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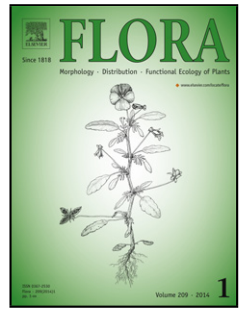

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Induced climate change impairs photosynthetic performance in *Echinocactus platyacanthus*, an especially protected Mexican cactus species

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Highlights

- Global warming is expected to affect physiological performance also of desert plants
- We therefore assessed the effects of induced warming in a protected cactus species
- We found 100% survival in young plants with induced warming
- Increased temperature affected the photosynthetic performance of young cacti
- Induced warming caused high non-photochemical quenching, to avoid photoinhibition

ABSTRACT

The responses of desert plants to climate warming have been poorly assessed, perhaps due to the overall expectation that desert vegetation will expand as a consequence of this component of climate change. However, determining what plant species will tolerate the expected increases in temperatures is a question that remains unanswered. The Chihuahuan Desert is the largest warm desert of North America, and predictive models of climate change indicate that summer temperatures in this desert will increase by 1–2 °C in the next decade. This study experimentally assessed the performance of an endangered cacti species from the Chihuahuan Desert under simulated warming conditions. Hexagonal open top chambers (OTCs) were used to simulate the effects of global warming on five-years-old individuals of the specially protected species *Echinocactus platyacanthus*. Temperature was 1.9 °C higher in open top-chambers than in control plots. In contrast, relative humidity was 3.1% higher in control plots than in open top-chambers. *Echinocactus platyacanthus* showed 100% survival for 14 weeks in both OTC and control plots. However, induced warming negatively affected the photosynthetic performance of this species. Cacti located within OTCs displayed lower maximum quantum efficiency of photosystem II (F_v/F_m), effective quantum yield of photosystem II (Φ_{PSII}), and electron transport rate (ETR) values, but higher non-photochemical quenching (NPQ) values, than cacti from control plots. This is the first study focused on the potential impact of climate warming on survival and photosynthetic performance of young individuals of a succulent species from American deserts. Induced warming negatively affected the photosynthetic performance of young *E. platyacanthus*, but it also increased non-photochemical quenching, a mechanism for avoiding photoinhibition.

Key words*:*Cactaceae; Global warming; Chlorophyll fluorescence; Stress tolerance

1. Introduction

Changes to the Earth's climate system during the last century have arisen from the accumulation of greenhouse gases in the atmosphere (Watson et al., 1990; IPCC, 2013). Together with other disturbances that humans have induced on natural ecosystems, including extensive deforestation and changes in albedo of ice or snow covered surfaces, such an accumulation of greenhouse gases is strongly influencing global temperatures (Le Treut et al., 2007). This human-induced global warming increases the extinction risk of plant species with low tolerances to raising temperatures (Malcolm et al., 2006). Nevertheless, the responses of plants to climate warming have been mainly assessed in tropical (e.g. Colwell et al., 2008) and temperate forests (De Frenne et al.,

2010) or in arctic and alpine ecosystems (Bokhorst et al., 2013), while little is yet known about the effects of warming on desert plants. This situation is perhaps due to the overall expectation that desert vegetation will expand as consequence of climate change (Prentice et al., 1992), but determining what plant species will tolerate the expected increases in temperatures is a question that remains unanswered.

The Chihuahuan Desert is the largest warm desert of North America, ranging from southwestern United States to the Central Mexican Highlands (Archer & Predick, 2008). Predictive models of climate change indicate that summer temperatures (June–September) in this desert will increase by 1–2 °C in the 2020 decade (Magaña et al., 2004). However, the major temperature changes by 2030 are predicted to occur during winter months (January–March), when monthly average temperatures might increase by up to 6 °C (Magaña et al., 2004). These predicted climate changes have triggered strong concerns in conservation biologists because the Chihuahuan Desert harbors an elevated richness of succulent plants (Rzedowski, 1991). Nevertheless, there is little information about how these plants will respond when facing increased temperatures, especially in their regeneration phase (Pérez-Sánchez et al., 2011). The expected increase in temperatures might surpass the thermal tolerance thresholds of native species and this could affect their recruitment and survival. Therefore, climate change could lead to local species extinctions across the Chihuahuan Desert during the next two decades. Thus, the work hypothesis of this study was that increased temperature stress due to induced climate warming would negatively impact on the specially protected *Echinocactus platyacanthus* Link & Otto (Cactaceae), causing lower photosynthetic performances than those observed in conspecific individuals subjected to current climate conditions. This is the first study focused on the potential impact of simulated climatic warming (using open-top-chambers) on survival and photosynthetic performance of young individuals of a succulent species, common in arid and semiarid areas of Mexico.

