Seasonal ecophysiological variations of *Echinocactus platyacanthus*, a specially protected cactus species: Effect of induced climate warming

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ABSTRACT

Cactus species are key components in American deserts and have a high socioeconomic value. Climate change exerts a threat to biodiversity, structure and functioning within deserts and many cactus species are predicted to face extinction because of climate change. Defining which plant species could tolerate climate change effects in desert ecosystems acquires crucial importance to promote conservation of these species. *Echinocactus platyacanthus* is a specially protected cactus species, widely distributed in desert areas of Mexico; however, long-term implications of climate change on survival and physiological responses of this species are still unclear. We assessed the effect of induced warming in the photosynthetic performance and survival on five-years old individuals of *Echinocactus platyacanthus* for a year. Open-top chambers (OTCs) were used to simulate the effect of global warming (a drive of climate change), while controls were exposed to the current climatic conditions. A generalized canonical correlation analysis was used to measure the intensity of the relationship among environmental variables (mean air temperature, evapotranspiration, global photon flux density, and rainfall), micro-environmental (mean temperature, mean relative humidity and photosynthetic photon flux density) and ecophysiological variables [effective quantum yield of photosystem II (Φ_{PSII}) and electron transport rate (ETR), both within and outside of OTCs]. OTCs had higher temperature than control plots through the seasons. *Echinocactus platyacanthus* showed higher seasonal variations in photosynthetic performance under warming than in current temperature; nevertheless, 100% survival in both treatments were found. The Φ_{PSII} and ETR values were lower in summer inside OTCs but increased in autumn and winter. We found a strongest correlation between environmental and micro-environmental variables, as well as between micro-environmental and ecophysiological ones, which support the

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premise that the young individuals of *E. platyacanthus* depends on the microenvironment to survive. Although after a continuous year under induced warming, individuals of *E. platyacanthus* showed a decrease in the Φ_{PSII} values during summer and spring and an increase in autumn and winter, survival was not affected. These results reflect the high tolerance in early developmental phases of *E. platyacanthus*, an adequate functioning of the photosynthetic apparatus of this species could be an efficient physiological mechanism to face future climate change.

1. Introduction

Climate change represents a severe threat to the biodiversity, structure and functioning of the ecosystems (Malcolm et al., 2006; IPCC et al., 2013). Deserts are one of the most diverse biomes, they host about 20% of plant diversity worldwide (White and Nackoney, 2003). Desert vegetation is expected to expand its distribution range because of climate change, as these plant species can rapidly adapt to water shortage and high temperatures (Tielbörger and Salguero-Gómez, 2014). However, because a given change in climate is expected to have the largest proportional effect on biodiversity in biomes characteristic of extreme climates, climate change models suggest that small changes in temperature or precipitation in deserts will result in large changes in species composition and biodiversity (Sala et al., 2000). In addition, climate change has a great influence on the distribution in arid and semi-arid regions, if the temperature will increase 1.5 or more degrees, then plants could reduce their distribution area and thus desertification may emerge (Chen et al., 2021). Therefore, defining the plant species that could tolerate the increases in temperatures is very important to promote conservation and management practices of desert species. In addition to warming, changes in the patterns of precipitation can also have a strong impact on plant species already stressed by drought in arid and semiarid ecosystems (Munson et al., 2013).

The Cactaceae family is a key component of diverse habitats in American continent, from arid deserts to tropical rainforests (Hunt, 2006; Ortega-Baes et al., 2010), including 1480 species (Goettsch et al., 2015). Cactus species have a high socioeconomic value because are widely used for ornaments, medicine, food and building materials (Anderson, 2001). Consequently, the wild Cactaceae populations are drastically affected due to overexploitation and modifications of their habitats (Goettsch et al., 2015). In addition, climate change is predicted to restrict the distribution of cactus species (Téllez-Valdés and Dávila-Aranda, 2003) affecting key processes such as flowering (Bustamante and Búrquez, 2008), germinability (Seal et al., 2017) and survival (Aragón-Gastélum et al., 2017). Thus, there is great concern to the conservation of many cactus species (Goettsch et al., 2015).

Mexico has a high richness (660 species) and endemism (518 species, 78%) of cactus species (Ortega-Baes and Godínez-Álvarez, 2006); 140 species (21%) are threatened, and 32 species (2.0%) are critically endangered according to IUCN Red List (Goettsch et al., 2015). Because the protection status of many cactus species, understanding the implications of loss of biodiversity of these species is crucial for developing effective conservation, propagation, and management strategies under climate change projections (Goodman et al., 2012).

