretical equation	Species	Equation	r^2
T_a	$g_S = A + B\,T_A + C\,T_A{}^2$	*Alnus acuminata*	$g_S = -\,4059.583\,T_A^2 + 345.473\,T_A + (-5.811)$	0.994
		Quercus xalapensis	$g_S = -1784.845\,T_A^2 + 171.448\,T_A + (-2.948)$	0.949
		Liquidambar styraciflua	$g_S = -2017.468\,T_A^2 + 198.647\,T_A + (-3.551)$	0.942
		Pinus ayacahuite	$g_S = -1580.765\,T_A^2 + 177.339\,T_A + (-3.307)$	0.981
PAR	$g_S = (a\mathrm{PAR}/b + \mathrm{PAR})$	*Alnus acuminata*	$g_S = 1007.364\ \mathrm{PAR} / (6.752 + \mathrm{PAR})$	0.929
		Quercus xalapensis	$g_S = 671.906\ \mathrm{PAR} / (8.675 + \mathrm{PAR})$	0.884
		Liquidambar styraciflua	$g_S = 723.639\ \mathrm{PAR} / (9.087 + \mathrm{PAR})$	0.964
		Pinus ayacahuite	$g_S = 738.749\ \mathrm{PAR} / (2.078 + \mathrm{PAR})$	0.978
VPD	$g_S = a + bVPD$	*Alnus acuminata*	$g_S = 2381.825 + (-466.341)\,VPD$	0.971
		Quercus xalapensis	$g_S = 1109.452 + (-169.337)\,VPD$	0.903
		Liquidambar styraciflua	$g_S = 1577.411 + (-304.068)\,VPD$	0.947
		Pinus ayacahuite	$g_S = 1129.183 + (-175.242)\,VPD$	0.979
E	$g_S = a + b\mathrm{E}$	*Alnus acuminata*	$g_S = 87.968 + 30.093\ \mathrm{E}$	0.93
		Quercus xalapensis	$g_S = 70.366 + 25.632\ \mathrm{E}$	0.978
		Liquidambar styraciflua	$g_S = 66.313 + 30.312\ \mathrm{E}$	0.963
		Pinus ayacahuite	$g_S = 52.092 + 23.123\ \mathrm{E}$	0.863
Ψ	$g_S = a + b\Psi$	*Alnus acuminata*	$g_S = 1716.049 + 222.668\ \Psi$	0.952
		Quercus xalapensis	$g_S = 1754.504 + 247.865\ \Psi$	0.985
		Liquidambar styraciflua	$g_S = 1230.826 + 284.702\ \Psi$	0.872
		Pinus ayacahuite	$g_S = 1064.502 + 192.232\ \Psi$	0.993

To corroborate both methods based on the statistical analysis, we plotted the predicted curves from the envelope function method for T_A, PAR, *VPD, E*, and Ψ against g_S, and the normalized g_S (g_{SNOR}) for the four species (Figure 2).

2.4 Discussion

Formation of functional groups can help us to understand how the organisms behave and respond to climate and environmental changes. We acknowledge that using only four species has limitations concerning this formation. However, regardless the species' number, we tested and evaluated the method's effectiveness. Here we used a multicriteria analysis to approach this aim (Saaty 1988). Using this approach had some advantages. It allowed us to define the problem to be solved and to identify the discriminating criteria in decision-making; finally, the objectives were undertaken with a multidisciplinary approach, maximizing our results.

Table 2.5. Functional groups formed from the calculated envelope function according to air temperature (T_A), photosynthetically active radiation (PAR), vapor pressure difference (*VPD*), transpiration (*E*), leaf water potential (Ψ) and stomatal conductance (g_S) from *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite* using Student-Newman-Keuls test.

Species	Cases	Mean	Homogeneous groups			
		T_A				
Pinus ayacahuite	100	26.8	X			
Liquidambar styraciflua	99	27.3111	X			
Quercus xalapensis	100	27.4	X			
Alnus acuminata	100	27.9	X			
		PAR				
Quercus xalapensis	100	155.0	X			
Liquidambar styraciflua	100	160.0	X			
Alnus acuminata	99	183.169	X			
Pinus ayacahuite	100	220.5		X		
		VPD				
Pinus ayacahuite	99	2.77251	X			
Liquidambar styraciflua	100	3.32728		X		
Quercus xalapensis	99	3.32979		X		
Alnus acuminata	99	3.48234			X	
		E				
Liquidambar styraciflua	99	16.638	X			
Alnus acuminata	99	18.8783	X	X		
Quercus xalapensis	100	19.4845	X	X		
Pinus ayacahuite	99	21.528		X		
		g_S				
Quercus xalapensis	100	571.745	X			
Liquidambar styraciflua	100	600.88		X		
Pinus ayacahuite	100	645.318			X	
Alnus acuminata	100	785.913				X
		Ψ				
Quercus xalapensis	99	-2.42512	X			
Liquidambar styraciflua	100	-2.10291		X		
Pinus ayacahuite	99	-1.96126		X		
Alnus acuminata	100	-0.930798			X	

The selection of our species was not arbitrary. We selected tree species to avoid the typical formation of functional groups based on life forms (tree, shrub, and herbaceous), with all of these species being part of the functional group of trees. The species are phenological and morphological different, and in particular with different kinds of leaves. And finally, the species are distributed along the altitudinal gradient in the region. This means that the species are subject to different regimes of temperature and precipitation (**Table 2.1**).

We observed the formation of same functional groups when analyzing PAR. When we considered the g_S similar groups were formed, but when using the envelope function method we observed four distinct groups, indicating that this method is more rigorous. The same results were observed when we analyzed *E*, where we could observe more subtle differences when analyzing this trait under the method of envelope functions. Similarly, when analyzing *VPD*, we noted that the general method only formed one group, but the envelope function method formed three groups, which reiterates that the analysis using the values of the envelope curves provides more detail data, perceiving more subtle differences. However, to analyze with more precision the variation of the parameters, the development of the graphic method could provide more information.

In the case of T_A we observed that *Q. xalapensis, L. styraciflua* and *A. acuminata* have the same physiological behavior in temperatures between 27.1 and 31 °C, which is consistent with the optimum temperature ranges of the three species (Table 1), and it is also consistent to data of altitudinal distribution of the three species; we can find the three species at 1300-1800 m asl, at lower altitudes where the temperature increases. At higher temperatures (31-34.2 °C), *P. ayacahuite* and *L. styraciflua* behave similarly. It is noteworthy that these are the only two species that do not share the altitudinal distribution; this might indicate the pine plasticity to adapt to high temperatures, because it has the highest distribution (2000-3500 m asl) and the lower optimum temperature (26.2 °C). Finally, with temperatures higher than 34 and up to 40 ºC, *A. acuminata* and *L. styraciflua* exhibit the same physiological behavior, indicating that these two species have a greater heat tolerance. This tolerance is very evident in the case of *A. acuminata*, consistent with the optimum temperature (29.7 °C), the envelope curve (Figure 2), and the altitudinal distribution (1300 to 2800 m asl). In the case of *L. styraciflua*, the result also was consisted with the distribution (the lowest of the four species, 400-1800 m asl).

For the case of PAR we noted in the graphs (**Figure 2.2**) that the behavior was similar for all four species, with a slight distinction in *P. ayacahuite,* and observing a greater affinity between *Q. xalapensis* and *L. styraciflua* (Figure 2). These data were consistent with both methods, with the isolation of *P. ayacahuite* in both; this can be corroborated also in the values of the equation of the envelope function method (Table 4), where the values of the sensitivity parameter *b* of PAR were similar for *A. acuminata, Q. xalapensis* and *L. styraciflua* (6.752, 8.675 and 9.087 respectively), against the *P. ayacahuite* value (2.078), indicating that the pine is more sensitive to PAR changes, therefore the pine is forming a separate functional group. *A. acuminata* is the next species in sensitivity, but it has a major tolerance to high radiation, *A. acuminata* can stand with values up to 1000 µmol m^{-2} s^{-1} (**Table 2.4**). As for *VPD,* this had the greatest difference between the two methods. We found a single functional group using the general method, and two groups with the envelope function method. When looking the graphs (**Figure 2.2**) we noted that at low values of *VPD* (2.51 - 2.85 kPa) all species behaved similarly. While increasing *VPD* (3.15 - 3.72 kPa) *A. acuminata* and *L. styraciflua* behaved similarly. With higher *VPD* (3.7 - 4.0 kPa) *A. acuminata* and *P. ayacahuite* behaved similarly, this can be corroborated with the highest altitudinal distribution of both species, where the higher altitude, the lower temperature.

Table 2.6. Functional groups formed using the two methods: the general method, and the envelope function method, using the parameters of stomatal conductance (g_S), leaf water potential (Ψ), transpiration (*E*), vapor pressure difference (*VPD*) and photosynthetically active radiation (PAR) for *Alnus acuminata*, *Quercus xalapensis*, *Liquidambar styraciflua*, and *Pinus ayacahuite*.

Parameter	**General Method**			**Envelope function method**			
	Functional Groups			**Functional Groups**			
g_s	*Q. xalapensis* *L. styraciflua*	*A. acuminata*	*P. ayacahuite*	*A. acuminata*	*Q. xalapensis*	*L. styraciflua*	*P. ayacahuite*
Ψ	*Q. xalapensis* *P. ayacahuite*	*A. acuminata*	*L. styraciflua*	*Q. xalapensis* *P. ayacahuite*	*A. acuminata*	*L. styraciflua*	
E	*Q. xalapensis* *L. styraciflua*	*A. acuminata*	*P. ayacahuite*	*Q. xalapensis* *L. styraciflua* *A. acuminata*	*Q. xalapensis* *A. acuminata* *P. ayacahuite*		
VPD	*Q. xalapensis* *L. styraciflua* *A. acuminata* *P. ayacahuite*			*Q. xalapensis* *L. styraciflua*	*A. acuminata*	*P. ayacahuite*	
PAR	*Q. xalapensis* *L. styraciflua* *A. acuminata*	*P. ayacahuite*		*Q. xalapensis* *L. styraciflua* *A. acuminata*	*P. ayacahuite*	PAR	*Q. xalapensis* *L. styraciflua* *A. acuminata*

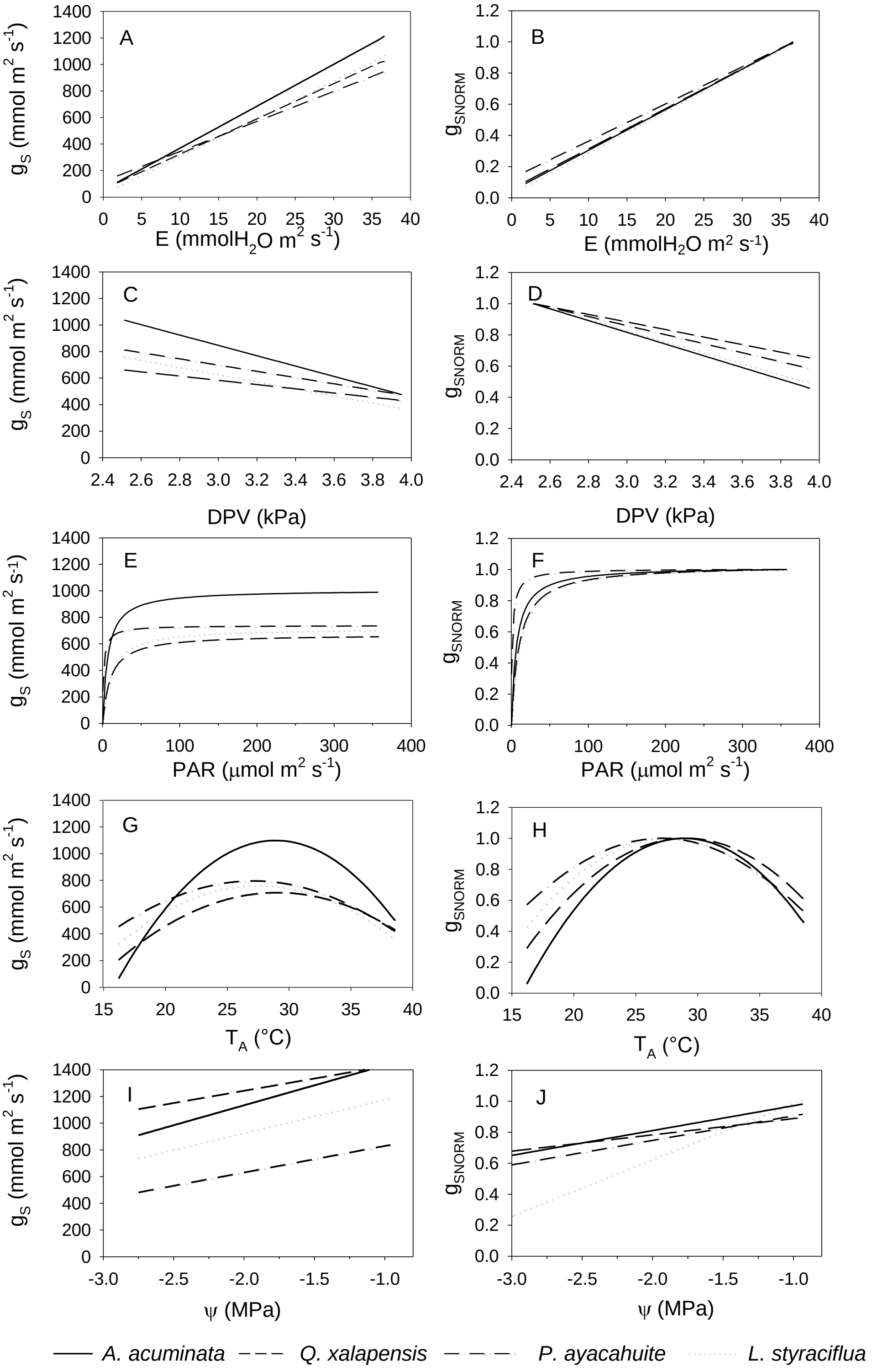

Figure 2.2. Diagram of the envelope function method for the parameters: transpiration (*E*), vapor pressure difference (*VPD*), photosynthetically active radiation (PAR), temperature (T_A), and leaf water potential (Ψ) plotted against stomatal conductance (g_S, A, C, E, G, I) and normalized stomatal conductance (g_{SNORM}, B, D, F, H, J) for *Alnus acuminata, Quercus xalapensis*, *Liquidambar styraciflua*, and *Pinus ayacahuite*.

In the case of *E* we found a similar behavior among the species (**Figure 2.2**). Both methods formed two functional groups, where *Q. xalapensis* and *L. styraciflua* behaved more similar than the others. This behavior can be corroborated with the graphic method. In the general method, *A. acuminata* and *P. ayacahuite* formed independent groups, and in the envelope function method, two groups were formed: 1) *L. styraciflua, Q. xalapensis* and *A. acuminata*, and 2) *Q. xalapensis*, *A. acuminata* and *P. ayacahuite* (Table 6). In the graphic method we observed that all species behaved similarly in $E < 10$ mmolH$_2$0 m^{-2} s^{-1}, and this is where the functional group formed by *Q. xalapensis*, *A. acuminata* and *P. ayacahuite* was found, with all species sharing higher altitudes (above 2000 m asl) where the temperature is lower, and thus g_S and *E* is lower preventing water loss through stomata. Above 20 mmolH$_2$0 m^{-2} s^{-1}, we found the functional group of *L. styraciflua, Q. xalapensis* and *A. acuminata*, where higher *E* can be related to lower altitudinal distribution (below 2000 m asl, and outside the *P. ayacahuite* distribution) with higher temperatures.

Concerning Ψ, both methods formed three groups: 1) *Q. xalapensis*, 2) *L. styraciflua* and *P. ayacahuite*, and 3) *A. acuminata*. Here we observed that *L. styraciflua* and *P. ayacahuite*, were the species which reached the lowest asymptotic g_S values, with *P. ayacahuite* being the most sensitive species to changes in Ψ (**Table 2.4**). The highest asymptotic g_S value corresponded to *Q. xalapensis*.

From the data found, we can say that the main difference between methods is that in the general method we analyzed the functional groups based on the values obtained from the individuals, whereas with the envelope function method we took and analyzed the estimated values from the envelope curves, and these values allowed us to extrapolate the results beyond the individuals, allowing analyzing physiological variations of a given population. Using this method also can help us to predict plant performance outside a species' native range (Sands et al., 2000; Rodriguez et al., 2002; Dye et al., 2004) by increasing temperature or reducing water or *VPD*, trying to simulate climate change scenarios or environmental changes. We encourage future functional groups formation using different physiological traits and climate variables, and under trying to observe how species respond to extreme conditions (i.e. high temperature).

In this work, we consider each method as a criterion to assess and evaluate the formation of functional groups through the multicriteria analysis. Thanks to this analysis, we noted that there are differences among methods. We found that the envelopes function method and the graphical method provided more detail; they are more susceptible to subtle differences and allowed us to infer better the physiological responses in g_S, Ψ and *E* to any disturbance or change in the climatic variables T_A, PAR or *VPD*.

We conclude that it is extremely important to define the physiological trait and the climate variable that will be used to form and to characterize the functional groups. The selected parameter to form functional groups should be considered at the beginning of the work and based on the objectives.

Capítulo 3

Vulnerabilidad potencial frente al cambio climático de cuatro especies arbóreas de la región montañosa central de Veracruz, México

Potential vulnerability to climate change of four tree species in the central mountain region of Veracruz, Mexico

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RESUMEN: Definimos vulnerabilidad como el grado en que el cambio climático puede dañar o perjudicar a un sistema, dependiendo no sólo de la sensibilidad del sistema, sino también de su capacidad para adaptarse a las nuevas condiciones climáticas. El cambio climático actual ya ha afectado a la biodiversidad de la Tierra, y es probable que la tasa de cambio se acelere en el futuro. Se espera que el cambio climático afecte el rendimiento, la estructura y distribución de los ecosistemas, las especies y los componentes genéticos. Los cambios en la temperatura y la precipitación, y en la frecuencia e intensidad de los eventos extremos, pueden influir directamente en el funcionamiento del ecosistema. Para determinar la vulnerabilidad o fragilidad de diferentes especies al cambio climático, se utilizó el método de las funciones envolvente, debido a su capacidad para analizar las variables que afectan directamente a las diferentes especies; midiendo el efecto de las variables climáticas sobre la conductancia estomática, esto nos proporcionó un análisis efectivo de la diversidad de respuestas eco-fisiológicos. El uso de este método para evaluar la vulnerabilidad ayudó a predecir los valores extremos que las especies podrían tolerar, y también brindó información sobre la sensibilidad de las especies. Se analizaron los efectos de la temperatura del aire, la radiación fotosintéticamente activa, el déficit de presión de vapor y el potencial hídrico foliar en la conductancia estomática en cuatro especies de árboles (*Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua* y *Pinus ayacahuite*) de diferentes rangos altitudinales en la región central de Veracruz, México, las grandes montañas. Conocer cómo vulnerabilidad afecta a las especies y los ecosistemas es un elemento clave para el mantenimiento de la biodiversidad regional.

Palabras clave: Vulnerabilidad · Cambio climático · Conductancia estomática · Temperatura del aire · Radiación fotosintéticamente activa · Déficit de presión de vapor · Potencial hídrico.

ABSTRACT: We define vulnerability as the extent to which climate change may damage or harm a system, depending not only on a system's sensitivity, but also on its ability to adapt to new climatic conditions. Current climate change has already affected the Earth's biodiversity, and the rate of change is likely to accelerate in the future. It is expected that climate change will affect the performance, structure and distribution of ecosystems, species and genetic constituents. Changes in temperature and precipitation, and in the frequency and intensity of extreme events, can directly influence ecosystem functioning. To determine the vulnerability or fragility of different species to climate change, we used the envelope function method, because of its capacity to analyze the variables that directly affect different species; by measuring the effect of climate variables on stomatal conductance, this provided an effective analysis of the diversity of eco-physiological responses. Using this method to assess vulnerability helped us predict the extreme values that the species could tolerate and also gave information about the species' sensitivity. We analyzed the effects of air temperature, photosynthetically active radiation, vapor pressure deficit and leaf water potential on the stomatal conductance in 4 tree species (*Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua* and

Pinus ayacahuite) from different altitudinal ranges in the central region of Veracruz, Mexico, the Great Mountains. Knowing how vulnerability affects the species and ecosystems is a key element of maintaining regional biodiversity.

Key words: Vulnerability · Climate change · Stomatal conductance · Air temperature · Photosynthetically active radiation · Vapor pressure deficit · Leaf water potential

3.1 INTRODUCTION

Vulnerability as an ordinary word refers to the capacity to be wounded; for instance, the degree to which a system is likely to experience harm due to exposure to a hazard (Turner et al. 2003). An extremely important hazard is climate change (IPCC 2001, 2007, Ford et al. 2006, Füssel 2007). Therefore, vulnerability to climate change can be defined as the extent to which climate change may damage or harm a system, depending not only on a system's sensitivity but also on its ability to adapt to new climatic conditions (Watson et al. 1996). Current climate change is already affecting the Earth's biodiversity at all scales of organization, from species to ecosystems, and the rate of change is likely to accelerate in the future (Walther et al. 2002). It is expected that climate change will affect the performance, structure and distribution of ecosystems, species and genetic constituents (Robledo & Forner 2005). The consequences of climate change on biotic communities and their biodiversity can be evidenced in shifts of species' distribution and phenology (Thomas et al. 2004, Parmesan 2006), species' distribution ranges, and the composition, structure and functioning of ecosystems (McCarty 2001).

Because climate is a spatially heterogeneous variable, the actual effects of climate change on biodiversity at regional scale can be severe due to particular conditions that affect and determine the species' presence/abscence (Gauch et al. 1974). Projected impacts on biodiversity include thermophilic plant species becoming more common as cold-tolerant species decline (Reid 2006). Different species groups might respond differently to changing conditions (Lindner et al. 2010). Most existing studies on forests rely on environmental envelope approaches, which suggest that there will be a shift in the natural species composition from coniferous dominated forests toward broadleaved species (e.g. Thuiller et al. 2006). However, it is still less understood how fast species will retreat from areas that no longer match their natural ecological niche (Lindner et al. 2010).

Climate change effects will affect all species; however, the severity of impacts on ecosystem goods and services will depend on the regional situation and the specific regional and local changes in climate, and the effects of increases in temperature will differ with location due to differences between bioclimatic zones (Lindner et al. 2010). An increase in temperature alone would enhance carbon intake, productivity and growth in boreal ecosystems and temperate regions (Kellomäki & Wang 1996, Saxe et al. 2001, Briceño-Elizondo et al. 2006); however, interaction with other climate- or site-related factors could alter the ecosystems' response. For the boreal, temperate oceanic, temperate continental, Mediterranean and mountainous forests of Eastern Europe, higher temperatures extend the growing season and may increase photosynthesis, particularly in the northern latitudes (Lindner et al. 2010); however, in other regions, such as our study region in Mexico, where water availability restricts productivity, detrimental effects on these measures are possible if precipitation does not increase. Negative effects of climate change are expected to be more severe in regions where droughts are the main constraint on forest growth and productivity, and where the temperature increase may affect the competitive relationships between tree species (Lasch et al. 2002).

Besides droughts, climate variability, heat waves and heavy precipitation events are likely to increase in intensity and frequency with unpredictable consequences on seasonality (IPCC 2007). Nevertheless, seasonality is not the only feature that can limit species' growth and distribution. The adaptation of plants to different elevations is seen as an analogy for climate adaptation (Hovenden & Brodribb 2000), where elevation influences the environmental variables of air temperature (T_A), photosynthetically active radiation (PAR), vapor pressure deficit (VPD) and rainfall by decreasing temperature with increasing altitude (Harper 1977, Hikosaka et al. 2002), and elevation influences the possibility of plants acclimation and adaptation to particular environmental conditions (Körner et al. 1986, Friend et al. 1989).

In this study, we used stomatal conductance (g_S) as an indicator of vulnerability to water and thermal stress because g_S is directly affected by time (over the course of the day), by climate variables such as temperature, and by physiological parameters such as water potential. Thus g_S is a key response of plants to climate, as it controls transpiration (*E*; water status) and CO_2 assimilation, playing an important role in photosynthesis and plant productivity (Jones 1992). Determining the vulnerability or fragility of different species in the face of climate change requires a model capable of analyzing the variables that directly affect the species and their ecophysiological responses (Lambers et al. 1998, Barradas et al. 2010). We considered the envelope function method as the model that was most capable of providing information about the eco-physiological responses of a species to T_A, PAR, *VPD* and water potential. This model analyzes the effect of each climate variable on g_S, and these effects are determined, in turn, from simple models that are referred to as envelope functions. The species' responses to different climate variables can be used to elucidate how populations might be affected by climate change and to address their potential vulnerability. The objective of this paper is to present the effect that climate change might have on 4 tree species from the central region of Veracruz, Mexico, through the envelope function method.

3.2 METHODS

Study Area

The central mountain region of Veracruz, Mexico (19º54'08'' N, 96º57'19'' W) (**Fig. 3.1**) is part of Neovolcanic Ridge and the Sierra Madre Oriental. Abrupt topography is the main characteristic of this region with a pronounced altitudinal gradient, from the sea level up to 5500 m asl, in a distance of 100 km, and with vegetation types that go from tropical montane cloud forest to semi-arid and arid communities (Gómez-Pompa 1978, Barradas 1983, García-García & Montañez 1991). Average annual temperatures range between 10 and 29 ºC, and annual precipitation ranges from 600 to 1200 mm, with a maximum of 3000 in wetter regions. Soils in the region are of volcanic origin or Andisols, with physical characteristics that favor good structural stability (Meza & Geissert 2003). They have low bulk density, high porosity with significant micro-porosity, significant amount of water micro-aggregates, complexation with organic matter, and very stable amounts of Fe and Al (Shoji et al. 1993).

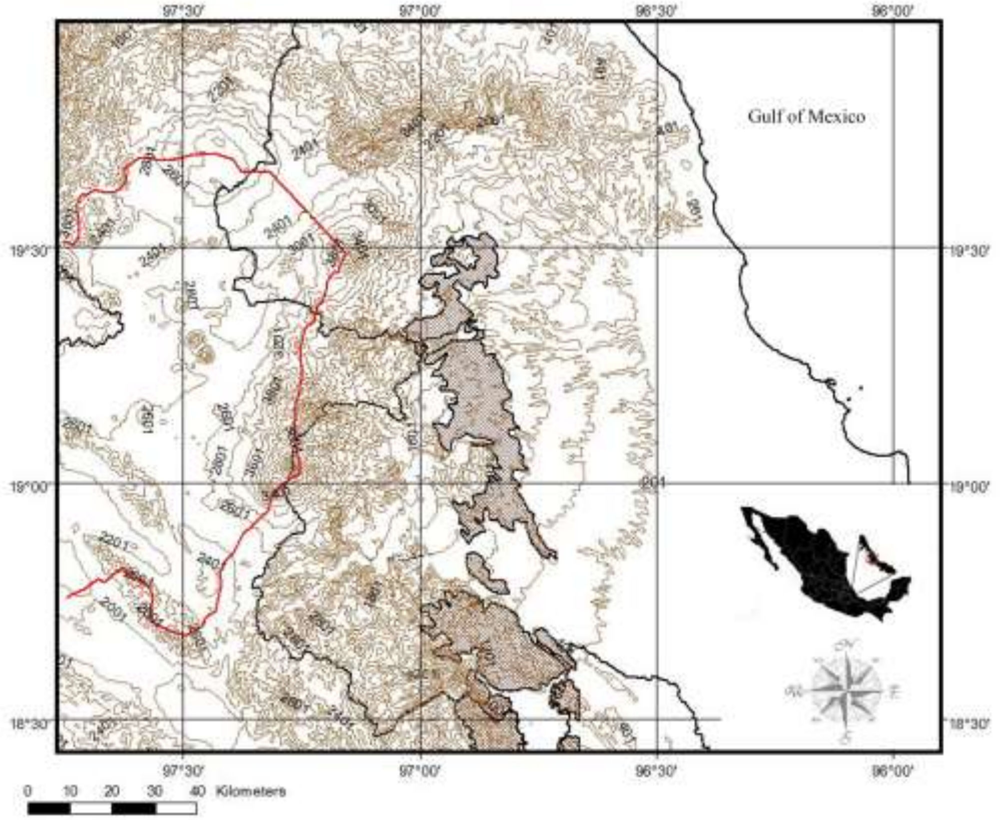

Figure 3.1. Location of the study area in the central mountain region of Veracruz, Mexico. Black line represents the stated division between Veracruz and Puebla; red line represents the watershed; brown lines represent contours.

Species selected

Four tree species were selected from different altitudinal ranges according to their dominance: *Alnus acuminata* Kunth, *Quercus xalapensis* Bonpl., *Liquidambar styraciflua* L. (1753), and *Pinus ayacahuite* Ehren (**Table 3.1**).

Plant material

Fifteen saplings of each species from 45 to 90 cm height were kept in a greenhouse. Individuals were transplanted in a mixture of peat moss that had been sterilized by autoclaving for 90 min. Saplings were kept at the humid greenhouse of the Institute of Ecology, UNAM, under well-watered conditions. All measures were made at the greenhouse in order to reach temperatures above the natural range of the species, to mimic climate change.

Table 3.1. Height, diameter, climatic requirements (temperature and precipitation ranges) and distribution (altitudinal range) of *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua* and *Pinus ayacahuite.*

Species	Height (m)	Diameter (cm)	Temperature range (ºC)	Precipitation range (mm)	Altitudinal range (masl)
Alnus acuminata	10 - 30	35 - 100	4 - 27	1000 - 3000	500 - 2800
Quercus xalapensis	30	45	12 - 18	1400 - 2300	400 - 2700
Liquidambar styraciflua	20 - 60	42 - 150	12 - 18	1000 - 2000	400 - 1800
Pinus ayacahuite	35-40	>100	13 - 17	800 - 1500	2000 – 3500

Stomatal conductance and Leaf water potential

We measured g_S in all individuals of each species on at least 2 fully expanded leaves per plant, with a steady-state diffusion porometer (LI-1600, LI-COR). Measurements were made from October 22 to December 7, 2012, at 07:00 h and from 10:00 to 18:00 h (local time) at 2 h intervals. Leaf water potential (Ψ) was measured in all individuals of each species on at least 2 fully expanded leaves per plant, with a pressure chamber (PMS) (Scholander et al. 1964, 1965, Turner 1981). Measurements were made over 2 d with diurnal variation and later only at 7 or 14 h in well-irrigated individuals.

Climatological measurements

All climatological measurements of air temperature (T_A), photosynthetically active radiation (PAR), transpiration (E), relative humidity (RH) and leaf temperature (T_L) were determined when measuring each leaf with a quantum sensor (LI-190SB, LI-COR Ltd., Lincoln, Nebraska, USA), a fine wire thermocouple, and a humicap sensor (Vaisala, Helsinki, Finland). Thermocouples were mounted in the porometer. The leaf–air vapor pressure deficit (VPD) was calculated from T_A, T_L and RH measurements. Climate measurements were made in the greenhouse daily from October 22 to December 7, 2012, at 7 and from 10 to 18 hours (h, local time) at 2 h intervals. Measurements of T_A, PAR, and VPD in the field were taken from September 29 to October 3.

The envelope function method

The envelope function method consists of selecting data of the probable upper limit of the function represented by a cloud of points in each of the diagrams produced by plotting stomatal conductance as a function of any variable (edaphic or climate). The method has three assumptions: 1) the envelope function represents the optimal stomatal response to a selected climate variable (e.g. photosynthetically active radiation); 2) the points below the selected function are the result of a change in any of the other variables (e.g. vapor pressure deficit and air temperature), and 3) there are not synergistic interactions (Jarvis 1976, Fanjul & Barradas 1985, Jones 1992, Ramos-Vázquez & Barradas 1998, Barradas et al. 2004).

The relationship of g_S in terms of air temperature (T_A) is given by the envelope values that fit a quadratic equation.

$$g_S = A + B\,T_A + C\,T_A^{\,2} \qquad (1)$$

where A, B and C are parameters of the parabola, making it possible to determine the optimum temperature (T_O) at which g_{SMAX} occurs, and the cardinal temperatures (minimum and maximum).

Envelope values of stomatal conductance (g_S) as a function of photosynthetically active radiation (PAR) are consistent with a hyperbolic function:

$$g_S = [a\mathrm{PAR}/(b + \mathrm{PAR})] \qquad (2)$$

where a is the asymptotic value of g_S or g_{SMAX}, and b is g_S sensitivity to changes in PAR.

While the g_S function in relation to vapor pressure deficit (*VPD*) generates a simple linear equation.

$$g_S = a + bVPD \qquad (3)$$

where b is g_S sensitivity to the *VPD*, and a is the zero drift.

Similarly, the stomatal response to water potential (Ψ) is also a simple linear equation:

$$g_S = a + b\Psi \qquad (4)$$

where b is g_S sensitivity to the Ψ, and a is the zero drift.

Potential distribution and Climate change model

To analyze the possible vulnerability in the region, we developed potential distribution maps for the species using *MaxEnt* program and *ArcView GIS 9.1*. We took data provided by the website Global Biodiversity Information Facility (accessed August 20, 2012), data from UNIBIO: Biological Collections of the National Autonomous University of Mexico, data collected at the Tropical Ecophysiology Lab, in the Institute of Ecology, and data collections from the Institute of Biology, the National Commission for the Knowledge and Use of Biodiversity (CONABIO), the National Forestry Commission (CONAFOR) and the Global Biodiversity Information (REMIB). We also took data on the average annual temperature and precipitation (INEGI). Concerning *MaxEnt*, this is an algorithm that has been adapted for the modeling of potential distribution of organisms (Phillips et al. 2006), calculating the statistical significance of a prediction, using a binomial test of omission given by ordained environmental variables, depending on a value expressed in percentage.

We carried out the analysis of the temperature climate change model in the study area with the Regionalized Climate Change Scenarios (SIECCRe) (SEMARNAT-INE-PNUD-UNAM-CCA/UNAM-GEF) (accessed August 20, 2012), and we developed the scenario for the years 2000-2099.

Statistical analysis

Statistical analyses were conducted using R v. 3.0.1 (R Development Core Team 2010). We analyzed the climatological variables of T_A, PAR and *VPD* to evaluate whether there were significant differences between greenhouse and field conditions. Additionally, differences among the 4 species (*A. acuminata, Q. xalapensis, L. styraciflua* and *P. ayacahuite*) in terms of g_S, T_A, PAR, *VPD* and Ψ

were evaluated using 1-way analysis of variance (ANOVA) for each variable. Homogeneity of variances was tested using Levene's test. Statistical significance was considered at 95% for all cases.

3.3 RESULTS

Regarding climatological measurements, we found not differences when comparing between field and greenhouse T_A (F = 2.733, $P = 0.104$). Greenhouse average temperature was 24.32 ºC, whereas the average temperature in the field was 23.76 ºC. As for *VPD* and PAR significant differences were found (F = 31.14, $P < 0.001$, and F = 15.24, $P < 0.001$, respectively). *VPD* average in the greenhouse was 2.03 kPa, whereas in the field was 1.31 kPa. PAR average in the greenhouse was 230 µmol m^{-2} s^{-1}, whereas in the field was 613.54 µmol m^{-2} s^{-1}.

After analyzing the variables g_S, T_A, PAR, *VPD* and Ψ between species, we found significant differences when comparing g_S, PAR, *E* and Ψ (**Table 3.2**). *A. acuminata* was the species that presented the highest values of g_S, T_A and E. *Q. xalapensis* had the highest *VPD* values, and *P. ayacahuite* had the highest PAR values (**Table 3.2**). For all the species we found the maximum climate variables (T_A, PAR and *VPD*) at 14 h. Concerning g_S, we observed that *A. acuminata* and *Q. xalapensis* had the highest values at 14 h, whereas *L. styraciflua* and *P. ayacahuite* had the highest values at 7 h. All the species had the lowest Ψ values at 14 h (**Fig. 3.2**).

Table 3.2. Stomatal conductance (g_S), leaf water potential (Ψ), air temperature (T_A), vapor pressure difference (*VPD*), photosynthetically active radiation (PAR) and transpiration (*E*) for *Alnus acuminata*, *Quercus xalapensis*, *Liquidambar styraciflua* and *Pinus ayacahuite*. The values represent the mean (±1 standard deviation) (n = 870 for each variable and for each species, except for □, n = 150 for each species) and ANOVA between species. *P < 0.05.

Species	**g_S (mmol m^{-2} s^{-1})**	**Ψ (Mpa)**	**T_A (ºC)**	***VPD* (kPa)**	**PAR (µmol m^{-2} s^{-1})**	***E* (mmol m^{-2} s^{-1})**
Alnus acuminata	433.96 (176.49)	-1.94 (0.98)	25.90 (3.81)	2.26 (0.5)	151.25 (63.62)	17.76 (8.82)
Quercus xalapensis	320.81 (125.53)	-1.65 (0.44)	25.84 (3.71)	2.28 (0.5)	152.69 (62.74)	13.13 (5.94)
Liquidambar styraciflua	329.66 (138.18)	-1.73 (0.57)	25.84 (3.56)	2.27 (0.48)	144.93 (60.23)	13.34 (6.13)
Pinus ayacahuite	377.54 (138.18)	- 0.57 (0.37)	25.84 (3.53)	2.22 (0.48)	182.73 (84.99)	14.07 (5.44)
F-value	310.8	115.9	0.033	2.376	18.86	47.66
***P* (>F)**	<2e-16*	<2e-16*	0.992	0.0681	3.95e-12*	<2e-16*

The envelope function method

From the envelope functions method we generated g_S curves versus T_A, PAR, *VPD* and Ψ (**Fig. 3.3**), and the equations for each climate variable, with their respective values of the parameters of the asymptotic value of g_S, and the g_S sensitivity to changes PAR, *VPD* and Ψ (**Table 3.3**). After analyzing the g_S-T_A curves, we obtained the optimum, the cardinal (minimum and maximum) temperatures, and the optimum thermal range (**Table 3.4**), where we found that *A. acuminata* was the species most capable to tolerate high temperatures, whereas *P. ayacahuite* was the less tolerant species. All the species presented values of T_O and T_R (**Table 3.4**) above from data reported in their natural distributions (**Table 3.1**).

Table 3.3. Calculated envelope functions for stomatal conductance (g_S) versus air temperature (T_A), photosynthetically active radiation (PAR), vapor pressure deficit (*VPD*), and leaf water potential (Ψ) for *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite* (r^2 is the coefficient of determination).

Parameter	Theoretical equation	Species	Equation	r^2
T_A	$g_S = A + BT_A + C\ T_A{}^2$	*Alnus acuminata*	$g_S = -\ 4059.583 + 345.473\ T_A - 5.811\ T_A{}^2$	0.994
		Quercus xalapensis	$g_S = -1784.845 + 171.448\ T_A - 2.948\ T_A{}^2$	0.949
		Liquidambar styraciflua	$g_S = 2017.468 + 198.647\ T_A - 3.551T_A{}^2$	0.942
		Pinus ayacahuite	$g_S = -1580.765 + 177.339\ T_A - 3.307\ T_A{}^2$	0.981
PAR	$g_S = a\text{PAR} / (b + \text{PAR})$	*Alnus acuminata*	$g_S = 1007.364\ \text{PAR} / (6.752 + \text{PAR})$	0.929
		Quercus xalapensis	$g_S = 671.906\ \text{PAR} / (8.675 + \text{PAR})$	0.884
		Liquidambar styraciflua	$g_S = 723.639\ \text{PAR} / (9.087 + \text{PAR})$	0.964
		Pinus ayacahuite	$g_S = 738.749\ \text{PAR} / (2.078 + \text{PAR})$	0.978
VPD	$g_S = a + (b\text{VPD})$	*Alnus acuminata*	$g_S = 2381.825 + (-466.341\ VPD)$	0.971
		Quercus xalapensis	$g_S = 1109.452 + (-169.337\ VPD)$	0.903
		Liquidambar styraciflua	$g_S = 1577.411 + (-304.068\ VPD)$	0.947
		Pinus ayacahuite	$g_S = 1129.183 + (-175.242\ VPD)$	0.979
Ψ	$g_S = a + b\ \Psi$	*Alnus acuminata*	$g_S = 1346.549 + 235.13\ \Psi$	0.952
		Quercus xalapensis	$g_S = 1558.1 + 248.12\ \Psi$	0.985
		Liquidambar styraciflua	$g_S = 1028.8 + 274.32\ \Psi$	0.872
		Pinus ayacahuite	$g_S = 861.32 + 190.17\ \Psi$	0.993

Concerning to PAR, *A. acuminata* had the highest asymptotic value of g_S, whereas *Q. xalapensis* was the most sensitive species to changes in PAR. Regarding Ψ, *L. styraciflua* was the most sensitive species, and *Q. xalapensis* and *A. acuminata* had the highest asymptotic value of g_S. For *VPD*, *A. acuminata* had the highest asymptotic value of g_S, and *Q. xalapensis* and *P. ayacahuite* were the most sensitive species to changes in *VPD* (**Table 3.3**).