2. Materials and methods

2.1 Study species

Echinocactus platyacanthus is a barrel-like cactus that can reach 2 m height and 80 cm in diameter (Jiménez-Sierra et al., 2007). This cactus is endemic to México, but overexploitation for food and ornamental proposals has heavily endangered the natural populations of this species (Jiménez-Sierra et al., 2007). For this reason, *E. platyacanthus* has been included as specially protected species in the framework of the environmental laws and regulations of México (SEMARNAT, 2010). According to Jiménez-Sierra et al. (2007) mean annual mortality in natural populations is highest for seedlings (19.7%) and lowest for adults (2.5%).

2.2 Study area

This study was conducted in the southernmost section of the Chihuahuan Desert, within the state of San Luis Potosí (México). The experimental site was located at an abandoned agricultural field (22° 14’ 11’’ N, 100° 51’ 46’’ W, 1844 m a.s.l.) where current vegetation is composed by sclerophyllous shrubs, cacti and other succulent plants. Mean annual temperature at the study site is 17.8 °C, but it can surpass 35 °C in summer and fall down below -1 °C in winter (Medina et al., 2005). Average annual precipitation is 341 mm and rainfall events are concentrated in the summer months June–September (Medina et al., 2005).

2.3 Seed collection

The effects of climate warming were assessed on young individuals of *E. platyacanthus* that were developed from seeds in the greenhouses of Instituto Potosino de Investigación Científica y Tecnológica (San Luis Potosí, México). For this, mature fruits were harvested in the field between summer and autumn 2007. Fruits were taken to the laboratory and cleaned to recover the seeds, which were germinated on peat moss trays within growth chambers (25 °C, 80% relative humidity, and photoperiod 12 h light/dark). Seedlings were later moved to the greenhouse and transplanted into individual plastic pots (one seedling per pot). These pots had a capacitance of 2 liters and were filled with a mixture of gravel (10%), sand (30%) and clay (60%). The plants were grown for five years in the greenhouse prior to be used in the experiment described below. Environmental conditions in the greenhouse were 33 °C, 80-90% of total daily photon flux density (PFD, 1300 μmol m^{-2} s^{-1}), and 60% relative humidity. The size of the plants after 5 years was 4 cm in height and 6 cm in diameter.

2.4 Open top-chambers design

Several manipulative systems have been proposed to simulate the influence of climate change on plants (*e.g.*, Bokhorst et al., 2013). Nevertheless, open-top chambers (OTCs) are still being the most common and simplest approach for assessing the responses of plants to climate warming in the field (De Frenne et al., 2010). In this study, hexagonal OTCs were used to simulate the effects of global warming on *E. platyacanthus*. These structures were built with UV-resistant transparent acrylic (3 mm thick; wavelength transmission < 280 nm) by following the design proposed by Marion (1996). The resulting OTCs were 50 cm tall, 150 cm wide in the open-top, and 208 cm wide at the base attached to ground. This OTC design allows daytime passive heating by increasing air temperature by 2–5 °C, as compared to the external environment (Musil et al., 2005, 2009).

2.5 Ambient and open top-chambers microenvironments

Because the larger increases in temperatures for the Chihuahuan Desert are expected in winter months, coinciding with the dry seasons, the experimental assessment of the responses of *E. platyacanthus* to induced warming was started in January 2013. The experiment was conducted within a 25 m x 25 m exclosure previously established at the study site. This exclosure was fenced with woven wire (2 m height) to avoid the access of cattle and people to the experiment. On January 7th 2013, twelve plots (5 m x 5 m = 25 m^2 each) were drawn within the exclosure by following a rectangular arrangement (3 plots width x 4 plots long). Six plots were randomly selected within the exclosure and an OTC was established at the center of each of these plots. The other six plots were maintained as controls. Temperature and relative humidity were continuously recorded within and outside OTCs to determine whether OTCs effectively modify microclimate. For this, we used microclimatic data-loggers (HOBO Pro v2, Onset Computer Corporation, MA, USA) programmed to record temperature and relative humidity every 1 h. A data-logger was located 20 cm above the ground at the center of each experimental plot, at 3–5 cm above plants, resulting in six data-loggers in plots containing open top chambers (OTCs) and six data-loggers in plots without OTCs. The incident photon flux density (PFD) 20 mm above the saplings was measured at mid-day with a quantum sensor (LI250-A, Li-Cor, Inc., Lincoln, Nebraska, USA).