Future warming and changes in the patterns of precipitation can have a strong impact on plant species already stressed by drought in arid and semiarid ecosystems (Munson et al., 2013). The most widespread warm desert of North America is the Chihuahuan Desert (Archer and Predick, 2008), ranging from southwestern United States to the Central Mexican Highlands. Climate change projections for the southern part of this region indicate that summer temperatures will increase by 1–2 °C by 2030 (Magaña et al., 2004). This critical outlook has created strong concerns in conservation biologists because the southernmost section of Chihuahuan desert harbors an elevated richness of cactus species (324 species and 5 hybrids; Hernández et al., 2004). However, there is still little information about the thermal tolerance thresholds for cactus species of this desert (see Aragón-Gastélum et al., 2014, 2017, 2018).

Early development phases (e.g., seedlings and/or young plants) of cactus are more sensitive to stress conditions than adult plants (Nobel, 1984; Flores et al., 2004), which could severely threaten the survival and physiological responses of wild populations of these species. In recent studies, negative impacts in seedlings and young plants of some cactus species from Chihuahuan Desert under simulated warming conditions were found, e.g. Aragón-Gastélum et al. (2014) documented a decrease of photosynthetic performance in young individuals of *Echinocactus platyacanthus* during a drought period (January-April). In addition, simulated warming caused a severe decline on seedling survival rate of three endemic and threatened cactus species, namely *E. platyacanthus*, *Ferocactus histrix* and *Stenocactus coptonogonus* during the three months of the growing season (Aragón-Gastélum et al., 2017). Specifically, survival rates of *E. platyacanthus* under warming markedly decreased during the first 20 day of the experiment, and all plants died after 65 days. In the control plots, more than 80% of the plants were alive after 105 days. Survival rates of *F. histrix* decreased within the OTCs until day 55 of the experiment, when all individuals were dead. Survival of this cactus species also decreased in the control plots until day 65 but, after this day, survival stabilized and more than 15% of the individuals reached 105 days in the experiment. For *S. coptonogonus*, while 100% mortality was found on day 105 of the experiment, more than 22% of the individuals located in the control plots were still alive. However, there are no studies to assess the effect of both seasonal drought and induced warming on survival and ecophysiological performance of succulent species, and these studies are needed to discern warming effects, which could vary between seasons.

Chlorophyll fluorescence estimate a series of variables related to the photosynthetic performance of plants located. The effective quantum yield of photosystem II (Φ_{PSII}) decrease as thermal stress increases and, thus, lower Φ_{PSII} values are expected for cacti under warming. In addition, the electron transport rate (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 Φ_{PSII} are indicative of reduced photosynthetic performance in plants (Aragón-Gastélum et al., 2014). Consequently, if induced warming negatively affects the performance of cacti, plants under warming should display lower ETR values than cacti from control plots.

In this work, the seasonal variations of daily mean air temperature, daily mean air relative humidity (RH), photon flux density (PFD), daily mean evapotranspiration (ET), daily rainfall and global photon flux density (GPFD), and their impact on photosynthetic performance and survival on five-year individuals of *E. platyacanthus* under simulated climatic warming conditions were evaluated. This species is *specially protected* by the environmental laws of Mexico (SEMARNAT, 2010), and it is also considered as a *near threatened species* in the Red List of the International Union for Conservation of Nature (Hernández et al., 2017). A decrease of photosynthetic performance in young individuals of *Echinocactus platyacanthus* during a drought period (January-April) has been found (Aragón-Gastélum et al., 2014), but the performance of this species under both seasonal drought and induced warming variations remains to be tested.

We hypothesized that photosynthetic responses and survival would be adversely affected due to the increased temperature stress by induced climate warming through all seasons of the year; also, we assessed response variables ecophysiological [(survival rate, effective quantum yield of photosystem II (Φ_{PSII}) and electron transport rate (ETR)], and environmental [(mean air temperature, RH, PPFD, GPFD, ET, and daily rainfall). We also examined the effects of environmental variables to describe the intensity of relations as well as their importance in photosynthetic responses and survival on five-year individuals of *E. platyacanthus* under induced climatic warming.

2. Materials and methods

2.1. Study species and seed collection

Echinocactus platyacanthus Link & Otto f. *visnaga* is a barrel-like cactus that can reach 2 m height and 80 cm in diameter (Jiménez-Sierra et al., 2007). Although it is endemic to México, this is one of the most widespread Mexican cacti (Trujillo-Argueta, 1984). It grows in the Chihuahuan Desert in the central northern part of the country and in the states of Puebla and Oaxaca; however, the overexploitation for food and ornamental purposes has seriously endangered its natural populations (Jiménez-Sierra et al., 2007).

Young individuals of *E. platyacanthus* were developed from seeds harvested in the Southern Chihuahuan Desert in San Luis Potosí, México, during summer and autumn 2008. Ripe fruits of study species were collected from at least 10 mother plants. This area is dominated by desert shrublands and has an annual rainfall of 300–450 mm and a mean temperature of 18–25 °C (INEGI, 2002).