Potential distribution and Climate change model

From the generated potential distribution of the species, we found that *P. ayacahuite* was the species with the most confined and limited distribution. In contrast, *A. acuminata* showed the widest distribution. The estimated areas of each species were: 1) *A. acuminata*: 3440.8 km^2; 2) *Q. xalapensis*: 2918.54 km^2; 3) *L. styraciflua*: 2179.75 km^2, and 4) *P. ayacahuite*: 765.61 km^2. The four species are distributed between the 10-22 ºC isotherms, where *P. ayacahuite* is located in the coldest range (10-12 ºC), *A. acuminata* is located between 14-22 ºC, *Q. xalapensis* and *L. styraciflua* are located in the warmest range (16-22 and 18-20 ºC, respectively) (**Fig. 3.4**).

Concerning the climate change model (SIECCRe), this showed an increase of 2-5 ºC for the year 2099. From this model we obtained the equation: $T = 0.0318$ (year) - 63.51, $r^2 = 0.84521$.

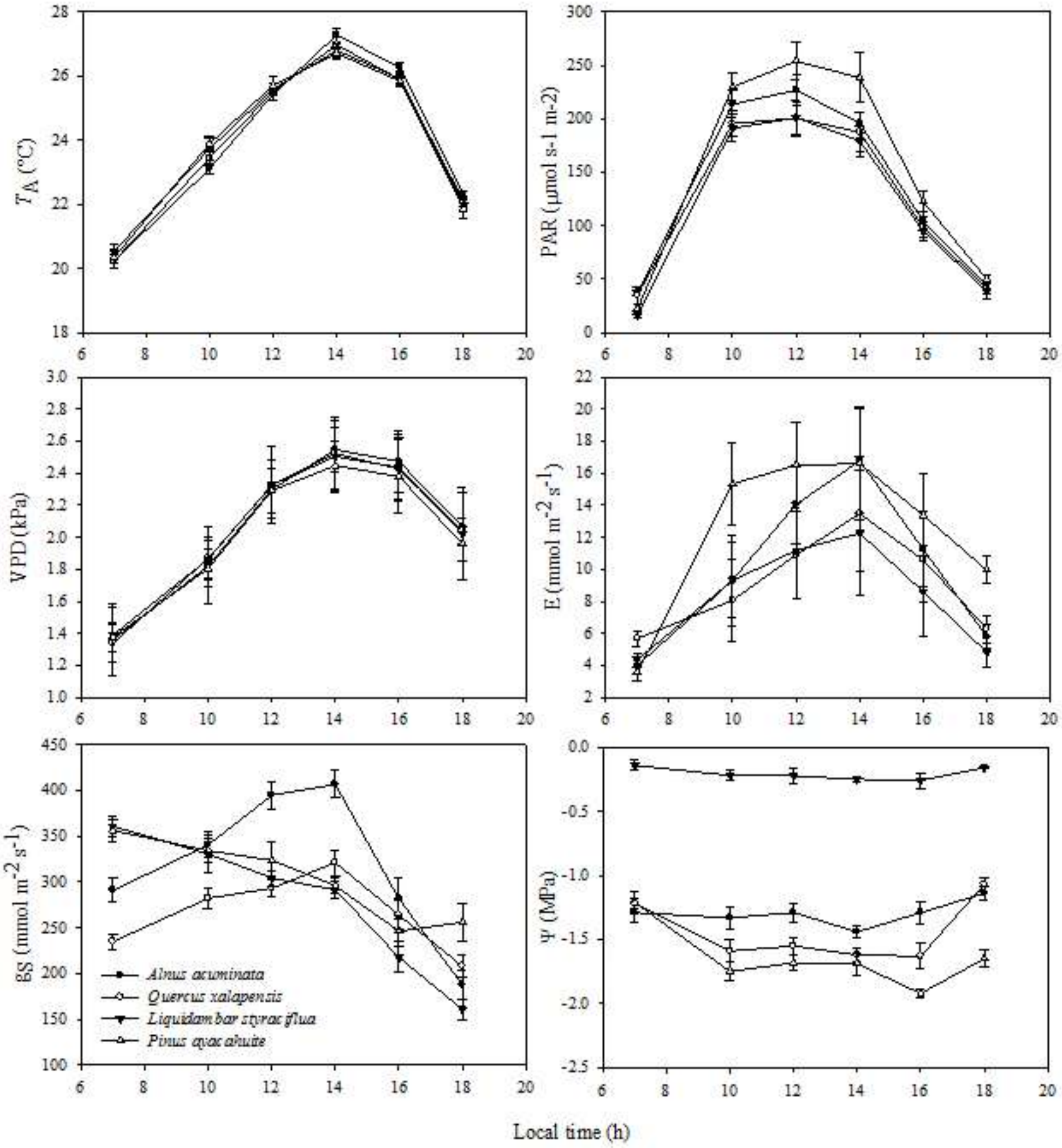

Figure 3.2. Diurnal variations of air temperature (T_A), photosynthetically active radiation (PAR), vapor pressure deficit (*VPD*), and transpiration (*E*), stomatal conductance (g_S), and leaf water potential (Ψ) for *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua* and *Pinus ayacahuite*. Data points represent the mean of 145 measurements on different leaves except for Ψ which were 75 measurements. Vertical bars represent the standard deviation of the mean.

Table 3.4. Cardinal (T_{min} and T_{MAX}), optimal temperature (T_O), and optimal thermal range (T_R) for the stomatal function of *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua* and *Pinus ayacahuite*. Data are mean ± SD.

Species	T_{min} **(°C)**	T_{MAX} **(°C)**	T_O **(°C)**	T_R **(°C)**
Alnus acuminata	16.1 (0.3)	41.5 (0.3)	29.7 (0.5)	22.17 - 37.17
Quercus xalapensis	15.7 (0.4)	39.5 (0.2)	28.2 (0.4)	20.65 - 37.39
Liquidambar styraciflua	15.1 (0.3)	37.8 (0.2)	27.5 (0.3)	19.55 - 36.19
Pinus ayacahuite	14.2 (0.3)	37.3 (0.2)	26.2 (0.2)	18.26 - 34.56

3.4 DISCUSSION

The possible effects of climate change on stomatal function can be inferred by determining the stomatal response to different climate variables observed using the envelope function method. However, there are limitations in considering only the stomatal function, and caution is advised because other factors such as temperature, irradiance, soil quality and nutrient availability might determine the species' distribution, and therefore influence their vulnerability. Another consideration is that the differential g_S response to the microenvironment (T_A, PAR and *VPD*) could be due to an acclimation of stomata to thermal variation in the environment. Data used in this study were collected in the greenhouse in order to obtain extreme values that cannot be found in the natural environment, allowing us to observe how species responded to extreme conditions (high temperature); however, this could be considered a limitation of our work, especially when comparing climate variables between the greenhouse and field, where we observed differences related to PAR and *VPD*. This difference may affect the stomatal response, causing midday stomatal closure in the field (Domec et al. 2006). However, for our purpose to observe the stomatal performance at high temperatures, we considered the method accurate. Thus, our results can help to better understand potential vulnerabilities to climate change and the possible shifts in disturbance scenarios of increased temperature. Nevertheless, we encourage future replications considering complementary field measurements.

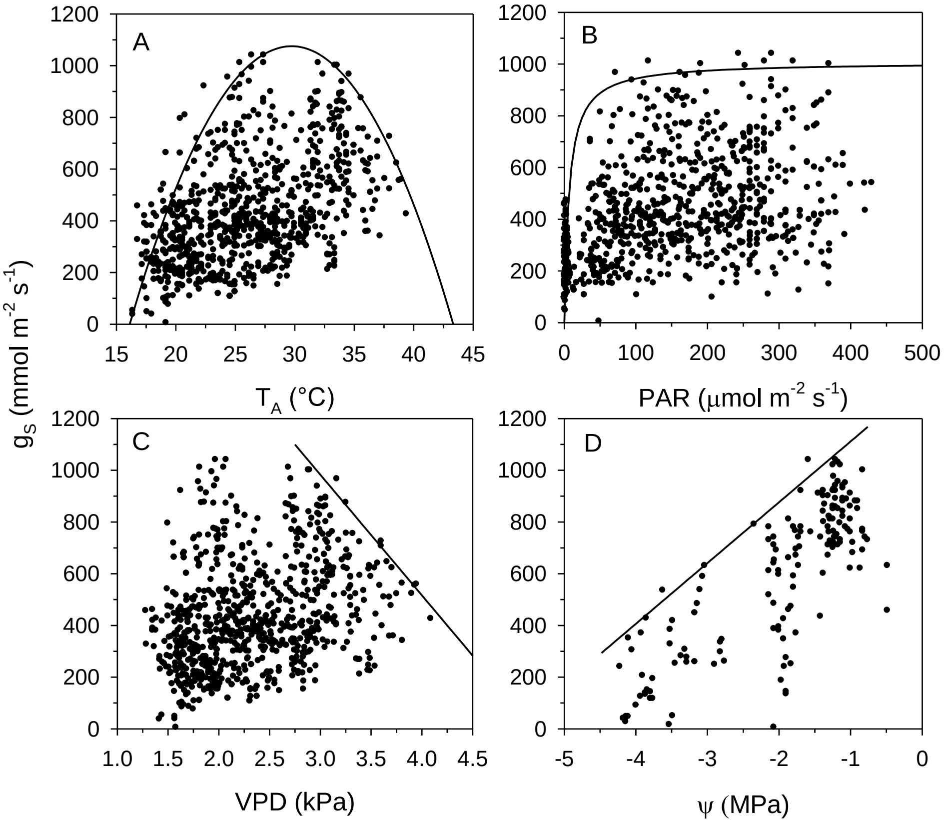

Figure 3.3. Scatter diagrams and probable boundary-line of stomatal conductance (g_S) plotted against air temperature (T_A, A), photosynthetically active radiation (PAR, B), vapor pressure deficit (*VPD*, C), and water potential (Ψ, D) for *Alnus acuminata.*

Based on the envelope function method, the values of the coefficient of determination (r^2) for the boundary-lines were indicative of a good approach to determine stomatal function ranges (**Table 3.3**). The fit of g_S vs. T_A, PAR, VPD and Ψ showed a higher sensitivity of g_S to the driving variables for the tested species, and although this model is not efficient for explaining stomatal variation between species, using the boundary-line function is a strong tool for separately analyzing the stomatal responses to the different driving variables (T_A, PAR, VPD and Ψ). Still, this model is individual-specific; therefore, care is needed when attempting to extrapolate the model parameters to other sites and individual trees.

Temperature

Concerning the stomatal response to temperature, the experiments in general show that when increasing temperature, the stomata open (Hovenden & Brodribb 2000); however, high temperatures can also cause stomata closure, making it possible to observe the optimal thermic range in which stomatal opening occurs (Jones 1992) depending on the characteristics of each plant (e.g. Mansfield 1971, Jarvis 1976, Rodriguez & Davies 1982, Delucia 1986, Honour et al. 1995, Medlyn et al. 2002). Increasing photosynthetic carbon gain by preopening stomata before dawn (Caird et al. 2007) might be an advantageous response in water-limited environments (Galmés et al. 2011). In the case of our species, we found that *A. acuminata* and *Q. xalapensis* presented the highest g_S at 14:00 h, whereas *L. styraciflua* and *P. ayacahuite* presented the highest g_S at 07:00 h, showing different functional mechanisms concerning the stomatal behavior. This might be related to different responses to changes in PAR in the greenhouse, as *A. acuminata* and *Q. xalapensis* responded by opening stomata with low PAR conditions at midday.

Comparing the climatic requirements of the species (**Table 3.1**) and the data obtained from the envelope function method related to the cardinal and optimal temperatures (**Table 3.4**), all the species have considerable tolerance to high temperatures, with an optimal temperature and an optimal thermal range above the temperatures reported in the field, consistent with the potential distribution of the species (Fig. 3.4). Regarding differences between the temperature range in the field and the cardinal temperature (T_{min}) found in our work, it is deduced that the species might distribute in colder regions below the thermal ranges found; however, we can infer that below these temperatures, stomatal performance decreases, as can be seen in Fig. 3.3a, where for *A. acuminata*, g_S below 16°C decreased up to 80% compared to the g_S at the optimum temperature. Although individuals can be found in colder regions, their stomatal performance may not be optimal.

Under greenhouse conditions, the species carried out their physiological functions in thermal ranges of 14 to >30°C. If we consider the climate change model, we can predict that the species might not be very vulnerable to the predicted temperature increase of 2°C; however, an increase of 5°C would represent greater risk to the stomatal function of these species, causing stomata closure and decrease of gas exchange and productivity, especially in individuals distributed in lower altitudes where temperature is higher. In addition, respiration, reproduction and germination may also be vulnerable to high temperatures, with potential negative effects on the life cycle of vulnerable species.

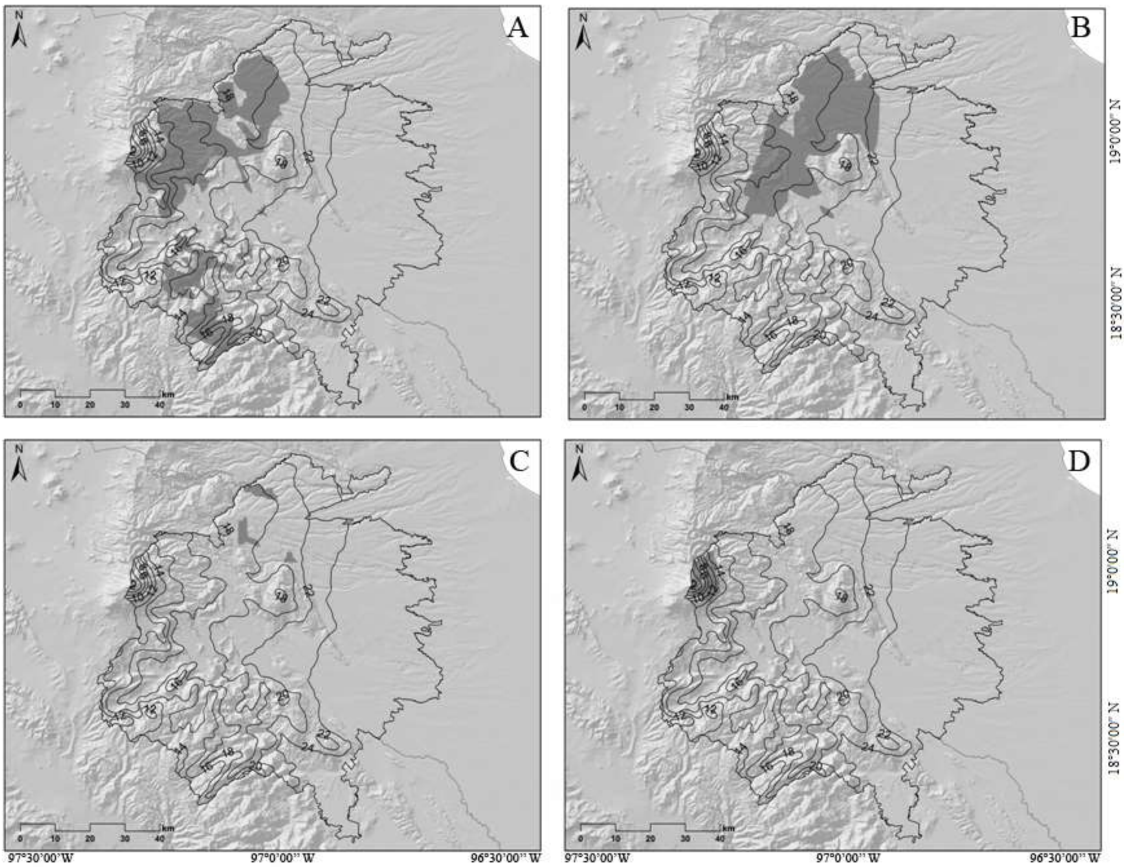

Figure 3.4. Potential distribution (shaded area) of *Alnus acuminata* (A), *Quercus xalapensis* (B), *Liquidambar styraciflua* (C) and *Pinus ayacahuite* (D), and annual average temperature (°C) distribution in the central mountain region of Veracruz, Mexico.

Photosynthetically active radiation

When analyzing PAR values from the model, we observed that the highest asymptotic value of g_S corresponded to *A. acuminata* and *Q. xalapensis.* Fast-growing species have high g_S values because they require more solar irradiance for growing (Ögren & Sundin 1996, De A. Sá et al. 1999, Gao et al. 2004). As for the g_S sensitivity, the most sensitive species to changes in PAR were *Q. xalapensis* and *P. ayacahuite*; this response could be one of the characteristics of ecosystem associations of pine-oak forest, and may be because these species are distributed at higher altitudes where the cloud cover is extensive, and this therefore increases the sensitivity to solar radiation (Barradas et al. 2001).

On most days, plants encounter light intensities that exceed their photosynthetic capacity (Ort 2001). In our study, all the species reached an asymptotic g_S value at specific PAR values. Consequently, we can predict that at some irradiance, the stomata would close without representing a major vulnerability for the species. However, the effects in PAR changes over the species are significant, especially considering the importance of this parameter in photosynthesis (Bunce 2000, Aasamaa & Sõber 2011). If stomata close, photosynthesis decreases. Even under conditions that may not be considered stressful, stomatal closing can substantially restrict CO_2 entry into leaves, causing even moderate irradiances in the top of the canopy to be in excess of photosynthetic capacity (Ort 2001).

Although PAR is fundamental in plant development (e.g. Mcelwee 1970, McCree 1981, Gordon & Rowe 1982, Jones 1992, Chazdon et al. 1996), an irradiance excess might have repercussions inducing stomatal closure, as we observed in the case of *L. styraciflua* and *P. ayacahuite*. Also, for species like *A. acuminata* and *P. ayacahuite*, which grow better under low PAR conditions (Eguiluz-Piedra 1978, Araya et al. 2000), an increment in this parameter would increase their vulnerability; this effect was observed for *A. acuminata* and *Q. xalapensis* in the greenhouse with their midday stomata opening. This behavior allows us to infer that conditions with low PAR are advantageous for these species, reducing their vulnerability by increasing g_S.

Vapor pressure deficit

We observed the highest asymptotic value of g_S corresponding to *A. acuminata* and *L. styraciflua*; also, they were the most sensitive species to changes in *VPD*. Both species have high water requirements during development, possibly due to their fast growth (CATIE 1995, Loewe & González 1997). *VPD* is critical for plant transpiration because with high *VPD*, plants release more water as vapor through stomata (transpiration); therefore, greater transpiration would translate to greater nutrient absorption, and thus a probable increase in photosynthesis and performance. However, with high *VPD* values, plants react by closing stomata to avoid excessive water loss by transpiration or dehydration, affecting photosynthesis and performance (Collatz et al. 1991, Bunce 1997). For some species, g_S decreased at midday during high evaporative demand, as in the case of *P. ayacahuite* and *L. styraciflua,* where this stomatal closure would induce a decrease in the magnitude of the transpiration flux at high *VPD* between leaf and air (Goldstein et al. 1986). From the model, we observed that *A. acuminata* and *L. styraciflua* are more likely to present stomatal closure easily, but we must consider that *A. acuminata* presented the highest g_S at 14:00 h, probable evidence of the tolerance of the species to high transpiration rates. *Q. xalapensis* and *P. ayacahuite* could be considered more vulnerable because low transpiration related to low *VPD* would mean less absorption of nutrients, less photosynthesis and lower performance. In addition, vulnerability related to *VPD* increases in conditions of low humidity and high temperatures during dry periods when transpiration is high (Moore et al. 2011).

Leaf water potential

Climate change models make more precise predictions with respect to temperature than to precipitation. Studies in the central region of Veracruz analyzed the precipitation tendencies for the period 1923 to 1997, finding negative tendencies, and suggesting potential reductions in precipitation of as much as 50% by the year 2023 (Cervantes et al. 2001, Barradas et al. 2010). Also, a decrease in rainfall on windward slopes was reported, as well as a diminished frequency of fog at some levels.

These changes have a direct repercussion on solar radiation, which is expected to be more intense where both rainfall and the frequency of fog decreased (Barradas et al. 2010).

Regarding Ψ, the highest asymptotic value of g_S corresponded to *Q. xalapensis* and *A. acuminata*, and both species are distributed in the higher precipitation ranges (Table 1). This condition might be correlated to conditions of good precipitation in the field (Mooney et al. 1983, Barradas et al. 2010, Abe et al. 2011) and well-irrigated conditions in the greenhouse. *L. styraciflua* was the most sensitive species to changes in Ψ; this may be due to the fast growth of the species, for which changes in Ψ affect stomatal response (Jarvis 1976, Bond 1999). We found significant differences when comparing the g_S response to Ψ, suggesting control of conductance produced by a signal from Ψ in our experiment (Bunce 1999); however, stomatal response might have been affected by leaf excision performed during the experiment. Previous studies have shown a kinetic effect on the stomatal response following leaf excision (During 1993, Powles et al. 2006) likely causing a decrease in photosynthesis and g_S by pressure changes in the xylem and by the stomata closure (During 1993). Caution is advised when analyzing the g_S response after leaf excision, especially in our study where defoliation was performed throughout the experiment. In conditions of high temperatures and solar irradiance, evaporation and water loss from the soil is expected, especially if there is no precipitation that can provide water to the substratum. Here, field capacity is very important. For the region, the content of water at field capacity varies from 0.23 to 0.30 $\text{cm}^3\ \text{cm}^{-3}$, whereas the water actually available to plants or usable water reaches values of 0.07 to 0.10 $\text{cm}^3\ \text{cm}^{-3}$ in forests (Geissert & Iba.e z 2008). In the field, this water storage allows the survival of species during drought periods. Climate variability is particularly important in connection with changes in precipitation (e.g. extended droughts) having more drastic consequences on tree growth and survival than gradual changes in average climate conditions (Fuhrer et al. 2006), because individuals are adapted to local water availability. Forests are particularly sensitive to climate change because the long life span of trees does not allow for rapid adaptation to environmental changes. There are several factors associated with climate change that can affect forest ecosystems (Lindner et al. 2010); these can act independently or in combination, as we observed in our analysis. We conclude that species are vulnerable not only to temperature increment but also to water loss, PAR and *VPD* increment. Caution must be taken regarding the raising temperatures predicted by the model and the precipitation decrease predicted by the tendencies. One factor that may mitigate vulnerability to climate change in the region would be migration to higher distributions where temperature is lower and where rainfall may be enhanced by the presence of clouds (Barradas et al. 2001). This migration process is subject to effective seed dispersion, although one option could be an assisted re-colonization of the species; however, an accurate analysis of soil requirements, proper germination conditions and space availability would be necessary to ensure this re-colonization. We recommend further analysis in the field considering the implications mentioned.

Capítulo 4

Vulnerabilidad ecofisiológica frente al cambio climático: respuestas al estres hídrico en cuatro especies arbóreas de la región montañosa central de Veracruz, México

Ecophysiological vulnerability to climate change: water stress responses in four tree species from the central mountain region of Veracruz, Mexico

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(*Regional Environmental Change*)

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RESUMEN: La vulnerabilidad ecofisiológica puede ser entendida como el grado de susceptibilidad o la incapacidad de un organismo para adaptar sus funciones fisiológicas a los cambios ecológicos y ambientales. Los cambios en la disponibilidad y la escasez de agua son críticos para las especies, quienes pueden responder diferencialmente a los distintos eventos de precipitación. Se analizó la respuesta del potencial hídrico (Ψ) y la conductancia estomática (g_S) al estrés hídrico para evaluar la vulnerabilidad eco-fisiológica y se evaluó la tolerancia a la sequía de cuatro especies arbóreas de la región montañosa central de Veracruz, México: *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua* y *Pinus ayacahuite*. El estrés hídrico se impuso por 15 días (excepto para *Q. xalapensis*) y luego se regó durante 25 días con el fin de evaluar la recuperación de las especies bajo tres tratamientos de riego: 16.67, 33.33, y 50% de capacidad de campo. Los individuos se monitorearon durante todo el experimento. El Ψ y la g_S se midieron diariamente, mostrando una disminución significativa y una recuperación diferencial para cada especie. *L. styraciflua* y *P. ayacahuite* necesitaron más agua y más días para recuperarse, mientras que *Q. xalapensis* necesitó menos agua y resistió más días sin agua. Encontramos a *A. acuminata* como una especie tolerante/evasiva de sequía. Después de analizar las tendencias de precipitación y temperatura para la región encontramos tendencias de precipitación negativas con un aumento en el número de días secos consecutivos, y encontramos tendencias positivas de temperatura. También desarrollado mapas de distribución potencial para todas las especies en la región, y después de analizar la precipitación y los cambios de temperatura, los mapas de distribución potencial, la resistencia al estrés hídrico, el número de días antes de la caída de las hojas, el Ψ y respuestas estomáticas, la cantidad de agua y el número de días necesarios para recuperarse, encontramos a *L. styraciflua* como las especies más vulnerable y *Q. xalapensis* como el menos vulnerable.

Palabras clave: Vulnerabilidad ecofisiológica · Potencial hídrico · Conductancia estomática · Estrés hídrico · Tolerancia a la sequía · Tendencias de temperatura y precipitación

ABSTRACT: Eco-physiological vulnerability can be understood as the degree of susceptibility or inability of an organism to adapt their physiological functions to ecological and environmental changes. Changes in water availability and water stress are critical for species, which may respond differentially to different precipitation events. We analyzed the response of leaf water potential (Ψ) and stomatal conductance (g_S) to water stress to assess the eco-physiological vulnerability and evaluated the drought tolerance of four tree species from the central mountain region of Veracruz, Mexico: *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite*. Drought stress was imposed for 15 days (except for *Q. xalapensis*) and then watered for 25 days in order to evaluate the species recovery under three watering treatments: 16.67, 33.33, and 50% field capacity. Individuals were screened throughout the experiment. Ψ and g_S were measured daily showing significant decrement and differential recovery for each species. *L. styraciflua* and *P.*

ayacahuite needed more water and more days to recover, whereas *Q. xalapensis* needed less water and resisted more days without water. We found *A. acuminata* as a drought tolerant/avoider species. After analyzing the precipitation and temperature trends for the region we found negative precipitation trends with an increase of consecutive dry days, and we found positive temperature trends. We also developed potential distribution maps for all the species in the region, and after analyzing the precipitation and temperature changes, the potential distribution maps, the resistance to water stress, the number of days before leaf drop, the Ψ and stomatal responses, the water amount and number of days required to recover, we found *L. styraciflua* as the most vulnerable species and *Q. xalapensis* as the least vulnerable.

Key words: Eco-physiological vulnerability · Leaf water potential · Stomatal conductance · Water stress · Drought tolerance · Precipitation and temperature trends

4.1 INTRODUCTION

Vulnerability has been defined by many authors (e.g. IPCC 2001, Buch & Turcios 2003, Brooks et al. 2005, Metzger et al. 2006). These definitions are separated into two categories. The first one involves the amount of (potential) damage caused to a system by a particular climate-related event or hazard (Jones & Boer 2003), and the second deals with a state that exists within a system before it encounters a hazard event (Allen 2003). However, in eco-physiological terms, there are not definitions related to vulnerability. After associating environmental variables with physiological responses, we propose the eco-physiological vulnerability as the degree of susceptibility or inability of an organism to adapt their physiological functions to ecological and environmental changes.

One critical environmental change is water availability. Water is one of the most important resources that influences primary productivity and vegetation structure in ecosystems (e.g. Smith & Nobel 1986, Polis 1991, Gutiérrez 1993, Squeo et al. 1994, 1998, Reynolds et al. 1999). Species may respond differentially to different precipitation events (Ehleringer et al. 1991, Zeppel et al. 2013, Oliveira et al. 2014). Also, species with different life forms appear to differ in their ability to use certain precipitation events (Squeo et al. 1999). Water availability directly affects gas exchange, productivity, species interactions and community structure (e.g. Ackerman 1979, Hadley & Szarek 1981, Ehleringer and Mooney 1983, Zeppel et al. 2013). Therefore, knowledge of how water is used and obtained by plants is critical for restoration plans, to increase productivity, and to assess species' vulnerability.

Within the tropics, water availability is the most important environmental factor determining tree species richness (Gentry 1988, Poorter et al. 2004, Ter Steege et al. 2006), composition (e.g. Bongers et al. 2004), and distribution (e.g. Holmgren & Poorter 2007). Perhaps the most important component of water availability is the seasonality of its distribution. The length of the dry period may vary from few days to up to eight months (Walter 1985, Walsh 1996), where plants are affected with reduced leaf water potential and stomatal conductance (Tobin et al. 1999, Cao 2000), having as consequence a reduction in growth (Engelbrecht & Kursar 2003, Bunker & Carson 2005) and survival (Engelbrecht & Kursar 2003, Poorter 2005) by the low water availability during drought periods. During the past decades, tropical forests have experienced a dramatic decrease in annual rainfall, and an increase in dry season length and rainfall variability (Malhi & Wright 2004). Besides, alterations in fog frequency and intensity are predicted to occur due to changes in sea-surface temperature and the height of the temperature inversion layer (Cereceda et al. 2002), loss of forest patch area and fragmentation, or changes in forest structure affecting fog capture (Hildebrandt & Eltahir 2006).

Our study area, the central region of Veracruz, contains very pronounced topographic variation along an altitudinal gradient (García-García & Montañez 1991, Barradas et al. 2010). As a result, climate in the region is defined by several forces as follows: 1) the complex interactions between the prevailing synoptic weather systems; 2) the mountainous topography; 3) the plant-atmosphere interaction, and 4) the proximity to the Gulf of Mexico (Barradas et al. 2010). Analyses of the precipitation trends for the period 1923-1997 revealed negative trends and suggested a possible regional climate change, implying potential reductions in precipitation of as much as 50% by the year 2023 (Lara-García 2000, Barradas et al. 2010). Also, decreased rainfall to windward, and decreased frequency of fog has been revealed at some elevations (Barradas et al. 2010, 2011). These changes also have repercussion on other climatic variables such as solar radiation, which is expected to be more intense where both, rainfall and the frequency of fog decreased (Barradas et al. 2011), increasing the vulnerability in the region.

One way to assess the vulnerability in the region is through the study of physiological traits; due to drought tolerance is closely related to these traits (Tyree et al. 2003). Species able to tolerate low leaf water contents and leaf water potentials survive longest in dry conditions (Poorter & Markesteijn 2008). The physiological traits of leaf water potential and stomatal conductance have been widely used as measures of plant water stress (e.g. Attiwill and Clayton-Greene 1984, Myers & Neales 1984, Filella & Penuelas 2003, Rice et al. 2004). Such traits have been identified as being indicative of drought tolerance (e.g. King 1997, Smith et al. 1997, Curran et al. 2009).

Taking this into account, our aims were: *i*) evaluate the drought tolerance of four tree species from the central mountain region of Veracruz analyzing the responses of leaf water potential (Ψ) and stomatal conductance (g_S) to water stress, and *ii*) assess the eco-physiological vulnerability through the link between two physiological traits (g_S and Ψ, although we acknowledge that this non-multifactor analysis limits the scope of our study), with the environmental variables of precipitation and temperature in the region.

4.2 METHODS

Study Area

The central mountain region of Veracruz, Mexico (19º54’08’’ N, 96º57’19’’ W) (**Fig. 4.1**) is part of Neovolcanic Ridge and the Sierra Madre Oriental. Abrupt topography is the main characteristic of this region with a pronounced altitudinal gradient, from the sea level up to 5500 m asl, in a distance of 100 km, and with vegetation types varying from tropical montane cloud forest to semi-arid and arid shrubs communities (Gómez-Pompa 1978, Barradas 1983, García-García & Montañez 1991). Average annual temperatures range between 10 and 29 ºC, and annual precipitation ranges from 600 to 1200 mm, with a maximum of 3000 mm in wetter regions. Soils in the region are of volcanic origin or Andisols, with physical characteristics that favor good structural stability (Meza & Geissert 2003). They have low bulk density, high porosity with significant micro-porosity, significant amount of water micro-aggregates, complexation with organic matter, and very stable amounts of Fe and Al (Shoji et al. 1993).

Selected species

Four tree species were selected according to their dominance at different elevations: *Alnus acuminata* Kunth, *Quercus xalapensis* Bonpl., *Liquidambar styraciflua* L. (1753), and *Pinus ayacahuite* Ehren (See **Table 3.1, Chapter 3**).

Plant material

Fifteen saplings of each species from 20-45 cm height were kept in the greenhouse. Individuals were transplanted into two-liter containers. Saplings were kept at the humid greenhouse of the Institute of Ecology, UNAM.

Stomatal conductance and leaf water potential

Stomatal conductance (g_S) was measured in all individuals of each species on at least four fully expanded leaves per plant, with a steady-state diffusion porometer (LI-1600, LI-COR, Lincoln, Nebraska, USA). Leaf water potential (Ψ, predawn and midday) was measured in all individuals of each species on at least two fully expanded leaves per plant in apparent good health, with a pressure chamber (PMS, Corvallis, Oregon, USA) (Scholander et al. 1964, 1965, Turner 1981). Measurements were made daily from April 21 to May 31, 2013, at 7 and 14 hours (h, local time) in order to include daily minimum and maximum water stress conditions.

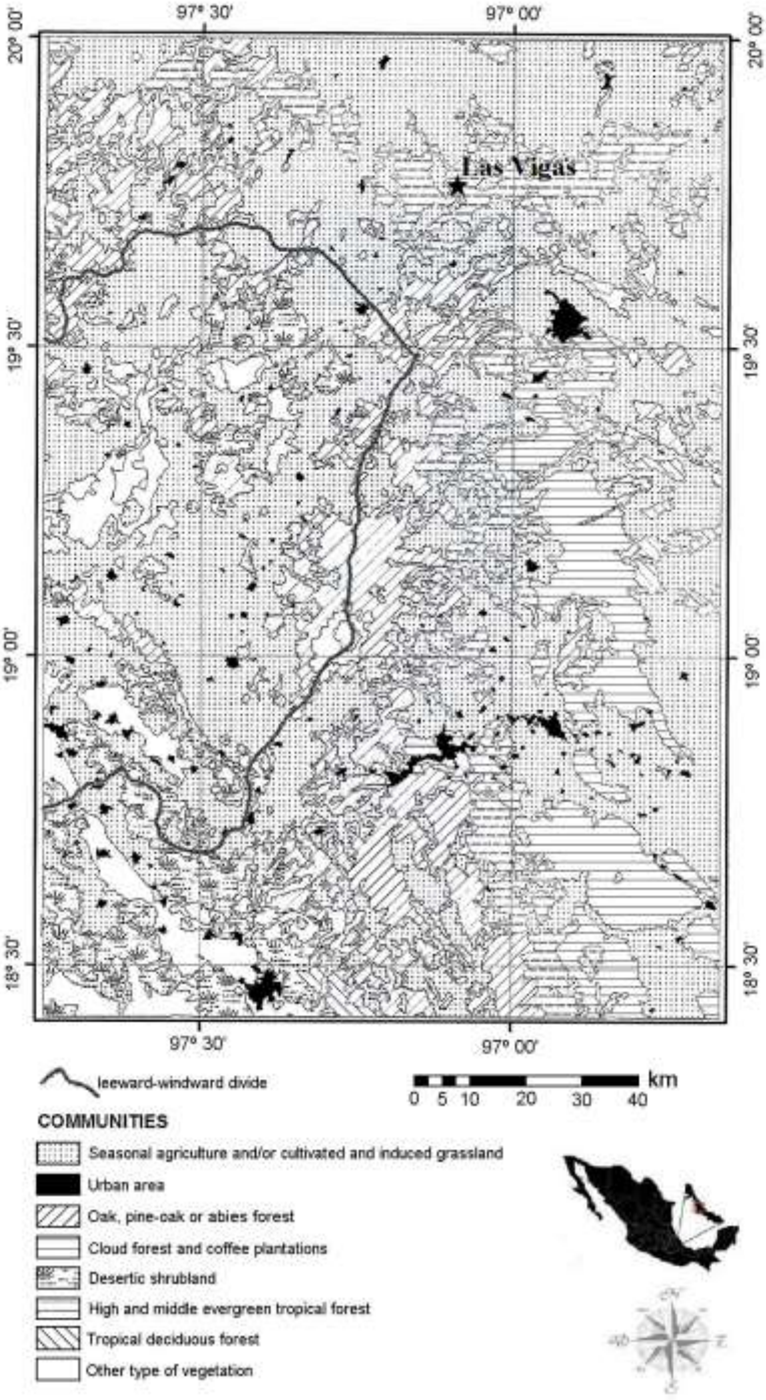

Figure 4.1. Study area, distribution of vegetation types, and the meteorological station at Las Vigas in the central mountain region of Veracruz, Mexico.

Transpiration and Specific Leaf Area

Transpiration (E) was measured in all individuals of each species on at least four fully expanded leaves per plant, with a steady-state diffusion porometer (LI-1600, LI-COR, Lincoln, Nebraska, USA). Measures were made daily from April 21 to May 31, 2013, at 7 and 14 hours (h, local time).

For specific leaf area (SLA), five individuals for each species were used to determine the surface area of the leaf divided by dry mass ($cm^2 g^{-1}$). For each individual, four fully expanded, non-damaged leaves were collected. Leaves were dried at 80 ºC to constant weight to obtain dry mass. The SLA values for the leaves were averaged to obtain a value for each species.

Experimental design

Two groups were formed. One control group included five individuals, and an experimental group of 10 individuals. Irrigation was calculated based on the area of the containers (29.85 cm^2), and on the water required for full irrigation (in milliliters). We calculated the irrigation regime assuming a field capacity of 20 mm (600 ml) for our containers.

After analyzing data related to precipitation frequency in the region we found that the most frequent precipitation ranges were 0-5 and 5-10 mm. Using these ranges we determined three watering treatments as follows: *i*) 3.35 mm (equivalent to 100 ml, 16.67% field capacity); *ii*) 6.7 mm (200 ml, 33.33% field capacity), and *iii*) 10 mm (300 ml, 50% field capacity). These irrigation treatments were used to elucidate the minimum amount of irrigation necessary for the individuals to recover after having been subjected to water stress.

The control group was watered daily throughout the experiment (40 days) with an irrigation of 16.75 mm (500 ml, 83.75% field capacity). The experimental group was watered on the first day of the experiment with 16.75 mm as well, and then the group was let to dry for 15 consecutive days for *A. acuminata, L, styraciflua* and *P. ayacahuite*, and 25 days for *Q. xalapensis*, until we observed leaf loss or wilting leaves.

For *A. acuminata, L, styraciflua* and *P. ayacahuite* on day 16 the experimental group was divided into two treatments. After day 16, both treatments were watered daily with different amounts of water during the rest of the experiment (days 16 to 40). From days 16 to 29, treatment 1 (T1) received an irrigation of 3.35 mm (100 ml), and from days 30 to 40 it received a second irrigation of 6.7 mm (200 ml). As for treatment 2 (T2), it received an initial irrigation of 20 mm (600 ml, 100% field capacity) in one single event on day 16, and from days 17 to 30 it received an irrigation of 3.35 mm (100 ml), and from days 30 to 40 it received an irrigation of 10 mm (300 ml). We increased the amount of water on day 30 because none of the species showed recovery of Ψ and g_S.

Because *Q. xalapensis* did not show signs of wilting on day 15, we let the experimental group to dry until we saw leaf loss on day 25. On day 26, the group was divided also into two treatments, and from days 26 to 40 both treatments were watered daily. T1 was watered with an irrigation of 3.35 mm (100 ml) from days 26 to 29, and then it received a second irrigation of 6.7 mm (200 ml) from days 30 to 40. T2 received an initial irrigation of 20 mm (600 ml, 100% field capacity) in one single event on day 26, then from days 26 to 29 it received an irrigation of 3.35 mm (100 ml), and from days 30 to 40 it received an irrigation of 10 mm (300 ml).

Potential distribution maps

To analyze the eco-physiological vulnerability in the region we developed potential distribution maps for the species. We took data provided by the website Global Biodiversity Information Facility (accessed August, 2012), data from Biological Collections of the National Autonomous University of Mexico (UNIBIO, accessed August, 2012), data collected at the Tropical Ecophysiology Lab in the Institute of Ecology (data available with the authors), and data collections from the Institute of Biology, the National Commission for the Knowledge and Use of Biodiversity (CONABIO, accessed August, 2012), the National Forestry Commission (CONAFOR, accessed August, 2012) and the Global Biodiversity Information (REMIB, accessed August, 2012). We also took data on the average annual precipitation (INEGI, accessed August, 2012) and developed the maps using *MaxEnt* program and *ArcView GIS 9.1*. Concerning *MaxEnt*, this is an algorithm that has been adapted for the modeling of potential distribution of organisms (Phillips et al. 2006), calculating the statistical significance of a prediction, using a binomial test of omission given by ordinal environmental variables, depending on a value expressed as a percentage.

Precipitation and temperature trends

We took data of precipitation and temperature from the meteorological station Las Vigas (19°38’20’’N, 97°06’35’’W, 2400 m asl, **Fig. 4.1**) and we examined the temperature and precipitation trends from the years 1922-2008. We analyzed data on the average annual precipitation (Pp_{A}), the annual maximum precipitation (Pp_{MA}), and the precipitation-frequency events in ranges of 5 mm. We also analyzed from the Expert Team for Climate Change Detection Monitoring and Indices (ETCCDI) (CCI/CLIVAR, accessed May, 2013), the basic climate indices of Consecutive Dry Days (CDD), Max 5-day precipitation amount (Rx5day), and we developed the consecutive dry day with less/more than 10 mm (CDD<10 mm, CDD>10 mm). For temperature we took data of average annual temperature (T_{AA}), average annual maximum/minimum temperature (T_{MA} / T_{mA}), and maximum/minimum annual temperature (T_{MM} / T_{mm}). This analysis was carried out with data from the Mexican National Weather Service (accessed May, 2013).