2.6 Chlorophyll fluorescence measures

One week after mounting OTCs in the field (January 14th 2013), all experimental plots received three pots with young individuals of *E. platyacanthus* (one individual per pot). The pots were placed on the soil. In those plots subjected to warming conditions, plants were placed at the center of OTCs directly below the open-top, to avoid overwarming due to proximity to the acrylic walls of these structures. All these cacti were watered every week to field capacity until the beginning of the experiment. Field capacity was determined in pots containing overwatered mixture and allowed to drain overnight. To reach field capacity, 200 mL water per pot was required. Nevertheless, the plants did not receive further watering during the experiment.

Three months after beginning the experiment (April 23rd 2013), we counted the number of *E. platyacanthus* individuals that survived within each plot. After that, two rounds of chlorophyll fluorescence measures were taken on all living cacti by using a portable pulse amplitude modulation fluorometer (Mini-PAM; H. Walz, Effeltrich, Germany). These data were used to estimate a series of variables related to the photosynthetic performance of plants located within and outside OTCs. The first round of chlorophyll fluorescence measures was conducted on dark-adapted cacti at predawn (between 05:00 and 06:00 h) in order to assess the maximum quantum efficiency of photosystem II. This variable was estimated as $F_v/F_m = (F_m - F_0)/F_m$, where F_v =

variable fluorescence determined in darkness, F_m = maximal level of fluorescence measured in darkness, and F_0 = minimal level of fluorescence measured in darkness (Maxwell and Johnson, 2000). The values for this ratio oscillate between 0.80 and 0.83 if environmental stress is negligible for plants, but these values decrease with increasing environmental stress (Maxwell and Johnson, 2000). In our case, lower F_v/F_m values were expected for *E. platyacanthus* individuals located within OTCs.

The second round of chlorophyll fluorescence measures was conducted at noon (between 13:00 and 14:00 h), when plants faced the maximum daily temperature. These data were used to estimate the effective quantum yield of photosystem II (Φ_{PSII}). This variable was computed as $\Phi_{PSII} = (F_m - F_t)/F_m$, where F_t is the chlorophyll fluorescence emitted by plants under steady-state illumination (i.e., light conditions in the field) and F_m is the maximum fluorescence emitted by chlorophyll when a saturating pulse of actinic light is superimposed to environmental levels of light (Genty et al., 1989). Similarly to the ratio F_v/F_m, the values of Φ_{PSII} should decrease as thermal stress increases and, thus, lower Φ_{PSII} were expected for cacti located within OTCs.

Because the fluorometer we used also measures the photon flux density (PFD) in the environment surrounding plants, we also calculated the electron transport rate (ETR) across the electron chain of chloroplasts. This variable was then estimated as ETR = Φ_{PSII} x PFD x 0.84 x 0.5, where PFD is the photosynthetic photon flux density recorded by the sensor in the leaf clip, 0.84 is the estimated mean proportion of incident light absorbed by the photosystems (Ehleringer, 1981) and 0.5 is the required factor for both photosystems to account for absorbed photons (Roberts et al., 1996).

Because ETR is directly and positively related to the generation of chemical energy (ATP and $NADPH/H^+$) that will be later used in the Calvin cycle, lower values of this variable are indicative of reduced photosynthetic performance in plants (Ritchie and Bunthawin, 2010). Therefore, if induced warming negatively affects the performance of *E. platyacanthus*, cacti located within OTCs should display lower ETR values than cacti from control plots.

Finally, because chlorophyll fluorescence was measured at both predawn and noon, we also calculated the non-photochemical quenching efficiency (NPQ) of cacti. This variable was calculated as NPQ = $(F_o - F_m)/F_m$, where F_o is the basal chlorophyll fluorescence emitted by cacti at predawn (dark-adapted plants), and F_m is the maximum fluorescence emitted by chlorophyll after imposing a saturating pulse of actinic light at noon. NPQ specifically refers to the mechanism used by plants to dissipate the excess of light energy captured by chlorophylls as heat. This mechanism of energy dissipation is linked to the xanthophyll cycle, and higher NPQ values are expected with increasing levels of environmental stress (Maxwell and Johnson, 2000). Therefore, if thermal stress induced by warming negatively affects *E. platyacanthus*, cacti located within OTCs should display higher NPQ values than cacti in control plots.

