

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

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ABSTRACT: We define vulnerability here 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, in Las Grandes Montañas. 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

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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 cli-

mate 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/absence. 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, negative effects 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 vari-

ables 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 eco-physiological 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.

2. METHODS

2.1. Study area

The central mountain region of Veracruz, Mexico (19° 54' 08" N, 96° 57' 19" W) (Fig. 1) is part of the Trans-Mexican volcanic belt and the Sierra Madre Oriental. Abrupt topography is the main characteristic of this region with a pronounced altitudinal gradient (from sea level to 5500 m a.s.l. 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°C, and annual precipi-

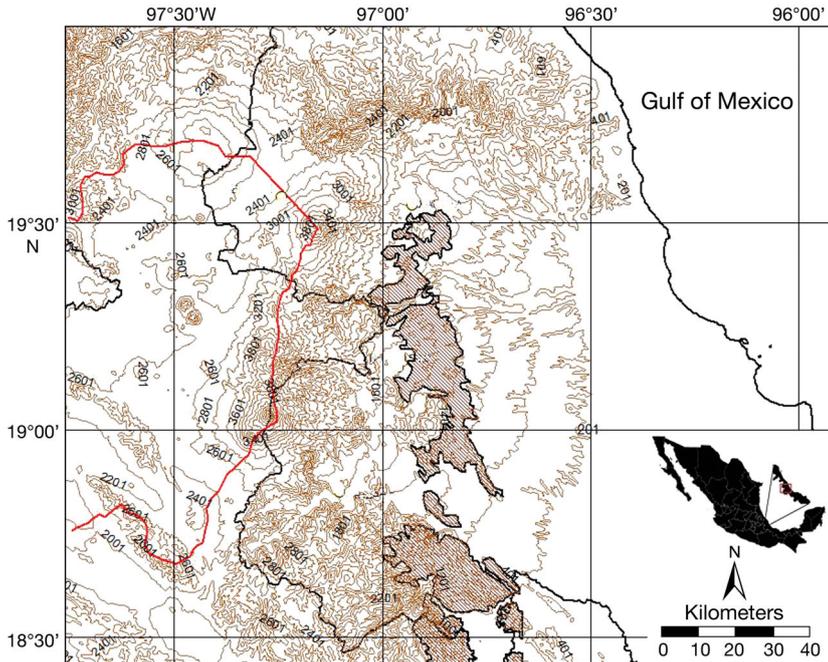


Fig. 1. Study area in the central mountain region of Veracruz, Mexico. Black line: stated division between Veracruz and Puebla; red line: watershed; brown lines and shaded area: contours and Mountain Cloud Forest, respectively

tation 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). The soils 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).

2.2. 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 1).

Table 1. Height, diameter, climatic requirements (temperature and precipitation ranges) and distribution (altitudinal range) of *Alnus acuminata*, *Quercus xalapensis*, *Liquidambar styraciflua* and *Pinus ayacahuite*

	Height (m)	Diameter (cm)	Temperature range (°C)	Precipitation range (mm)	Altitudinal range (m a.s.l.)
<i>Alnus acuminata</i>	10–30	35–100	4–27	1000–3000	500–2800
<i>Quercus xalapensis</i>	30	45	12–18	1400–2300	400–2700
<i>Liquidambar styraciflua</i>	20–60	42–150	12–18	1000–2000	400–1800
<i>Pinus ayacahuite</i>	35–40	>100	13–17	800–1500	2000–3500

2.3. 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.

2.4. 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 07:00 and 14:00 h every day in well-irrigated individuals.

2.5. Climatological measurements

All climatological measurements of T_A , PAR, E , relative humidity (RH) and leaf temperature (T_L) were determined when measuring each leaf with a quantum sensor (LI-190SB, LI-COR), a fine wire thermocouple and a humicap sensor (Vaisala, Helsinki). Thermocouples were mounted in the porometer. The leaf–air 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 10:00 to 18:00 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.

2.6. 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 g_S as a function of any variable (edaphic or climate). The method has 3 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. VPD and T_A), and (3) there are no 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 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 parabolic function, making it possible to determine both the optimum temperature (T_O) at which $g_{S_{MAX}}$ occurs and the cardinal temperatures (minimum and maximum).