Statistical analysis

Statistical analyses were conducted using R version 3.0.1 (R Development Core Team 2010). We analyzed all Ψ and g_{S} data collected daily from the four species to find significant differences between hours (7 vs. 14 h), and between the four watering treatments (control/16.75, 3.35, 6.7 and 10 mm), with the anova with repeated measures test (rANOVA) using as factors water irrigations and time. Statistical significance was considered to be $P < 0.05$.

To analyze the temperature trends in the region and to observe if the trends were significant we performed the Mann-Kendall analysis (Nasrallah et al. 1990). We also analyzed the trend of the series with *XLSTAT* statistical package to determine if there was an increase or decline in the trends data generated in the period 1922-2008.

4.3 RESULTS

For the well-irrigated group (control) we found that *A. acuminata* and *Q. xalapensis* presented the highest g_S at 14 h, whereas *L. styraciflua* and *P. ayacahuite* were at 7 h. For Ψ, all the species presented the lowest values at 14 h, with *L. styraciflua* being the species with the highest values, and *Q. xalapensis* with the lowest (**Table 4.1**). Drought stress caused decreased in g_S and increased negatively in Ψ as it can be noticed in **Table 4.1** when comparing control and experimental groups, where for all the species g_S decreased over 50%. We also observed a significant decrease in Ψ, for *L. styraciflua* we noticed a decrement over 75%.

Table 4.1. Average of the drought traits of stomatal conductance (g_S) and leaf water potential (Ψ) for the well-irrigated group (control) and the experimental group (treatments 1 and 2) at 7 and 14 h (local time) during the 40 days-experiment.

Species	Drought trait			
	g_S (mmol m^{-2} s^{-1})		**Ψ (MPa)**	
	7 h	14 h	7 h	14 h
		Well-irrigated group		
Alnus acuminata	1156.51± 25.57	1253.29± 22.39	-1.15 ± 0.02	-1.22 ± 0.03
Quercus xalapensis	925.39 ± 9.42	1178.30± 31.60	-1.24 ± 0.02	-1.55 ± 0.01
Liquidambar styraciflua	1024.15± 24.17	928.19 ± 19.38	-0.15 ± 0.01	-0.23 ± 0.01
Pinus ayacahuite	608.44 ± 11.07	520.04 ± 11.70	-1.17 ± 0.01	-1.52 ± 0.01
		Experimental group		
Alnus acuminata	625.85 ± 232.93	667.66 ± 246.73	-1.96 ± 0.92	-2.05 ± 1.00
Quercus xalapensis	574.45 ± 168.50	659.84 ± 257.81	-1.93 ± 0.75	-2.28 ± 0.70
Liquidambar styraciflua	499.31 ± 148.74	449.79 ± 149.86	-0.44 ± 0.17	-0.60 ± 0.30
Pinus ayacahuite	388.63 ± 135.53	281.38 ± 124.68	-2.09 ± 0.71	-2.55 ± 0.72

As for the experimental group, *A. acuminata* presented the highest g_S at 14 h. In similar way, *Q. xalapensis* presented the highest g_S at 14 h; except during the water stress period before the second irrigation (from day 12 to 24,) where g_S was higher at 7 h. In contrast, *L. styraciflua* and *P. ayacahuite* presented the highest g_S at 7 h. All the species had the lowest Ψ values at 14 h. After letting individuals dry, *A. acuminata* and *L. styraciflua* presented leaf loss on day 12, and reached Ψ of -4.14 MPa (s.d. ± 0.12) and -1.29 MPa (s.d. ± 0.23), respectively. *P. ayacahuite* presented leaf loss on day 13, with -4.13 MPa (s.d. ± 0.09) as the lowest Ψ. *Q. xalapensis* lasted 25 days with no water before leaf loss, reaching -4.34 MPa (s.d. ± 0.13).

Concerning transpiration (E) all species reached the lowest values at 7 h on day 15, except *Q. xalapensis*, which reached the lowest E of 1.56 mmol m^{-2} s^{-1} (s.d. ± 0.7) on day 25. On day 15, *L. styraciflua* had E of 6.58 mmol m^{-2} s^{-1} (s.d. ± 0.93), *P. ayacahuite* 8.41 mmol m^{-2} s^{-1} (s.d. ± 1.2), and *A. acuminata* 7.21 mmol m^{-2} s^{-1} (s.d. ± 0.82) (**Fig. 4.2**). We observed that water stress significantly affected transpiration at the end of the stress period and caused the reduction of g_S. The highest SLA corresponded to *A. acuminata* (67.38 ± 63.92 cm^2 g^{-1}), followed by *L. styraciflua* (46.01 ± 43.65 cm^2 g^{-1}), *P. ayacahuite* (14.13 ± 13.41 cm^2 g^{-1}), and *Q. xalapensis* (8.22 ± 7.79 cm^2 g^{-1}).

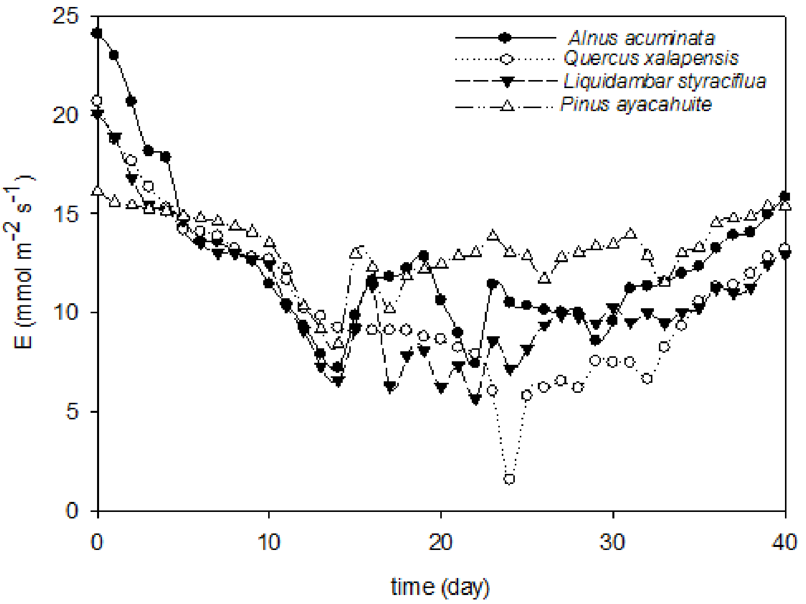

Figure 4.2. Changes in transpiration (E) during 40 days of the water stress experiment for *Alnus acuminata, Quercus xalapensis*, *Liquidambar styraciflua*, and *Pinus ayacahuite*.

For all the species we found similar responses in the g_S vs. Ψ plots, where high g_S values were correlated to high Ψ (**Fig. 4.3**). After analyzing the slope values from each species (see **Fig. 4.3** legend) we found that *L. styraciflua* was the most sensitive species to changes in g_S related to Ψ, followed by *Q. xalapensis, A. acuminata* and *P. ayacahuite*; this because the higher the value of the slope, the greater the changes of g_S related to Ψ. The decrease pattern of g_S with Ψ provided the strongest trace to the drought survival mechanism employed by these species.

For both traits, g_S and Ψ, we found significant differences for all the species when comparing between hours (7 vs. 14 h) showing that all the individuals were more stressed at 14 h. We also found for g_S and Ψ significant differences for all the species when comparing the four watering treatments (control/16.75, 3.35, 6.7 and 10 mm) (**Table 4.2**).

Alnus acuminata

On day 12 of the treatment two individuals lost their leaves completely, and after six days of irrigation at field capacity they had sprouts. During the first 12 days, g_S and Ψ dropped drastically. In terms of recovery, this was faster with respect to Ψ than g_S. With irrigation at field capacity (20 mm) and with the 3.35 mm irrigation, plant response was immediate, even presenting higher values than the control group (**Fig. 4.4**). A constant irrigation of 3.35 mm was not sufficient for the species to recover showing a decrease in g_S and Ψ (**Fig. 4.4**). However, by increasing irrigation at 6.7 and 10 mm the species begun to recover reaching similar values to the control group after 10 days of irrigation. Therefore, *A. acuminata* required ca. 67 mm to recover after the water stress period; this without considering the water that might have been evaporated or transpired.

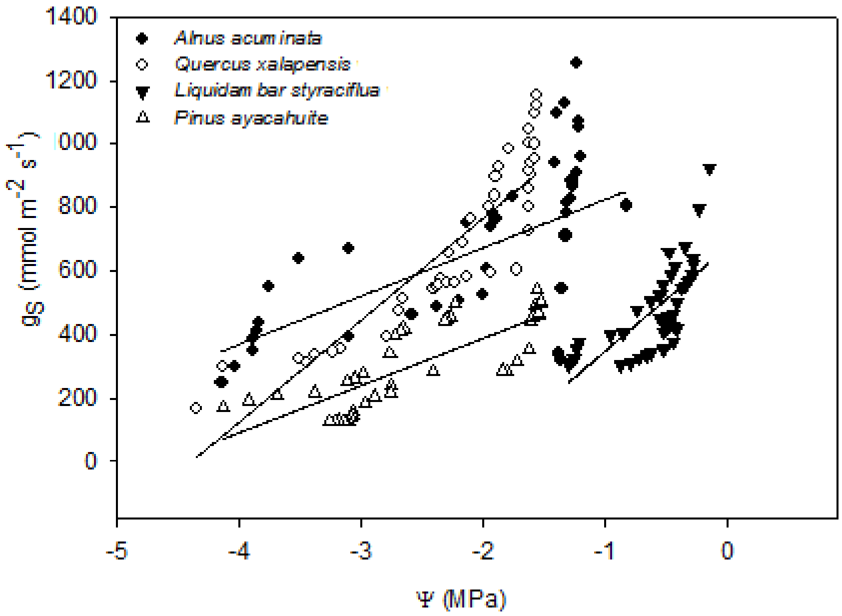

Figure 4.3. Plot of the daily averages of stomatal stomatal conductance (g_S) against the leaf water potential (Ψ) during the experiment (treatment 2, 14 hrs) and their respective linear regresions for *Alnus acuminata* ($g_S = 151.41\ \Psi + 975.42$, $R^2 = 0.33$), *Quercus xalapensis* ($g_S = 319.86\ \Psi + 1405.8$, $R^2 = 0.79$), *Liquidambar styraciflua* ($g_S = 327.22\ \Psi + 674.7$, $R^2 = 0.52$), and *Pinus ayacahuite* ($g_S = 148.24\ \Psi + 684.92$, $R^2 = 0.63$).

Table 4.2. Statistical analysis of the anova with repeated measures (rANOVA) of the traits: stomatal conductance (g_S) and the leaf water potential (Ψ), for the four species, *Alnus acuminata, Quercus xalapensis, Liquidambar styraciflua,* and *Pinus ayacahuite*, comparing time (7 vs. 14 hours) and comparing the four watering treatments: control/16.75 mm (C), 3.35 mm (T1), 6.7 mm (T2) and 10 mm (T3).

Trait		**F-value**	***P* (>F)**	**Watering treatment**	C	T1	T2
g_S	Species	301.835	<2e-16 *	T1	< 2e-16**	-	-
	Watering treatment	2815.693	< 2e-16 *	T2	6.2e-16**	4.6e-07**	-
	Time	6.512	0.0108*	T3	0.00031**	< 2e-16**	6.3e-05**
Ψ	Species	756.1	<2e-16 *	T1	< 2e-16**	-	-
	Watering treatment	740.3	<2e-16 *	T2	6.2e-16**	4.6e-07**	-
	Time	409.0	<2e-16 *	T3	0.00031**	< 2e-16**	6.3e-05**

Statistical significance $P < 0.05$*, P value adjustment method: holm**

Quercus xalapensis

Quercus xalapensis lasted the longest time with no irrigation, 25 days, and even one individual without irrigation survived 30 days. *Q. xalapensis* presented the lowest Ψ on day 25 (**Fig. 4.4**). Like *A. acuminata*, the recovery was faster with respect to Ψ than g_S. With an irrigation of 6.7 or 10 mm the individuals begun to recover reaching similar values to the control group after nine days of irrigation (**Fig. 4.4**). *Q. xalapensis* required ca. 60.3 mm to recover after the water stress period; this without considering the water that might have been evaporated or transpired.

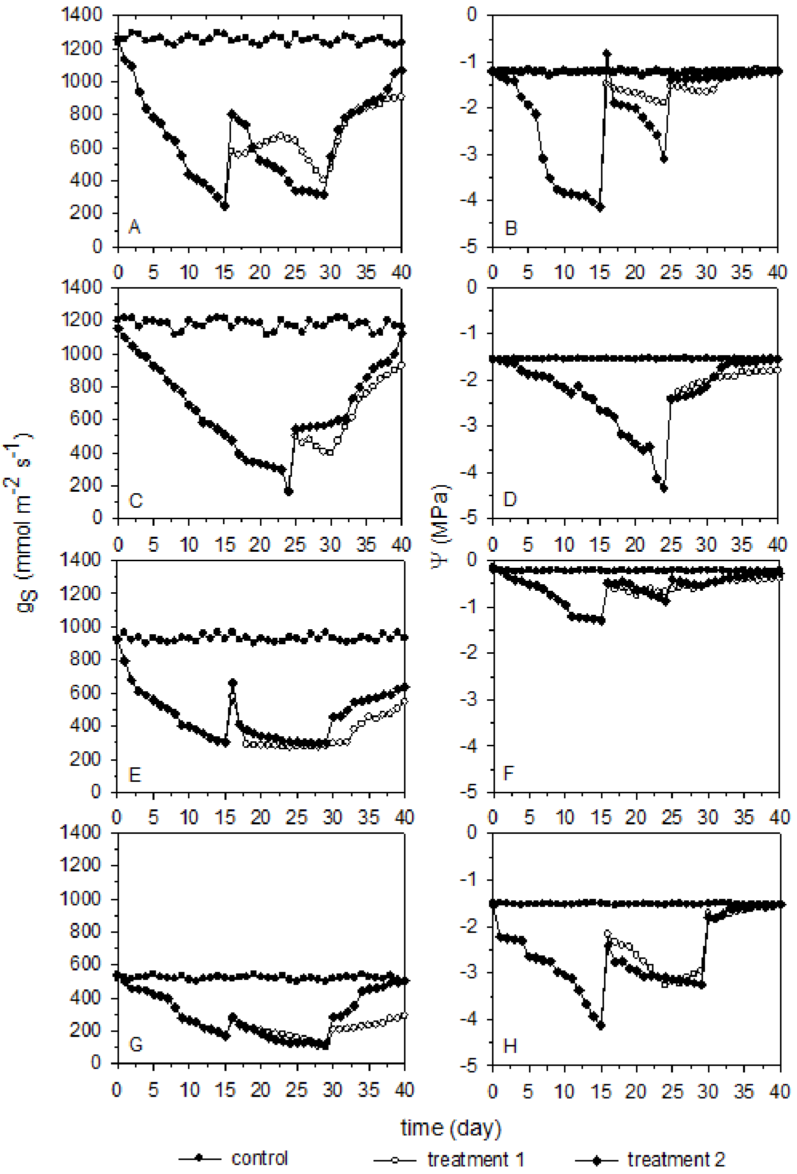

Figure 4.4. Changes in stomatal conductance (g_S, A, C, E, G), and leaf water potential (Ψ, B, D, F, H) during 40 days of the water stress experiment at 14 h (local time). Control group: Well irrigated (16.77 mm). For *Alnus acuminata* (A, B), *Liquidambar styraciflua* (E, F) and *Pinus ayacahuite* (G, H): treatment 1) irrigation from day 16 to 29 (3.35 mm) and irrigation from day 30 to 40 (6.7 mm), treatment 2) irrigation on day 16 (20 mm), irrigation from day 17 to 30 (3.35 mm) and irrigation from day 30 to 40 (10 mm). For *Quercus xalapensis* (C, D): treatments 1) irrigation from day 26 to 29 (3.35 mm) and irrigation from day 30 to 40 (6.7 mm), treatment 2) irrigation on day 26 (20 mm), irrigation from day 26 to 29 (3.35 mm) and irrigation from day 30 to 40 (10 mm).

Liquidambar styraciflua

On day 12 of the treatment one individual lost its leaves completely, and after 15 days of irrigation at field capacity it had sprouts. *L. styraciflua* had the highest Ψ even before wilting (**Fig. 4.4**). A constant irrigation of 3.35 mm was no sufficient to recover; even g_S and Ψ values continued dropping. An irrigation of 6.7 mm was not sufficient for recovering (**Fig. 4.4**); an irrigation of 10 mm was necessary to notice recovery in terms of g_S, and after 15 days of constant watering we found similar Ψ between experimental and control groups. *L. styraciflua* required ca. 150 mm to recover after the water stress period; without considering the water that might have been evaporated or transpired.

Pinus ayacahuite

On day 13 of the treatment the individuals presented signs of wilting. Similar to *L. styraciflua*, with a constant irrigation of 3.35 or 6.7 mm there were not signs of recovery (**Fig. 4.4**). An irrigation of 10 mm was necessary to notice g_S recovery, and after 11 days of constant irrigation the experimental group reached similar Ψ to the control group. *P. ayacahuite* required ca. 110 mm to recover after the water stress period; without considering the water that might have been evaporated or transpired.

Potential distribution maps

From the potential distribution maps generated we found that *P. ayacahuite* had the most confined and limited distribution. In contrast, *A. acuminata* showed the widest distribution. The estimated area of each species was: 1) *A. acuminata*: 3440.8 km^2; 2) *Q. xalapensis*: 2918.54 km^2; 3) *L. styraciflua*: 2179.75 km^2, and 4) *P. ayacahuite*: 765.61 km^2. The four species are distributed between the 1000-2000 mm isohyets, where *P. ayacahuite* is located in the driest range (1000-1200 mm), whereas *A. acuminata, Q. xalapensis* and *L. styraciflua* are located in the ranges with more precipitation (1500-2000 mm) (**Fig. 4.5**).

Precipitation and temperature trends

Concerning precipitation, we found trends to be significant in Pp_{A}, Pp_{MA}, CDD, Rx5day, and CDD<10 mm (Table 4). We found an annual decrease of 3.74 mm, and an annual maximum precipitation decrease of 0.67 mm between the years 1922 and 2008. We also found a decrease in the CDD<10mm of 0.03 days, and a decrease of 0.027 days for the CDD>10 mm. We also found a decrease of 1.29 mm in the Rx5day, but for the CDD we observed an increase of 0.18 days (**Fig. 4.6**). Between 1922-2008, 24,326 days had 0 mm, 2,225 days had 5 mm, and 1,170 days had 10 mm. However, there were only 19 days with 60 mm, 16 days with 65 mm, 2 days with 110 mm, and one day with 150 mm; these precipitation events are related to the precipitation required for trees to recover from drought, which for *Q. xalapensis* was 60.3 mm, for *A. acuminata* was 67 mm, for *P. ayacahuite* was 110 mm, and for *L. styraciflua* was 150 mm. After projecting these trends to the year 2099, we found an increase up to 45 consecutive dry days, a decrease in the Pp_{A} of 374.64 mm, a decrease in the Pp_{MA} of 80.53 mm, and a decrease of 129.15 mm in the Rx5day.

As for the temperature trends analysis, we found trends to be significant in the average annual (T_{AA}), and the maximum annual (T_{MA}) (**Table 4.3**). We found an increase of 0.0123 ºC per year in (T_{AA}), therefore following this tendency, T_{AA} will increase 1.12 °C by the year 2099. It is worth to notice that there are increments on T_{AA} and T_{MA} but a decreasing in T_{mA}. Maximum annual temperature tendency showed an increase of 0.0306 ºC per year, and T_{mA} a decrease of 0.0043 ºC per year (-0.37 °C towards 2099); an increase of 0.98 ºC for the lowest temperature in the year, and an increase 1.35 ºC for the highest temperature in the year for the region in the year 2099 (**Fig. 4.7**).

Table 4.3. Statistical analysis of the precipitation trends of average annual precipitation (Pp_A), annual maximum precipitation (Pp_{MA}), consecutive dry days (CDD), Max 5-day precipitation amount (Rx5day), and consecutive dry day with less/more than 10 mm (CDD<10 mm, CDD>10 mm). And statistical significance of the temperature trends of average annual (T_{AA}), maximum annual (T_{MA}), minimum annual (T_{mA}), highest temperature in the year (T_{MM}), and lowest temperature in the year (T_{mm}) using the Mann-Kendall analysis. Data from the Mexican National Weather Service.

Precipitation tendency	Pp_A	Pp_{MA}	**CDD**	**Rx5day**	**CDD<10 mm**	**CDD>10 mm**
Tau of Kendall	-0.191	-0.266	0.235	-0.169	-0.166	-0.135
P-value	0.012*	< 0.0001*	0.002*	0.027	0.041*	0.106

Temperature tendency	T_{AA}	T_{MA}	T_{mA}	T_{MM}	T_{mm}	-
Tau of Kendall	0.380	0.369	-0.077	0.090	0.149	-
P-value	< 0.0001*	< 0.0001*	0.314	0.250	0.057	-

Statistical significance $P < 0.05$*

4.4 DISCUSSION

Relation between leaf water potential and stomatal conductance

Changes in leaf water potential, soil moisture, and evaporative demand will indirectly drive changes in stomatal conductance and transpiration (Fuchs and Livingston 1996, Comstock & Mencuccini 1998, Hubbard et al. 2001). Additionally, due to the evaporation of water through stomata on the leaf surface, the rate of transpiration is directly related to the surface area. Thus, the analysis of leaf water potential can be used to explain and predict patterns of plant water use with respect to soil and atmospheric environment, large differences between species and ecosystems (Sperry et al. 2002), and also eco-physiological vulnerability of species within an ecosystem.

We found in our study that g_S is highly sensitive to Ψ□ and also that g_S response is closely correlated with the plant response to water stress causing stomatal closure (Brodribb & Holbrook 2003). These results indicated that stomatal closure is primarily coordinated with Ψ (**Fig. 4.3**). Across all the traits that we measured, differences were found among species, implying functional diversity and a mechanism for coexistence (Ackerly 2004). We observed for all the species that recovery was faster by Ψ than by g_S or *E*. Our findings suggest that stomatal closure occurred in response to soil dryness at a threshold soil water deficit. This response appeared to be linked to the soil water experienced by the majority of the roots (Irvine et al. 1998). As Ψ declined, stomata closed more readily with the increasing atmospheric water deficits, with complete closure occurring below -4.5 MPa, the stomatal closure prevented water potentials declining below this value.

Pinus ayacahuite and *A. acuminata* had a marked steeper decrease in g_S related to Ψ (**Fig. 4.3**). Such stomatal response is indicative of drought-avoider species, such is the case of *A. acuminata*; that is, they close their stomata at lower water potentials to avoid water stress (Smith et al. 1997). This suggests that the carbon gain/water use trade off used by *A. acuminata* involves exploiting good conditions and avoiding water stress during drought (Curran et al. 2009). In the opposite case we found *P. ayacahuite,* a drought-resistant species physiologically adapted to dry conditions. Finding these differential g_S responses provided evidence of different physiological adaptations to water-stress.

Comparison between species

Alnus acuminata and *L. styraciflua* are drought-deciduous species, losing most of their leaves during drought, but not necessarily seasonally. Such a classification can be supported by the pattern of leaf loss and change in canopy of these species over the course of our experiment. Also, *A. acuminata* and *L. styraciflua* had significantly higher SLA than the other two species; this also suggests these species are drought-avoiders, in that they avoid water stress by dropping their foliage during drought.

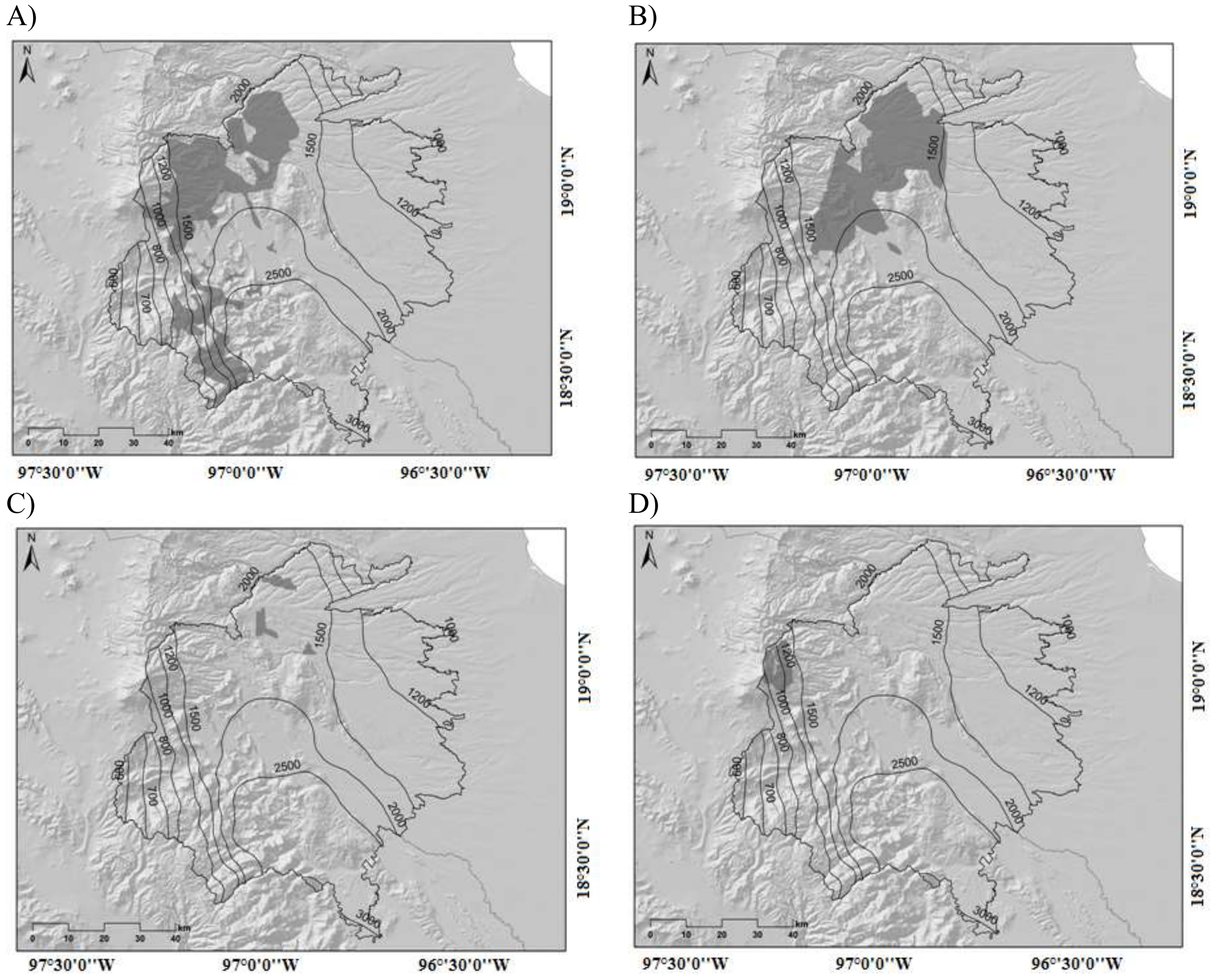

Figure 4.5. Potential distribution (shaded area) of *Alnus acuminata* (A), *Quercus xalapensis* (B), *Liquidambar styraciflua* (C) and *Pinus ayacahuite* (D), and annual average precipitation (mm) distributions in the central mountain region of Veracruz, Mexico.

For *Q. xalapensis* and *P. ayacahuite,* it appears they utilized similar mechanisms to survive drought. Both can be characterized as species that maintain metabolic activity during water stress (particularly *P. ayacahuite* which had shallow g_S vs. Ψ response curve), and are both sclerophyllous (low SLA) (Curran et al. 2009, Deines et al. 2011). More evidence of this drought tolerance can be observed in the Ψ of the control group for both species, presenting similar and lower values than those of the other species (Table 2). The drought tolerance of *Q. xalapensis* could well be related to the sclerophyllous nature of their leaves. However, there were some notable differences between species, where *P. ayacahuite* consistently recorded lower Ψ than the others species. *P. ayacahuite* also had significantly lower g_S than *A. acuminata* and *L. styraciflua* during the experiment, suggesting that in better conditions both species had higher carbon assimilation rate than *P. ayacahuite*. This assumption is supported by the low SLA of *P. ayacahuite*; species with low SLA are considered to exhibit a conservative resource capture strategy, with low light-catching area per unit of dry mass allocated to this purpose (Westoby 1998).

Interestingly, *A. acuminata, Q. xalapensis* and *P. ayacahuite* had g_S vs. Ψ response curves similar. This is unusual, as deciduous species are generally characterized for having higher Ψ than evergreen and sclerophyllous species (Eamus 1999), although there are exceptions (Medina & Francisco 1994). It seems that the deciduousness of *A. acuminata* might serve to minimize rather than avoid water stress, and that it is relatively drought-tolerant for a deciduous species. For *L. styraciflua,* it had the highest g_S vs. Ψ response curve of all the species indicating its low drought tolerance.

Effect of drought stress on leaf water potential

When analyzing Ψ, we observed that *Q. xalapensis* took the longest to reach its lowest values (lasted 25 days with no irrigation; Fig. 2C), making this the most efficient species at preventing the water loss and therefore, the least vulnerable. In contrast, *L. styraciflua* consistently had the highest Ψ across all the experiment. Also, *L. styraciflua* lasted fewer days before wilting (only 12), making it the most vulnerable species to water loss. Similar Ψ between species were observed on day 16 for *A. acuminata* and *P. ayacahuite*, and on day 25 for *Q. xalapensis*. The low Ψ and the high resistance to water stress by *Q. xalapensis* may be due for its sclerophyllous nature mentioned before, but also because the species might have other mechanisms to meet water stress such as osmotic potential adjustment and/or higher cell wall elasticity modulus, which measures the stiffness of the cell wall (Burgert and Dunlop 2011). Also, water stress resistance may result from the adaptation to the altitudinal distribution of the species where the precipitation is lower. Another important characteristic in *Q. xalapensis* behavior was its maximum stomatal opening at 7 h during the water stress period, whereas in good irrigation conditions the maximum opening was recorded at 14 h. This behavior could be evidence of the high adaptability of the species to low precipitation and water stress preventing water loss by transpiration.

For *A. acuminata* we observed an immediate response in Ψ after the first irrigation. The stress group (treatment 1) even produced higher Ψ than the control group; with minimum (3.35 mm) and at field capacity (20 mm) irrigation the species responded similarly, indicating that regardless of the amount of water, *A. acuminata* is highly susceptible to changes in precipitation. *L. styraciflua* was the species that needed more precipitation and days to recover after the water stress period; it required a precipitation of ca. 150 mm, besides, this species had the highest Ψ even before leaf drop. This may be because the species grows in areas where precipitation is not a limiting factor, and perhaps the species in its evolutionary history did not have to face a water stress-environment. However, high Ψ compared to those of the other species do not necessary meant that the species was less stressed. These water potential differences suggest that different species have different minimum Ψ (Goldstein et al. 1986), which for *L. styraciflua* were not less than -1.5 MPa, whereas the minimum Ψ for the other species could reach values lower than -4 MPa. *P. ayacahuite* responded similarly to *Q. xalapensis* after irrigation; however, *P. ayacahuite* needed more irrigation to recover, ca. 110 mm.

Transpiration and specific leaf area

In the case of E we found similar responses between the four species (**Fig. 4.2**). For *A. acuminata, Q. xalapensis* and *P. ayacahuite* such a response might be attributed to their higher distributions in field (above 1500 m asl) where temperature is lower, and thus g_S and E are lower preventing water loss through stomata. Soil water stress occurs when growth and transpiration become restricted in response to a decline in soil moisture (Breda et al. 2006, Chen et al. 2014). In general, forests species (in particular, *Pinus*) have traits that have made them more drought tolerant than other species (Duursma et al. 2008). Our results also indicate that non-irrigated individuals avoided drought by maintaining low transpiration rates, may be due to reduced leaf area and reduced transpiration per unit leaf area compared to irrigated individuals.

Concerning SLA, this is an index of sclerophylly (Witkowski & Lamont 1991), which has been functionally linked with drought tolerance (Groom & Lamont 1997, Salleo et al. 1997), and has been positively correlated with rainfall across a wide range of habitats (e.g. Fonseca et al. 2000, Lamont et al. 2002). Low SLA is indicative of a conservative resource capture strategy (Westoby 1998). This strategy can be observed in *Q. xalapensis* and *P. ayacahuite*, both species distributed at higher altitudes where precipitation is lower, suggesting that dry rainforest taxa may have slow growth rates as a means to cope with lower and less reliable rainfall, and also might be an indicator of high water-use efficiency, which was observed in *Q. xalapensis*. Sclerophyill species might be more sensitive to climate change. This sensitivity would be increased by extreme temperatures, which will favor deciduous species (Valladares et al. 2004), such as *A. acuminata*. If this scenario is feasible, climate change will promote an ecosystem with more deciduous and shrubs species, with less productivity and higher transpiration rates linked to better water-use efficiency.

Precipitation and temperature trends

Regarding precipitation and temperature, we corroborated that precipitation decreased and temperature increased in the region. If these trends continue, they will represent a major risk for all the species. High temperatures are related to soil water loss through evaporation, and also causing stomata closure and decrease of gas exchange and productivity (Jones 1992). As for precipitation, Ehleringer et al. (1991) postulated that changes in precipitation predicted by global climate models would result in a gradual increase in the frequency of herbaceous perennials and succulents, while the frequency of woody species may decline. Because all the species in our study are woody species, changes in precipitation and temperature would possess an incremental impact on their vulnerability. Moreover, it has been hypothesized that severe soil water deficits in one month cause hydraulic and physiological responses that are carried over into subsequent years (Innes 1993). For species that present slow recovery, like *L. styraciflua* and *P. ayacahuite*, these longer recovery periods would enhance the vulnerability of the species.

Besides the precipitation reduction in the region, we found an increase in the consecutive dry days (CDD, **Fig. 4.6**). If the CDD increases, field capacity of the region becomes an important water source. Previous studies in our study area described the content of water at field capacity for the region, varying from 0.23-0.30 $cm^3 \, cm^{-3}$ in the soils. These values indicate a potential availability of water in the first 20 cm, equivalent to 440-680 $m^3 \, ha^{-1}$, with the water content at wilting point varying from 0.17-0.21 $cm^3 \, cm^{-3}$ (Geissert & Ibañez 2008). But if drought periods increase, water loss from the soil is inevitable. Good root systems might compensate for the water loss by searching more efficiently for water sources. Species may therefore explore the moister deeper soil layers by producing deep roots (Poorter & Hayashida-Oliver 2000).

We must recognize some limitations in our study, mainly due to the use of only two physiological traits, (Ψ and g_S) as indicators of drought tolerance and water stress; however, photosynthetic capacity and the water use efficiency (WUE) are important parameters to acknowledge how plants adapt to climate change and change their distributions (Wright et al. 2004, Nicotra et al. 2010). In particular, WUE is used to describe the trade-off between water loss and carbon gain during plant photosynthesis carbon assimilation processes (Baldocchi 1994, Yu et al. 2004, Zeppel 2013) reflecting the coupling relationship between carbon and water cycles (Yu et al. 2008). Also, it is important to mention that biotic interactions play and important role in the species survival and for plant fitness (Wright et al. 2004). As for our experimental design, we considered that the number of individuals and the number of days must be increased for future replications, as plants would have acclimatized to the new dry conditions in our experiment; however it must be considered that g_S and Ψ should be measured as simultaneously as possible. Regarding the precipitation and temperature trends, our analysis did not consider the CO_2 increment levels that global climate models do. Climate models predict a temperature increment of 1 to 4.5 ºC with a maximum of 6 ºC (IPCC 2013). Also, the rising CO_2 concentrations might increase the WUE (e.g. Wullschleger et al. 2002, Xu & Hsia, 2004).

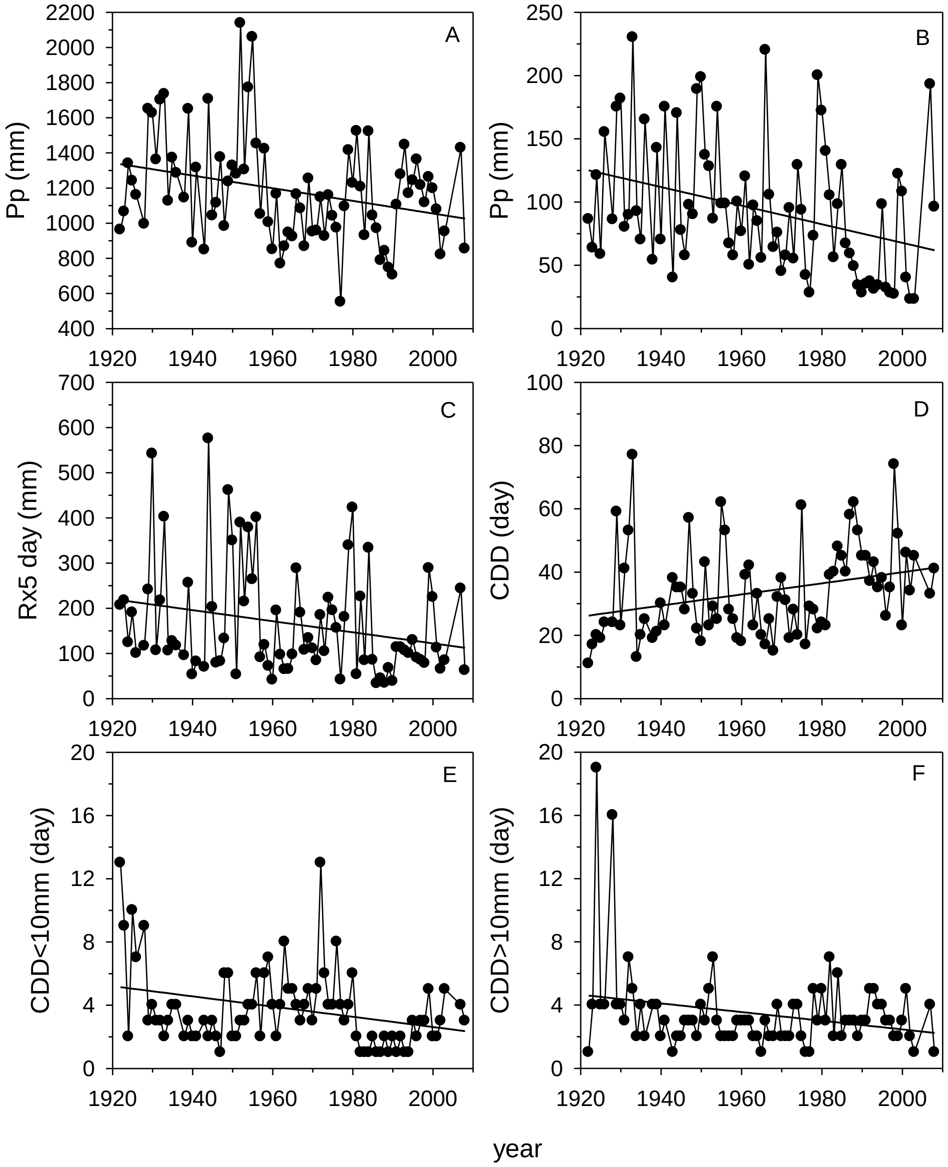

Figure 4.6. Trends of annual precipitation (*Pp*A) (A), annual maximum precipitation (*Pp*MA), (B), Max 5-day precipitation amount (Rx5day) (C), consecutive dry days (CDD) (D), consecutive dry days with less than 10 mm (CDD<10 mm) (E), and consecutive dry days with more than 10 mm (CDD>10 mm) (F). Data from the meteorological station Las Vigas, in the central mountain region of Veracruz, years 1922-2008.

It is important to mention that we used saplings instead of adult individuals (e.g. Poorter & Markesteijn 2008, Deines et al. 2011, Curran et al. 2013) for our experimental design mainly because regional patterns in species composition and distributions in rainforests have been attributed to differential survival of saplings during drought (Engelbrecht et al. 2007, Baltzer et al. 2008), being this stage the critical phase of the plant life cycle in influencing survival (Tyree et al. 2003, Poorter & Markesteijn 2008, Markesteijn 2010). Saplings are more sensitive to drought than adults because of their shallower roots that limit access to soil water (Gerhardt 1996, Coomes & Grubb 2000, Tyree et al. 2003, Poorter & Markesteijn 2008). However, dry season survival under field conditions may be much higher than the one found in our experiment, because wild saplings grow in unlimited soil volume and benefit from incidental rains, also species are able to survive with the little water remaining in the soil and with coastal fog (Rundel et al. 1991, Arroyo et al. 1993, Gutiérrez 1993, Dawson 1998, Poorter & Markesteijn 2008, Markesteijn et al. 2010).

Despite these limitations, we have produced a study that would serve as a background for future experiments, encouraging its reproduction with more adequate sample sizes, longer-term experiments including CO_2 fertilization, WUE increments, inclusion of biotic interactions, evaluation of rooting depth in the experimental setup, and analysis of different watering treatments according to the regional climate patterns.