2.7 Statistical analyses

Biotic and abiotic measures were based on 6 replicates (from 6 OTC and 6 controls). Each replicate had 3 plants, and the value for a replicate was based on their average. The biotic (F_v/F_m, ΦP_{SII}, NPQ and ETR) and abiotic variables (air temperature, relative humidity and PFD) were analyzed through one-way ANOVA. Most data fulfilled the requirements of variance homogeneity and homoscedasticity, except abiotic variables, thus these data were analyzed through non-parametric ANOVA (Kruskal-Wallis One Way ANOVA on Ranks).

3. Results

Mean air temperature (Figure 1a) and relative humidity (Figure 1b) significantly differed ($P < 0.001$) between open top-chambers and control plots. Temperature was on average 1.9 °C higher in open top-chambers than in control plots. In contrast, relative humidity in control plots was 3.1% higher than in open top-chambers. Maximum and minimum mean temperatures were 41.7 °C and 4.8 °C in the OTC's, as well as 34.2 °C and 4.7 °C in the control plots. The light intensity received at mid-day by plants inside OTCs (1922.1 ± 47.5 μmol m^{-2} s^{-1}) was similar to that received by plants in the control plots (1941.9 ± 9.4 μmol m^{-2} s^{-1}), without significant differences between treatments ($P = 0.825$).

Echinocactus platyacanthus showed 100% survival in both OTC and control plots. However, induced warming negatively affected the photosynthetic performance of this species. The F_v/F_m values were significantly higher in the control plots than in the open top-chambers ($F_{1,10} = 22.427$, $P < 0.001$; Table 1). The quantum yield of photosystem II (Φ_{PSII}) was higher in the control than in the OTC plots ($F_{1,10} = 23.001$, $P < 0.001$; Table 1). ETR values were also higher in the control than in the OTC plots ($F_{1,10} = 18.539$, $P < 0.005$; Table 1), and NPQ values were higher in the OTC than in the control plots ($F_{1,10} = 20.150$, $P < 0.005$; Table 1).

4. Discussion

The recorded 1.9 °C increase in mean daily air temperature in the OTC's over the treatment period fitted to 1–2 °C increase predicted for the Chihuahuan Desert under summer in the next decade, although did not fit for winter months for which predictive models suggest increase up to 6 °C (Magaña et al., 2004). OTC plots also had lower relative humidity than control plots, which was also expected because of the warming inside and the semiarid climate. Low relative humidity diminishes the atmospheric water vapor and therefore the water condensation in the soil; affecting the water uptake by the superficial roots of some succulents (Von Willert et al., 1992; Martorell & Ezcurra, 2002; Matimati et al., 2012). Thus, increased temperature and decreased relative humidity inside OTCs were expected to affect the performance of *E. platyacanthus*. We hypothesize that the lower Φ_{PSII} values found in OTC plots than in controls were a consequence of the lower relative humidity inside OTCs which could have reduced water uptake.

OTC effects on spectral composition of global radiation were ignored, and radiation from the chamber walls was partly neglected (Jetten, 1992; Nussbaum & Fuhrer, 2000). Thus, the effects of the acrylic walls on spectral composition and its possible effects on chlorophyll concentration and chlorophyll fluorescence measurements remain to be tested.

The Φ_{PSII} values were lower than the F_v/F_m ratios in both OTC and control plots. This decrease in the values of the ratio between variable and maximum fluorescence during the day is related to increases in the emission of fluorescence when chlorophylls are exposed to more light than can be handled by the electron transport chain in the thylakoid membrane (Duan et al., 2005). However, cacti inside OTCs always displayed lower Φ_{PSII} and ETR values than those in control plots. This suggests that plants under induced warming were exposed to intense physical stress, as compared to plants in control plots. Our findings are in agreement with Musil et al. (2009) who found a decline in both photochemical efficiency and ETR for the succulent *Cephalopyllum* *spissum*, a South African succulent species, following short (2-h) exposures to heat of increasing intensity in the temperature range 42–54 °C.

In addition, because ETR is positively related to the ability of plants to assimilate CO_2 (Kitao et al., 2003; Kakani et al., 2008), these results suggest diminished photosynthetic performance of cacti under induced warming. In a contrary way, induced warming caused high NPQ which indicates that cacti within OTCs required dissipation of quantities of light energy in excess of those required for photochemistry or of those re-emitted to the environment as fluorescence (Krause and Jahns, 2004; Müller et al., 2001).