Envelope values of g_S as a function of PAR are consistent with a hyperbolic function:

$$g_S = [aPAR/(b + PAR)] \quad (2)$$

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

The g_S function in relation to 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 (Ψ) 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.

2.7. Potential distribution and climate change model

To analyze the possible vulnerability in the region, we developed potential distribution maps for the spe-

cies using the MaxEnt program and ArcView GIS 9.1. We took data provided by the website Global Biodiversity Information Facility (www.gbif.org, 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 mean annual temperature and precipitation (INEGI). MaxEnt 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 to 2099.

2.8. 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. RESULTS

Regarding climatological measurements, we found no differences when comparing field and greenhouse T_A ($F = 2.733$, $p = 0.104$). The greenhouse average temperature was 24.32°C, whereas the average temperature in the field was 23.76°C. As for VPD and PAR, significant differences were found ($F = 31.14$, $p < 0.001$, and $F = 15.24$, $p < 0.001$, respectively). The average VPD in the greenhouse was 2.03 kPa,

Table 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 Ψ , $n = 150$ for each species) and ANOVA between species. * $p < 0.05$

	g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	Ψ (MPa)	T_A ($^{\circ}\text{C}$)	VPD (kPa)	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	E ($\text{mmol m}^{-2} \text{s}^{-1}$)
<i>Alnus acuminata</i>	433.96 \pm 176.49	-1.94 \pm 0.98	25.90 \pm 3.81	2.26 \pm 0.5	151.25 \pm 63.62	17.76 \pm 8.82
<i>Quercus xalapensis</i>	320.81 \pm 125.53	-1.65 \pm 0.44	25.84 \pm 3.71	2.28 \pm 0.5	152.69 \pm 62.74	13.13 \pm 5.94
<i>Liquidambar styraciflua</i>	329.66 \pm 138.18	-1.73 \pm 0.57	25.84 \pm 3.56	2.27 \pm 0.48	144.93 \pm 60.23	13.34 \pm 6.13
<i>Pinus ayacahuite</i>	377.54 \pm 138.18	-0.57 \pm 0.37	25.84 \pm 3.53	2.22 \pm 0.48	182.73 \pm 84.99	14.07 \pm 5.44
F-value	310.8	115.9	0.033	2.376	18.86	47.66
p (>F)	$< 2.0 \times 10^{-16}$ *	$< 2.0 \times 10^{-16}$ *	0.992	0.0681	3.95×10^{-12} *	$< 2.0 \times 10^{-16}$ *

whereas in the field, it was 1.31 kPa. The average PAR in the greenhouse was 230 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas in the field, the average PAR was 613.54 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

After analyzing the variables g_s , T_A , PAR, VPD and Ψ between species, we found significant differences when comparing g_s , PAR, Ψ and E (Table 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). For all the species, we found the maximum climate variables (T_A , PAR and VPD) at 14:00 h. Concerning g_s , *A. acuminata* and *Q. xalapensis* had the highest values at 14:00 h, whereas *L. styraciflua* and *P. ayacahuite* had the highest values at 07:00 h. All the species had their lowest Ψ values at 14:00 h (Fig. 2).

3.1. The envelope function method

From the envelope function method, we generated g_s curves versus T_A , PAR, VPD and Ψ (Fig. 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 in PAR, VPD and Ψ (Table 4). After analyzing the g_s - T_A curves, we obtained the optimum and cardinal (minimum and maximum) temperatures, and the optimum thermal range (Table 4). *A. acuminata* was the species most capable of tolerating high temperatures, whereas *P. ayacahuite* was the least tolerant species. All the species presented values of T_O and T_R (Table 4) above that of data reported in their natural distributions (Table 1).