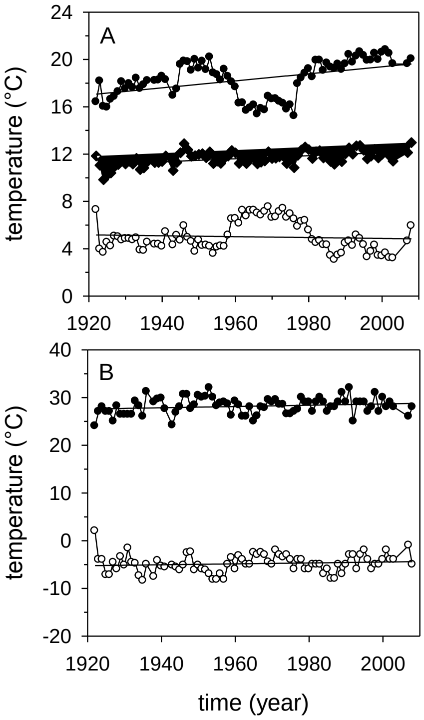

Figure 4.7. Trends of average annual temperature (T_{AA}) (A, closed circle), average maximum temperature (T_{MA}) (A, closed diamond), average minimum temperature (T_{mA}) (A, open circle), highest temperature in the year (T_{MM}) (B, closed circle), and lowest temperature in the year (T_{mm}) (B, open circle). Data from the meteorological station Las Vigas, in the central mountain region of Veracruz, years 1922-2008.

Capítulo 5

Comparación de la vulnerabilidad ambiental de once especies arbórea del bosque de niebla de montaña del este de México: un índice de vulnerabilidad

Comparing the environmental vulnerability of eleven tree species from the montane cloud forest of eastern Mexico: a vulnerability index

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RESUMEN: El bosque mesófilo de montaña (BMM) es uno de los ecosistemas más amenazados a pesar de su alto valor estratégico para el desarrollo sostenible, el papel que desempeña en el mantenimiento del ciclo hidrológico, y como reserva de biodiversidad endémica. Para México, este bosque es considerado como el ecosistema terrestre más amenazado a nivel nacional debido a los cambios de uso del suelo y los efectos del cambio climático global. Para comparar y evaluar la vulnerabilidad ambiental en el BMM medimos dos rasgos fisiológicos (conductancia estomática y potencial hídrico foliar), cuatro variables climáticas (temperatura del aire, radiación fotosintéticamente activa, déficit de presión de vapor, disponibilidad de agua) y la distribución geográfica potencial de once especies arbóreas de este bosque. Se evaluaron las respuestas de conductancia estomática utilizando el método de las funciones envolventes (MFE), y después de analizar estas respuestas se desarrolló un índice de vulnerabilidad que nos permitió comparar la vulnerabilidad ambiental entre las especies. Propusimos el MFE como una herramienta útil para evaluar la vulnerabilidad regional mediante la comparación de especies. Nuestros resultados mostraron respuestas diferenciales en todas las especies y para todas las variables estudiadas; sin embargo, el índice de vulnerabilidad permitió concluir que la especies más vulnerables fue *Liquidambar styraciflua*, y *Persea longipes* fue la menos vulnerable. También se encontró que temperaturas por encima de 34 ºC, y déficit de presión de vapor por encima de 2.9 kPa con una humedad relativa inferior al 30% ponen en peligro el rendimiento de la conductancia estomática de todas las especies. También encontramos al potencial hídrico foliar como la variable que más influye sobre las especies estudiadas, seguido por déficit de presión de vapor, lo que muestra que, incluso en el BMM, el agua es un factor determinante para el desarrollo de las especies.

Palabras clave: Vulnerabilidad ambiental · índice de vulnerabilidad · método de la función envolvente · conductancia estomática · potencial hídrico foliar · temperatura del aire · radiación fotosintéticamente activa · déficit de presión de vapor · distribución potencial · bosque de mesófilo de montaña

ABSTRACT: The montane cloud forest (MCF) is one of the most threatened ecosystems, in spite of its high strategic value for sustainable development, the role it plays in the hydrological cycle maintenance, and as reservoir of endemic biodiversity. For Mexico, this forest is considered as being the most threatened terrestrial ecosystem at national level due to land-use changes and the effects of global climate change. To compare and assess the environmental vulnerability in the MCF we measured two physiological traits (stomatal conductance and leaf water potential), four climate variables (air temperature, photosynthetically active radiation, vapor pressure deficit, water availability) and the potential geographic distribution of eleven tree species from this forest. We evaluated the stomatal conductance responses using the envelope function method (EFM), and after analyzing these responses we developed a vulnerability index that allowed us to compare the environmental vulnerability between species. We proposed the EFM as a useful tool to assess regional environmental vulnerability by comparing species. Our results showed differential species responses to all the studied variables; however, the vulnerability index allowed us to conclude that the most vulnerable species was *Liquidambar styraciflua,* and the less vulnerable *Persea longipes*. We also found that temperatures above 34 ºC, and vapor pressure deficit above 2.9 kPa with relative humidity below 30% jeopardized the stomatal conductance performance of all species. We also found leaf water potential as the most influential variable over the studied species followed by vapor pressure deficit, showing that even in the MCF water is a determinant factor for species' development.

Key words: Environmental vulnerability · vulnerability index · envelope function method · stomatal conductance · leaf water potential · air temperature · photosynthetically active radiation · vapor pressure deficit · potential distribution · montane cloud forest

5.1 INTRODUCTION

The montane cloud forest posses high strategic value for sustainable development, plays a key role in the hydrological cycle maintenance, and is a reservoir of endemic biodiversity (Toledo-Aceves et al., 2011). For Mexico, this forest is one of the most bio-diverse ecosystem (González-Espinosa et al., 2012); however, it is also considered the most threatened terrestrial ecosystem at national level due to changes in land-use, the effects of global climate change, and local and regional environmental changes (e.g. CONABIO, 2010; Toledo-Aceves et al., 2011; Calderon Aguilera et al., 2012).

Globally, climate and environmental changes are increasingly recognized as a complex phenomenon involving shifts in many dimensions of Earth's atmospheric functions (Houghton et al., 1995). Three general expectations exist for species' responses to these changes: movement, adaptation (evolutionary change or physiological acclimatization), or extintion (Holt, 1990). If species are sufficiently mobile, they may track the geographic position of their ecological niches; if species are capable of rapid evolutionary change or have a wide range of physiological tolerances, adjustment to changing conditions and landscapes may be possible. Failing mobility and adaptability, extintion is the likely result (Holt, 1990; Melillo et al., 1995). Changes on climate are expected to shift the species distribution along environmental gradients if their current environmental tolerance is exceeded (Miller and Urban, 1999).

Modeling can be used to predict shifts in the vegetation's distribution under climatic change, and to simulate responses of vegetation (Zolbrod and Peterson, 1999). In theory the species presence/absence and abundance is highest where optimal conditions exist (Gauch et al., 1974). However, global vegetation patterns are already shifting in response to changes in temperature and precipitation (Parmesan, 2006; Allen et al., 2010). Therefore, anticipating potential shifts in local vegetation are critical to develop adaptive strategies. However, predicting the vegetation response to climate change requires consideration of interacting physical and biological processes (Halofsky et al., 2013). With climatic conditions predicted to continue changing over the next century (IPCC, 2014), conservationists and environmental managers would like to know where species are likely to remain within, or expand from their current distributions, and conversely, situations where species are likely to become vulnerable (Coops and Waring, 2011).

Vulnerability is defined as the degree to which a system is susceptible to, or unable to cope with, adverse effects of climate changes, including climate variability and extreme climate events (IPCC, 2001). Ecophysiological vulnerability is the degree of susceptibility or inability of an organism to adapt their physiological functions to ecological and environmental changes (Esperón-Rodríguez and Barradas 2014a). Assessment of vulnerability is important, as it enables identification of areas or species at risk, and the threats posed by the diminution or loss of such resources that will threaten future efforts towards sustainable development.

To determine and compare the environmental vulnerability of eleven tree species from the montane cloud forest of eastern Mexico, we selected stomatal conductance as a vulnerability indicator. We measured four climate variables to assess the species' vulnerability: air temperature, photosynthetically active radiation, vapor pressure deficit and water availability, measured through the physiological trait of leaf water potential, in the field and in the greenhouse. Data from the greenhouse allowed us to observe the species' response in non-natural conditions by increased temperature. We also added the species' potential distribution to our analysis as a vulnerability enhancer. We approached this study with the envelope function method. This method is capable of analyzing variables that directly affect the species, providing an effective tool to analyze the diversity of ecophysiological responses (Lambers et al., 1998; Barradas et al., 2010). From the physiological responses that different species may have to different climate and physiological variables, it is explored how the species can be affected by the potential vulnerability to changes in these variables. This study presents a first attempt to develop a comparative vulnerability index with ecophysiological implications.

5.2 METHODS

Study Area

The montane cloud forest located in the central mountain region of Veracruz in eastern Mexico (19º54'08'' N, 96º57'19'' W, **Figure 3.1; Chapter 3**) forms part of Neovolcanic Ridge and the Sierra Madre Oriental. Abrupt topography is the main characteristic of the region with a pronounced altitudinal gradient, from the sea level up to 5500 m asl at a distance of 100 km (Barradas et al., 2010). Average annual temperatures range between 10 and 29 ºC, and annual precipitation ranges from 600 to 1200 mm, with a maximum of 3000 mm in wet regions. Soils in the region are of volcanic origin or Andisols, with physical characteristics that favor good structural stability (Meza and Geissert, 2003). They have low bulk density, high porosity with significant micro-porosity, significant amount of water micro-aggregates, complexation with organic matter, and stable amounts of Fe and Al (Shoji et al., 1993).

Species selected

Eleven tree species from the montane cloud forest were selected: *Carpinus caroliniana* Walter, *Clethra mexicana* DC., *Cornus florida* var. *urbiniana* (Rose) Wangerin, *Liquidambar styraciflua* L., *Ostrya virginiana* (Mill.) K.Koch, *Persea longipes* Meisn., *Quercus candicans* Née, *Q. germana* Schltdl. & Cham., *Q. xalapensis* Bonpl., *Tapirira mexicana* Marchand, and *Ulmus mexicana* Planch. In **Table 5.1** we present the climate requirements and altitudinal ranges for all the species (CONABIO, accessed April, 2014).

Table 5.1. Height, diameter, climate requirements (temperature and precipitation ranges), and distribution (altitudinal range) for eleven tree species from the montane cloud forest in Mexico (CONABIO, accessed April, 2014).

Species	**Height (m)**	**Diameter (cm)**	**Temperature range (ºC)**	**Precipitation range (mm)**	**Altitudinal range (m asl)**
Carpinus caroliniana	10 - 15	30	12- 14	1200 - 1500	1000 - 2500
Clethra mexicana	15 - 20	20 – 100	12 - 23	600 - 2000	500 – 3300
Cornus florida var. *urbiniana*	10	30	12 - 21	700 - 2000	1725 - 1950
Liquidambar styraciflua	20 – 60	40 - 150	12 - 18	1000 - 2000	400 - 1800
Persea longipes	15	20- 40	16 - 22	400 - 1700	500 - 2500
Ostrya virginiana	5 - 18	25 - 30	12- 18	700 - 2000	100 - 1500
Quercus candicans	15 - 20	100	12 - 22	1500 - 1700	1200 - 2700
Quercus germana	20	20 - 60	12 - 18	1500 - 2600	1200 - 2800
Quercus xalapensis	30	45	12 - 18	1400 - 2300	400 - 2700
Tapirira mexicana	30	100	18 - 20	1500 - 2000	200 - 1400
Ulmus mexicana	25 - 40	100 - 250	16 - 20	1900 - 3800	900 - 2200

Plant material

We measured five individuals of each species in the field and under greenhouse conditions. Five saplings of each species from 45 to 90 cm height were kept in the greenhouse. Individuals were transplanted into two-liter containers with a mixture of peat moss after having been sterilized in an autoclave for 90 minutes. Saplings were kept at the humid greenhouse of the Institute of Ecology, UNAM under well-watered conditions simulating field conditions.

For a typical day, greenhouse mean temperature was 24.09 ± 5.08 ºC, maximun temperature was registred at 14 hours (h, local time, 28.26 ± 1.78 ºC) and minimum at 8 h (17.33 ± 0.50 ºC). Mean relative humidity (HR) was 36.56 ± 1.77 %, being maximun at 8 h (38.37 ± 4.24 %), and minimum at 16 h (33.38 ± 0.64 %). Photosynthetically active radiation average was 133.57 ± 96. □mol m^{-2} s^{-1}, with maximun values at 12 h (289.06 ± 65.90 □mol m^{-2} s^{-1}) and minimum at 18 h (26.58 ± 14 □mol m^{-2} s^{-1}).

Stomatal conductance and Leaf water potential

Stomatal conductance (g_S) and leaf water potential (Ψ) measurements were taken in the field and greenhouse one week after transplanting the sapplings. Because of the age differences bewteen individuals from the field and the greehouse, we selected the leaf age as a parameter to perform the measurements, measuring mature leaves from all individuals.

We considered that both measurements must be taken as simultaneously as possible for all the species in the field and greenhouse. Field measurements were taken from September 29 to October 3, 2013; and greenhouse measurements were taken from October 7 to 14, 2013. Stomatal conductance (g_S) was measured daily in all individuals of each species in the field and greenhouse, on at least two fully expanded leaves per plant, with a steady-state diffusion porometer (LI-1600, LI-COR, Lincoln, Nebraska, USA) from 8 to 18 h at 2 h intervals; however, due to high air humidity conditions in the field, data from 8 h were not considered in our diurnal variation analysis. Leaf water potential (Ψ) was measured daily in all individuals of each species only in the field, on at least two fully expanded leaves per plant, with a pressure chamber (PMS, Corvallis, Oregon, USA) (Scholander et al., 1964, 1965; Turner, 1981) at 8 and 14 h to register the maximum and minimum values.

In order to observe the g_S response to high temperatures, greenhouse was adapted to reach high T_A values, by closing it during the last two days of the experiment. Greenhouse conditions mentioned above do not considered these values.

Climatological measurements

Air temperature (T_A), photosynthetically active radiation (PAR), and relative humidity (RH) were determined next to each measured leaf with a quantum sensor (LI-190SB, LI-COR Ltd., Lincoln, Nebraska, USA), a fine wire thermocouple, and a humicap sensor (Vaisala, Helsinki, Finland). Leaf temperature (T_L) was also measured with thermocouples which were mounted in the porometer. The leaf–air vapor pressure deficit (*VPD*) was calculated from T_A, T_L and RH measurements. Climate measurements were made daily from September 29 to October 12, 2013, from 8 to 18 hours (h, local time) at 2 h intervals, in the field and under greenhouse conditions.

Potential distribution maps

We developed potential distribution maps for all the species. We took data provided by the website Global Biodiversity Information Facility (accessed April, 2014), data from Biological Collections of the National Autonomous University of Mexico (UNIBIO, accessed April, 2014), data collected at the Tropical Ecophysiology Lab in the Institute of Ecology (data available with the authors), and data collections from the Institute of Biology, the National Commission for the Knowledge and Use of Biodiversity (CONABIO, accessed April, 2014), the National Forestry Commission (CONAFOR, accessed April, 2014) and the Global Biodiversity Information (REMIB, accessed April, 2014), and developed the maps using MaxEnt program and ArcView GIS 10.2. Concerning MaxEnt, this is an algorithm that has been adapted for the modeling of potential distribution of organisms (Phillips et al., 2006), calculating the statistical significance of a prediction, using a binomial test of omission given by ordinal environmental variables, depending on a value expressed as a percentage. To estimate the area occupied by each species, we used the regions where there were more than 60% probability of finding the species.

The envelope function method (EFM)

The EFM analyzes the relation between g_S response to climate and physiological variables (T_A, PAR, VPD and Ψ). As a result, we obtained graphics that represent the optimal stomatal response to one selected variable (Jarvis, 1976; Fanjul and Barradas, 1985; Jones, 1992; Ramos-Vázquez and Barradas, 1998; Barradas et al., 2004). The method analyzes the effect of each variable on g_S, and it is determined from simple models that are referred to as envelope functions. This model consists of selecting data from the probable upper limit of the function represented by a cloud of points in each of the diagrams produced by plotting g_S as a function of any variable (edaphic or climate). The model has three theoritic assumptions: 1) the envelope function represents the optimal stomatal response to a selected climate variable (e.g. PAR); 2) the points below the selected function are the result of a change in any of the other variables (e.g. T_A and VPD), and 3) there are no synergistic interactions between variables (edaphic or climate) (Jarvis, 1976; Fanjul and Barradas, 1985; Jones, 1992; Ramos-Vázquez and Barradas, 1998; Barradas et al., 2004).

The relation of g_S in terms of air temperature (T_A) is given by the envelope values that fit a quadratic equation:

$$g_S = A + B\,T_A + C\,T_A^2 \qquad (1)$$

where A, B and C are parameters of the parable, being possible to determine the optimum temperature (T_O) at which the maximum stomatal conductance (g_{SMAX}) occurs, and the cardinal temperatures (minimum and maximum). From the plot T_A *vs.* g_S we also obtained the optimal thermic interval (T_R) for all the species (considering this interval from the maximum stomatal opening up to 30% closure), and the maximum temperature (T_{MAX}) before the g_S decrease by 50%, because we considered that this decrease represented potential vulnerability and stress to jeopardize the stomatal performance.

Envelope values of stomatal conductance (g_S) as a function of photosynthetically active radiation (PAR) are consistent with a hyperbolic function:

$$g_S = [a\mathrm{PAR}/(b + \mathrm{PAR})] \qquad (2)$$

where a is the asymptotic value of g_S or g_{SMAX}, and b is g_S sensitivity to changes in PAR.

While the g_S function in relation to vapor pressure deficit (VPD) generates a simple linear equation.

$$g_S = a + bVPD \qquad (3)$$

where b is g_S sensitivity to the VPD, and a is the zero drift. Using the plots, we calculated the minimum VPD value (VPD_{min}) before the stomatal conductance decrease by 50%.

Similarly, the stomatal response to leaf water potential (Ψ) is also a simple linear equation:

$$g_S = a + b\Psi \qquad (4)$$

where b is g_S sensitivity to the Ψ, and a is the zero drift. We also calculated the maximum Ψ value (Ψ_{MAX}) before the stomatal conductance decrease by 50%.

We used data of all the variables (g_S, T_A, PAR, VPD and Ψ) from the field and the greenhouse to estimate all the functions and the coefficients mentioned above.

Vulnerability index

For our study we considered the parameter *b* from the envelope function model as a vulnerability indicator. Parameter *b* represents the slope of the equations of the variables PAR, *VPD* and Ψ. The higher the *b*, the greater the slope. High *b* values indicate that these variables (PAR, *VPD* and Ψ) limit and affect more the g_S response, compared with lower slopes where the variables' effects on the stomatal response is minor. The higher the *b* value, the greater the vulnerability; thus, small changes in the climate or physiological variables represent major changes in the g_S response.

We developed a vulnerability index that can be used to compare vulnerability among species (I*sp*), but also among functional groups or species from different altitudinal ranges or ecosystems (I_V) by obtaining the average values of all the individuals I*sp* of each group. The index is composed by five vulnerability components: air temperature (V_{TA}), photosynthetically active radiation (V_{PAR}), vapor pressure deficit (V_{VPD}), leaf water potential ($V_{□}$) and distribution (V_D). The vulnerability index is the average of all these components:

$I_{sp} = (V_{TA} + V_{PAR} + V_{VPD} + V_{\Psi□}□□□ V_D) / 5$ (5)

$I_V = \sum_{n=1}^{n} I_{sp} / n$ (6)

As for the vulnerability components, V_{TA} is obtained by dividing the temperature from the optimal range of each species (T_{Rspn}) by the broadest thermal range of all the species (T_{RMAX}):

$V_{TA} = 1 - (T_{Rspn} / T_{RMAX})$ (7)

Regarding the components V_{PAR}, V_{VPD}, V_{Ψ}□, these are obtained by dividing the resulting parameter *b* of each species (b_{spn}) from the corresponding envelope function (PAR, *VPD* and Ψ) between the maximum *b* value of all the species (b_{MAX}):

V_{PAR} , V_{VPD} , V_{Ψ}□□= b_{spn} / b_{MAX} (8)

The component V_D, was obtained by dividing the distribution of each species (D_{spn}) by the broadest distribution of all the species D_{MAX}.

$V_D = 1 - (D_{spn} / D_{MAX})$ (9)

The highest vulnerability level corresponds to values close to 1 and the lowest to values close to 0.

Statistical analysis

Statistical analyses were conducted using R version 3.0.1 (R Development Core Team 2010). We used the non-paramatrical test Kruskal-Wallis to evaluate our data whether there were significant differences for three cases: *i*) to compare the climatological variables of T_A, PAR and *VPD* between greenhouse and field conditions; *ii*) to compare for each species the variables of g_S, T_A, PAR, *VPD* between greenhouse and field conditions, and *iii*) to compare the variables of g_S, T_A, PAR, *VPD,*

Ψ□among all the species under greenhouse and field conditions. Statistical significance was considered at 95% for all cases.

Influence of each variable (T_A, PAR, VPD, Ψ) across the eleven species was evaluated through a Principal Components Analysis (PCA). For this purpose, the dataset was organized into a single 4 variable X 11 species matrix, and the PCA was based on the correlation matrix of variables (Jongman et al., 1987). The PCA was used to identify the principal sources of variability. We calculated the relative importance (RI) of each component by measuring the length of each vector (Legendre and Legendre, 1998). The RI values estimated were multiplied for the vulnerability components (V_{TA}, V_{PAR}, V_{VPD}, V_{Ψ}□) of all the species to obtain the weighted or adjusted values.

5.3 RESULTS

To compare the species' response to the drifting variables we included in the comparison of climatological conditions between field and greenhouse the values of high T_A and VPD reached during the last days of the experiment (when the greenhouse was closed). We found no differences between greenhouse and field when comparing T_A (Kruskal-Wallis H = 1.5504, df = 1, $P = 0.2131$); whilst VPD (Kruskal-Wallis H = 11.0253, df = 1, $P = 0.0008988$) and PAR (Kruskal-Wallis H = 5.890, df = 1, $P = 0.015$) had significant differences. Greenhouse mean temperature was 25.62 ± 5.88 ºC, whereas the average temperature in the field was 24.02 ± 3.87 ºC. VPD average in the greenhouse was 1.64 ± 0.79 kPa, whereas in the field it was 1.48 ± 0.40 kPa. PAR average in the greenhouse was 133.57 ± 96.70 □mol m^{-2} s^{-1}, whereas in the field it was 675.55 ± 591.55 □mol m^{-2} s^{-1}.

We found significant differences when comparing for each species all the variables of g_S, T_A, PAR, VPD between greenhouse and field conditions (**Supplementary Table S5.1**); and we also found significant differences when comparing in the field the variables g_S, VPD and Ψ, and in geenhouse g_S and PAR between all the species (**Supplementary Table S5.2**). The highest g_S in field and greenhouse were recorded for *Q. xalapensis*, followed by *C. caroliniana*, whereas the lowest g_S corresponded to *L. styraciflua* and *O. virginiana*. The lowest Ψ belonged to *Q. xalapensis* and *Q. germana*, and the highest were *L. styraciflua* and *C. mexicana*. Similarly, the environmental parameters of PAR, VPD and T_A, varied between species and between field and greenhouse, where variations between species were related to variations in the measurement conditions (**Table 5.2**).

We observed different diurnal responses for some species. In the field all species showed the highest g_S at 10 or 18 h; however, under greenhouse conditions, some species showed the highest g_S at 12-14 h (*C. caroliniana, C. mexicana, C. florida, Q. candicans*, and *Q. xalapensis*). For Ψ□we observed that all the species had the lowest values at 14 h (**Table 5.3**). At 8 and 14 h *L. styraciflua* presented the highest values; in contrast, *Q. xalapensis* presented the lowest values. At 14 h we observed the highest Ψ in *L. styraciflua* (-0.34 MPa) and *C. mexicana* (-0.95 MPa), whereas *Q. xalapensis* (-3.48 MPa) and *Q. germana* (-2.03 MPa) had the lowest values (**Table 5.3**).

Table 5.2. Stomatal conductance (g_S), leaf water potential (Ψ), air temperature (T_A), vapor pressure difference (*VPD*) and photosynthetically active radiation (PAR) for eleven tree species from the tropical montane cloud forest in the field and in the greenhouse. The values represent the mean and the standard deviation (N = 250 for the field and 420 for the greenhouse for each species; except for Ψ, N = 100 for each species). No Ψ data were collected in the greenhouse to prevent stomatal response might be affected by the kinetic effect of the leaf excision.

	g_S (mmol m^{-2} s^{-1})		**T_A (ºC)**		***VPD* (kPa)**		**PAR (μmol m^{-2}s^{-1})**		**Ψ (MPa)**
Species	**Field**	**Greenhouse**	**Field**	**Greenhouse**	**Field**	**Greenhouse**	**Field**	**Greenhouse**	**Field**
Carpinus caroliniana	1049.13 (227.02)	883.52 (145.60)	26.1 (3.24)	23.93 (3.69)	1.65 (0.39)	1.56 (0.35)	665.54 (700.05)	117.96 (85.56)	-0.97 (0.37)
Clethra mexicana	1036.42 (182.37)	772.70 (140.58)	26.38 (2.66)	24.63 (3.77)	1.64 (0.33)	1.75 (0.34)	975.34 (735.35)	156.72 (126.88)	-0.66 (0.30)
Cornus florida var. *urbiniana*	1035.74 (182.18)	771.92 (139.19)	25.50 (3.05)	26.53 (2.32)	1.55 (0.32)	1.90 (0.21)	633.25 (626.30)	196.26 (140.19)	-0.98 (0.57)
Liquidambar styraciflua	950.27 (214.60)	688.32 (72.43)	26.06 (3.48)	26.47 (2.38)	1.76 (0.42)	1.86 (0.24)	455.85 (483.92)	143.40 (104.54)	-0.28 (0.07)
Ostrya virginiana	904.12 (357.95)	719.01 (62.35)	25.78 (4.14)	26.35 (2.30)	1.81 (0.53)	1.83 (0.24)	788.45 (743.76)	117.60 (89.35)	-1.13 (0.53)
Persea longipes	960.88 (197.54)	737.18 (68.90)	26.23 (3.07)	26.36 (2.37)	1.68 (0.39)	1.83 (0.23)	760.79 (658.95)	189.73 (138.96)	-1.26 (0.51)
Quercus candicans	1028.75 (154.25)	834.06 (114.77)	26.10 (2.76)	26.36 (2.31)	1.62 (0.34)	1.80 (0.24)	937 (735.31)	153.32 (116.07)	-0.89 (0.53)
Quercus germana	971.02 (189.21)	776.92 (92.65)	26.03 (3.04)	26.34 (2.42)	1.68 (0.38)	1.80 (0.26)	655.20 (652.41)	120.21 (99.80)	-1.46 (0.63)
Quercus xalapensis	1056.81 (474.03)	884.48 (193.61)	25.93 (3.65)	26.30 (2.36)	1.81 (0.45)	1.79 (0.26)	631.04 (610.54)	104.58 (75.97)	-2.86 (0.64)
Tapirira mexicana	1045.26 (191.60)	791.60 (88.24)	26.24 (2.71)	26.04 (2.24)	1.60 (0.33)	1.76 (0.25)	742.16 (712.10)	119.27 (87.06)	-0.93 (0.37)
Ulmus mexicana	1005.35 (182.48)	784.97 (63.37)	26.11 (2.98)	25.90 (2.20)	1.64 (0.38)	1.74 (0.24)	807.53 (738.32)	133.86 (96.64)	-1.21 (0.46)

The envelope function method analysis and the vulnerability index

We compared the parameters and the curves generated by the envelope function method between the eleven species performing the method for all the variables (T_A, PAR, *VPD* and Ψ) for each species (one case study is shown in **Figure 5.1**). We also obtained for each species the parameter values corresponding to each function (**Supplementary Tables S5.3, S5.4, S5.5, S5.6**).

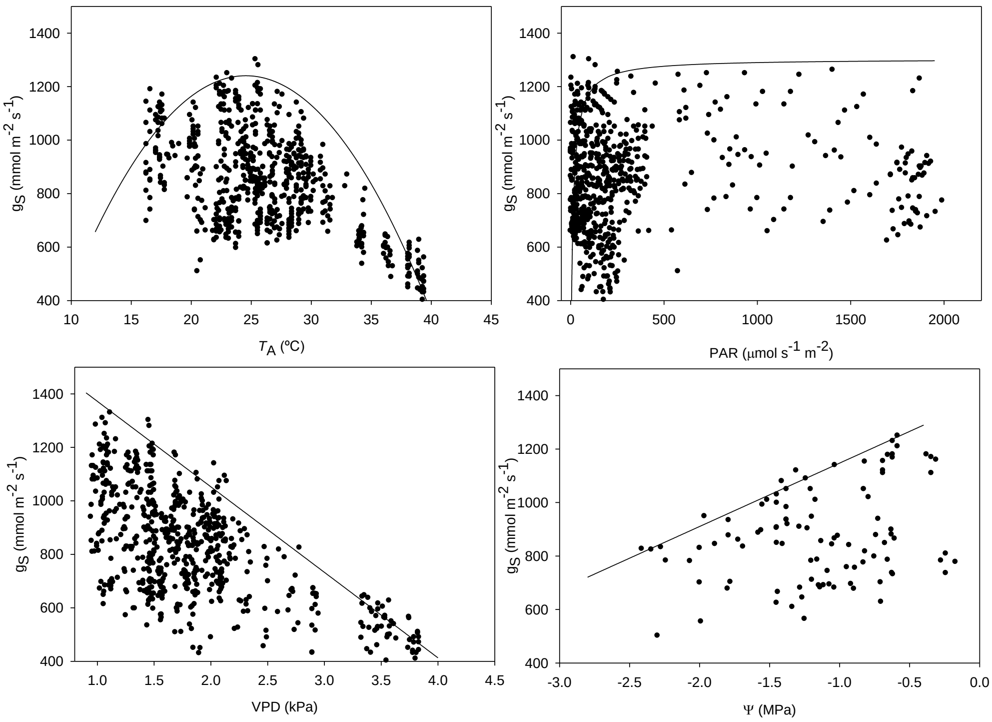

Figure 5.1. Scatter diagrams and probable boundary-line of stomatal conductance (g_S) plotted against air temperature (T_A), photosynthetically active radiation (PAR), vapor pressure deficit (*VPD*), and leaf water potential (Ψ) for *Quercus candicans*.

Table 5.3. Leaf water potential (Ψ) at 8 and 14 h (local time), and minimum Ψ value (Ψ_{MAX}) when stomatal conductance decreased by 50% for eleven tree species from the montane cloud forest in Mexico. Values represent the mean and the standard deviation (n = 50).

	Ψ (MPa)		
Species	**8 h**	**14 h**	**Ψ_{MAX}**
Carpinus caroliniana	-0.56 (0.05)	-1.32 (0.09)	-1.45
Clethra mexicana	-0.31 (0.10)	-0.95 (0.05)	-1.35
Cornus florida var. *urbiniana*	-0.40 (0.07)	-1.50 (0.29)	-3.04
Liquidambar styraciflua	-0.22 (0.03)	-0.34 (0.04)	-0.37
Ostrya virginiana	-0.66 (0.22)	-1.63 (0.12)	-1.73
Persea longipes	-0.78 (0.11)	-1.76 (0.07)	-1.81
Quercus candicans	-0.29 (0.07)	-1.38 (0.21)	-3.03
Quercus germana	-0.76 (0.15)	-2.03 (0.25)	-2.36
Quercus xalapensis	-2.21 (0.07)	-3.48 (0.04)	-3.51
Tapirira mexicana	-0.47 (0.04)	-1.26 (0.09)	-2.15
Ulmus mexicana	-0.83 (0.06)	-1.65 (0.07)	-2.35

We found in our results that all the species presented similar T_O (range: 19.4-24.6), optimal thermal ranges, and similar T_{MAX} (range: 30-35 ºC), with an optimal temperature for all the species of 21.9 ± 1.8 ºC, which was expected since all the species share the same habitat, this was also corroborated by not finding significant differences when comparing T_A between species (**Table S5.2**). For T_A, we considered species with the narrowest ranges as the most vulnerable. Using that measure, *C. mexicana* and *C. caroliniana* were the most vulnerable, and *U. mexicana* and *Q. candicans* the least vulnerable species. The T_O ranged from 19.4 °C (*O. virginiana*) to 24.6 ºC (*C. mexicana*). As for the optimal thermic intervals, the broadest range corresponded to *U. mexicana* and *Q. candicans* with 12.4-31.7 and 12.9-30.4 °C respectively. In contrast, the narrowest interval corresponded to *C. Mexicana* (17.7-31.8 °C). For T_{MAX} the highest temperatures corresponded to *Q. xalapensis* (35 ºC) and *Q. candicans* (34.4 ºC), and the lowest to *C. caroliniana* (31 ºC) and *O. virginiana* (32.1 ºC) (**Table 5.4**). For all species we observed a significant decrease in stomatal opening above 34 °C, where the most significant decrement corresponded to *O. virginiana*, with a decrease of 63%.

Concerning PAR, *VPD* and Ψ, the most vulnerable species were the ones with the highest values of parameter *b* of each equation. For PAR, *O. virginiana*, followed by *Q. xalapensis* and *Q. germana* reached the highest asymptotic values; observing a small difference between the eleven species with respect to this parameter (**Supplementary Table S5.4**). As for vulnerability, *C. mexicana* and *T. mexicana* were the most vulnerable species to changes in PAR, and *L. styraciflua* and *P. longipes* were the least vulnerable (**Table 5.6**).

Regarding *VPD*, *C. caroliniana* and *O. virginiana* reached the highest asymptotic g_S values, and they also were the most vulnerable species (**Supplementary Table S5.5**). As for VPD_{min}, for all the species the critical temperature and relative humidity values were above 33.8 ºC and less than 30% of humidity, where *Q. germana* presented the lowest VPD_{min} and *Q. candicans* the highest (**Table 5.5**). According to this parameter, the most vulnerable species were *C. caroliniana* and *O. virginiana*, and the least vulnerable were *Q. candicans* and *P. longipes* (**Table 5.6**).

Table 5.4. Optimal temperature (T_O), optimal thermal range (T_R), and maximum temperature when stomatal conductance decreased by 50% (T_{MAX}) for the stomatal function for eleven tree species. Values represent the mean and the standard deviation (n = 35).

Species	T_O (ºC)	T_R (ºC)	T_{MAX} (ºC)
Carpinus caroliniana	20.8 (0.2)	14.2 - 30.1	31.0
Clethra mexicana	24.6 (0.3)	17.7 - 31.8	33.4
Cornus florida var. *urbiniana*	23.6 (0.2)	15.3 - 33.1	32.8
Liquidambar styraciflua	20.4 (0.4)	12.5 - 29.9	34.2
Ostrya virginiana	19.4 (0.2)	11.9 - 30.5	32.1
Persea longipes	21.4 (0.4)	12.9 - 30.4	34.1
Quercus candicans	24.2 (0.4)	14.1 - 33.3	34.4
Quercus germana	20.6 (0.2)	12.1 - 30.7	34.2
Quercus xalapensis	20.4 (0.4)	12.8 - 29.9	35.0
Tapirira mexicana	23.4 (0.5)	12.8 - 31.4	34.2
Ulmus mexicana	22.6 (0.5)	12.4 - 31.7	33.4

For Ψ, *C. caroliniana* and *Q. xalapensis* reached the highest asymptotic values; whereas *C. florida* and *Q. candicans* had the lowest values (**Supplementary Table S5.6**). In terms of vulnerability, *L. styraciflua* and *C. caroliniana* were the most vulnerable species and *Q. candicans* and *C. florida* were the least vulnerable (**Table 5.6**). Concerning Ψ_{MAX} , we confirmed that the most vulnerable species were *L. styraciflua* and *C.caroliniana*, whilst *C. florida* and *Q. candicans* were less vulnerable (**Table 5.3**).

Table 5.5. Minimum vapor pressure deficit (VPD_{min}) when stomatal conductance decreased by 50%, and associated values of air temperature (T_A) for eleven tree species from the montane cloud forest in Mexico.

Species	VPD_{min} (kPa)	T_A (°C)
Carpinus caroliniana	2.93	34.4
Clethra mexicana	3.02	34.8
Cornus florida var. *urbiniana*	3.13	34.9
Liquidambar styraciflua	2.87	34.2
Ostrya virginiana	2.86	34.4
Persea longipes	2.96	34.2
Quercus candicans	3.18	34.8
Quercus germana	2.83	34.2
Quercus xalapensis	2.88	34.0
Tapirira mexicana	2.94	34.4
Ulmus mexicana	2.86	33.8

From the potential distribution maps generated we found that *Q. germana* had the most confined and limited distribution, and was considered the most vulnerable species. In contrast, *C. mexicana* showed the widest distribution, and was considered the least vulnerable species according to the index (**Table 5.6**). The estimated area of each species was: 1) *C. mexicana*: 3369.06 km^2; 2) *O. virginiana*: 3264.77 km^2; 3) *C. caroliniana*: 3211.49 km^2; 4) *Q. candicans*: 3169.55 km^2; 5) *P. longipes*: 3157.08 km^2; 6) *U. mexicana*: 2712.70 km^2; 7) *Q. xalapensis*: 2408.90 km^2; 8) *L. styraciflua*: 2013.27 km^2; 9) *T. mexicana*: 1872.71 km^2; 10) *C. florida*: 1504.29 km^2, and 11) *Q. germana*: 906.88 km^2 (**Figure 5.2**).

After analyzing the PCA, we found that all the variables had a similar influence in all the species, with similar vector lengths (**Supplementary Table S5.7, Figure S5.1**). However, we found that □ was the variable with the highest relative importance (100%), followed by *VPD* (99.27%), T_A (97.85%), and PAR (82.94%). We considered a relative importance of 100% for potential distribution due to the metodological implications used to estimate this variable. All the values obtained by the respective component index of each species were weighted using the RI values, and averaged later.

Regarding our vulnerability index, we found that the most vulnerable species was *L. styraciflua* and the least vulnerable was *P. longipes* (**Table 5.6**).

Table 5.6. Vulnerability indices (I_{sp} and I_V) of eleven tree species from the montane cloud forest, Veracruz, Mexico, considering five components: Vulnerability to temperature (V_{TA}), vulnerability to photosynthetically active radiation (V_{PAR}), vulnerability to vapor pressure deficit (V_{VPD}), vulnerability to leaf water potential (V_Ψ), and vulnerability to geographical distribution (V_D). The highest values (high vulnerability) and the lowest values (low vulnerability) for each component are indicated in bold.

Species	V_{TA}	V_{PAR}	V_{VPD}	V_Ψ	V_D	I_{sp}
Carpinus caroliniana	0.17	0.65	**0.99**	0.27	0.05	0.42
Clethra mexicana	**0.25**	**0.83**	0.71	0.12	**0.00**	0.38
Cornus florida var. *urbiniana*	0.08	0.32	0.68	0.04	0.55	0.34
Liquidambar styraciflua	0.10	**0.14**	0.76	**1.00**	0.40	**0.48**
Ostrya virginiana	0.04	0.46	0.93	0.14	0.03	0.32
Persea longipes	0.10	0.15	0.68	0.17	0.06	**0.23**
Quercus candicans	0.01	0.50	**0.67**	**0.04**	0.06	0.25
Quercus germana	0.03	0.32	0.75	0.07	**0.73**	0.38
Quercus xalapensis	0.11	0.68	0.85	0.11	0.28	0.41
Tapirira mexicana	0.03	0.76	0.79	0.08	0.44	0.42
Ulmus mexicana	**0.00**	0.35	0.74	0.07	0.19	0.27
				I_V		0.36

5.4 DISCUSSION

The envelope function method (EFM) and the importance of stomatal conductance (g_S)

To understand how changes in temperature, irradiance, and soil water balances actually affect photosynthesis, growth, and in our particular case g_S, we used the EFM which allowed us to predict plant performance outside a species' native range (Rodriguez et al., 2002; Dye et al., 2004), allowed us to describe the g_S responses to the different variables (T_A, PAR, *VPD*, and Ψ), and we were also able to assess and compared the species vulnerability through the use of a vulnerability index within the ecosystem.

In this study we used the g_S response as a vulnerability indicator, considering that g_S is a key response of plants to climate, controling transpiration (water status) and CO_2 assimilation, and playing an important role in photosynthesis and plant productivity (Jones, 1992). Thus, when determining g_S responses to different climatic factors in combination with the models from the EFM, the possible effects of climate change can be inferred. And, although we acknowledge that g_S is not the only physiological trait that can be used to assess vulnerability, we used it considering that g_S provides a reflection of micro-environmental conditions and physiological processes.

However, it must be considered that g_S is species-specific and the g_S response to environmental variables might be reflection of the species plasticity (Buckley and Mott, 2013). Also, this response might be a plant phenotypic plasticity and resilience to climate changes and to environmental factors (Nicotra et al., 2010; Gratani, 2014). Differences among species represent their different evolutionary histories and their particular niche adaptations, and although all the species studied share the same environment, they respond differentially to environmental factors. Therefore, when we compared the g_S response among species, we also compared and evaluated the vulnerability linked to specific adaptations of each species.The study of the environmental g_S responses, also helped us to understand the control of transpiration and assimilation in natural and artificial environments, in our case the greenhouse.