We found 100% survival for *E. platyacanthus* in both OTC and control plots, which is contrary to findings for southern African quartz-field succulents (Musil et al., 2005), which after 4-months summer treatment, displayed between 2.1 and 4.9 times greater plant and canopy mortalities in the open top chambers than in the control plots. It is possible that high survivorship for *E. platyacanthus* plants is related with high non-photochemical quenching values, because high NPQ is a mechanism for avoiding photoinhibition (Barker et al., 2002). Non-photochemical quenching was not investigated for African quartz-field succulents, but we hypothesized that it was low.

Our hypotheses that cacti located within OTCs displayed lower F_v/F_m, Φ_{PSII}, and ETR, as well as higher NPQ values, than cacti from control plots were corroborated. Nobel (2010) suggests that desert succulents have high tolerance to water and temperature stress; however, predictions of global change studies propose that succulents will decrease in species range due to increased temperature and diminished precipitation (Butler et al., 2012; Dávila et al., 2013). Ureta et al. (2012) studied two threatened *Mammillaria* species (Cactaceae) with contrasting distribution ranges under climate change scenarios, and suggested that the most widespread species would be less affected by climate change, proposing that past selection on plasticity allows it to survive under variable conditions. Interestingly, *E. platyacanthus* is one of the most widespread Mexican cactus species (Jiménez-Sierra et al., 2007) and young plants of this species showed 100% survivorship under simulated warming. In addition, it is possible that adult individuals of *E. platyacanthus* are less sensitive to temperature increases than young plants, because adult *E. platyacanthus* preferentially tilt towards the south, which reduces temperatures on the apical meristems during the hot season (Herce et al., 2014).

Most predictions of global changes have been suggested for adult plants, but there are no studies taking into account other plant development phases, such as seeds, seedlings or young plants which are more susceptible to extreme temperatures (Drennan, 2009) or drought (Delgado-Sánchez et al., 2013). The seasonal variation of *E. platyacanthus* performance inside OTC's to evaluate the hypothesis on 6 °C increase in the next 30 years remains to be studied. Nevertheless, after induced warming by 1.9 °C for three months, we found 100% survival of young *E. platyacanthus*. However, this simulated global warming reduced photosynthetic efficiency and also resulted in high non-photochemical quenching to avoid photoinhibition. The long-term consequences of these physiological responses for plant fitness have still to be investigated.

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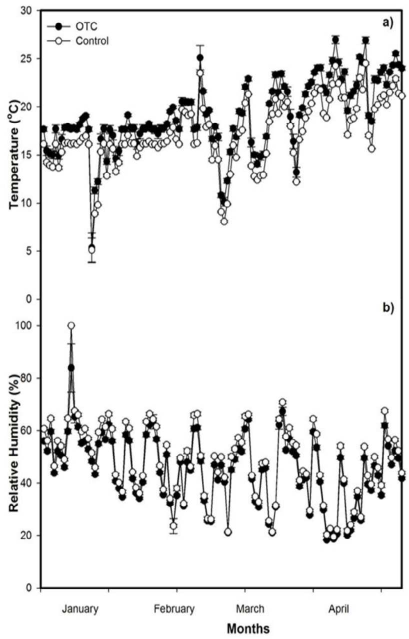
Figure Caption:

Fig. 1 Daily changes (± SE) in mean air temperature (a) and mean relative humidity (b) in open top-chambers (black circles) and control plots (white circles), over 120 days. Significant differences between treatments were found ($P < 0.05$).

Table 1

Effect of induced warming on photosynthetic performance of young plants of *Echinocactus platyacanthus*. Different letters indicate significant differences between treatments ($P < 0.05$).

Variable	OTC	Control
	Mean (± S.E.)	**Mean (± S.E.)**
$\mathbf{F_v/F_m}$	0.630 ± 0.025 [b]	0.760 ± 0.01 [a]
$\mathbf{\Phi_{PSII}}$	0.199 ± 0.02 [b]	0.327 ± 0.02 [a]
ETR (μmol m^{-2} s^{-1})	142 ± 18.3 [b]	266 ± 16.1 [a]
NPQ	0.755 ± 0.08 [a]	0.484 ± 0.06 [b]



OTC
Control
a)
b)
Temperature (°C)
Relative Humidity (%)
January
February
March
April
Months

Figure 1