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

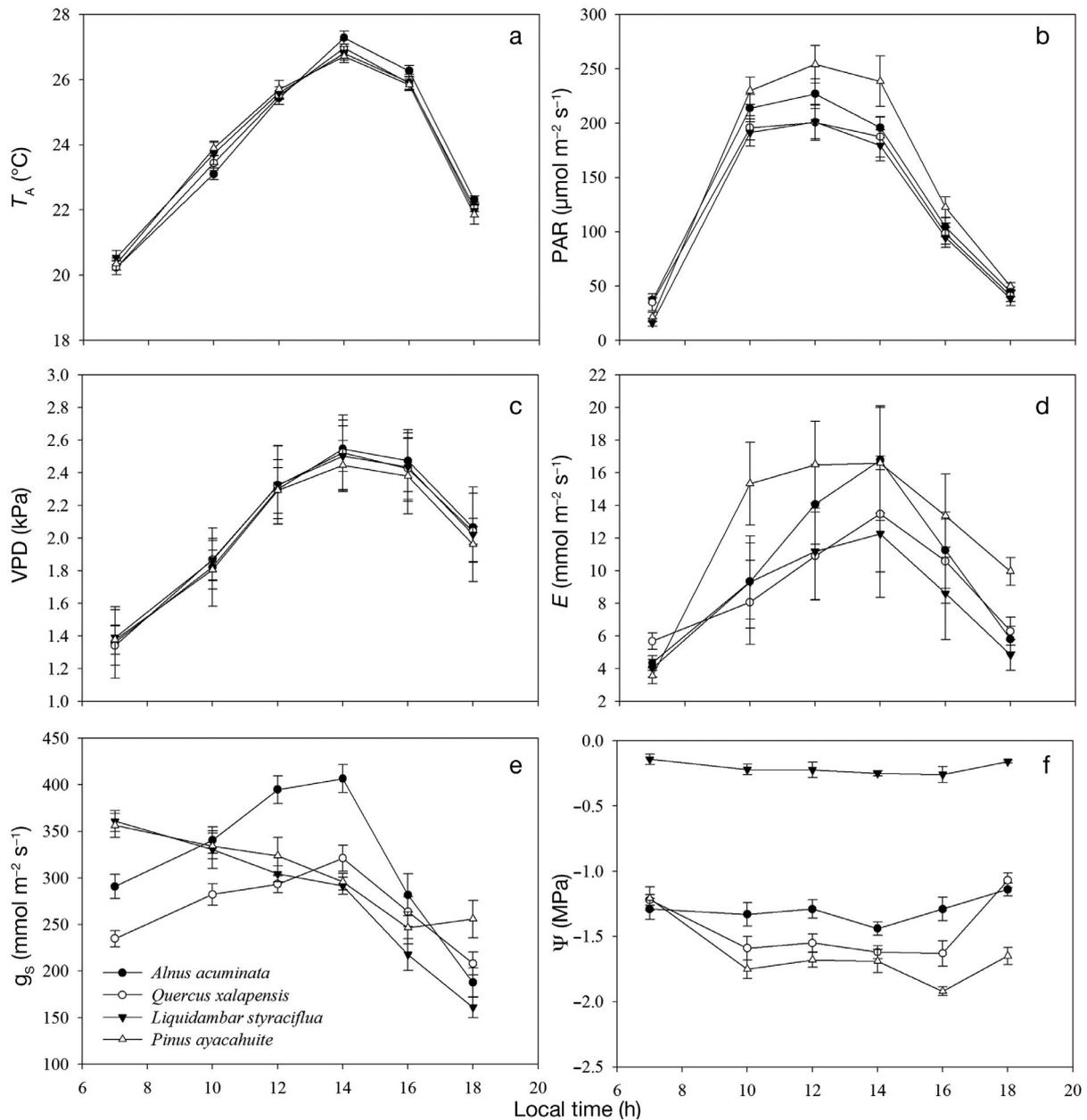


Fig. 2. Diurnal variations of (a) air temperature (T_A), (b) photosynthetically active radiation (PAR), (c) vapor pressure deficit (VPD), (d) transpiration (E), (e) stomatal conductance (g_s), and (f) leaf water potential (Ψ) for *Alnus acuminata*, *Quercus xalapensis*, *Liquidambar styraciflua* and *Pinus ayacahuite*. Data points represent the mean of 145 measurements on different leaves except for Ψ , which were based on 75 measurements. Vertical bars represent the standard deviation of the mean

Concerning 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).

3.2. Potential distribution and climate change model

From the generated potential distribution of the species, *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 km²; (2) *Q. xalapensis*: 2918.54 km²; (3) *L. styraciflua*: 2179.75 km², and (4) *P. ayacahuite*: 765.61 km².