From the envelope function method we observed that the values of the coefficient of determination (r^2) for the boundary-lines were indicative of a suitable approach to stomatal function ranges. The fit of g_S *vs.* T_A, PAR, *VPD* and Ψ□showed a higher sensitivity of g_S to the driving variables. Changes in stomatal sensitivity to T_A and *VPD* can be attributable to a wider range of g_S responses registered in the field as a possible effect of the differences measured between T_A related to high humidity in the region. This differential response of g_S to the microenvironment (T_A and *VPD*) might be due to an acclimation of stomata to the thermal variation of the environment. In general, the values of the coefficients of determination of the model were indicative of an agreement between observed g_S values and the values generated from the model. And, although the model itself is not efficient for explaining stomatal variation in different time and places, the use of the boundary-line function is a strong tool for analyzing separately the g_S responses.

It has been demonstrated from studies in tropical forests and pastures that empirical approximations, such as the EFM, are site specific (Wright et al., 1996; Barradas et al., 2004). Our results reported here comparing conditions between field and greenhouse corroborated the site specificity due to particular environmental conditions, but also that this method might be considered as individual-specific. Therefore, care is needed when attempting to extrapolate the method parameters to other sites and individuals in different conditions and time, especially if it is not including data from the field and greenhouse.

Due to these considerations we considered the importance of combining data from the field and greenhouse, proving that data from both environments are complementary. We enriched the data from greenhouse by exposing plants to extreme conditions, which cannot be found in the natural environment (high temperature). In addition, we observed that the g_S response is not always the same in the field and greenhouse, as we found differences between the g_S diurnal variations. In the field, all the species presented the lowest g_S at midday, and the highest g_S at sunset or dawn. Plants may be able to increase their photosynthetic carbon gain by preopening stomata before dawn (Caird et al., 2007). This might be especially advantageous in water-limited environments because of a higher potential for early morning carbon gain when T_A and *VPD* are lower (Galmés et al., 2011). Stomatal opening and closing rates are affected directly by T_A, *VPD* and water status.

Midday stomatal closure should be a well-developed characteristic in species that are regularly confronted with drought stress. In the greenhouse, water was not a limiting factor, which allowed stomatal opening at midday. We found midday stomatal closure in some of the woody species studied. However, species-specific differences in sensitivity to high leaf temperatures and to large humidity deficits, and species-specific differences in the tendency to exhibit midday stomatal closure, were found only in the greenhouse in potted studied plants under artificial conditions and not in the natural habitat. Also, midday stomatal closure commonly occurs during periods of high light intensity, which contributes to increased leaf temperature and consequently to increased humidity due to temperature differences between leaf and air. Differences found between field and greenhouse might be caused by PAR. PAR intensity might be regulatintg the oxidative stress during iddday in the field, but this did not occur in the greenhouse due to the low PAR intensity. Light intensity might have stimulated stomatal opening at temperatures between 25 and 35 ºC, whereas increased leaf temperature or increased air humidity would lead to stomatal closure.

Concerning Ψ□ in some plant species in arid ecosystems, midday stomatal closure has been correlated with changes in Ψ□(Roy and Mooney, 1982), similar to our results in the field and greenhouse. Previous studies also found significant differences when comparing the g_S response to □□under experimental conditions, reporting that stomatal response might be affected by the kinetic effect of the leaf excision involved during the □ measurment. This effect probably causes a decrease in photosynthesis and g_S by pressure changes in the xylem and by stomata closure (During 1993; Bunce 1999; Powles et al. 2006). Therefore, we did not measure Ψ in the greenhouse. Nevertheless, we encourage future replications measuring □□in the greenhouse, but considering these implications.

Species vulnerability

In this study, we found that temperatures above 34 ºC, and *VPD* values above 2.9 kPa with RH below 30% limited g_S performance of all the species. The decrease in g_S has been attributed to a decrease in Ψ□(e.g. Comstock and Mencuccini, 1998), to increasing *VPD* and T_A (e.g. Maroco et al., 1997), or to a combination of these factors; but if we consider species individually we observed differences among the g_S responses. These responses allowed us to considered *L. styraciflua C. caroliniana* and *T. mexicana* as the most vulnerable species; whereas *P. longipes*, and *Q. candicans* were the least vulnerable.

Concerning Ψ, the most important variable according to the RI from the PCA, we found significant differences, especially when comparing the most vulnerable species (*L. styraciflua*) and the least vulnerable (*Q. candicans*). Stomatal conductance was highly correlated to *VPD* and T_A but not as much to Ψ. This suggests that the control of stomatal opening is mainly a function of the atmospheric evaporative demand rather than a response to the plant water status (Meinzer, 2002), may be because water is not a limiting factor in the montane cloud forest and under greenhouse conditions. However, Ψ should not be underestimated, particularly in arid environments or in regions where water is a limiting factor. Also, changes in □ are not necessary related to low □□values; this was corroborated in our results, where *Q. candicans* was the least vulnerable species, whilst *Q. xalapensis* reached the lowest Ψ (**Table 5.3**). Opposite to this finding, *L. styraciflua* was the most vulnerable species with the highest Ψ□(**Table 5.3**).

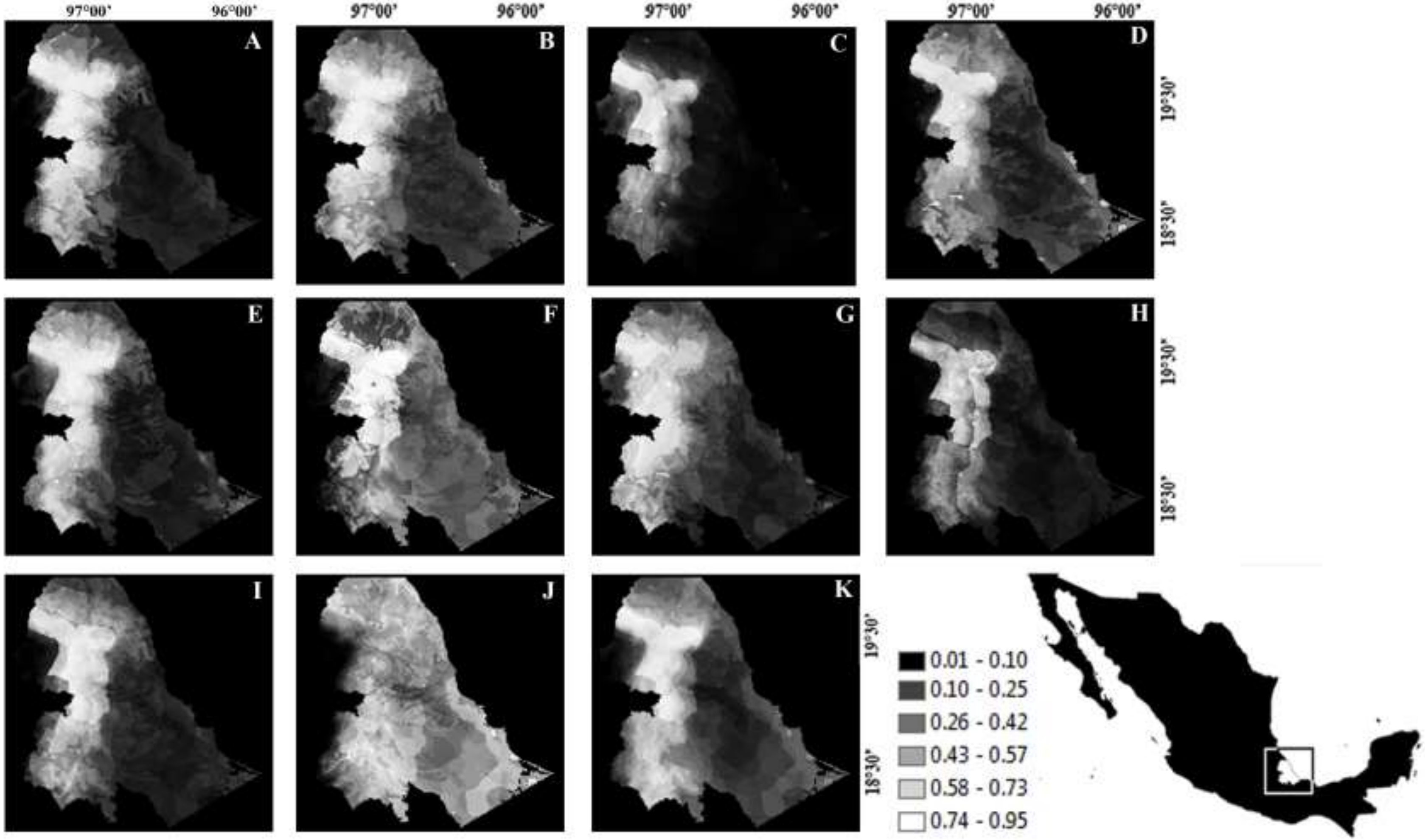

Figure 5.3. Potential distribution and the probability color scale of *Carpinus caroliniana* (A), *Clethra mexicana* (B), *Cornus florida* var. *urbiniana* (C), *Liquidambar styraciflua* (D), *Ostrya virginiana* (E),), *Persea longipes* (F), *Quercus candicans* (G), *Q. germana* (H), *Q. xalapensis* (I), *Tapirira mexicana* (J), and *Ulmus mexicana* (K) in the central mountain region of Veracruz, Mexico.

Concerning the geographical distribution, we considered that the species distribution is an accurate and complementary component for our vulnerability analysis. Species with more confined distributions are more likely to suffer the impacts of environmental and climate changes, particularly those species that require more specific micro- and climatic conditions. The potential species distribution represents an indirect reflection of temperature, precipitation and other climate parameters that establishes the presence/absence of a given species.

The vulnerability index: ecological relevance and limitations

In this work we considered the sensitivity of the species, the parameter *b* from the EFM, as a vulnerability indicator, reflecting g_{S} sensitivity to changes in the variables of each species. As a result, a species with a broader thermal range, and lower values of the parameter *b*, was considered to be better fitted to face and tolerate environmental changes, whereas a species whose thermal range was narrower, and the vulnerability parameter was higher, was considered less tolerant and more vulnerable to disturbances.

The use of sensitivity as a vulnerability indicator has been proposed previously by other authors (e.g. Tremblay-Boyer and Ross-Anderson, 2007; Young et al., 2010; Loehle, 2014). The importance of sensitivity relies on its capacity to explain the species' adaptations to external factors as a means of identifying what causes vulnerability differences (Berry et al., 2006). Also, vulnerability is a function of the character, magnitude and rate of climate change and variation to which a system is exposed, its sensitivity, and its adaptive capacity (IPCC, 2001). Predicted sensitivity to temperature and precipitation changes is of particular importance. Species requiring specific precipitation and temperature regimes may be less likely to find similar areas as climate change and previously associated temperature and precipitation patterns uncouple (e.g. Hawkins et al., 2008; Laidre et al., 2008). Also, species dependent on habitats that are maintained by regular disturbances (e.g. fires or flooding) are vulnerable to changes in the frequency and intensity of these disturbances (IPCC, 2001; Archer and Predick, 2008), also species with more confined distributions are more vulnerable.

We acknowledge that our index has some limitations. It only considers two physiological traits, g_{S} and Ψ, three climate variables, T_{A}, PAR and *VPD*, and the species distribution, and although we recognize that there are other traits and variables relevant to describe species vulnerability, we considered our index accurate, due to the g_{S} importance, and because it is useful to compare vulnerability among species. Also, the evaluated climate variables helped us to understand the species response to climate variability, by measuring directly the effect of T_{A}, and indirectly the effect of water availability through Ψ. Changes in PAR and *VPD* are also affected indirectly by T_{A} and water availability; where the PAR increment will concur with the substrate temperature and water loss from the soil, and changes in T_{A} and humidity will cause effects on *VPD*. Due to these interactions we considered that the five components of our index ($V_{T\mathrm{A}}$, V_{PAR}, V_{VPD}, $V\Psi$, $V_{D\square}\square$) could provide an accurate vulnerability status of a given species.

Another limitation of our index is the fact that it is only comparative; however, we found it efficient because it gathers information about variables that might be affected by environmental changes (T_A, PAR, *VPD* and Ψ). Nonetheless, we do not consider that this detracts from the effectiveness and assertiveness of the index. We also encourage using more physiological traits and climate variables for future research. Another consideration, concerning to diurnal variation, is that T_A, PAR and *VPD* are not the only variables that vary during day. The antioxidant capacity of leaves also varies during the day and seasonally (Ni et al., 2012), and althoug this variable was not considered for our study, it should be addressed its importance, considering that this variable might jeopardize the g_S response if, in a future scenario of climate change, the variable will change at different times of the day.

The index allows to prioritize the approach of vulnerability studies by telling which species is most vulnerable. Also, the index might be used to compare species, functional groups or species from different ecosystems, taking into account the limitations mentioned above. Irrespective of these considerations, we consider that our index has great ecological relevance, because it links physiological responses to climate variables. We encourage future replications in other ecosystems using other physiological traits and climate variables. We also encourage the development of a homonym index for other taxonomical groups, such as animals.

Future implications

Gradual increases in temperature, changes in rainfall patterns, or modification in solar radiation will likely impact on growth, regeneration and natural rates of mortality (Chapin et al., 2010). Previous studies from our study region revealed negative precipitations and positive temperature trends (Esperón-Rodríguez and Barradas 2014a, 2014b), suggesting a possible regional climate change, implying potential reductions in precipitation of as much as 50% by the year 2023, and increment of consecutive dry days by the year 2099 (Cervantes et al., 2001; Barradas et al., 2010; Esperón-Rodríguez and Barradas 2014a). Also, decreased rainfall and fog frequency is expected (Barradas et al. 2010, 2011). These changes also have repercussions on other climatic variables such as solar radiation, which is expected to be more intense where both rainfall and the frequency of fog decreased (Barradas et al., 2011).

It is also important to consider that interactions of species under climate change will probably be altered, thus influencing potential distributions (Davis et al., 1998). We must consider the expected change in species distributions regarding dispersal abilities. Dispersal abilities will play an important role for the species to reach places where the environmental conditions will be more favorable for their establishment, growth, and eventual reproduction.

Increases in temperature predicted by climate change models reflect species vulnerability against these changes. Species might respond to this vulnerability by migrating to higher elevations where temperature is lower. Management plans and policies that incorporate the response of species and ecosystems are required to assist species to respond to rapid environmental changes (del Barrio et al., 2006). It must be considered that if a species does not have the ability to migrate to higher elevations due to the lack of effective seed dispersal, this migration process could be assisted, starting with the most vulnerable species. However, it is important to mention that the climate variables are not the only parameters delimiting the species' distribution. Factors such as deforestation, agriculture and urban growth, counteract the species' conservation. Scientists and policymakers must work together to implement proper plans and actions that not only guarantee the preservation of the species but also benefit the local communities.

5.5 CONCLUSIONS

We proposed the EFM as a useful tool for assessing regional environmental vulnerability by comparing species with the development of the vulnerability index in a case study in the montane cloud forest of eastern Mexico. This method allowed us to integrate climate and physiological variables. Our results showed that species responded differentially to the variables of T_A, PAR, *VPD* and Ψ. However, the vulnerability index allowed us to conclude that the most vulnerable species was *L. styraciflua*. In terms of temperature *C. mexicana* and *C. caroliniana* were also vulnerable, and in terms of geographical distribution, *Q. germana* and *C. florida* were the most vulnerable species.

Finding Ψ□as the variable with more influence over the species studied followed by *VPD*, showed that even in the MCF water is a determinant factor for the species' establishment and development. The EFM needs to be considered with caution due to the differences between species and sites. Further use with other species, in other regions and ecosystems should pay attention to what microclimatic conditions are important in determining the local environmental vulnerability and how is the impact of each variable on the complex environment. Our vulnerability index can be considered as an ecophysiological index, which evaluates and compares the species' vulnerability through the link of physiological traits, climate variables and geographical distribution.

SUPPLEMENTARY MATERIAL

Table S5.1. Kruskal-Wallis analysis between greenhouse and the field for stomatal conductance (g_S), air temperature (T_A), vapor pressure difference (*VPD*) and photosynthetically active radiation (PAR) for eleven species from the montane cloud forest of eastern Mexico. For all cases statistical significance $P < 0.05$.

	g_S		T_A		*VPD*		PAR	
Species	**H**	***P***	**H**	***P***	**H**	***P***	**H**	***P***
Carpinus caroliniana	51.256	< 0.0001	2.456	0.117	9.419	0.0021	15.863	< 0.0001
Clethra mexicana	75.383	< 0.0001	6.285	0.043	25.125	< 0.0001	31.569	< 0.0001
Cornus florida var. *urbiniana*	76.024	< 0.0001	6.769	0.009	27.090	< 0.0001	12.562	0.0003
Liquidambar styraciflua	51.973	< 0.0001	3.006	0.082	7.832	0.005	6.895	0.008
Persea longipes	44.108	< 0.0001	3.186	0.074	12.549	0.0003	11.984	0.0005
Ostrya virginiana	9.6372	0.001	1.7908	0.180	1.962	0.161	34.767	< 0.0001
Quercus candicans	66.188	< 0.0001	3.082	0.079	12.502	0.0004	26.070	< 0.0001
Quercus germana	32.135	< 0.0001	2.062	0.150	6.567	0.0103	27.823	< 0.0001
Quercus xalapensis	3.597	0.057	2.440	0.118	1.942	0.163	22.622	< 0.0001
Tapirira mexicana	50.596	< 0.0001	2.477	0.115	12.120	0.0004	38.577	< 0.0001
Ulmus mexicana	41.165	< 0.0001	3.572	0.167	9.668	0.007	16.857	0.0002

Table S5.2. Stomatal conductance (g_S), leaf water potential (Ψ), air temperature (T_A), vapor pressure difference (*VPD*) and photosynthetically active radiation (PAR) Kurskal-Wallis analysis under field and greenhouse conditions for the eleven species.

Conditions	**Test/Probability**	g_S	Ψ	T_A	**VPD**	**PAR**
Field	H	71.8538	108.8216	2.8268	24.5303	14.7839
	P	< 0.0001*	< 0.0001*	0.9852	0.00631*	0.1401
Greenhouse	H	54.1054	-	1.7863	13.552	57.1896
	P	< 0.0001*	-	0.9977	0.1944	< 0.0001*

Statistical significance $P < 0.05$*

Table S5.3. Parameters of the calculated envelope functions for stomatal conductance versus air temperature (T_A) for eleven tree species from the montane cloud forest. A, B and C are parameters of the parable. r^2 is the coefficient of determination.

Species	**A (mmol m^{-2} s^{-1})**	**B (mmol m^{-2} s^{-1})**	**C (mmol m^{-2} s^{-1})**	r^2
Carpinus caroliniana	-359.51	143.82	-3.22	0.835
Clethra mexicana	-1344.29	201.47	-4.03	0.816
Cornus florida var. *urbiniana*	-1063.24	187.42	-3.80	0.916
Liquidambar styraciflua	-99.91	130.09	-3.05	0.890
Ostrya virginiana	-444.13	186.62	-4.38	0.847

Persea longipes	-207.36	127.94	-2.98	0.830
Quercus candicans	-995.001	182.15	-3.71	0.931
Quercus germana	-205.41	138.98	-3.18	0.882
Quercus xalapensis	-337.34	157.66	-3.66	0.846
Tapirira mexicana	-382.05	147.36	-3.29	0.962
Ulmus mexicana	-400.21	150.34	-3.37	0.956

Table S5.4. Parameters of the calculated envelope functions for stomatal conductance versus photosynthetically active radiation (PAR) for eleven tree species from the montane cloud forest. *a* is the asymptotic value of g_S or g_{SMAX}, and *b* is g_S sensitivity to changes in PAR. r^2 is the coefficient of determination. The highest asymptotic values (*a*), and sensitivity to changes in PAR (*b*) are indicated in bold.

Species	***a* (mmol m^{-2} s^{-1})**	***b* (mmol m^{-2} s^{-1})**	**r^2**
Carpinus caroliniana	1567.03	14.12	0.967
Clethra mexicana	1375.53	**18.09**	0.825
Cornus florida var. *urbiniana*	1420.84	6.99	0.899
Liquidambar styraciflua	1424.002	3.14	0.995
Ostrya virginiana	**1876.69**	10.19	0.807
Persea longipes	1343.39	3.21	0.878
Quercus candicans	1303.93	10.88	0.808
Quercus germana	1575.27	7.05	0.812
Quercus xalapensis	**1578.07**	14.79	0.926
Tapirira mexicana	1492.35	**16.73**	0.922
Ulmus mexicana	1379.56	7.61	0.894

Table S5.5. Parameters of the calculated envelope functions for stomatal conductance versus vapor pressure deficit (*VPD*) for eleven tree species from the montane cloud forest. *a* is the zero drift, and *b* is g_S sensitivity to*VPD*. r^2 is the coefficient of determination. The highest asymptotic values (*a*), and sensitivity to changes in *VPD* (*b*) are indicated in bold.

Species	***a* (mmol m^{-2} s^{-1})**	***b* (mmol m^{-2} s^{-1})**	**r^2**
Carpinus caroliniana	**2144.11**	**-478.54**	0.977
Clethra mexicana	1737.48	-344.43	0.987
Cornus florida var. *urbiniana*	1711.29	-332.62	0.976
Liquidambar styraciflua	1802.71	-367.18	0.964
Ostrya virginiana	**2129.69**	**-450.08**	0.970
Persea longipes	1674.20	-325.83	0.954
Quercus candicans	1691.81	-319.72	0.986
Quercus germana	1788.61	-363.78	0.959
Quercus xalapensis	1976.09	-412.47	0.997
Tapirira mexicana	1847.12	-382.83	0.986
Ulmus mexicana	1721.83	-357.36	0.986

Table S5.6. Parameters of the calculated envelope functions for stomatal conductance versus leaf water potential (Ψ) for eleven tree species from the montane cloud forest. *a* is the zero drift, and *b* is g_S sensitivity to Ψ. r^2 is the coefficient of determination. The highest asymptotic values (*a*), and sensitivity to changes in *VPD* (*b*) are indicated in bold.

Species	***a* (mmol m^{-2} s^{-1})**	***b* (mmol m^{-2} s^{-1})**	**r^2**
Carpinus caroliniana	**2962.75**	**1531.77**	0.998
Clethra mexicana	1629.32	690.47	0.926
Cornus florida var. *urbiniana*	1436.71	251.86	0.987

Liquidambar styraciflua	2849.89	**5627.52**	0.997
Ostrya virginiana	2199.43	785.25	0.978
Persea longipes	2458.17	970.66	0.999
Quercus candicans	1384.54	237.04	0.965
Quercus germana	1638.80	377.56	0.972
Quercus xalapensis	**2998.05**	628.77	0.987
Tapirira mexicana	1630.89	434.32	0.946
Ulmus mexicana	1623.39	392.87	0.995

Table S5.7. Length of the vectors of the principal component analysis (PCA), their relative importance and Eigenvector scores of plant traits in the first three principal components analysis axes. Values are ranked in order of absolute magnitude along PCA axes. Values in parentheses indicate variance accounted for by each axis.

Trait	**Length**	**RI**	**PCA1 (62.54%)**	**PCA2 (21.31%)**	**PCA3 (15.24%)**
Leaf water potential (Ψ)	2.737	1.000	-1.492	2.2945	-0.7853
Vapor pressure deficit (*VPD*)	2.717	0.9926	2.715	0.1029	-0.7579
Air temperature (T_A)	2.678	0.9784	2.662	0.2930	-0.8928
Photosynthetically active radiation (PAR)	2.270	0.8294	1.898	1.2457	1.7191

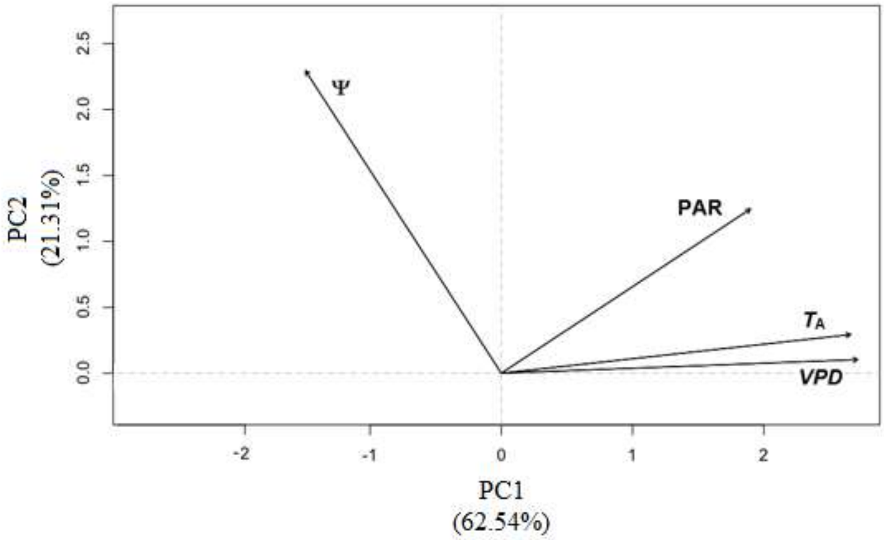

Figure S5.1. Principal Components Analysis (PCA) for the leaf water potential (Ψ), vapor pressure deficit (*VPD*), air temperature (T_A) and photosynthetically active radiation (PAR). Values in parentheses indicate variance accounted for by each axis.

Capítulo 6

Vulnerabilidad socio-económica frente al cambio climático en la región central montañosa del este de México

Socio-economical vulnerability to climate change in the in the central mountainous region of eastern Mexico

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(Sometido)

RESUMEN: Se espera que los efectos del cambio climático sean más grave para algunos segmentos de la sociedad que otros debido a la ubicación geográfica, el grado de asociación con ambientes sensibles al clima, y a características culturales, económicas o políticas particulares de cada población humanas. La vulnerabilidad social se define como la susceptibilidad de una población determinada a ser dañada por la exposición a un peligro, lo que afecta directamente su capacidad para prepararse, responder y recuperarse. En México, la variabilidad climática asociada con el cambio climático tiene un importante impacto socio-económico y ambiental, y para la región de las Grandes Montañas, Veracruz, la vulnerabilidad socio-económica es de gran preocupación, ya que 62,42% del territorio se dedica a actividades agrícolas, mientras que 36.37% presenta diferentes tipos de vegetación, incluyendo el bosque mesófilo de motaña, que es un ecosistema amenazado. Se analizaron los datos relacionados con precipitación total anual y temperatura promedio anual de 26 estaciones meteorológicas, encontrando diferentes tendencias de temperatura y precipitaciones. También desarrollamos escenarios de cambio climático con base en estas tendencias con proyecciones hacia os años 2025, 2050, 2075 y 2100, encontrando considerables cambios climáticos locales con reducciones en las precipitaciones de más de 700 mm y un aumento de la temperatura de ~9 ºC para el año 2100. Las áreas deforestadas ubicadas a barlovento fueron considerados más vulnerables, lo que representa un riesgo potencial para el medio ambiente natural, las comunidades locales y los principales cultivos (caña de azúcar, café y maíz). Encontramos que la vulnerabilidad aumenta en las zonas donde se incrementa la temperatura y disminuye la precipitació..

Palabras clave: Cambio climático · vulnerabilidad económica · vulnerabilidad social · Región de las Grandes Montañas · Veracruz · México

ABSTRACT: Effects of climate change are expected to be more severe for some segments of society than others because of geographic location, degree of association with climate-sensitive environments, and unique cultural, economic or political characteristics of particular landscapes and human populations. Social vulnerability is defined as the susceptibility of a given population to be harmed from exposure to a hazard, directly affecting its ability to prepare for, respond to, and recover. In Mexico, climate variability associated with climate change has an important socio-economic and environmental impact, and for the region of the Great Mountains, Veracruz, socio-economic vulnerability is of great concern, with 62.42% of the territory comprised to agricultural activities, whereas 36.37 % presents different vegetation types, including the montane tropical cloud forest, which is a threaten ecosystem. Data related to total annual precipitation and average annual temperature from 26 meteorological stations were analyzed and different temperature and precipitations trends were found within the region. We also developed climate change scenarios based on these trends with projections to 2025, 2050, 2075 and 2100, finding considerable local climate changes with reductions in precipitation of over 700 mm and increases in temperature of ~9 ºC for the year 2100. Deforested areas located at windward were considered more vulnerable, representing potential risk for natural environments, local communities and the main crops they cultivate (sugarcane, coffee and corn). We found that vulnerability increases in areas where temperature increases and precipitation decreases.

Key words: Climate change · economical vulnerability · social vulnerability · Great Mountains Region· Veracruz · Mexico

6.1 INTRODUCTION

Climate change is increasingly accepted as a major issue facing human societies (Houghton et al. 2001), and it is recognized as one of the most serious challenges facing the world, the people, the environment and the economy (Lindner et al. 2010). Climate change will increase the intensity and frequency of extreme weather events (IPCC 2001). Impacts of extreme climate events are therefore, the principal climate phenomenon enhancing vulnerability (Adger 1996). Climate change is expected to alter precipitation patterns and increase temperature. Temperature has increased at unprecedented rates in the last 100 years, and warming trends are particularly pronounced at higher latitudes (Houghton et al. 2001). Also, frequency and intensity of extreme events have increased in recent years (IPCC 2001). Changes in mean and variance of rainfall and temperature, extreme weather events, food and agriculture production and prices, water availability and access, nutrition and health status are expected. The most adverse impacts are predicted to occur in the developing world because of the geographic exposure, reliance on climate sensitive sectors, low incomes, and weak adaptive capacity. Socio-economic impacts are likely to be profound and will impact humans through a variety of direct and indirect pathways (Cline 2007; IPCC 2007).

Effects of climate change are expected to be more severe for some segments of society than others, because of geographic location, degree of association with climate-sensitive environments, and unique cultural, economic and political characteristics of particular landscapes and human populations (Lynn et al. 2011). In the IPCC report “the Regional Impacts of Climate Change: An Assessment of Vulnerability”, it is argued that the vulnerability of a region depends to a great extent on its wealth, where poverty limits adaptive capabilities (Watson et al. 1998). The report argues that socio-economic systems typically are more vulnerable in developing countries where economic and institutional circumstances are less favorable, and vulnerability is higher in places with greater sensitivity to climate change (Watson et al. 1996). Socio-economic factors that determine the adaptive capacity to climate change include economic development, technology and infrastructure, information, knowledge and skills, institutions, equity and social capital (McCarthy et al. 2001). Also, vulnerability is influenced by social, economic, cultural and political conditions, and processes operating at multiple scales over time and space, and change in these non-climatic conditions playing an important role in determining vulnerability (Ford et al. 2010).

Social vulnerability is defined as the susceptibility of a given population to be harmed from exposure to a hazard, directly affecting its ability to prepare for, respond to, and recover (Hewitt 1997). It is also defined as the exposure of groups or individuals to stress as a result of social and environmental change, where stress refers to unexpected changes and disruption of livelihoods (Adger 1999). Vulnerability is a socially constructed phenomenon influenced by institutional and economic dynamics. A system's vulnerability to climate change is determined by its exposure, physical setting, ability and opportunity to adapt to change (Granados 2012). Social vulnerability and equity in the context of climate change are important because some populations may have less capacity to prepare for, respond to, and recover from climate-related hazards and effects. Such populations may be disproportionately affected by climate change and natural hazards (Lynn et al. 2011).

Vulnerability to climate change

Vulnerability to climate change is defined as the degree to which a system is susceptible to, or unable to cope with, adverse effects of climate change, where vulnerability is a function of a system's sensitivity to change in climate, and the ability to adapt the system to climate changes (IPCC 2001). Also, vulnerability to climate change is the propensity of human and ecological systems to suffer harm and their ability to respond to stresses imposed as a result of climate change effects (Adger et al. 2007). The United Nations (2004) identified four internal vulnerability factors as relevant for disaster reduction; economic, social, physical and environmental. In the present work, our aim is to consolidate both approaches to make a socio-economic analysis based on climatic changing conditions caused by climate change.

Vulnerability, Poverty and Agriculture

Although related, vulnerability and poverty are different concepts; but it has been found that poor people are usually among the most vulnerable (Moser 1998). Poverty is an important aspect of vulnerability because it is directly associated to resource access. Poverty affects vulnerability through individuals' expectations of impacts of hazards and their ability to invest to alleviate risks; also affects coping and recovery from extreme events and reduces resilience to impacts (Adger 1999). Impacts of climate changes fall disproportionately on people that have contributed the least to cause the climate change problem, and have the least resources to cope with it (Mendelsohn et al. 2006), with food security being one issue of major concern. Adaptation to climate change to ensure adequate food security must take into account the diversity of the vulnerable populations and their capacity to respond to global climate change (Handmer et al. 1999).

Climate change is likely to affect crop yields and agriculture differently from region to region (Parry et al. 1999). Agriculture is inherently sensitive to climate conditions, and is vulnerable to global climate change (Parry and Carter 1998). Adaptation is an important component of any policy response to climate change in this sector (Reilly and Schimmelpfennig 1999). Studies show that without adaptation, climate change is generally problematic for agricultural production, economies and communities (Wheaton and McIver 1999). But agricultural systems are vulnerable to climate variability, whether naturally forced or due to human activities. Food crops productivity is inherently sensitive to climate variability due to changes in precipitation. Producers need to have physical, agricultural, economic and social resources to moderate, or adapt to, the impacts of climate variability (Challinor et al. 2007).

6.2 Materials and Methods. A case study: the region of the Great Mountains, Veracruz, Mexico

Study area

The Region of the Great Mountains (RGM) is located in the south-central part of Veracruz (19º54'08'' N, 96º57'19'' W) (**Figure 6.1**) with a surface of 6350.85 km^2, bordered on north by the Capital Region, on east by the region Sotavento, on west by the state of Puebla, southeast by the Region Papaloapan, and on south by the state of Oaxaca. The region is part of the Neovolcanic Ridge and the Sierra Madre Oriental. Abrupt topography is the main characteristic, going from sea level to up 5500 m asl in a distance of 100 km. Vegetation types go from tropical cloud forest to semi-arid and arid communities (Gómez-Pompa 1978; Barradas 1983). Average annual temperature ranges between 10-29 ºC, and annual precipitation ranges from 600-1200 mm, with a maximum of 3000 mm.

Vegetation and land-use

The region is known for its land-use guidance to primary sector activities with more than 67.9% of its territory intended to pasture and agricultural activities. According to the National Institute of Statistics and Geography (INEGI, 2013), 62.42% of the territory (3779.32 km^2) is comprised to agricultural activities, whereas 36.37% (2202.57 km^2) presents different vegetation types, and only 1.18 % (71.89 km^2) of the territory has urban cover (**Table 6.1, Figure 6.1**).

Socio-economic data collection

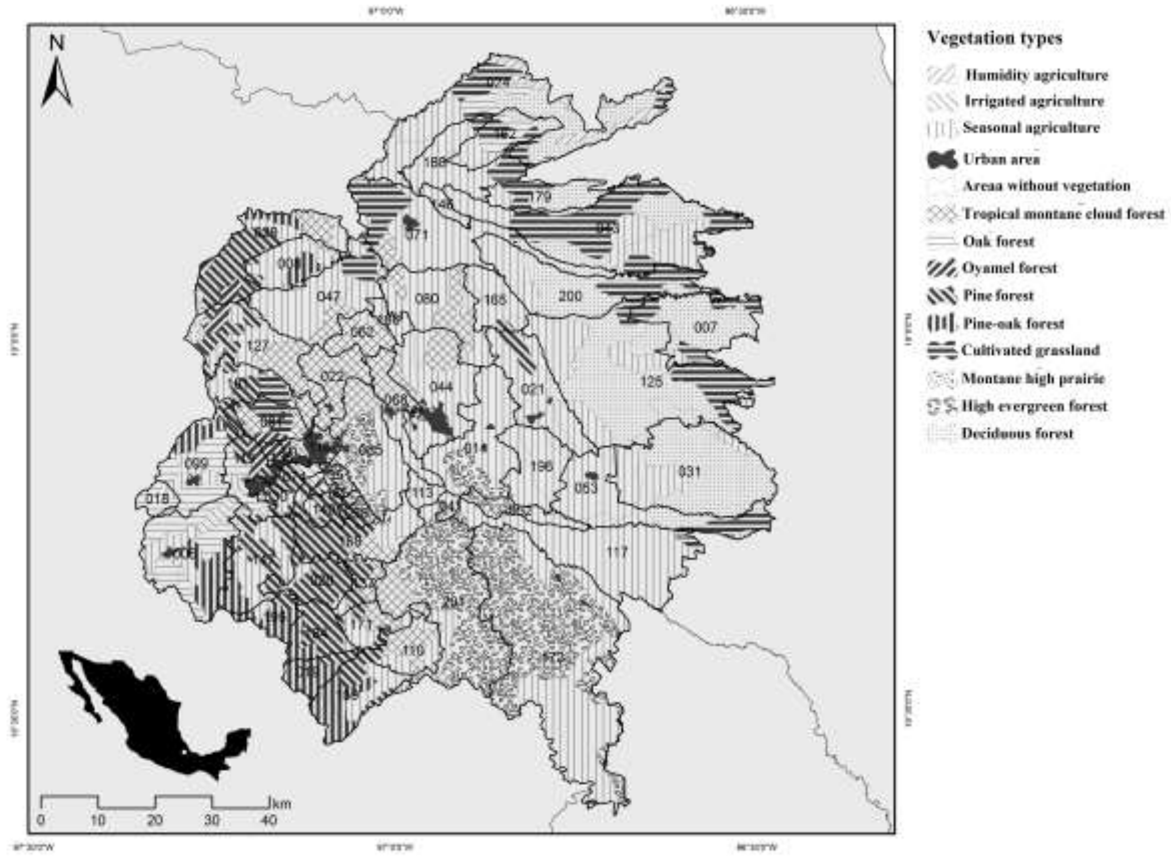
We gathered information related to population, agricultural and forestry activities and finance from the Regional Planning Studies (ERP for its acronym in Spanish, 2011), the National Council of Population (CONAPO for its acronym in Spanish, 2011), and the Veracruz State Government (accessed July 15, 2014). We analyzed all municipalities within the region, and we compared the most and the least vulnerable municipalities: Aquila and Córdoba.

We also analyzed the human development index (HDI) and the marginalization level for the region. The marginalization level is a measure of intensity of deficit and deprivation, and lack of population related to education, housing and monetary income, categorized it five levels: very high, high, medium, low and very low. CONAPO considers four structural dimensions of marginalization: housing, education, employment income, and population distribution. The marginalization index is a measure-summary that permits to differentiate states and municipalities from the country according to the global impact that suffers the population as a result of the absence of access to education, inadequate housings, insufficient monetary income and perception in small locations. This index considers the percentage of illiterate population older than 15 years old, the percentage of population older than 15 years without elementary school, percentage of population living in dwellings without toilet, without electricity, without access to water, with some level of overcrowding, with floor of earth, in localities with less than 5,000 inhabitants, and with income lower than 2 minimum wages (CONAPO 2001).

Table 6.1. Vegetation types and covered area in the region of the Great Mountains, Veracruz.

Vegetation type	Area (km^2)
Area without vegetation	1.09
Cultivated grassland. Secondary vegetation of Deciduous forest	6.80
Montane high prairie	11.45
Irrigated agriculture	28.34
Seasonal agriculture. Secondary vegetation of deciduous forest	31.33
Cultivated grassland. Seasonal agriculture	32.19
Humidity agriculture	36.27
Deciduous forest	42.91
Oyamel forest	48.30
Urban area	71.89
Secondary vegetation of Deciduous forest. Cultivated grassland	151.72
Secondary vegetation of Deciduous forest. Induced grassland	213.54
Oak forest	220.47
Pine-Oak forest	231.68
Seasonal agriculture. Cultivated grassland	234.36
Secondary vegetation of deciduous forest. Seasonal agriculture	427.16
Pine forest	472.97
Cultivated grassland	481.08
Seasonal agriculture. Secondary vegetation of Semi-evergreen seasonal forest	515.75
Tropical montane cloud forest	530.79
High evergreen forest	644.00
Seasonal agriculture	1620.78

In contrast, the HDI is a measure of relative performance compared to a reference standard. This index was created to emphasize that people and their capabilities should be the ultimate criteria for assessing the development of a country, not economic growth alone. Three dimensions compose the index: health, education and income (CONAPO 2001), and is a summary measure of average achievement in key dimensions of human development considering a long and healthy life, being knowledgeable and have a decent standard of living. The HDI is the geometric mean of normalized indices for each of the three dimensions. Health dimension is assessed by life expectancy at birth component of the HDI is calculated using a minimum value of 20 years and maximum value of 85 years. The education component is measured by mean of years of schooling for adults aged 25 years and expected years of schooling for children of school entering age. The standard of living dimension is measured by gross national income per capita (Human Development Report 2014; accessed July 15, 2014).