The harvested fruits were transferred to the laboratory where seeds were removed. The seeds were germinated on peat moss trays inside growth chambers (25 °C, 80% RH, photoperiod 12 h light/dark and 30–40 μmol m^{-2} s^{-1} PFD). The seedlings were later moved to the greenhouse and transplanted into individual plastic pots (one seedling per pot). These pots 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 being used in the experiment described below. Mean greenhouse conditions were 33 °C, 1300 μmol m^{-2} s^{-1} PFD, and 60% RH. The size of the plants after five years was 4 cm in height and 6 cm in diameter.

2.2. Study area

Our experimental site was located at an abandoned agricultural field (22° 14' 11'' N, 100° 51' 46'' W, 1844 m a.s.l.), in the

Fig. 1. Section of abandoned agricultural field used to induce global warming in the municipality of Soledad de Graciano Sanchez, San Luis Potosí, Mexico. A) Experimental site, B) Example of hexagonal open top-chamber (OTC) used to simulate the effects of global warming, C) Experimental design showing open top-chambers (OTC) and control plots, and D) Five-years old individuals of *Echinocactus platyacanthus*.

southernmost section of the Chihuahuan desert, in the municipality of Soledad de Graciano Sánchez, San Luis Potosí , Mexico (Aragón-Gastélum et al., 2014). Mean annual temperature is 17.8 °C, but it can be higher than 35 °C in summer and be as low as 1 °C in winter (Medina-García et al., 2005). Annual rainfall in the study area is 341 mm and is concentrated in the summer months; the rainy season occurs between June and October (Medina-García et al., 2005). The vegetation is dominated by sclerophyllous shrubs, cacti and succulent monocots scattered among woody species (Aragón-Gastélum et al., 2014).

2.3. Open top-chambers design

Hexagonal OTCs were used to simulate the effects of global warming. Passive open top-chambers (OTCs) are the most common and simplest tool to assess the responses of plants to climate warming in the field (Bokhorst et al., 2013). The OTCs have the advantage of being passive warming devices that do not require technological support (Hollister and Webber, 2000). These structures are built with UV–resistant transparent acrylic (3 mm thick; wavelength transmission < 280 nm) by following the design proposed by Marion (1996). Thus, we obtained OTCs with 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 1.9–5 °C, respect to the external environment in desert ecosystems (Musil et al., 2005, 2009; Aragón-Gastélum et al., 2014, 2017, 2018, 2020).

2.4. Environment and open top-chamber microenvironments

The experiment was carried out within a 25 m x 25 m exclosure previously established at the study site (Fig. 1). This exclosure was fenced with woven wire (2 m height) to avoid the access of cattle and people to the experiment. On June 1st, 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 enclosure and one OTC was established at the center of each of these plots. The other six plots were maintained as controls; the distance between plots was five meters (Aragón-Gastélum et al., 2014, 2017, 2018, 2020).

Temperature and relative humidity were steadily recorded within and outside OTCs to determine whether OTCs effectively modify microclimate. We used microclimatic data-loggers (HOBO Pro v2, Onset Computer Corporation, Bourne, Massachusetts, USA), which were programmed to record temperature and RH every 1 h during all experiment. A data-logger was installed 10 cm above the ground at the center of each experimental plot, at 3–5 cm above plants, resulting in six randomly selected OTCs and six control plots. The daily mean, minimum and maximum temperatures and daily mean relative humidity of the air were calculated for both the OTC and control plots. Additionally, data of daily rainfall (mm), daily mean evapotranspiration = ET (mm) and global photon flux density = GPFD (μmol m^{-2} s^{-1}) were obtained from the meteorological station of National Institute of Forestry, Agriculture and Livestock (INIFAP-San Luis Potosí, México), which is adjacent to the study area described above. The experiment was conducted from June 1st, 2013 to May 31st, 2014.

2.5. Chlorophyll fluorescence and survival measures

On June 1st, 2013, all experimental plots received five pots with five years-old individuals of *E. platyacanthus* (one individual per pot). The pots were placed on the soil. In these plots subjected to warming conditions, five pots 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 and for plants to receive the same amount of rainfall as control plots. All cacti were watered every week to field capacity before 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. The plants did not receive further artificial watering during the experiment, but they did receive rainfall.

On June 14th, we conducted the first chlorophyll fluorescence measures on all 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. These chlorophyll fluorescence measures were taken 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 calculated $\Phi_{PSI} = (F'_m - F_t)/F'_m$, where F_t is the chlorophyll fluorescence emitted by plants under steady-state illumination (e.g., light conditions on 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).