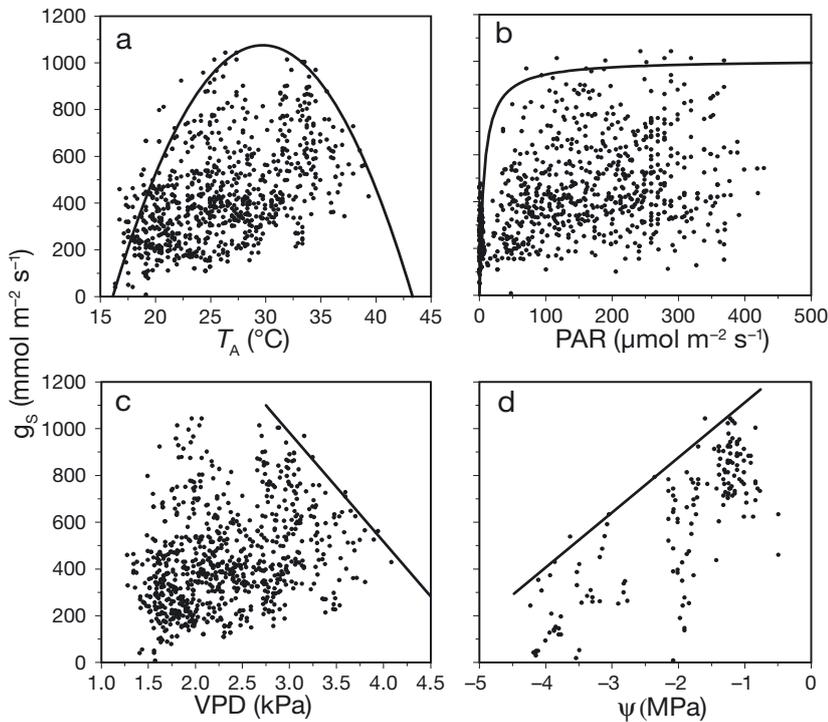


Fig. 3. Scatter diagrams and probable boundary-line of stomatal conductance (g_s) plotted against (a) air temperature (T_A), (b) photosynthetically active radiation (PAR), (c) vapor pressure deficit (VPD) and (d) water potential (Ψ) for *Alnus acuminata*

Table 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 \pm SD

	T_{\min} (°C)	T_{\max} (°C)	T_O (°C)	T_R (°C)
<i>Alnus acuminata</i>	16.1 \pm 0.3	41.5 \pm 0.3	29.7 \pm 0.5	22.17–37.17
<i>Quercus xalapensis</i>	15.7 \pm 0.4	39.5 \pm 0.2	28.2 \pm 0.4	20.65–37.39
<i>Liquidambar styraciflua</i>	15.1 \pm 0.3	37.8 \pm 0.2	27.5 \pm 0.3	19.55–36.19
<i>Pinus ayacahuite</i>	14.2 \pm 0.3	37.3 \pm 0.2	26.2 \pm 0.2	18.26–34.56

The 4 species are distributed between the 10 and 22°C isotherms, where *P. ayacahuite* is located in the coldest range (10–12°C), *A. acuminata* is located between 14 and 22°C, and *Q. xalapensis* and *L. styraciflua* are located in the warmest range (16–22 and 18–20°C, respectively) (Fig. 4).

The climate change model (SIECCRe) showed an increase of 2 to 5°C for the year 2099. From this model, we obtained the following equation: $T = 0.0318 (\text{year}) - 63.51$, $r^2 = 0.84521$.

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.

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). 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.