006 - Acultzingo
008 - Alpatláhuac
014 - Amatlán De Los Reyes
018 - Aquila
019 - Astacinga
020 - Atlahuilco
021 - Atoyac
022 - Atzacan
029 - Calcahualco
007 - Camarón De Tejeda
030 - Camerino Z. Mendoza
031 - Carrillo Puerto
062 - Chocamán
041 - Coetzala
043 - Comapa
044 - Córdoba
047 - Coscomatepec
052 - Cuichapa
053 - Cuitláhuac
068 - Fortín
071 - Huatusco
074 - Huiloapan De Cuauhtémoc
080 - Ixhuatlán Del Café
081 - Ixhuatlancillo
085 - Ixtaczoquitlán
127 - La Perla
137 - Los Reyes
098 - Magdalena
099 - Maltrata
101 - Mariano Escobedo
110 - Mixtla De Altamirano
113 - Naranjal
115 - Nogales
117 - Omealca
118 - Orizaba
125 - Paso Del Macho
135 - Rafael Delgado
138 - Río Blanco
140 - San Andrés Tenejapan
146 -Sochiapa
147 -Soledad Atzompa
159 - Tehuipango
162 - Tenampa
165 - Tepatlaxco
168 - Tequila
171 - Texhuacán
173 - Tezonapa
179 - Tlacotepec De Mejía
024 - Tlaltetela
184 - Tlaquilpa
185 - Tlilapan
186 - Tomatlán
188 - Totutla
195 - Xoxocotla
196 - Yanga
200 - Zentla
201 - Zongolica

Figure 6.1. Location, vegetation types, and municipalities of the region of the Great Mountains, Veracruz.

Climatological data collection: Precipitation and temperature trends

We took data from all active meteorological stations from the region, but because of the low number of stations with adequate data (only eight: Coscomatepec, El Coyol, Ixhuatlán del Café, Huatusco, Naranjal, Tenampa, Totutla and Villa Tejeda), we also selected fifteen meteorological stations from the north region, and three stations from the south region in Puebla state (San Bernardino Lagunas, Telpatlán and Alcomunga), this in order to elucidate how is changing the climate in the region (**Figure 6.3**). We analyzed all data available related to total annual precipitation and average annual temperature. This analysis was carried out with data from the Mexican National Weather Service (accessed July 17, 2014).

Using data concerning precipitation and temperature trends, we developed climate change scenarios of temperature and precipitation with projections to 2025, 2050, 2075 and 2100 using *Surfer* 9.11 software.

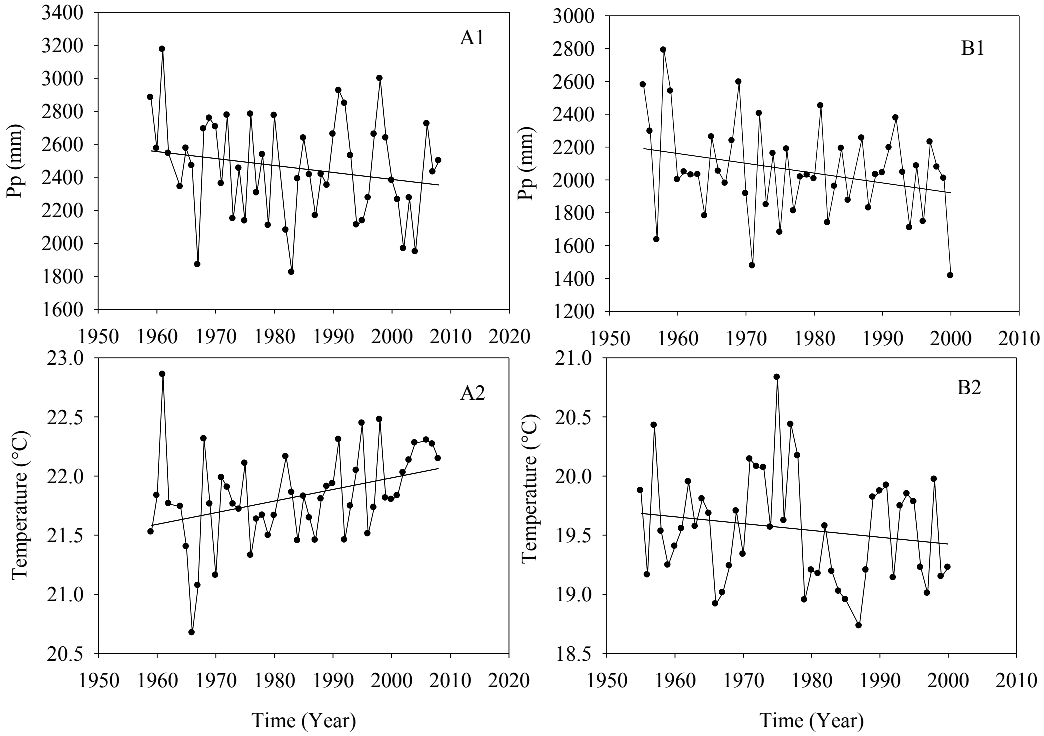


Figure 6.3. Precipitation and temperature trends for the meteorological station of El Naranjal (A1, A2), and Huatusco (B1, B2) from the region of the Great Mountains, Veracruz.

Statistical analysis

We performed the Mann-Kendall analysis (Nasrallah et al. 1990) to analyze whether temperature and precipitation trends were significant. We also analyzed data with *XLSTAT* statistical package to determine whether trends increase or decrease.

6.3 RESULTS

Population

Fifty-seven municipalities conform the region (**Figure 6.2**). Twenty-two are completely rural, and only two are metropolitan areas: Orizaba and Córdoba. 98.6% of the urban settlements have less than 5,000 inhabitants. In the year 2000, population was 1,237,461. 10.5% were included in the range of 5-9 year old. 539,090 individuals lived in rural conditions, and 698,371 lived in urban concentrations. 57.1% are beneficiaries to health services, 64.4% of households have cement/firm floor, and 13.3% do not have floor; 14.2% of households do not have piped water service, and 18.9% have no drainage, also 3% of households do not have electricity. As for access to transportation, the region has 1,938.3 km road network comprised (ERP 2011).

Agricultural and forestry activities

The region has a wide variety of crops, highlighting sugarcane, coffee, corn, chayote, potatoes, lemon, beans, gladiola, and hevea rubber. Sugarcane is the major crop with 58.6% of total production value, followed by coffee, corn, and chayote (19.8, 10.2 and 3.8% respectively). Concerning harvested area, cherry coffee is the most representative crop, with an area of 816.29 km^2, followed by sugarcane and corn with 791.27 and 577.03 km^2 respectively. 43 municipalities cultivate corn, 31 bean, 26 coffee, and 17 sugarcane (ERP 2011).

Finance

According to the Laws of Revenue for the State Municipalities for the Fiscal year of 2011, the municipalities of the region have 234.05 million USD from their own income, equity and federal contributions to meet the population demands, with a public spending/municipalities of 278.55 millions USD, where Córdoba and Orizaba had the major incomes and spending (ERP 2011).

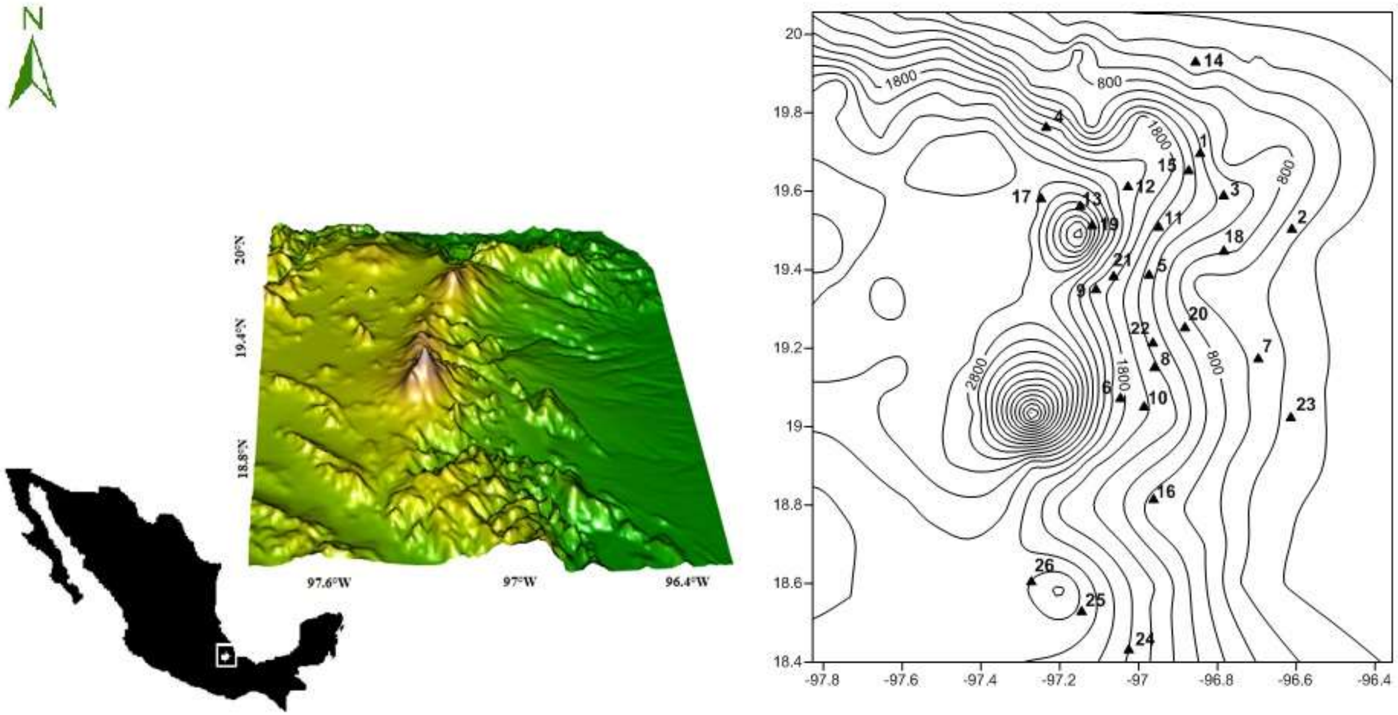
Contrasting municipalities: marginalization and human development

We considered Orizaba and Córdoba, the metropolitan areas, as less vulnerable. Córdoba is the largest municipality with a population of 196,541 inhabitants, and an extension of 159.9 km^2 (135.6 km^2 are used for agricultural activities and 15.8 km^2 are urban areas), whereas Orizaba has a population of 120,995 inhabitants, an extension of 27.9 km^2 (3.8 km^2 are used for agricultural activities and 14 km^2 are urban areas). 17.6% of Córdoba's population lives in food poverty, whit a low degree of marginalization (marginalization index of -1.1793), and a high human development level (HDI = 0.8370) comprising education, health and income. Economically active population is 85,004 (primary sector 3.4%, secondary sector 18.9%, and tertiary sector 73.1%), and economic participation rate is 55.2%. Main crops are sugarcane (445,152 Mg with an estimated value of 14,679,122.62 USD), coffee (6 996 Mg with an estimated value of 2,212,918.75 USD), and corn (2 557 Mg with an estimated value of 716,921.15 USD). Córdoba has a total gross production of 1,298,481,003.97 USD with total fixed assets of 439,941,279.95 USD (Veracruz State Government, accessed July 15, 2014).

In contrast, municipalities such as Aquila, Coetzala and Sochiapan, are more vulnerable because of their population is completely rural, having populations of 1797, 2144 and 12,409 inhabitants, respectively. For example, Aquila has an extension of 20.6 km^2, of which more than half (11.9 km^2) is destined for agricultural activities, 4.2 km^2 is forest, with no urban areas. 54.1% of the population lives in food poverty, 83.9% lives in poverty equity, and 55.2% has drain availability. Aquila has a very high degree of marginalization (marginalization index of 1.5558), and with a medium human development level (HDI = 0.6306). Economically active population is 700 (primary sector 74.6%, secondary sector 5.5%, and tertiary sector 19.7%), and economic participation rate is 54.5%. Population depends on corn production (1,040 Mg with an estimated value of 363,916.97 USD). Aquila has a total gross production of 22,062.76 USD, with total fixed assets of 46,181.55 USD (Veracruz State Government, accessed July 15, 2014). When we contrast these municipalities, important differences concerning vulnerability are noted (**Table 6.2**; **Supplemental Table S6.1**).

T**able 6.2**. Poverty and marginalization indicators, human development index and housing characteristics for two contrasting municipalities in the region of the Great Mountains, Veracruz, México (Data from 2010; Veracruz State Government, accessed July 15, 2014).

Poverty indicators	**Municipality**	
	Córdoba	**Aquila**
Population living in food poverty	17.6 %	54.1%
Population in capacity poverty	26.4%	64.1%
Population living in patrimony poverty	52.5%	83.9%
Marginalization and indicators	**Reference**	
Marginalization level	Low	Very High
Marginalization index	-1.1793	1.5558
Place in the state context	200	15
Place in the national context	2,153	169
Illiterate population (15 years or more)	6.2%	39.1
Population without complete primary education (15 years or more)	21.3%	66.0%
Occupants in dwellings without drainage or exclusive toilet	1.0%	25.5%
Occupants in dwellings without electricity	0.8%	6.2%
Occupants in houses without running water	12.4%	36.6%
Homes with some level of overcrowding	40.4%	69.5%
Occupants in houses with dirt floors	8.2%	46.9%
Population in towns with less than 5000 inhabitants	17.5%	100%
Employed population with income up to 2 minimum wages	51.5%	80.3%
Human development index	**Reference**	
Level of human development	High	Medium
Human Development Index	0.8370	0.6306
Education index	0.8529	0.5974
Health Index	0.9105	0.6592
Index entry	0.7477	0.6356
Housing characteristics	**Percentage**	
With availability of piped water	91.8%	72.0%
With availability drainage	97.1%	55.2%
With availability of electricity	99.1%	95.0%



1 - Acatlán
2 - Actopan
3 - Almolonga
4 - Altotonga
5 - Briones
6 - Coscomatepec
7 - El Coyol
8 - Huatusco
9 – Ixhuacán
10 – Ixhuatlán del Café
11 - La Joya
12 - Las Vigas
13 - Los Pescados
14 - Misantla
15 - Naolinco de Victoria
16 - Naranjal
17 - Perote
18 - Rancho Viejo
19 - Tembladeras
20 - Tenampa
21 - Teocelo
22 - Totutla
23 - Villa Tejeda
24 - Alcomunda
25 – San Bernardino Lagunas
26 – Telpatlán

Figure 6.2. Location of the 26 meteorological stations in the region of the Great Mountains, Veracruz, and contour lines distribution (range 200 m) for the region.

Precipitation and temperature trends

We found positive and negative trends related to average annual temperature and total annual precipitation. For precipitations, 15 stations had negative trends and 11 were positive; as for temperature, 16 stations had an increase and 10 had a decrement in temperature (**Table 6.3**). After analyzing **figure 6.4,** we noted that temperature/precipitation distribution is not uniform, finding particular local trends.

Table 6.3. Precipitation and temperature trends from 26 meteorological stations in the Region of the Great Mountains, Veracruz.

Meteorological station			**Coordinates**				**Increase / decrease**	
			Latitude	**Longitude**	**Elevation (m asl)**	**Data (years)**	**Precipitation (mm year^{-1})**	**Temperature (°C year^{-1})**
1	Acatlán	30338	19.6958	-96.8439	1751	1980-2008	-2.4765	-0.0011
2	Actopan**	30003	19.5028	-96.6111	250	1954-2008	-3.1451*	0.0143*
3	Almolonga	30007	19.5883	-96.7842	730	1971-2008	1.1793	0.0197*
4	Altotonga	30008	19.7625	-97.2347	1867	1960-2008	3.0385	0.0071
5	Briones	30452	19.5083	-96.9494	1349	1985-2008	4.781	-0.0273
6	Coscomatepec	30032	19.0717	-97.0461	1530	1954-2007	7.157	-0.0674*
7	El Coyol**	30047	19.1722	-96.6964	545	1980-2008	-8.6085	0.0358*
8	Huatusco	30066	19.15	-96.9597	1284	1955-2008	-5.9775*	-0.0058
9	Ixhuacán**	30336	19.3486	-97.1083	1802	1980-2007	-8.9545	0.0444
10	Ixhuatlán del Café**	30072	19.05	-96.9861	1350	1981-2008	-1.9043*	0.0415*
11	La Joya	30455	19.6108	-97.0272	2,175	1991-2008	-2.3604	-0.1039*
12	Los Pescados	30097	19.5614	-97.1481	2395	1980-2008	1.0373	0.069*
13	Las Vigas**	30211	19.382	-97.0635	2400	1922-2008	-3.7464*	0.0351*
14	Misantla	30108	19.9292	-96.8556	310	1926-2008	-2.3604	-0.0132*
15	Naolinco de Victoria**	30114	19.6519	-96.8731	1542	1956-2008	-2.5545	0.0172*
16	Naranjal**	30115	18.8139	-96.9622	697	1959-2008	-4.2314	0.0271*
17	Perote	30128	19.5808	-97.2478	2392	1967-2007	3.3255	-0.0098*
18	Rancho Viejo	30140	19.4469	-96.7836	914	1969-2008	-3.7932	-0.0209*
19	Tembladeras	30175	19.5122	-97.1181	3102	1966-2008	3.0546	0.0178
20	Tenampa	3017	19.2517	-96.8825	1015	1980-2004	-8.6901	-0.0162

		7						
21	Teocelo**	30179	19.3861	-96.9736	1188	1946-2008	-3.139	0.1525
22	Totutla	30187	19.2125	-96.9639	1446	1960-2008	8.1987	0.0232
23	Villa Tejeda	30364	19.0222	-96.6139	348	1983-2008	4.3279	-0.0081
24	Alcomunga	21009	18.4306	-97.025	2485	1956-2009	15.664	0.136
25	San Bernardino Lagunas**	21053	18.6039	-97.2725	1693	1955-2009	-1.5411	0.0617
26	Telpatlán	21084	18.5281	-97.1447	2212	1955-2009	1.4843	0.0023

*Significant trends ($P < 0.05$)
**Potential areas where the increment in temperature and the decrement in precipitation, increase the vulnerability to fire and crop productivity.

Because of the mountain massif configuration, trends in temperature and precipitations are affected by terrain, orography and by flow of moisture-bearing winds, which are distributed unevenly. Stations located at windward in high areas with deforestation, presented decrement in precipitation (**Figure 6.2**). In some cases, such as in Naolinco Victoria, temperature increased because of sensible heat, which results in increased surface temperature. Stations where precipitation increases at leeward presenting positive temperature trends are located at higher altitude, where vegetation retains moisture before it is transported at higher elevations. An example of this phenomenon is observed in El Coyol, with a temperature increase and a decrease in rainfall because of lack of vegetation at leeward by the introduction of livestock and farming. However, there are cases where this phenomenon is not observed, as in Los Pescados, where temperature and precipitation increased; here, the agricultural activity could cause an increment in temperature by increasing soil surface temperature, but being located at higher altitude (2395 m asl) and at windward, precipitation increases because moisture is deposited by the orography regardless deforestation. For Rancho Viejo and Acatlán, temperature and precipitation decreased. Precipitation decreased by lack of moisture at leeward due to deforestation, and temperature is diminished possibly by topography and cold winds coming from north.

Climate in this region is affected by local and site-specific conditions, where the mountainous and rugged terrain, and winds affect the humidity entrance of the Gulf of Mexico. Deforestation has a very strong local effect, which can be observed in the changing trends between nearby stations. Yet, these climate conditions may respond to other factors, such as changes in land-use, human settlements and global and regional climate change.

Statistical analysis

Only 14 meteorological stations had significant statistical trends. This result may be because of the lack of data available for many stations (less than 30 years). Still, we considered all stations to evaluate climatic conditions and create the climate change scenarios. Nevertheless, this study should be considered more an exploratory assessment of the possible changes in temperature and precipitation, rather than future predictions.

Vulnerability and climate change in the region

Vulnerability increases with respect to changes in temperature and precipitation (Esperón-Rodríguez and Barradas 2014a, 2014b). Previous studies from the region analyzed precipitation trends finding negative trends implying potential reductions in precipitation of as much as 50% by the year 2023 (Barradas et al. 2010). An increase of consecutive dry days has also been predicted (Esperón-Rodríguez and Barradas 2014b). Also, it was reported the decrease of rainfall to windward and fog frequency (Barradas et al. 2004, 2010, 2011). These changes have repercussion on other climatic variables like solar radiation, which is expected to be more intense where rainfall and fog decrease (Barradas et al. 2011).

In spite not all meteorological stations had significant statistical trends, we used all data to develop our climate change scenarios. Although we recognize that caution must be taken for this analysis, we found considerable changes in temperature and precipitation, finding reductions in precipitation of over 700 mm and increases in temperature of ~9 ºC for the year 2100 (**Table 6.4**; **Figures 6.5, 6.6**). Regardless the trends statistical significance, changes in temperature and precipitation are occurring in the region.

Table 6.4. Projections of maximum and minimum changes in temperature (T_{MAX}, T_{min}; ºC) and precipitation ($\mathrm{Pp}_{\mathrm{MAX}}$, $\mathrm{Pp}_{\mathrm{min}}$; mm) for the years 2025, 2050, 2075 and 20100 in the region of the Great Mountains, Veracruz, Mexico. For all years, T_{MAX} was found in La Joya; T_{min} was found in Los Pescados; $\mathrm{Pp}_{\mathrm{MAX}}$ was found in Totutla, and $\mathrm{Pp}_{\mathrm{min}}$ was found in Ixhuacán.

Year	T_{MAX}	T_{min}	$\mathrm{Pp}_{\mathrm{MAX}}$,	$\mathrm{Pp}_{\mathrm{min}}$
2025	1.25	-0.83	107.45	-98.38
2050	3.84	-2.55	331.32	-303.35
2075	6.44	-4.28	555.18	-508.32
2100	9.04	-6.00	779.04	-713.29

A) B)

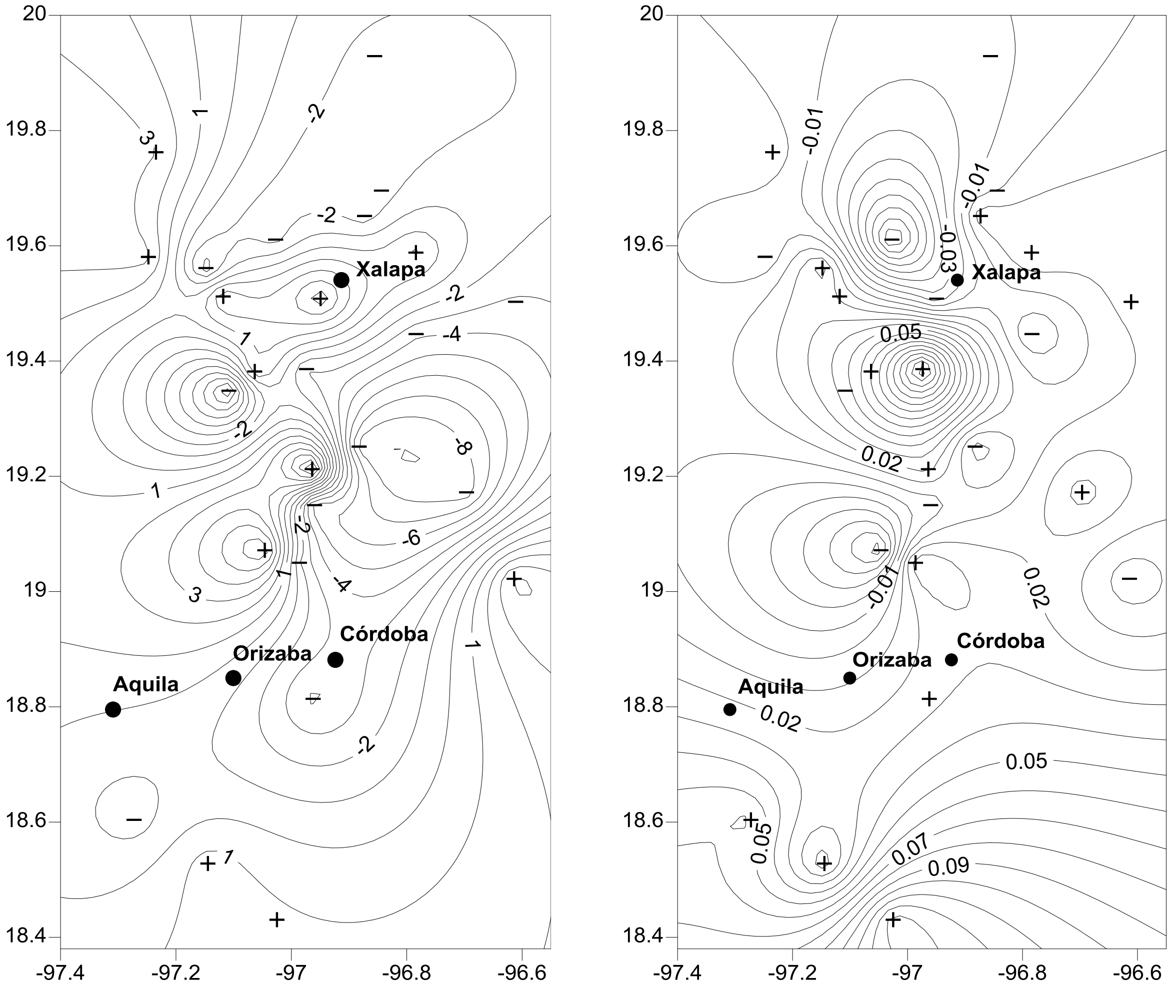


Figure 6.4. . Increment (+) and decrement (-) of precipitation (A, mm year^{-1}) and temperature (B, °C year^{-1}) in the 23 meteorological stations from the region of the Great Mountains, Veracruz.

6.4. DISCUSSION

Isolated from social reality, vulnerability studies are incomplete. This paper outlines a framework for analyzing the socio-economic vulnerability to the impacts of global warming-induced by climate change in the RGM, Veracruz.

The central insight to the adaptation process is that vulnerability is socially differentiated (Adger 1999). Vulnerability is not the same for different populations living under different environmental conditions or faced with complex interactions of social norms, political institutions and resource endowments, technologies and inequalities (Adger 1996). For our region, it is noteworthy the analysis of the degrees of marginalization and human development. Concerning marginalization level, 16 municipalities (28%) had very high, 23 (40.35%) had high, 10 (17.54%) had medium, five (8.77%) had low, and only three municipalities (Alpatláhuac, Orizaba and Río Blanco) representing 5.25% had very low marginalization level. Concerning the degree of human development, we found that 84.21% (48 municipalities) had medium, 14% (eight municipalities) had high, and only one municipality (Tehuipango) had low degree of human development (**Supplemental Table S6.1**). The region has severed problems related to marginalization enhancing vulnerability and potential risks.

We also observed differences among municipalities, illustrated when comparing Córdoba and Aquila (**Table 6.2**). The majority of the economical active population in Córdoba focuses on the tertiary sector (73.1%), whereas in Aquila is the primary sector (74.6%); and also, the estimated value of crop production in Aquila represents the 0.02% of the value estimated in Córdoba. Despite differences in population size, it can be inferred that vulnerability in small municipalities that rely mostly on agriculture (mainly corn) increases compared to big municipalities. Related to precipitation and temperature trends, we observed that both municipalities are located in the area where precipitation has decreased and temperature increased (**Figure 6.4**), making them vulnerable to possible drought and fires. In 2009 there were 42 wildfires in an area of 3.52 km^2. Maltrata was the most affected municipality with seven fires, followed by Nogales with six fires (0.2 km^2), whereas in Tequila five fires were reported (1.05 km^2) (ERP 2011). Fire must be considered as a vulnerability enhancer where temperature increases and precipitation decreases (**Table 6.3**).

Climate change will also affect biodiversity and ecosystem's goods and services relying on for human health (Haines et al. 2006). There are several mechanisms by which climate can affect health (Haines and Patz 2004). Extremes of temperature and rainfall, such as floods, drought and heat waves, have direct immediate effects on mortality as well as long-term effects (Haines et al. 2006). Intrinsic and extrinsic factors can contribute to different levels of risk to heat related illness or death. Intrinsic factors are those that are inherent to the individual, such as age or medical condition, whereas extrinsic factors are those that are external to the individual, such as living conditions or access to transportation (Cooley et al. 2012). Regarding intrinsic factors, vulnerability increases in the region because most of the population is included in the range of 5-9 years old (10.5% of total population), and from the total population only 57.1 % are beneficiaries to health services (ERP 2011). As for extrinsic factors, 64.4 % of households have cement floor or firm, and 13.3 % do not have floor; 14.2 % of households do not have piped water service, and 18.9 % have no drainage, also 3% of households do not have electricity. As for access to transportation, the region has 1938.3 km road network comprised mostly as well paved, with rural road lines and small roads, and a paved federal highway (ERP 2011). High percentage of the population can be considered as vulnerable. Besides intrinsic and extrinsic factors, poverty, and social and geographic isolation also affects how people are impacted by climate change (Cooley et al. 2012).

Severity of impacts on ecosystem's goods and services will depend on the regional situation and specific climatic changes (Schröter et al. 2005). While all people are dependent upon the function of natural ecosystems, connection between natural world and their livelihood is more direct for some groups, in particular those dependent upon a particular natural resource, such as agriculture or subsistence farmers (Cooley et al. 2012). Cropping patterns in agricultural producing areas are primarily determined by regional climatic conditions. Farmers would respond to climate change *inter* *alia* by altering the crops mixture they grow, which would reduce some climate-change-related losses (Butt et al. 2005). We found that more than 60% of the territory is comprised to agricultural activities, highlighting the importance of this activity. All municipalities have agricultural activities, more than half of them depend almost entirely on agriculture, where 51% of the municipalities rely on two or three crops. One possible solution to mitigate the climate change adverse effects would be to diversify the agricultural areas implementing more crops. Other possible solution could be changing the cropping pattern in warm regions, shifting towards patterns used in hotter regions (Butt et al. 2006).

Land-use change also impacts natural ecosystems. Reforesting can be a useful tool to mitigate impacts and to keep vegetation cover. The "ProÁrbol" program reported in 2009, that 4,278 seedlings were planted, representing a reforested area of 62.31 km^2 (ERP 2011). However, reforesting must be carried out with caution and considering the precipitation/temperature trends, planting species tolerant to changes in the local conditions, and considering natural environments and croplands. Besides, future vulnerability studies must be assessed by analyzing how climate change will affect the natural ecosystems, and whether the communities' coping strategies will have the capacity to deal with these scenarios.

As it was mentioned early, sugarcane is the major crop in the region, followed by cherry coffee and corn, with coffee as the most extensive plantation (ERP 2011). This characteristic is beneficial, because coffee plantations are developed under the same environmental conditions of the tropical cloud forest, therefore coexistence and recombination (replacement) of species make them complementary (García-Franco et al. 2008). The system "coffee plantation-tropical cloud forest" maintains a large and vast forest cover. Because of its structure and species diversity, coffee plantations are of great importance for implementation of environmental services (Olguin et al. 2011). Encouraging coffee production might represent an advantage to preserve natural vegetation.

In the region, all ecosystems are vulnerable, including agricultural areas. Increase/decrease in precipitation and temperature can limit the species' growth and development, and increase substantially vulnerability. We found changes in precipitation and temperature, and although we did not found significant statistical differences in all meteorological stations, attention must be paid, because changes in precipitation and temperature are occurring, and the climate change scenarios predict changes in temperature and precipitation, where both climate variables present considerable increments and decrements (**Table 6.4**; **Figures 6.5, 6.6**). 16 stations presented positive temperature trends, representing an important increment in temperature. Stations that presented a temperature decrement are located above 1000 m asl, and temperature increment can be observed in the coastal region, where deforestation has increased (Barradas et al. 2004, 2011).

For precipitation, 15 stations had negative trends. This finding is very relevant because water is one of the most important resources that influence vegetation structure in ecosystems, and primary productivity (Reynolds et al. 1999). Also if precipitation and cloud cover decrease, fog frequency decreases as well, but solar radiation, and air and substrate temperatures increase. For the central region of Veracruz it has been predicted a decrement not only in rainfall, but also in fog frequency (Barradas et al., 2010, 2011; Esperón-Rodríguez and Barradas 2014b), which increases vulnerability. We found that precipitation increases in the east at windward, or in the coastal region but at low altitudes (less than 800 m asl). Previously, Barradas et al. (2001, 2004) hypothesized that changes in precipitation trends and fog frequency are mainly because of deforestation. This is because the increment of the air heating could increase the cloud base, which is formed largely by the forced ascent of moist air from the Gulf of Mexico.

Lack of water affects crop's growth and productivity (Kramer 1980), where drought is probably the most important factor limiting crop yields and species' distribution (Jones and Corlett 1992). A decrease in precipitation represents high risk for agriculture. High quality coffee requires more than 3000 mm, and with less than 1000 mm plant growth is limited; also, a very prolonged drought period conducts to defoliation and death. Optimum temperature goes from 17 to 23 ºC, but temperatures lower than 10 ºC cause chlorosis and stop growth of young leaves, also is recommended relative humidity less than 85% (Barva 2011). Vulnerability is high for coffee, especially where temperature increases and precipitation decreases; moreover, a decrement in coffee production has economical repercussion at national level. Currently, Veracruz's coffee production represents approximately 27.4% of the national product (ranking second at national level), with a coffee fragmented area of 1520 km^2, equivalent to 13.92% of the total of vegetation in the state (Olguín et al. 2011).

Sugarcane's growth is directly related to temperature. Optimum temperature for germination ranges between 32-38 ºC. Germination drops below 25 °C, and is optimal between 30-34 ºC, reducing around 35 °C, and stops above 38 ºC. Temperatures above 38 °C reduce photosynthesis rate and respiration increases. For ripening are preferred relatively low temperatures (12-14 °C), and exerted a strong influence on reducing the vegetative growth rate and enrichment. As for precipitation, a total rainfall between 1100-1500 mm is suitable, providing adequate and abundant light during growth, followed by a dry period for ripening (Subirós-Ruiz 1995). For sugarcane, temperature changes may limit growth. However, a decrease in precipitation and clouds' reduction may increase irradiance favoring this crop.

As for corn, from planting to maturity it requires 500-800 mm, depending on variety and climate, but its average water requirement per cycle (one year) is 650 mm. 6-8 mm/day are necessary during early stages of development. Optimum germination temperature ranges between 18-21 ºC, germination below 13 °C is reduced significantly, and below 10 °C no germination occurs. Photosynthesis and development is maximum between 30-33 °C. Practically no cultivation occurs where average temperature is lower than 19 ºC or when average temperature during night at summer falls below 13 ºC. The largest areas of corn production are located where the warmer months ranges between 21-27 °C and with a frost-free period of 120-180 days. The combination of temperatures above 38 ºC plus water stress during early formation and development prevent grain formation;

whereas temperatures below 15.6 °C delayed significantly flowering and maturity (Ruíz et al. 1999). For corn, vulnerability increases whit temperature changes. Fortunately, corn is tolerant to low precipitation. In regions where precipitation decreases and irradiance increases, corn can be benefited. However, corn has high economical importance (75% of the municipalities cultivate corn). Also, the region's culture is based on a corn-nutrition feeding; therefore, consequences in a production decrement would enhance vulnerability.

The RGM has an important economical participation in the country, particularly with coffee. A region with economical importance and a significant poor population highlights the relevance of the socio-economic vulnerability to climate change, where measures must be taken to prevent economic loss and social harm. Crops more tolerant to low precipitation must be promoted in areas where precipitation trends are negative. Cultivation aims to ensure a more efficiently water use (yield of product/water consumed); nevertheless, this benefit would be unlikely when the limiting factor is water (Galmés et al. 2011). In the region, a precipitation reduction can be translated to economic loss.

6.4 CONCLUSIONS

The RGM is socio-economically vulnerable to climate change. Poverty, rural populations and dependency on agriculture to support the economy enhance vulnerability. Changes in precipitation and temperature, and future climate change scenarios highlight the importance to implement measures to protect the most vulnerable population, promoting crops that adapt better to the predicted climate conditions. Local, regional and state climate analyses must be emphasized to climate impacts and mitigation strategies, where communities must develop and implement adaptation plans. Local governments and regional planning agencies should conduct detailed studies to understand better the potential impacts of climate change. Also, local planning processes need to involve the most vulnerable communities when developing appropriate mitigation and adaption strategies.

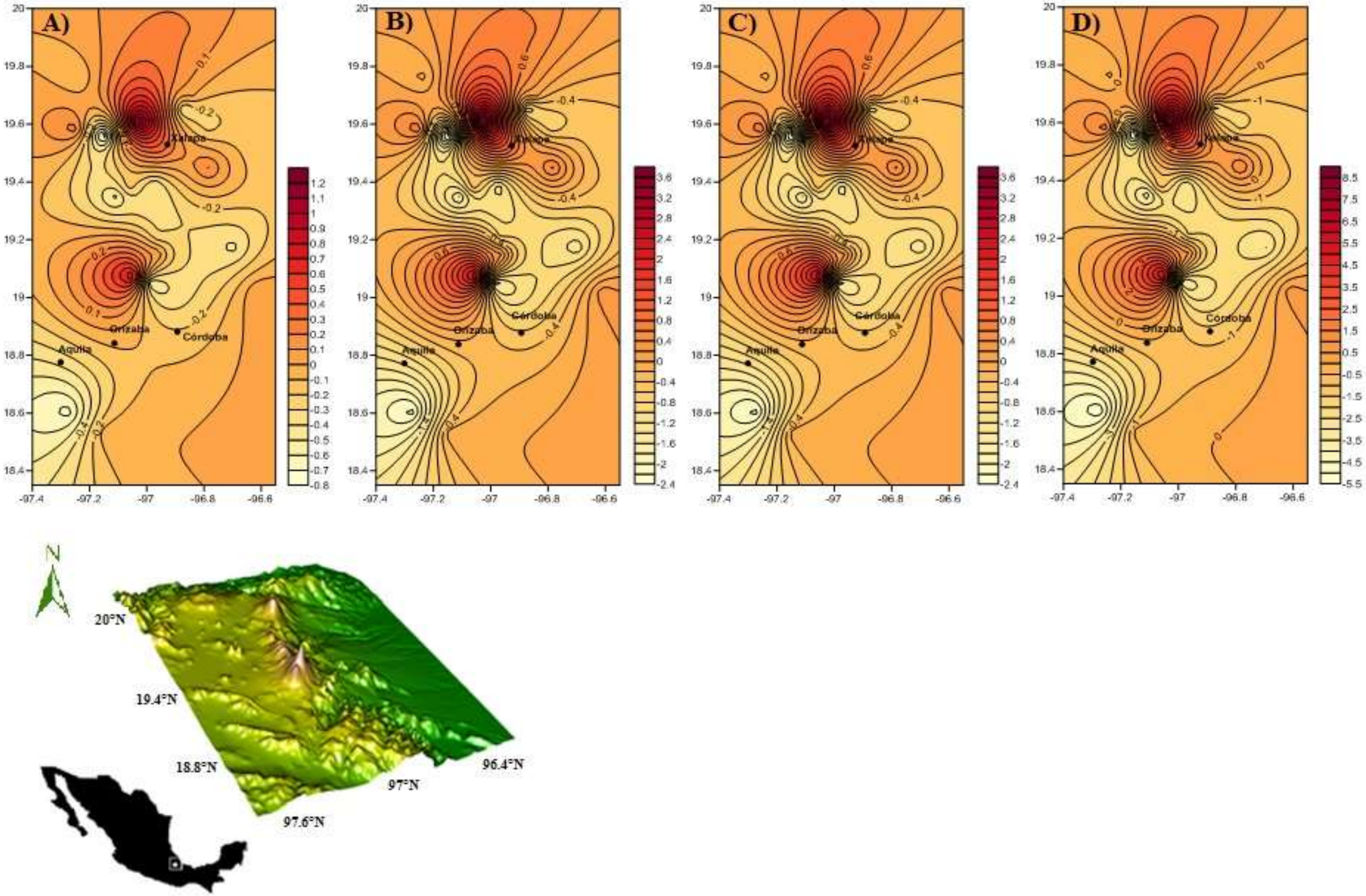


Figure 6.5. Climate change scenarios in temperature (ºC; color scale) for the years 2025 (A), 2050 (B), 2075 (C) and 2010 (D), based on the temperature trends of 26 meteorological stations in the region of the Great Mountains, Veracruz.

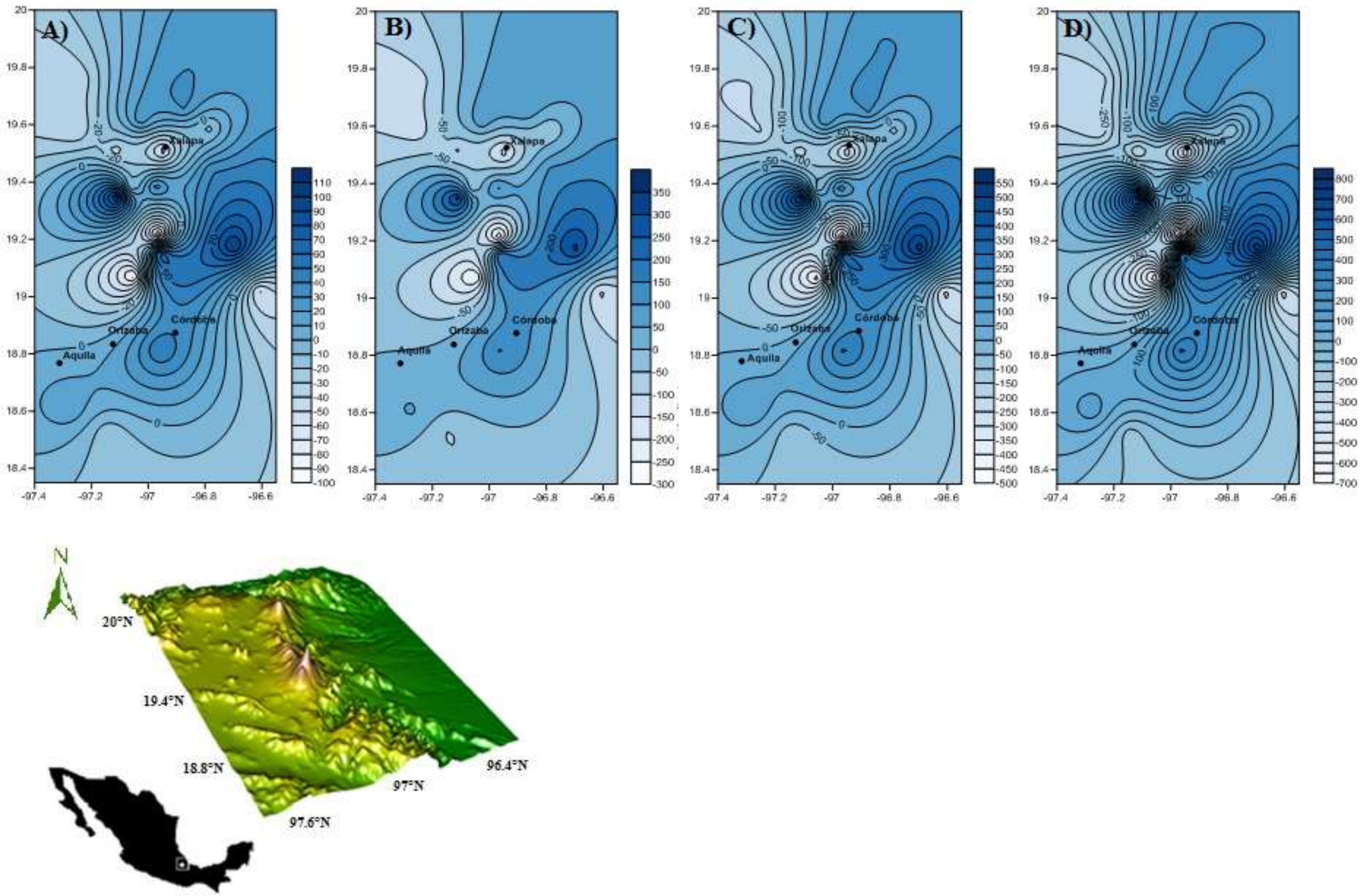


Figure 6.6. Climate change scenarios in precipitation (mm; color scale) for the years 2025 (A), 2050 (B), 2075 (C) and 2010 (D), based on the precipitation trends of 26 meteorological stations in the region of the Great Mountains, Veracruz

SUPPLEMENTAL MATERIAL

Table S6.1. Geographic data, marginalization level, marginalization index, level of human development, and human development index for the 57 municipalities of the region of the Great Mountains, Veracruz, Mexico (Data from 2010; Veracruz State Government, accessed July 15, 2014).

Municipality	**Localities**		**Surface (km^2)**	**Percentage of state territory (%)**	**Population density (inhabitants/km^2)**	**Marginalization level**	**Marginalization index**	**Level of human development**	**Human development index**
	Urban	**Rural**							
Acultzingo	1	38	167.9	0.2	124.9	High	0.5412	Medium	0.7218
Alpatláhuac	0	38	71	0.1	136.4	Very High	1.1665	Medium	0.6532
Amatlán de los Reyes	4	72	151.1	0.2	279.8	Medium	-0.2780	Medium	0.7847
Aquila	0	6	20.6	< 0.1	87.1	Very High	1.5558	Medium	0.6306
Astacinga	0	26	38.6	0.1	155.3	Very High	1.4120	Medium	0.6116
Atlahuilco	0	36	62.1	0.1	158.1	Very High	1.9712	Medium	0.6379
Atoyac	2	73	122.7	0.2	187.4	Medium	-0.5482	High	0.8023
Atzacan	2	14	65.2	0.1	307.9	High	0.3571	Medium	0.7079
Carrillo Puerto	0	96	249.2	0.3	65.5	High	0.8307	Medium	0.7011
Camarón de Tejeda	0	30	125.8	0.2	49.5	High	0.0760	Medium	0.7531
Calcahualco	0	33	134.2	0.2	96.3	Very High	1.5070	Medium	0.6189
Camerino Z. Mendoza	2	3	21.5	< 0.1	1,941.4	Low	-1.0401	High	0.8203
Coetzala	0	5	9.5	< 0.1	226.9	High	1.0335	Medium	0.6789
Comapa	1	66	311.8	0.4	60.0	High	1.0098	Medium	0.6853
Córdoba	5	91	159.9	0.2	1,229.2	Low	-1.1793	High	0.8370
Coscomatepec	3	59	157.7	0.2	333.1	High	0.7509	Medium	0.6714
Cuichapa	2	19	34.7	< 0.1	335.6	Medium	-0.1428	Medium	0.7625
Cuitláhuac	1	73	150.2	0.2	174.9	Medium	-0.5424	Medium	0.7943
Chocamán	2	17	44.4	0.1	418.6	High	0.2492	Medium	0.7062
Fortín	4	57	61.6	0.1	970.1	Low	-1.0758	High	0.8459
Huatusco	1	70	202.5	0.3	269.5	Medium	-0.2458	Medium	0.7599
Huiloapan de	1	4	18.7	< 0.1	361.7	Medium	-0.5409	Medium	0.7945

Cuauhtémoc									
Ixhuatlán del Café	2	29	129.5	0.2	165.3	High	0.5655	Medium	0.7069
Ixhuatlancillo	3	16	52.6	0.1	402.4	High	0.1246	Medium	0.7362
Ixtaczoquitlán	7	55	137.4	0.2	476.0	Low	-0.6723	High	0.8081
La Perla	1	49	199.9	0.3	94.7	Very High	1.5064	Medium	0.6121
Los Reyes	0	20	33.8	< 0.1	162.3	Very High	1.6858	Medium	0.6583
Magdalena	0	8	13.8	< 0.1	212.1	High	1.0213	Medium	0.7052
Maltrata	1	31	110.9	0.2	152.4	High	-0.0340	Medium	0.7345
Mariano Escobedo	2	48	69.6	0.1	488.0	Medium	-0.4146	Medium	0.7770
Mixtla de Altamirano	0	43	66.3	0.1	156.7	Very High	2.9278	Medium	0.5469
Naranjal	0	12	18.6	< 0.1	242.3	High	0.5519	Medium	0.7388
Nogales	2	24	63.6	0.1	545.5	Low	-0.9404	High	0.8187
Omealca	1	58	214.7	0.3	105.1	High	0.1825	Medium	0.7464
Orizaba	1	4	27.9	< 0.1	4,338.3	Very Low	-1.7241	High	0.8872
Paso del Macho	1	134	399.0	0.6	73.1	Medium	-0.1457	Medium	0.7524
Rafael Delgado	2	16	26.7	< 0.1	759.1	High	0.1522	Medium	0.7358
Río Blanco	1	3	15.2	< 0.1	2,669.8	Very Low	-1.5577	High	0.8593
San Andrés Tenejapan	0	9	21.9	< 0.1	123.9	Very High	1.0879	Medium	0.6582
Sochiapa	0	11	16.2	< 0.1	215.8	High	0.4605	Medium	0.6814
Soledad Atzompa	1	34	115.7	0.2	184.9	Very High	1.7716	Medium	0.5947
Tehuipango	0	51	94.8	0.1	247.8	Very High	2.8054	Low	0.4985
Tenampa	0	14	65.3	0.1	95.7	High	1.0204	Medium	0.6764
Tepatlaxco	0	12	59.8	0.1	138.0	Very High	1.2612	Medium	0.6871
Tequila	1	38	99.7	0.1	146.9	Very High	1.6768	Medium	0.6596
Texhuacán	0	18	44.0	0.1	120.2	Very High	1.1850	Medium	0.6552
Tezonapa	2	137	524.6	0.7	100.2	High	0.9426	Medium	0.7321
Tlacotepec de	0	5	65.4	0.1	60.6	High	0.5058	Medium	0.7078

Mejía									
Tlaltetela	1	42	278.5	0.4	52.5	High	0.6979	Medium	0.6851
Tlaquilpa	0	66	57.2	0.1	125.0	Very High	43.8	Medium	0.6326
Tlilapan	1	6	11.1	< 0.1	441.1	High	0.3656	Medium	0.7144
Tomatlán	1	9	18,9	< 0.1	358.8	Medium	23.5	Medium	0.7704
Totutla	1	31	97.8	0.1	167.8	High	0.5247	Medium	0.6891
Xoxocotla	0	17	37.2	0.1	138.9	Very High	1.4993	Medium	0.6471
Yanga	1	42	89.1	0.1	196.0	Medium	-0.3859	Medium	0.7980
Zentla	0	52	178.7	0.2	69.3	High	0.2760	Medium	0.7414
Zongolica	1	146	280.1	0.4	149.7	Very High	1.3342	Medium	0.6977

Capítulo 7

Rasgos de sequía y la predictibilidad del potencial osmótico en vegetación de Nueva Zelanda

Drought traits and predictability of osmotic potential in vegetation from New Zealand

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(Sometido)

RESUMEN: La disponibilidad de agua es uno de los factores ambientales más importantes que afectan a la variabilidad en la estructura y la composición de las comunidades, el funcionamiento de las plantas y la productividad primaria. Por lo tanto, es importante entender qué especies podrían ser más vulnerables a las reducciones en la disponibilidad de agua, ya que se prevé para muchas regiones del mundo experimentarán condiciones de sequía a causa del cambio climático. Para evaluar la tolerancia a la sequía, se seleccionaron 14 especies nativas de árboles y arbustos nativos de Nueva Zelanda, y se realizó un análisis de los rasgos estructurales y funcionales suaves (densidad de la madera, saturada contenido saturado de agua de la madera, área foliar, área foliar específica, contenido relativo de agua de la hoja, grueso de la hoja) y duros (potencial osmótico a turgencia completa, potencial osmótico, presión de turgencia, potenciales hídrico foliar, conductancia estomática). Seleccionamos al potencial osmótico a turgencia completa como un indicador de la sequía para nuestro análisis, teniendo en cuenta que este rasgo duro es un factor determinante de la respuesta fisiológica del estrés hídrico de la planta. Generamos modelos para predecir el potencial osmótico a turgencia completa, y posteriormente se evaluaron siguiendo el criterio de información de Akaike, encontramos que el modelo g_S/LA como el mejor predictor. Entre las especies analizadas, *Lophozonia menziesii* fue la más vulnerable a la sequía, mientras que *Plagianthus regius* fue la menos vulnerable.

Palabras clave: Rasgos de sequía · potencial osmótico · criterio de información de Akaike · vulnerabilidad · indicador de sequía

ABSTRACT: Water availability is one of the most important environmental factors affecting the variability in community structure, composition, plant functioning, and primary productivity. Hence, it is important to understand which species might be most susceptible to reductions in water availability, as it is predicted for many regions of the world because of climate change. To assess drought tolerance, we selected 14 native tree and shrub species from New Zealand and conducted an analysis of structural and functional traits measuring soft (wood density, wood saturated water content, leaf area, specific leaf area, leaf relative water content, and leaf thickness) and hard traits (osmotic potential at full turgor, osmotic potential, turgor pressure, minimum seasonal water potential, and stomatal conductance). We selected osmotic potential at full turgor as a drought indicator for our analysis, considering this trait is a physiological determinant of plant water stress response. We generated models to predict osmotic potential at full turgor, and subsequently evaluated them following Akaike's information criterion, finding that g_S /LA is the best predictor. Among the analyzed species, *Lophozonia menziesii* was the most vulnerable to drought stress, whereas *Plagianthus regius* was the least vulnerable.

Key words: Drought traits · osmotic potential · Akaike's information criterion · vulnerability · drought indicator

7.1 INTRODUCTION

Water availability is one of the most important environmental factors affecting the variability in community structure, composition, plant functioning, and primary productivity (Reynolds et al. 1999; Engelbrecht et al. 2007). Lack of water is one of the most unfavorable environmental stress factors affecting plant growth and performance, with its effects being the most harmful among environmental stress agents (Kramer 1980). Also, drought, which is a condition of insufficient moisture caused by a deficit in precipitation over some time period (McKee et al. 1993), negatively affects plant performance by reducing recruitment, growth and survival (McDowell et al. 2013; Zeppel et al. 2013). Drought frequency and severity is projected to increase in many parts of the world, because of anthropogenic climate change (IPCC 2014). Therefore, determining which species might be most susceptible to drought becomes a priority if we are to understand the impacts of climate change on plant communities.

One approach to assessing the likely response of a plant species to drought is by measuring its functional traits (Bartlett et al. 2012a). Functional traits are those attributes of a plant, which impact fitness indirectly via their effects on growth, reproduction and survival (Violle et al. 2007), and may be divided into easy and hard traits. Hard traits are tightly linked to plant functions, but are often difficult to measure; whereas easy traits are relatively quick and easy to measure, but are often less tightly linked to function (Hodgson et al. 1999; Wright et al. 2010). Easy traits are often correlated with hard traits, which may be more accurate indicators of plant functions responsible for responses or effects at ecosystem or biome scale, but which are difficult to quantify for large numbers of species in many regions of the world (Hodgson et al. 1999; Cornelissen et al. 2003). Easy traits are especially useful when assessing large numbers of individuals or species (Cornelissen et al. 2003). However, first we must determine how well these easy traits correspond to key hard traits (Weiher et al. 1999).

A number of hard traits have been linked to plant responses to drought, including osmotic potential at full turgor (π_O), osmotic potential ($\square_{\pi}$), turgor pressure (TP), minimum seasonal water potential (Ψ_w), and stomatal conductance (g_S) (Table 1). These traits have been used to assess physiological drought tolerance for decades (Bartlett et al. 2012a) and have been used to examine the relationship between plants and water supply within or across biomes (Larcher 2003; Nobel 2009). Hard traits are recognized as indicators of drought resistance and tolerance, and also water use efficiency. Some of these traits show a strong association with water availability, and they can also be used to predict drought tolerance and distributions with respect to water supply (Table 1).

Although $\square_{\pi}$, Ψ_w, TP and g_S have been used widely to explain drought tolerance (O'Toole and Cruz 1980; Breshears et al. 2009; Markesteijn et al. 2010), recent studies identify osmotic potential as a suitable drought tolerance indicator (Lenz et al. 2006; Bartlett et al. 2012a, 2012b; Bartlett et al. 2014), as it is recognized as key determinant of plant water stress responses and predictor of distributions with respect to water supply and drought tolerance (Bartlett et al. 2012a). However, despite its potential use for quantifying drought tolerance (Lenz e et al. 2006; Bartlett et al. 2012a, 2012b), only a few studies to our knowledge have tested the direct relationship between π_O and water availability and its relationship to widely measured easy traits (Lenz et al. 2006; Bartlett et al. 2012b).

A number of easy traits have also been correlated to drought resistance, including wood density (WD), wood saturated water content (WCsat), leaf area (LA), specific leaf area (SLA), leaf relative water content (LRWC), and leaf thickness (LT) (Cunningham et al. 1999; Cornelissen et al. 2003; Mitchell et al. 2008). These traits are indicators of drought tolerance and they have been used to observe changes in water content, and plant water status. Some of these traits have been correlated with rainfall (i.e. in areas with low rainfall plants tend to have smaller leaves), and also can be correlated to xylem resistance to cavitation, and hence drought tolerance (**Table 7.1**).

There is a clear need to readily assess drought tolerance in a wide range of species. Differences among species in drought tolerance will determine their current and future distributions, which might include probability of extinctions (Engelbrecht et al. 2007; Feeley et al. 2011), because environmental and climate changes are predicted to increase incidence and severity of droughts in ecosystems worldwide (IPCC 2014). Therefore, predicting the climate change impacts on plant performance and survival is a major challenge facing plant science and ecology (Grierson et al. 2011). Consequently, our aims were to 1) assess drought tolerance of 14 native tree and shrub species from New Zealand forests, by measuring a range of easy (WD, WCsat, LS, SLA, LRWC and LT) and hard drought traits (π_o, □□, TP, □$_w$ and g_S), and 2) evaluate which traits are most related to the key drought tolerance trait of osmotic potential at full turgor.

7.2 MATERIALS AND METHODS

Study area and species selection

The study area is located in the Canterbury Region in New Zealand (**Fig. 7.1**). All sampling was undertaken in the gardens at Landcare Research and Lincoln University, both located in the town of Lincoln, 22 km south of Christchurch, New Zealand, at 15 m asl (43°39’ S, 172º29’ E). Climate is humid with an annual precipitation of 663 mm. The driest month is April with 43 mm. Lincoln has a mean annual air temperature of 10.8 ºC, with January and February the warmest months and June and July the coldest. Mean annual soil temperature at 10 cm depth is 10.7 º, at 30 cm is 11.9 º and at 91 cm is 12 ºC. Annual number of days of frost is 39 (screen frost) and 91 (ground frost) (data from 1881-1970; Cox 1978). Soils are a complex of upland yellow-brown earths, brown granular, and intergrades between these two (Griffiths 1974).

We selected 14 native tree and shrubs species from New Zealand: *Aristotelia serrata*, *Coprosma robusta*, *Dodonaea viscosa*, *Fuchsia excorticata*, *Fucospora cliffortioides*, *Fuscospora fusca*, *Griselinia littoralis*, *Hoheria angustifolia*, *Kunzea ericoides, Lophozonia menziesii*, *Pittosporum eugenioides*, *Pittosporum tenuifolium*, *Plagianthus regius*, and *Pseudopanax arboreus* (Supplemental Table S7.1).

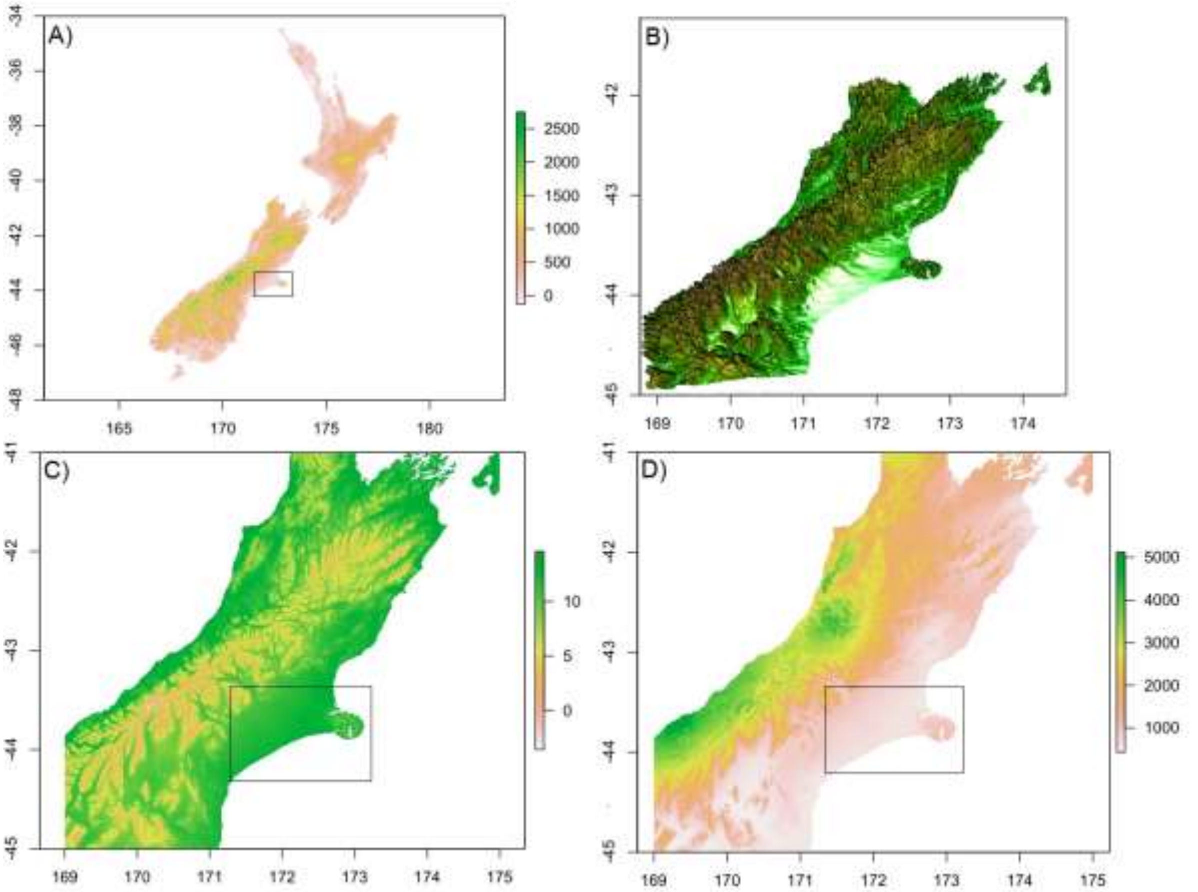

Figure 7.1. Location of the study area showing elevation (m asl, A and B), mean annual temperature (ºC, C) and total annual precipitation (mm, D). Data from WorldClim-Global Climate Data (http://www.worldclim.org/ Accessed January 2015).

Plant Structural and Functional traits: Easy and Hard traits

We measured five hard and six easy traits considered indicators of drought tolerance (Table 7.1). All six easy traits and two hard traits (WD, WCsat, LS, SLA, LRWC, LT, Ψ_w and g_S) were used to construct models for to simplify the estimation of π_O (Supplemental Table S7.2).

Data collection

Field and lab work were undertaken from 3 – 15 March 2014, during late summer / early autumn. Traits were measured for five adult individuals of each 14 species, using mature fully expanded leaves without herbivore damage.

For wood traits (WD and WCsat), small pieces of wood were collected from the trees, and then wood density was calculated using Archimedes' method (Falster and Westoby 2005). Wood density of all samples was determined by taking a 3 cm-long segment cut from one end of each sample at a regular branch thickness (~ 1 cm of diameter); its fresh volume was measured by water displacement with an analytical balance. We also measured fresh mass (FM) of these stems. Prior to oven-drying, we immersed the stems in distilled water for 24 h (until saturation) and later stems were re-weighed to determine saturation mass (SM) (Borchert 1994a). Using these data, we calculated water content (WC, % FM) = 100 (FM - DM)/FM and saturation water content (WCsat, % DM) = 100

(SM - DM)/DM (Borchert 1994b). Wet mass and volume were determined and stems were dried for 72 h at 100 °C and weighed to determine saturated water content (WCsat). Wood density was measured as dry mass divided by fresh volume.

For leaf traits, four leaves per individual were collected. To measure LA, individual leaf laminas were measured without petiole or rachis by taking photographs of each leaf and using the software ImageJ. Then, leaves were dried for 72 h at 70 °C and weighed to determine dry mass. SLA was determined by dividing the surface area of the fresh leaf and dry mass. LT was measured using a dial gauge micrometer (0.01 mm; Insize Inc., Cheektowaga, NY) at three points along the lamina on a fresh leaf, taking care to avoid major veins or the midrib. For LRWC, samples were weighed to give fresh mass (FM). Segments were then floated on distilled water for 4 h at room temperature in laboratory lighting that was close to the compensation point for photosynthesis (Barrs and Weatherley 1962). Then, leaves were re-weighed to give the 'fully turgid' or hydrated mass (HM), after which they were dried for 48 h in an oven at 80 ºC to give the dry mass (D). LRWC was calculated according to Weatherley (1950):

$$\text{LRWC} = (\text{FM} - \text{DM}) / (\text{HM} - \text{DM}) \times 100 \qquad (1)$$

For the hard traits we used 2-5 leaves per individual, making measures daily at midday (1300 h). We obtained the Ψ_π using a vapor pressure osmometer (VAPRO 5520). First we collected leaves, then they were torn and submerged in liquid nitrogen, then were centrifuged for 4 minutes at 12 rpm, and finally samples were read in an osmometer. Ψ_w was measured by obtaining the stem water potential using a pressure chamber (PMS, Corvallis, Oregon, USA) (Scholander et al. 1964; Turner 1981), and g_S was measured using a leaf porometer (Decagon SC-1, Washington, USA). πo was calculated using $\Psi_\pi$and RWC modified from Nguyen-Queyrens et al. (2002):

$$\pi o = (\Psi_\pi \times \text{LRWC} - \text{RWCa}) / (1 - \text{RWCa}) \qquad (2)$$

where RWCa (the RWC of apoplastic water) is a constant value of 0.1.
Turgor pressure, TP was calculated as:

$$\text{TP} = \Psi_w - \Psi_\pi \qquad (3)$$

All trait values were averaged to obtain a mean value for each individual and later they were averaged for each species.

Statistical analysis

Correlation between traits across the 14 species was evaluated through a Principal Components Analysis (PCA). For this purpose, the dataset was organized into a single 11 trait x 14 species matrix, and the PCA was based on the correlation matrix of variables (Jongman et al. 1987). PCA was used to identify relationships between traits and to compare species samples using the multidimensional character of the dataset. Also, we used a one-way analysis of variance (ANOVA) to test for statistical differences among species for each trait. Homogeneity of variances was tested using Levene's Test. Statistical significance was considered at 95% for all cases.

Model selection was conducted by pre-selecting combinations of easy traits (WD, WCsat, LA, SLA, and LT) considered likely to influence to π_O, and then we added to this analysis the hard traits g_S and Ψ_w. The hard traits Ψ_π and TP and the easy trait LRWC were not included in any of the models because they are directly involved in the calculation of π_O, and therefore are not independent.

The selected models for predicting π_O were evaluated through Akaike's information criterion (AICc) (Akaike 1974). AICc was selected over AIC as the total sample size was low and AIC can perform poorly when there are too many estimated parameters (Anderson 2008). AICc also enabled the ranking of the importance of each trait to the overall model set. To do so, the AICc weight values were summed for all models containing a given trait and the totals for each trait were then ranked (Burnham and Anderson 2001). AICc weights are the relative likelihood of each model: the bigger the Delta AICc (Δ_{AICc}), the smaller the weight and the less plausible the model. Model performance was evaluated through leave-one-out cross-validation, leading to the estimation of the root mean squared error (RMSE) produced by each model. We evaluated all models with and without the species' effect; however, we found that considering the species improved models performance increasing their predictability (low RMSE) and their explicability (high R^2) (Table 7.2; Supplemental Table S7.3).

All statistical analyses were conducted using the statistical environment software R (RCoreTeam 2013), specifically the package AICcmodavg (Mazerolle 2013).

Table 7.1. List of traits measured, their units, and description of their relevance to drought tolerance.

Symbol/abbreviation	Trait	Units	Relevance	References
Hard traits				
π_o	Osmotic potential at full turgor	MPa	Key trait driving π_{tlp} (permanent wilting point) across species during seasonal and experimental droughts; hence, powerful trait for predicting drought tolerance and distributions with respect to water supply	Lenz et al. 2006; Bartlett et al. 2012a, 2012b
Ψ_π	Osmotic potential	MPa	Recognized as an indicator of drought resistance and Indicator of water use efficiency, and shows a strong association with water availability within and across biomes	Jongdee et al. 2002; Blum 2005
Ψ_w	Minimum seasonal leaf/steam water potential	MPa	Reflection of the water availability in the soil in the season when water is most limited – hence indicator of drought tolerance	Scholander et al. 1964; Turner 1981; Ackerly 2004; Wyse et al. 2013; Esperón-Rodríguez and Barradas 2014
TP	Turgor pressure	MPa	When plants lose water through stomata, this dehydrates the cells inducing a loss of pressure, drought-tolerant plants protect their dehydrating cells from shrinking as they lose turgor pressure. Saltier cell sap in each plant cell allows the plant to maintain turgor pressure during dry times and to continue photosynthesizing and growing as drought ensues	Tyree 1976; Blake et al. 1991; Torrecillas et al. 1996
g_S	Stomatal conductance	mmol m^{-2} s^{-1}	Recognized as an indicator of plant water stress and drought avoidance. High g_S represent high water loss through transpiration, reducing productivity. Other plant species close stomata to prevent water loss	Rice et al. 2004; Buckley 2005; Buckley and Mott 2013; Wyse et al. 2013
Soft traits				
WD	Wood density	mg mm^{-3}	Correlated with xylem resistance to cavitation and hence drought tolerance	Tyree and Sperry 1989; Maherali et al. 2004; Rice et al. 2004
WC_{sat}	Wood saturated water content	% dry mass	Measure of stem water storage capacity	Borchert 1994a, 1994b
LA	Leaf area	cm^2	Correlated with rainfall, it is recognized that plants occurring in areas of low rainfall tend to have smaller	Cornelissen et al. 2003; Sack et al. 2012; Sack and Scoffoni 2013

			leaves than those in more favorable regions. Small leaves have the capacity to shed heat without using evapotranspiration. Also, smaller leaves have denser venation, which can increase drought tolerance by providing an efficient water transport that contribute to drought tolerance by routing water around blockages caused by drought-induced xylem embolism	
SLA	Specific leaf area	cm^2 mg^{-1}	Index of sclerophylly. Linked with drought tolerance	Salleo et al. 1997; Cunningham et al. 1999; Cornelissen et al. 2003
LRWC	Leaf relative water content	% fresh mass	Indicator of plant water status and water content	Saura-Mas and Lloret 2007
LT	Leaf thickness	μm	Indicator of water deficit and used to observe changes in water content dehydration. During water deficit stress, leaf thickness decreased dramatically by as much as 45%	Marenco et al. 2009; Seelig et al. 2010

Table 7.2. AICc model selection statistics and proposed predicting models for the osmotic potential at full turgor (π_O), considering the traits stomatal conductance (g_S), water potential (Ψ_w), wood density (WD), wood water saturated content (WCsat), leaf area (LA), specific leaf area (SLA) and leaf thickness (LT); the values of the Akaike information criterion (AICc), the AICc accumulated change (Δ_{AICc}), the root mean squared error (RMSE), the error rate for each model (% error) and the R^2 associated to each model . All models considered the species' effect. AICc weights are the relative likelihood of each model: the bigger the Delta AICc (Δ_{AICc}), the smaller the weight and the less plausible the model.

Model	AICc	Δ_{AICc}	AICcWt	RMSE	% error	R^2
g_S/LA	-263.9431	0.00000	0.55839	0.17356	0.25165	0.69427
g_S/(LA+SLA)	-261.8575	2.08559	0.19681	0.17443	0.25292	0.69299
g_S/(LA+LT)	-261.5332	2.40994	0.16735	0.17442	0.25291	0.69228
g_S/(LA+SLA+LT)	-259.2641	4.67900	0.05382	0.17512	0.25392	0.69067
g_S/WCsat	-256.3748	7.56828	0.01269	0.17431	0.25275	0.67728
g_S/(WD+WCsat)	-256.0448	7.89829	0.01076	0.17467	0.25326	0.67998
Ψ_w/WCsat	-247.1634	16.77973	0.00013	0.17646	0.25585	0.65534
LA+SLA+ LT+ WD+WCsat	-243.9368	20.00631	0.00003	0.17700	0.25664	0.65873
g_S/ Ψ_w	-241.8263	22.11679	0.00001	0.17652	0.25594	0.63817
Ψ_w/(LA+SLA)	-240.9215	23.02156	0.00001	0.17893	0.25944	0.64347
WD+WCsat	-239.4747	24.46842	0.00000	0.17722	0.25697	0.63588
(WD+WCsat)/(LA+SLA+LT)	-238.9321	25.01104	0.00000	0.17896	0.25949	0.64631
Ψ_w/(LA+SLA+LT)	-238.5228	25.42030	0.00000	0.17925	0.25990	0.64127
LA+SLA	-237.0808	26.86229	0.00000	0.17919	0.25982	0.62960
g_S+□Ψ_w	-236.9529	26.99024	0.00000	0.17986	0.26080	0.62926
Ψ_w /g_S	-236.0332	27.90988	0.00000	0.17936	0.26007	0.62682
LA+SLA+LT	-234.5316	29.41145	0.00000	0.17980	0.26070	0.62682
g_S/□Ψ_w	-234.111	29.83209	0.00000	0.17994	0.26091	0.62166
g_S	-231.3943	32.54884	0.00000	0.17987	0.26081	0.61017
(LA+SLA+LT)/(WD+WCsat)	-231.2438	32.69927	0.00000	0.18038	0.26154	0.62635
Ψ_w	-226.6876	37.25547	0.00000	0.18168	0.26343	0.59685
Null	-221.7813	42.16182	0.00000	0.18165	0.26339	0.57816
LT	-221.3491	42.59398	0.00000	0.18185	0.26368	0.58118

7.3 RESULTS

Which traits and trait combinations are most correlated with π_O?

For this study, g_S and LA had the highest AICc weights, indicating the importance of both traits when predicting π_O; whereas, □□ had the lowest weight, showing that this trait is not as useful to predict π_O (**Table 7.3**). The ratio g_S / LA was the most efficient variable to predict π_o (**Fig. 7.2**). Thus, π_O increases negatively when g_S decrease and when LA increases (**Fig. 7.3**). Interestingly, none of the models considering only easy traits had high predictive value (**Table 7.2**).

Comparing Δ_{AICc} values provided models for evaluating relative model strength. Accordingly, the model that showed the best performance among the candidate model set was:

$$\pi_O = (-1.264 + a) + 0.0000002524 * (g_S / \text{LA}) \qquad (5)$$

where *a* is the coefficient from the model indicating the species' effect, and is specific of each species (**Fig. 7.3B**). Coefficients are as follows: a) *A. serrata*, -1.264; b) *C. robusta,* -4.4629e-2; c) *D. viscosa* -2.3448e-2; d) *F. excorticata,* -1.1438e-1; e) *F. cliffortioides,* -2.4586e-2; f) *F. fusca,* -1.2372e-1; g) *G.*

littoralis, -1.8867e-1; h) *H. angustifolia,* -1.3693e-1; i) *K. ericoides*, 7.8418e-2; j) *L. menziesii*, 1.1621e-1; k) *P. eugenioides*, -4.1066e-2; l) *P.tenuifolium*, -4.2327e-2; m) *P. regius*, -3.0272e-1, and n) *P. arboreus*, -3.8911e-1.

The next two top-ranked models were also highly plausible (Δ_{AICc} approximately 2 or less) and consisted of variations of the best model, using as predictors g_S /(LA+SLA), and g_S /(LA+LT). Two other models were also considered plausible: g_S /(LA+ SLA+LT) and (g_S /WCsat). The model that considered only easy traits (LA, SLA, WD, WCsat, LT) was ranked eight, but was not considered plausible (Δ_{AICc}>12; **Table 7.2**).

Table 7.3. AICc weight for all models contained each trait was summarized to give a ranking of the importance of each trait.

Trait	AICc Weight Summation
Stomatal conductance (g_S)	0.9998
Leaf area (LA)	0.9764
Specific leaf area (SLA)	0.2507
Wood water saturated content (WCsat)	0.2358
Leaf thickness (LT)	0.2212
Minimum seasonal water potential (Ψ_w)	0.1444
Wood density (WD)	0.1079

Which species are the most drought tolerant?

We found significant differences among species for all traits (**Table 7.4**; **Supplemental Table S7.4**). The species with the highest WD was *D. viscosa*, whereas *P. arboreus* had the lowest WD. Contrary to WD, for WCsat, *P. arboreus* had the highest values and *D. viscosa* the lowest. *Pseudopanax arboreus* had the highest LA and *K. ericoides* the lowest; *F. excorticata* had the highest SLA, and *K. ericoides* the lowest. As for LRWC, *H. angustifolia* had the highest and *K. ericoides* the lowest. LT was highest for *G. littoralis* and lowest for *F. fusca*.

Concerning hard traits, the highest Ψ_π and π_O corresponded to *L. menziesii*, and the lowest to *P. regius*. As for Ψ_w and TP, *P. arboreus* had the highest and *H. angustifolia* the lowest. *Plagianthus regius* had the highest g_S and *P. arboreus* the lowest. Species with the highest hard traits were considered as the most vulnerable (*L. menziesii* and *P. arboreus*). In Table 4 and Supplemental Table S5 we summarized the results obtained for the hard and easy traits.

The two first PCA axes explained 49.49% of the dataset variance (PC1= 32.56% and PC2= 16.93%). Relative importance of traits, according to the length of their associated vectors, showed that the most important trait was π_O, followed by Ψ_π and WCsat, whereas the least important trait was

LRWC (**Table 7.5**). The first axis was most associated with the traits π_O, Ψ_π, Ψ_w and WCsat, whereas the second axis was more influenced by the traits WD, LA, TP and g_S. Angles among vectors showed that all easy traits correlated to each other, except for WD. WD had an inverse relation with all soft traits. As for hard traits, we found an inverse relation between g_S and Ψ_w; whereas π_O and $\Psi\pi$ were closely correlated, we did not find a relationship among these and any of the other traits. Also, the PCA ordination showed that TP is related to easy traits (WCsat, LA, SLA, LT and LRWC). WD and g_S were correlated, and they are inversely correlated to the aforementioned traits (**Fig. 7.4**).

Concerning the relation among traits with species, the hard traits π_O and Ψ_π were strongly associated with *L. menziesii*, *A. serrata*, and *P. eugenioides*. Ψ_w and TP did not seem to be influencing directly any species, and g_S was associated with *P. tenuifolium* and *H. angustifolia.* The easy traits LA, LT and WCsat were associated with *P. arboreus*, indicating the possible vulnerability of this species to drought. WD was associated with *D. viscosa* and *K. ericoides*; *C. robusta* was strongly associated with SLA and LRWC; *F. fusca* did not presented a clear association to any trait (**Fig. 7.4**).

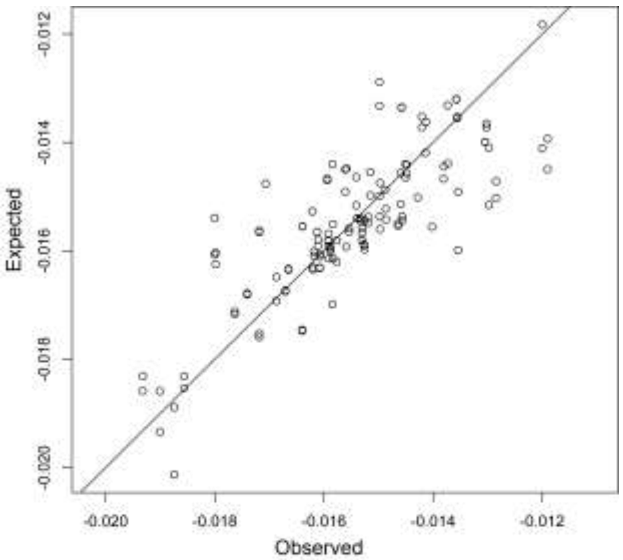

Figure 7.2. Effectiveness evaluation of the model (g_S / LA) (stomatal conductance / leaf area) to predict the osmotic potential at full turgor (π_O), through the criterion of root mean square error.

Table 7.4. Averages and standard deviation (in parenthesis) of wood density (WD), wood saturated water content (WCsat), leaf area (LA), specific leaf area (SLA), leaf relative water content (LRWC), leaf thickness (LT), osmotic potential at full turgor (π_O), osmotic potential (Ψ_π), osmotic adjustment (OA), minimum seasonal water potential (Ψ_w), turgor pressure (TP), and stomatal conductance (g_S) for fourteen New Zealand native tree species.