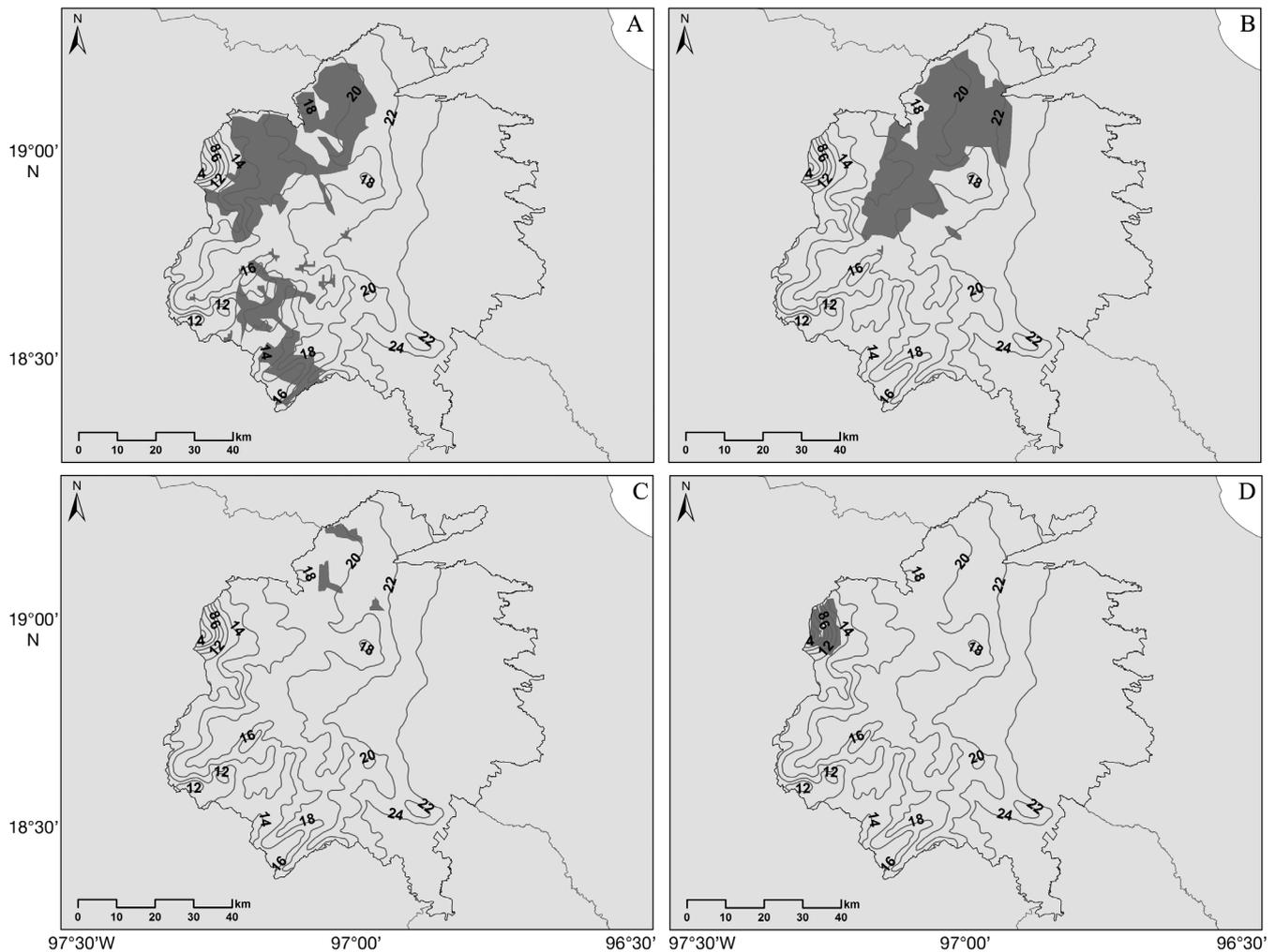


Fig. 4. Potential distribution (shaded area) of (A) *Alnus acuminata*, (B) *Quercus xalapensis*, (C) *Liquidambar styraciflua* and (D) *Pinus ayacahuite* and annual average temperature ($^{\circ}\text{C}$) distributions in the central mountain region of Veracruz, Mexico

4.1. Temperature

Concerning the stomatal response to temperature, the experiments in general show that when increasing temperature, the stomata open (Hovenden & Brodrribb 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. ayacahu-*

ite 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 1) and the data obtained from the envelope function method (Table 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. 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. 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 the vulnerable species.

4.2. PAR

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 & Söber 2011). If stomata close, photosynthesis decreases. Even under conditions that may not be considered stressful, stomatal closing can substantially restrict CO₂ 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 .

4.3. VPD

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).

4.4. 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, as well as a diminished frequency of fog at some levels. These changes have direct repercussions on solar radiation, which is expected to be more intense where both rainfall and the frequency of fog decreases (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 the Ψ in our experiment (Bunce 1999); however, stomatal response might have also been affected by the 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 the pressure changes in the xylem and by the stomata closure (During 1993). Therefore, caution is advised when analyzing the g_s response after submitting the individuals to 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. This type of vulnerability is extremely relevant, given the decrease in precipitation predicted in the region. 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 & Ibanez 2008). In the field, this water storage allows the survival of species during drought periods. Climate variability is partic-

ularly 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 temperature and precipitation (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. For the study region, we conclude that the species are vulnerable not only to the 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.

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