Species	**WD (mg mm^{-3})**	**WCsat (%)**	**LA (cm^2)**	**SLA (cm^2 mg^{-1})**	**LRWC (%)**	**LT (μm)**	**π_O (MPa)**	**Ψ_π (MPa)**	**Ψ_w (MPa)**	**TP (MPa)**	**g_S (mmol m^{-2} s^{-1})**
Aristotelia serrata	0.56 (0.17)	68.53 (19.35)	24.71 (8.82)	133.22 (36.24)	94.39 (0.45)	22.75 (2.0)	-1.37 (0.14)	-1.50 (0.06)	-0.93 (0.15)	0.56 (0.08)	417 (19.84)
Coprosma robusta	0.61 (0.01)	87.65 (2.59)	14.07 (4.02)	58.57 (9.07)	94.38 (0.69)	34.05 (1.17)	-1.52 (0.03)	-1.62 (0.04)	-0.82 (0.07)	0.61 (0.41)	389.7 (28.17)
Dodonaea viscosa	0.84 (0.03)	43.87 (2.82)	10.35 (3.12)	93.42 (23.52)	90.53 (1.60)	24.10 (3.34)	-1.49 (0.05)	-1.59 (0.07)	-1.55 (0.05)	0.03 (0.12)	316.75 (26.35)
Fuchsia excorticata	0.59 (0.17)	95.99 (42.53)	21.61 (6.39)	139.28 (60.32)	95.54 (0.91)	39.05 (2.63)	-1.52 (0.27)	-1.62 (0.28)	-0.75 (0.05)	0.80 (0.26)	388.87 (145.14)
Fucospora cliffortioides	0.57 (0.12)	72.71 (13.45)	0.52 (0.11)	62.59 (15.78)	93.80 (3.39)	21.72 (2.33)	-1.57 (0.07)	-1.75 (0.09)	-1.2 (0.10)	0.58 (0.14)	320.55 (36.95)
Fuscospora fusca	0.55 (0.03)	73.78 (10.17)	5.22 (0.87)	113.89 (32.28)	95.59 (2.23)	19.94 (1.21)	-1.59 (0.01)	-1.77 (0.02)	-0.92 (0.18)	0.87 (0.17)	261.85 (31.79)
Griselinia littoralis	0.58 (0.02)	95.11 (4.77)	16.30 (3.75)	59.02 (15.71)	86.65 (3.31)	57.90 (3.45)	-1.58 (0.02)	-1.68 (0.03)	-1.33 (0.15)	0.35 (0.15)	271.07 (28.30)
Hoheria angustifolia	0.65 (0.07)	79.13 (12.63)	1.56 (0.48)	93.75 (33.37)	95.95 (0.94)	22.35 (1.80)	-1.66 (0.10)	-1.74 (0.10)	-1.9 (0.10)	-0.18 (0.12)	305.07 (103.81)
Kunzea ericoides	0.72 (0.04)	62.86 (5.79)	0.086 (0.02)	50.64 (19.17)	68.53 (57.25)	25.56 (0.80)	-1.48 (0.15)	-1.60 (0.15)	-1.18 (0.07)	0.42 (0.15)	324.12 (56.14)
Lophozonia menziesii	0.51 (0.06)	90.71 (17.90)	1.34 (0.49)	104.14 (71.39)	94.88 (7.97)	22.50 (1.67)	-1.35 (0.08)	-1.43 (0.06)	-0.9 (0.26)	0.54 (0.25)	231.57 (32.55)
Pittosporum eugenioides	0.68 (0.04)	70.31 (5.21)	22.38 (5.57)	106.79 (34.19)	95.39 (1.14)	20.40 (2.23)	-1.39 (0.16)	-1.62 (0.22)	-0.82 (0.07)	0.91 (0.18)	251.15 (86.65)
Pittosporum tenuifolium	0.72 (0.01)	62.64 (3.62)	4.83 (1.19)	74.78 (18.71)	93.64 (2.14)	26.55 (3.29)	-1.53 (0.08)	-1.78 (0.06)	-1.28 (0.07)	0.52 (0.12)	286.35 (26.56)
Plagianthus regius	0.60 (0.07)	89.32 (11.01)	9.34 (2.69)	102.64 (18.39)	87.95 (1.68)	21.85 (0.91)	-1.85 (0.09)	-1.93 (0.10)	-1.8 (0.10)	0.12 (0.04)	429.22 (144.02)
Pseudopanax arboreus	0.37 (0.15)	141.81 (46.04)	55.99 (22.74)	95.23 (40.68)	95.74 (3.37)	32.50 (7.29)	-1.58 (0.20)	-1.66 (0.22)	-0.62 (0.07)	1.02 (0.30)	140.30 (38.35)

7.4 DISCUSSION

The main questions of our research were: Can easily measured traits be used as surrogates for osmotic potential at full turgor? And, which trees and shrubs are the most likely to survive drought? We found no support for using easy-to-measure traits alone as surrogates for osmotic potential at full turgor. The model that performed as the best predictor of π_O included both hard and easy traits (g_S / LA). We found considerable differences in drought resistance traits among species, which has implications for changes in forest composition under various climate change scenarios. Furthermore, we identified *L. menziesii* as the most vulnerable species concerning π_O.

Easy traits cannot be used as surrogates for osmotic potential at full turgor

Many efforts have been made attempting to link drought resistance with physiological and structural traits (**Table 7.1**). Osmotic potential has been used widely to explain drought tolerance (Callister et al. 2008; Sakthivelu et al. 2008), as reduced osmotic potential allows the plant to maintain turgor, and therefore turgor-dependent processes such as cell expansion and stomatal aperture can continue even at low water potential (Nguyen-Queyrens et al. 2002). Although osmotic potential at turgor loss point, or wilting (π_{tlp}), is also recognized as a major physiological determinant of plant water stress response (Bartlett et al. 2012a, 2012b, 2014), π_O is a key driver of π_{tlp} (Lenz et al. 2006; Bartlett et al. 2012a, 2012b), and so π_O was used to infer drought tolerance and the ability to withstand low leaf water potentials (Bonal and Guehl 2001; Tyree et al. 2003).

As was expected, the hard traits π_O and Ψ_π were closely correlated to each other with high relative importance (**Table 7.5**; **Fig. 7.4**). We also found an important inverse relation between g_S and Ψ_w, a characteristic of avoider species (White et al. 2000; Esperón-Rodríguez and Barradas 2014), although only three of the study species are deciduous; *A. serrata, F. excorticata*, and *P. regius*. A deciduous leaf habit coupled with greater hydraulic conductivity of xylem of deciduous species makes them more able to survive drought by avoiding it (Valladares et al. 2004), but if drought persists, species might die. However, one of these deciduous species (*A. serrata*) was among the most drought tolerant of our study species, having high π_O (**Table 7.4**; **Supplementary Table S7.5**). Deciduous species with traits indicative of drought tolerance have been observed in other ecosystems, including deserts (Smith et al. 1997) and subtropical dry forest (Curran et al. 2009), showing that some species have a combination of drought avoidance and tolerance traits.

We also found a correlation between Ψ_w and TP. Previous studies have shown that plants subjected to dehydration may avoid reduced water potential and maintain turgor by reduction of their turgor-loss volume (TLV) via tissue shrinkage associated with elastic adjustment of their cell walls (Torrecillas et al. 1996; Marshall and Dumbroff 1999). Also, the correlations among TP and leaf traits has been reported before, where leaf shrinkage caused by dehydration has been used as drought indicator (Scoffoni et al. 2014). Another correlation found was g_S and WD. Previous findings have shown that midday g_S was correlated positively with midday stem water potential, where species with higher stem hydraulic conductivity and greater daily reliance on stem hydraulic capacitance were able to maintain higher stem water potential and higher g_S at midday (Zhang et al. 2013). This finding shows that g_S is not only related to leaf traits, but it may also be related to other structural parameters such as WD.

Table 7.5. Length of the vectors of the principal component analysis (PCA) and their relative importance. Eigenvector scores of plant traits in three main PCA axes obtained from a matrix of 12 traits X 14 species. Values are ranked in order of absolute magnitude along PCA axes. The four highest eigenvector scores for each PCA axis are indicated in bold. Values in parentheses indicate variance accounted for by each axis.

Trait	**Length**	**Relative importance**	**PCA1 (32.56%)**	**PCA2 (16.93%)**	**PCA3 (11.56%)**
Osmotic potential at full turgor	1.8193	100%	-0.9534	1.5495	-0.1266
Osmotic potential	1.6852	92.62%	-0.9468	1.3941	-0.3508
Wood water saturated content	1.6172	88.89%	-1.3444	-0.8989	-0.3567
Minimum seasonal water potential	1.6067	88.31%	-1.5582	0.3921	0.2339
Wood density	1.5196	83.52%	1.2954	0.7946	-0.0416
Leaf area	1.5106	83.03%	-1.4103	-0.5416	-0.0079
Turgor pressure	1.3111	72.07%	-1.3080	-0.0911	0.4534
Stomatal conductance	0.8231	45.24%	0.8152	-0.1141	0.6448
Leaf thickness	0.7868	43.25%	-0.5162	-0.5939	-1.0224
Specific leaf area	0.4908	26.98%	-0.4862	-0.0672	1.2369
Leaf relative water content	0.3983	21.89%	-0.3836	-0.1073	1.0013

Our aim was to determine if π_O could be estimated adequately by a model using only easy traits. We found that the best such model was the one that included all easy traits: LA, SLA, LT, WD and WCsat. However, this model was not considered plausible (Δ_{AICc} >12; Anderson 2008), and so we conclude that the commonly-used easy drought traits which we measured are no suitable surrogates for π_O; therefore, drought studies should continue to measure this hard trait.

This finding that easy traits alone cannot be used as surrogates for π_O was supported whether we included species as a fixed or random effect in the model analysis (**Table 7.2**; **Supplemental Table S7.3**). We found better model performance, evidenced in lower RMSE and higher R^2, when species was a fixed effect (**Table 7.2**). If we used species as a random effect, that would imply that the π_O response of all the species is the same (Hubbell 2001), but the better performance of the models when species was a fixed effect (**Table 7.2**; **Supplemental Table S7.3**) suggests that the differences among species were important when considering drought traits. Models with species as a fixed effect had more parameters than those with species as a random effect (AIC can perform poorly when there are too many parameters, see Material and Methods), but regardless of the parameter number the RMSE and R^2 scores were higher for the first set of models. Although intuitive, these results further confirm that species possess different combinations of drought traits.

In our study species, π_O was most correlated to stomatal conductance per unit of leaf area, with π_O becoming less negative when the LA increases and g_S decreases (**Fig. 7.3A**). Plants require more strength to obtain water and keep full turgor when leaf area is higher. Also, low g_S might be a reflection of low water availability in the environment (Aasamaa and Sõber 2011; Esperón-Rodríguez and Barradas 2014). Thus, lower π_O are required to absorb water and to maintain turgor. In drying soil, stomata initially regulate water loss from the leaves to maintain xylem pressure (Ψ_X; measured as water potential below 0) within a range that will protect the xylem from extensive embolism (Tyree and Sperry 1989; Sperry et al. 1998). As drought continues, stomatal closure slows but does not halt the decline of xylem pressure and hydraulic capacity. If soil water is not replenished before complete hydraulic failure occurs then the plant will desiccate and potentially die (Choat et al. 2012).

Which trees and shrubs are the most likely to survive drought?

Drought tolerance is closely related to physiological traits. Species able to tolerate low levels of leaf water content and leaf water potentials survive longest in dry conditions (Tyree et al. 2003). Hence, the physiological ability of cells and meristems to remain alive in dry conditions is also an important component of drought survival (Poorter and Markesteijn, 2008). In our study, we considered as less vulnerable the species capable to reach lowest hard traits values (excluding g_S): *P. regius* and *H. angustifolia*; whereas species such as *L. menziesii* and *P. arboreus* were considered the most vulnerable (Table 4; Supplemental Table S5). Concerning easy traits, species with low values of leaf traits (LA, SLA and LT) might be considered less vulnerable (Mitchell et al. 2008; Curran et al. 2009; Deines et al. 2011); in our study, this was the case for *K. ericoides* (**Table 7.4**; **Supplemental Table S7.5**).

For *K. ericoides,* its drought tolerance has been reported before, proving that this species survives in dry locations having the ability to reach low water potentials (Innes and Kelly 1992). For *L. menziesii*, we also corroborated its vulnerability concerning g_S and water potentials; which has been shown previously comparing this species to *F. cliffortioides* (Sun et al. 1995). Former studies inferred drought tolerance from climatic limits associated with species distribution (Leathwick and Whitehead 2001; Hall and McGlone 2006), and although we measured physiological and morphological traits, we found similarities in both studies, identifying *G. littoralis* as a potential species to be found in drought climates. We also corroborated the sensitivity of *L. menziesii* and *F. fusca*. Differences in responses to water deficits among species appear to reflect differences in climate regimes (Read et al. 2010). If we considered more vulnerable the species with more confined and higher distribution with low precipitation (Leathwick and Whitehead 2001), *F. cliffortioides, K. ericoides* and *L. menziesii* can be considered as more vulnerable (**Supplemental Table S7.1**). When considering also annual degree-day sum limits and annual soil moisture deficit limits (Hall and McGlone 2006), we found *K. ericoides, P. eugenioides* and *P. arboreus* as the least vulnerable species.

We conclude that hard-to-measure drought traits such as π_O can be used to screen species and assess which species might be most vulnerable to future droughts. We propose the model (g_S / LA) as a tool to estimate π_O.

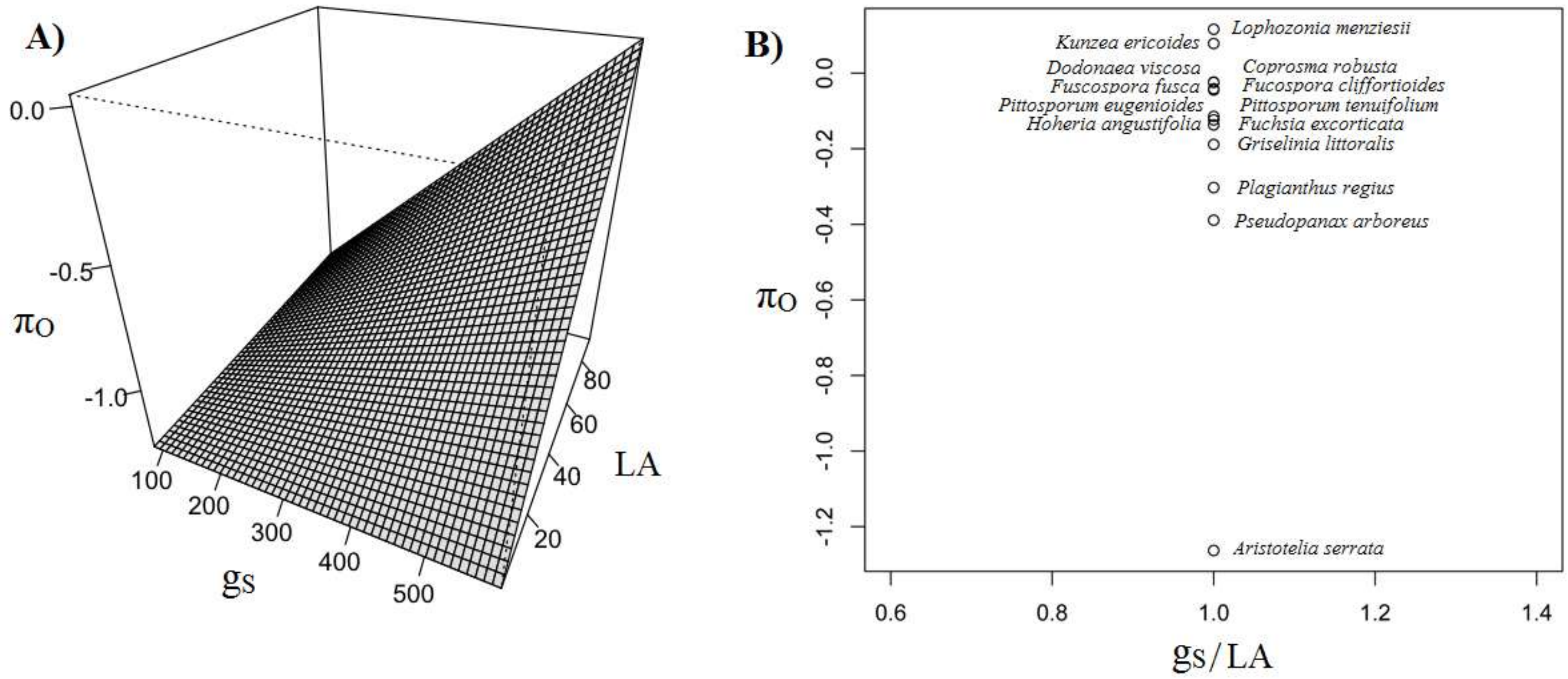

Figure 7.3. Graphical representation of the model (g_S / LA) (stomatal conductance / leaf area) to predict the osmotic potential at full turgor (π_O) for *Aritotelia serrata* (A), and the π_O variability found among 14 tree and shrubs species from New Zealand (B).

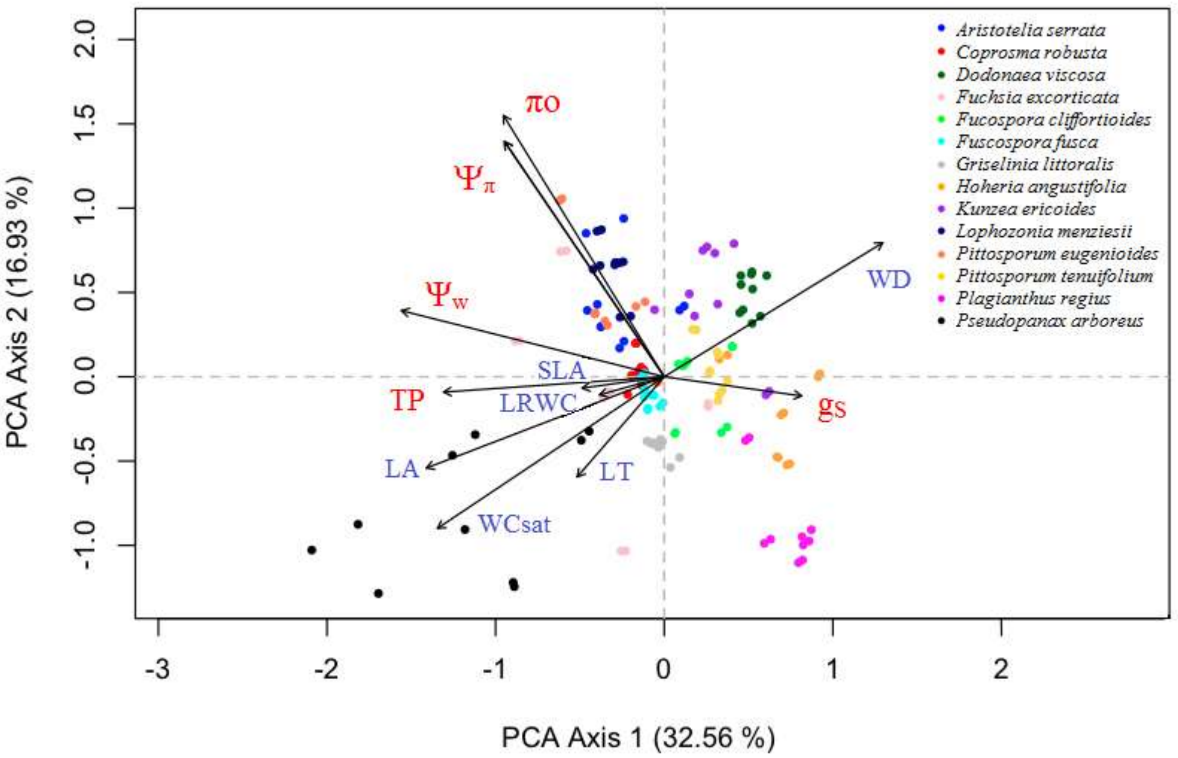

Figure 7.4. Principal Components Analysis (PCA) for hard traits (red): osmotic potential at full turgor (πo), osmotic potential (Ψ_π), osmotic adjustment (OA), minimum seasonal water potential (Ψ_w), turgor pressure (TP), and stomatal conductance (g_S), and soft traits (blue): wood density (WD), wood saturated water content (WCsat), leaf area (LA), specific leaf area (SLA), leaf relative water content (LRWC), and leaf thickness (LT); and the PCA species scores for 14 tree and shrub species from New Zealand.

SUPPLEMENTAL MATERIAL

Table S7.1. Scientific and common name, family, height and diameter, habitat and distribution (Dawson & Lucas 2012) of fourteen New Zealand native tree and shrub species.

Scientific name	Scientific authority	Family	Height (m)	Diameter (m)	Habitat	Distribution
Aristotelia serrata	(J.R.Forst. et G.Forst.) W.R.B.Oliv	Elaeocarpaceae	10	0.30	From moist lowland to montane forest	Throughout New Zealand
Coprosma robusta	Raoul	Rubiaceae	6	0.30	Forest margins and in shrubland from the coast and lowlands to middle elevations	Three Kings Islands and through the North and South islands
Dodonaea viscosa	Jacq.	Sapindaceae	10	0.30	Coastal and lowland open forest	Throughout the North Island, Banks Peninsula and Greymount in the South Island
Fuchsia excorticate	(J.R.Forst. et G.Forst.) L.f.	Onagraceae	12	0.30	From disturbed lowland to mid-montane forest	Throughout New Zealand
Fucospora cliffortioides	(Hook.f.) Heenan et Smissen	Nothofagaceae	15	0.75	Mountain and subalpine forest and shrubland, mostly in drier sides	Coromandel, North Island, and through the South Island
Fuscospora fusca	(Hook.f.) Heenan et Smissen	Nothofagaceae	30	2.0	From moister mid-mountain forest to lowlands	Coromandel, North Island, and through the South Island
Griselinia littoralis	Raoul	Griseliniaceae	10	1.5	From higher elevations to lowlands	Throughout New Zealand
Hoheria angustifolia	Raoul	Malvaceae	15	0.30	Lowland forest. Sometimes forming groves	From Taranaki and Hawke's Bay southwards, North Island
Kunzea ericoides	(A.Rich)	Myrtaceae	20 - 30	0.60	Wetlands, river gravels and dry hillsides	North and South islands
Lophozonia menziesii	(Hook.f.) Heenan et Smissen	Nothofagaceae	25	1.5	Mountain forest and subalpine shrubland, on wetter sides	Coromandel, North Island, and through the South Island
Pittosporum eugenioides	A.Cunn.	Pittosporaceae	12	0.60	Lowland and lower-montane forest, mostly on margins and in second	North and South islands

					growth	
Pittosporum tenuifolium	Sol. ex Gaertn.	Pittosporaceae	8	0.30 - 0.40	In coastal to lower-montane forest including margins and in second growth	North and South islands
Plagianthus regius	(Poit.) Hochr.	Malvaceae	15	1	In lowlands and lower mountains, fertile and frosty river flats, and in damps hollows	Throughout New Zealand
Pseudopanax arboreus	(L.f.) Allan	Araliaceae	8	0.30	Lowland forests and shrubland	North and South islands

Table S7.2. Possible relation between osmotic potential at full turgor (π_O) and water potential (Ψ_w), stomatal conductance (g_S), wood density (WD), wood water saturated content (WCsat), leaf area (LA), specific leaf area (SLA), leaf relative water content (LRWC) and leaf thickness (LT).

Hard trait	**Model**	**Justification**
π_O =	LA+SLA+ LT+ WD+WCsat	All soft traits might be correlated to π_O
	LA+SLA+LT	All leaf traits are correlated to π_O. The bigger the leaf, the lower the π_O to maintain the osmotic potential at full turgor
	WD+WCsat	Wood traits correlate with π_O. High WCsat and low WD increase the π_O, as there is more water in the plant
	(LA+SLA+LT)/(WD+WCsat)	Higher leaf traits, and lower wood traits decrease π_O
	LT	As the LT increases, π_O decreases to keep full turgor
	WCsat	As the WCsat increases, π_O increases due to water availability
	g_S	As g_S increases, transpiration and water loss increase, therefore π_O decreases to keep the full turgor
	Ψ_w	Both traits, Ψ_w and π_O, decrease under dry conditions
	g_S/□Ψ_w	As water is lost through stomata, and Ψ_w decreases to obtain water from the soil, π_O also decreases
	g_S/(LA+SLA+LT)	π_O is associated to changes in the g_S and a combination of leaf traits. Adding LA, SLAT and LT increased the leaf size and might increased the g_S by increased stomata
	g_S/LA	π_O is associated to changes in g_S and a combination of leaf traits: the bigger the leaf area the lower the π_O, and the bigger the leaf area the higher the g_S
	g_S/(LA+SLA)	Increasing SLA decreases the π_O
	g_S/(LA+LT)	High values of LT decrease the π_O as it requires more strength to maintain full turgor
	g_S/WCsat	Increasing WCsat and decreasing g_S, increases π_O, as there is more water in the plant and less water loss throw stomata
	g_S/(WD+WCsat)	Increasing the WCsat and decreasing WD and g_S, increases π_O, as there is more water in the plant and less water loss throw stomata
	Ψ_w/WCsat	π_O increases when there is water in the soil related to high values of Ψ_w and WCsat
	Ψ_w/(LA+SLA+LT)	Low Ψ_w represents low water availability, and high leaf traits represent lower π_O to maintain full turgor

Table S7.3. AICc model selection statistics and proposed predicting models for the osmotic potential at full turgor (π_O), considering the traits stomatal conductance (g_S), minimum seasonal water potential (Ψ_w), wood density (WD), wood water saturated content (WCsat), leaf area (LA), specific leaf area (SLA) and leaf thickness (LT); the values of the Akaike information criterion (AICc), the AICc accumulated change (Δ_{AICc}), the AICc weight and the error rate for each model. Models do not consider the species' effect. AICc weights are the relative likelihood of each model: the bigger the Delta AICc (Δ_{AICc}), the smaller the weight and the less plausible the model.

Model	**AICc**	**Δ_{AICc}**	**AICcWt**	**RMSE**	**% error**	**R^2**
Ψ_w /g_S	-1461.197	0.0000	7.9097 e-21	0.001336	0.1763	0.325
g_S/WCsat	-1453.471	7.7252	1.6620 e-22	0.001567	0.1801	0.286
Ψ_w/(LA+SLA+LT)	-1447.391	13.8059	7.9476 e-24	0.001405	0.1864	0.255
g_S/□Ψ_w	-1445.245	15.9516	2.7184 e-24	0.001307	0.1870	0.243
g_S	-1445.071	16.1257	2.4917 e-24	0.001547	0.1860	0.236
Ψ_w	-1439.276	19.8786	3.8156 e-25	0.001380	0.1885	0.228
g_S/(LA+SLA+LT)	-1425.014	21.9210	1.3742 e-25	0.001510	0.1894	0.223
g_S/(LA+SLA)	-1424.365	36.1830	1.0993 e-28	0.001506	0.2012	0.125
(WD+WCsat)/(LA+SLA+LT)	-1422.914	36.8322	7.9457 e-29	0.001675	0.2012	0.128
g_S/(LA+LT)	-1422.181	38.2831	3.8465 e-29	0.001492	0.2031	0.119
g_S/(WD+WCsat)	-1414.114	39.0155	2.6671 e-29	0.001547	0.2036	0.122
g_S+□Ψ_w	-1412.004	47.0823	4.7246 e-31	0.001387	0.2086	0.047
Ψ_w/WCsat	-1410.858	49.1931	1.6444 e-31	0.001382	0.2112	0.041
g_S/LA	-1408.549	50.3384	9.2748 e-32	0.001492	0.2122	0.040
LT	-1408.346	52.6479	2.9227 e-32	0.001576	0.2117	0.016
LA+SLA+LT+WD+WCsat	-1407.791	52.8508	2.6408 e-32	0.001600	0.2117	0.000
(LA+SLA+LT)/(WD+WCsat)	-1407.073	53.4053	2.001 e-32	0.001569	0.2116	0.035
WD+WCsat	-1406.572	54.1239	1.3973 e-32	0.001591	0.2122	0.014
Ψ_w/(LA+SLA)	-1406.382	54.6250	1.0876 e-32	0.001398	0.2131	-0.004
WCsat	-1404.484	56.7227	9.8934 e-32	0.001581	0.2124	-0.006
LA+SLA	-1403.491	47.7056	3.8295 e-33	0.001570	0.2145	-0.012
LA+SLA+LT	-1401.960	59.2364	2.3310 e-33	0.001617	0.2157	0.005

Table S7.4. ANOVA analysis. Differences of the traits among 13 native tree and shrub species from New Zealand: *Aristotelia serrata, Dodonaea viscosa, Coprosma robusta, Fuchsia excorticata, Fucospora cliffortioides, Fuscospora fusca, Griselinia littoralis, Hoheria angustifolia, Kunzea ericoides, Lophozonia menziesii, Pittosporum eugenioides, P. tenuifolium, Plagianthus regius* and *Pseudopanax arboreus.* All results are significant $P < 0.05$.

Trait	**F**	***P***
Osmotic potential (Ψ_π)	14.05	<0.0001
Osmotic potential at full turgor (π_O)	15.39	<0.0001
Osmotic adjustment (OA)	15.65	<0.0001
Minimum seasonal water potential (Ψ_w)	209.6	<0.0001
Turgor pressure (TP)	93.02	<0.0001
Stomatal conductance (g_S)	18.37	<0.0001
Wood density (WD)	17.3	<0.0001
Wood water saturated content (WCsat)	15.22	<0.0001
Leaf area (LA)	44.59	<0.0001
Specific leaf area (SLA)	6.189	<0.0001
Leaf relative water content (LRWC)	2.168	0.0145
Leaf thickness (LT)	123.9	<0.0001

Table S7.5. Ordering of the species 1, *Aristotelia serrata*; 2, *Coprosma robusta*; 3, *Dodonaea viscosa*; 4, *Fuchsia excorticata*; 5, *Fucospora cliffortioides*; 6, *F. fusca*; 7, *Griselinia littoralis*; 8, *Hoheria angustifolia*; 9, *Kunzea ericoides*; 10, *Lophozonia menziesii*; 11, *Pittosporum eugenioides*; 12, *P. tenuifolium;* 13, *Plagianthus regius*; and 14, *Pseudopanax arboreus*, according to the values obtained for traits of wood density (WD), wood water saturated content (WCsat), leaf area (LA), specific leaf area (SLA), leaf relative water content (LRWC), leaf thickness (LT), osmotic potential at full turgor (π_O), osmotic potential (Ψ_π), osmotic adjustment (OA), minimum seasonal water potential (Ψ_w), turgor pressure (TP) and stomatal conductance (g_S).

-							**Species**								**+**
WD	*14*	*10*	*6*	*1*	*5*	*7*	*4*	*13*	*2*	*8*	*11*	*9*	*12*	*3*	**WD**
WCsat	*3*	*12*	*9*	*1*	*11*	*5*	*6*	*8*	*2*	*13*	*10*	*7*	*4*	*14*	**WCsat**
LA	*9*	*5*	*10*	*8*	*12*	*6*	*13*	*3*	*2*	*7*	*4*	*11*	*1*	*14*	**LA**
SLA	*9*	*2*	*7*	*5*	*12*	*3*	*8*	*14*	*13*	*10*	*11*	*6*	*1*	*4*	**SLA**
LRWC	*9*	*7*	*13*	*3*	*12*	*5*	*2*	*1*	*10*	*11*	*4*	*6*	*14*	*8*	**LRWC**
LT	*6*	*11*	*5*	*13*	*8*	*10*	*1*	*3*	*9*	*12*	*14*	*2*	*4*	*7*	**LT**
π_O	*13*	*8*	*6*	*5*	*7*	*14*	*12*	*2*	*4*	*3*	*9*	*11*	*1*	*10*	π_O
$\Psi\pi$	*13*	*12*	*6*	*5*	*8*	*7*	*14*	*2*	*4*	*11*	*9*	*3*	*1*	*10*	$\Psi\pi$
OA	*13*	*8*	*6*	*7*	*14*	*5*	*12*	*2*	*4*	*3*	*9*	*11*	*1*	*10*	**OA**
Ψ_w	*8*	*13*	*3*	*7*	*12*	*5*	*9*	*1*	*6*	*10*	*2*	*11*	*4*	*14*	Ψ_w
TP	*8*	*3*	*13*	*7*	*9*	*12*	*10*	*1*	*5*	*2*	*4*	*6*	*11*	*14*	**TP**
g_S	*14*	*10*	*10*	*6*	*7*	*12*	*8*	*3*	*5*	*9*	*4*	*2*	*1*	*13*	g_S

Capítulo 8

Discusión y conclusiones finales

Vulnerabilidad

La Vulnerabilidad se refiere a la capacidad de ser herido; por ejemplo, el grado en que es probable que un sistema experimente un daño debido a la exposición a un peligro (Turner et al. 2003). Para este trabajo, nosotros consideramos al cambio climático como un potenciador de vulnerabilidad (IPCC 2001, 2007, Ford et al. 2006, Füssel 2007). Por lo tanto, la vulnerabilidad frente al cambio climático es definida como el grado en que el cambio climático puede dañar a un sistema, dependiendo de la sensibilidad del sistema y de su capacidad para adaptarse a las nuevas condiciones climáticas (Watson et al. 1996). Sin embargo, esta definición deja fuera la respuesta fisiológica de los organismos y su capacidad de adaptarse a esas nuevas condiciones, por lo que en términos ecofisiológicos, la vulnerabilidad es el grado de susceptibilidad o de la incapacidad de un organismo para adaptar sus funciones fisiológicas a los cambios ecológicos y ambientales (Esperón-Rodríguez y Barradas 2014a).

Pero la vulnerabilidad no solo afecta la respuesta de los organismos al medio ambiente en términos fisiológicos, la vulnerabilidad abarca también la esfera social, política y económica, y si dejamos a un lado estos componentes, cualquier trabajo de vulnerabilidad queda incompleto. Es por esto, que en este trabajo también se abordó la vulnerabilidad socio-económica, la cual se define como la susceptibilidad que tiene una población a ser dañada por la exposición a un peligro, que afecta directamente su capacidad para prepararse, responder y recuperarse (Hewitt 1997). También se define como la exposición de los grupos o individuos al estrés como resultado de un cambio social, económico y ambiental, donde el estrés se refiere a los cambios y la interrupción inesperada de los medios que favorecen la vida (Adger 1999). La vulnerabilidad es un fenómeno socialmente construido influenciado por las dinámicas institucionales y económicas. La vulnerabilidad social es en parte, producto de las desigualdades sociales. Las características de las comunidades y su medio ambiente, el nivel de urbanización, las tasas de crecimiento, y la vitalidad económica contribuyen a la vulnerabilidad socio-económica de los lugares (Cutter et al. 2003).

Importancia de la conductividad estomática (g_S)

En esta tesis se utilizó la respuesta de la g_S como un indicador de vulnerabilidad, teniendo en cuenta que la g_S es una respuesta fundamental de las plantas al clima, ya que controla la transpiración (estado del agua) y la asimilación de CO_2, jugando un papel muy importante en la fotosíntesis y la productividad de la planta (Jones 1992). Por lo tanto, al determinar la respuesta de la g_S a diferentes factores climáticos (Jarvis 1976;. Wright et al. 1996) es posible inferir los posibles efectos del cambio climático. Y si bien reconocemos que la g_S no es el único rasgo fisiológico que se puede utilizar para evaluar la vulnerabilidad, se utilizó este parámetro considerando que la g_S es un buen reflejo de las condiciones micro-ambientales y los procesos fisiológicos de las especies a las condiciones locales particulares.

El estudio de las respuestas estomáticas nos ayuda a comprender el control de la transpiración y la asimilación en ambientes naturales y artificiales (Barradas et al. 1994), en nuestro caso, el efecto en el invernadero. En ambientes naturales y artificiales, la apertura y el cierre de los estomas se ven afectados directamente por las variables como la temperatura del aire (T_A), la radiación fotosintéticamente activa (PAR), el déficit de presión de vapor (*VPD*) y el estado hídrico (Ψ).

El método de las funciones envolventes.

Para entender cómo los cambios en las variables T_A, PAR, *VPD* y Ψ afectan a la fotosíntesis, el crecimiento, y en nuestro caso particular, la g_S, se requiere un método que nos ayudan a evaluar la vulnerabilidad de las especies dentro del ecosistema (Cooperativas y Waring 2011). Este método debe ser capaz de predecir el rendimiento de la planta fuera del rango nativo de la especie (Sands et al. 2000; Rodríguez et al. 2002; Tinte et al. 2004). La posible desventaja del método es que se requiere un conocimiento detallado para definir la respuesta fisiológica de las especies a las variaciones de T_A, PAR, *VPD*, de la precipitación y de las propiedades del suelo (Cooperativas y Waring 2011). Estudios previos sobre el efecto de las variables micro-ambientales y fisiológicas sobre g_S han demostrado la existencia de una gran diversidad de respuestas estomáticas a diferentes factores microclimáticos y fisiológicos (Fanjul y Barradas 1985; Roberts et al. 1990; Pitman 1996; Meinzer et al. 1997; Comstock y Mencuccini 1998; Barradas et al. 2004; Esperón-Rodríguez y Barradas 2014a,b). En el presente trabajo consideramos el método de las funciones envolventes para describir las respuestas de la g_S a diferentes variables.

De las respuestas de g_S, se puede explorar cómo las poblaciones pueden incrementar su vulnerabilidad potencial frente a cambios en T_A, PAR, *VPD* y Ψ, y es posible inferir el efecto del cambio climático global, local y regional. Estudios previos han demostrado la utilidad de usar este método para observar la respuesta de g_S (Fanjul y Barradas 1985; Ramos-Vázquez y Barradas 1998; Barradas et al. 2004, 2011; Gerosa et al. 2012; Esperón-Rodríguez y Barradas 2014a, b). Y además, se añadió el uso de este método para evaluar y comparar la vulnerabilidad de las especies a través de la utilización de un índice de vulnerabilidad dentro del ecosistema, y también se utilizó el método para caracterizar y analizar la formación de grupos funcionales.

Del método de las funciones envolventes se observó que los valores del coeficiente de determinación (r^2) eran indicativos de una buena aproximación a los rangos de función de los estomas. El ajuste de las curvas g_S *vs.* T_A, PAR, *VPD* y Ψ mostró una mayor sensibilidad de la g_S a las variables. En general, los valores de los coeficientes de determinación del modelo fueron indicativos de una mejor concordancia entre los valores de g_S observados y los valores generados a partir del modelo. Reconocemos que aunque el modelo en sí mismo no es eficiente para explicar la variación de los estomas en diferente tiempo y lugares, el uso de este método es una fuerte herramienta para analizar por separado las respuestas de g_S a las diferentes variables (T_A, PAR, *VPD*, Ψ) dentro del ecosistema.

Además, al comparar los resultados entre las condiciones de campo e invernadero, se corroboró la especificidad de sitio debido a las condiciones ambientales específicas. De esta manera, este método podría ser considerado como individuo-específico. Por lo tanto, es necesario tener cuidado al intentar extrapolar los parámetros del método a otros sitios en diferentes condiciones y tiempo, especialmente si no se considera los datos de campo e invernadero. Aún así, nuestros resultados pueden ayudar a una mejor comprensión de la respuesta potencial de las variables climáticas y los posibles cambios en escenarios de perturbación.

Asimismo, encontramos la efectividad del método de las funciones envolventes para caracterizar y formar grupos funcionales. Con este método tomamos y analizamos los valores estimados a partir de las curvas envolventes, y estos valores nos permitieron extrapolar los resultados más allá de los individuos, lo que permite analizar las variaciones fisiológicas de una población determinada. El uso de este método también puede ayudar a predecir el rendimiento de plantas fuera de sus rangos nativos (Sands et al. 2000; Rodríguez et al. 2002; Tinte et al. 2004)

Implicaciones futuras

Los aumentos graduales en la temperatura, cambios en los patrones de lluvia y las modificaciones en la radiación solar probablemente tendrán un impacto en el crecimiento, la regeneración y la tasa natural de mortalidad de las poblaciones vegetales; mientras que los cambios más abruptos en el clima pueden dar lugar a grandes incendios, heladas, sequías y brotes de insectos y enfermedades (Chapin et al., 2010). Además, también se espera un aumento en el riesgo de sequía en muchas regiones (Nitschke y Innes, 2008) lo que afectará la distribución de las especies. Existen tres expectativas generales para las respuestas de las especies a estos cambios: el movimiento, la adaptación (ya sea en términos de cambio evolutivo o de aclimatación fisiológica), o la extinción (Holt 1990). Si las especies son suficientemente móviles, es posible el desplazamiento de la posición geográfica de sus nichos ecológicos; si las especies son capaces de un rápido cambio evolutivo o tienen una amplia gama de tolerancias fisiológicas, la adaptación a las condiciones cambiantes podrá ser posible. A falta de movilidad y adaptabilidad, la extinción es el resultado probable (Holt 1990;. Melillo et al. 1995). Se espera que los cambios en el clima cambien la distribución de las especies a lo largo de gradientes ambientales si su actual tolerancia ambiental se ve superada (Miller y Urban, 1999). Además, las interacciones de las especies bajo condiciones de cambio climático probablemente se verán alteradas, influyendo así sus distribuciones potenciales (Davis et al. 1998), por lo que debemos tomar en cuenta la capacidad de dispersión frente al cambio esperado en la distribución de las especies. La capacidad de dispersión jugará un papel importante para las especies para llegar a lugares donde las condiciones ambientales sean más favorables para su establecimiento, crecimiento y reproducción.

Los aumentos de temperatura predichos por los modelos de cambio climático reflejan vulnerabilidad de las especies frente a estos cambios. Las especies podrían responder a esta vulnerabilidad mediante la migración a zonas más elevadas, donde la temperatura es más baja. Por lo tanto, se requieren planes y políticas de gestión que incorporen la respuesta de las especies y los ecosistemas para ayudar a las especies a responder los cambios ambientales rápidos (del Barrio et al. 2006). Debe tenerse en cuenta que si una especie no tiene la capacidad de migrar a elevaciones más altas debido a la falta de dispersión eficaz, este proceso de migración podría estar asistido, empezando por las especies más vulnerables. Sin embargo, es importante mencionar que las variables climáticas no son los únicos parámetros que delimitan la distribución de las especies. Factores tales como la deforestación, la agricultura y el crecimiento urbano, juegan un papel de extrema importancia para la conservación. Científicos y políticos deben trabajar juntos para implementar planes adecuados y acciones que no sólo garanticen la preservación de las especies, sino también beneficien a las comunidades locales.

Como conclusiones finales podemos decir que la región de las Grandes Montañas es vulnerable frente al cambio climático, encontrado cambios en las tendencias de temperatura y precipitación. Además, en este trabajo se encontró que la vulnerabilidad no sólo se da en términos ambientales y ecofisiológicos, sino también en términos socio-económicos. También encontramos que la vulnerabilidad de las especies es diferencial, encontrando especies y grupos funcionales más vulnerables que otros, en particular a cambios en el estado hídrico de las especies.

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