The fluorometer was also used to measure the photon flux density (PFD; μmol m^{-2} s^{-1}) into the environment surrounding plants, then, we also calculated the electron transport rate (ETR) across the electron chain of chloroplasts. This variable was then estimated as ETR = Φ_{PSI} x PFD x 0.84 × 0.5, where PFD is the 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 reflection factor for both photosystems to absorb photons (Roberts et al., 1996).

We also counted the number of alive individuals of *E. platyacanthus* in OTCs and control plots. The Φ_{PSII} and ETR values were registered every three weeks in both treatments, whereas survival was weekly monitored from June 1st, 2013 to May 31st, 2014 to evaluate the seasonal variations in photosynthetic performance as well as persistence in *E. platyacanthus* young plants.

2.6. Statistical analyses

Response variables were based on six replicates (six OTCs and six controls) and the value for a replicate was based on their average.

Thus, to evaluate the seasonal variation of photosynthetic performance in *E. platyacanthus*, the ecophysiological (Φ_{PSII} and ETR) and micro-environmental (PFD) variables in both treatments (OTC and controls plots) were grouped by seasons (five measurements by season) and subjected to repeated measures one-way ANOVA after that the requirements of variance homogeneity and homoscedasticity were corroborated. Daily average of air temperature and RH (within and outside OTCs) as well as GPFD, ET and rainfall data were analyzed by one-way ANOVA through seasons.

A generalized canonical correlation was conducted. The goal of this analysis was to examine the relationships between more than two sets of variables, to measure the intensity of the relationships and to delineate strategies of simple canonical correlation by pairs of canonical variates (Yáñez-Espinosa et al., 2006; Delgado-Sánchez et al., 2013). In addition, a canonical discriminant analysis was used to understand the complex relationship between three groups of original variables (environmental, microenvironmental and ecophysiological measurements) and the relative contribution of these variables (within each group) to explain the effect of our experimental design, describing the linear combination of the original variable coefficients (canonical variables) that maximally discriminates among groups (Delgado-Sánchez et al., 2013).

Finally, a redundancy analysis (RDA) was performed to calculate the variance in a set of original variables explained by a canonical variate of another set (McGarigal et al., 2000). ANOVAs were performed with Statistica 8; discriminant analyses were performed with XLSTAT (2014.2.02 v, Addinsoft, NY, USA).

3. Results

3.1. Microenvironmental variables

Between June 1st 2013 and May 31st 2014, mean daily air temperature was 19.3 ± 0.2 °C (SE) inside OTCs and 17.7 ± 0.08 °C in control plots. This variable was significantly affected by the treatments ($F_{(3,2052)} = 22.28$, $P < 0.001$) and the interaction warming X season ($F_{(3,2052)} = 82.32$, $P < 0.001$), in that these values were always higher in the OTC plots than in control plots in all seasons (Table 1).

Average air relative humidity was $66.0 \pm 0.9\%$ within OTCs and $67.4 \pm 0.7\%$ in control plots. We found no significant effects of warming ($F_{(1,6)} = 2.00$, $P = 0.1573$), but season ($F_{(3,2052)} = 93.62$, $P < 0.001$), and the interaction between both factors were significant ($F_{(3,2052)} = 155.17$, $P < 0.001$), in that relative humidity was higher in the control plots than in OTCs in all seasons but in winter (Table 1). PFD mean was 1465.6 ± 26.0 µmol m^{-2} s^{-1} within OTCs and 1460.6 ± 18.3 µmol m^{-2} s^{-1} in control plots. This variable was no affected by warming ($F_{(1,6)} = 0.008$, $P = 0.9293$), and season ($F_{(5,1190)} = 1.485$, $P = 0.1917$); however, the interaction between both factors was significant ($F_{(5,1190)} = 5.868$, $P < 0.001$) in that the PFD values were increased in both OTCs and control plots across seasons (Table 1).

During the study period, mean maximum temperatures averaged 36.8 ± 0.6 °C within OTCs and 31.0 ± 0.6 °C in control plots, whereas mean minimum temperature was 7.4 ± 0.1 °C in control plots and 7.6 ± 0.1 °C inside OTCs. Maximum temperature was significantly affected by the treatment X season interaction ($F_{(3,2052)} = 164.61$, $P < 0.001$) in that these values were higher in the OTC than in control plots in summer and spring than in the other combined treatments (Table 1). Minimum temperature did not differ between control plots and OTCs ($F_{(1,6)} = 0.472$, $P = 0.4924$), but season ($F_{(3,2052)} = 113.286$, $P < 0.001$) and the interaction between both factors were significant ($F_{(3,2052)} = 42.620$, $P < 0.001$) in that the values of this variable decreased in cold seasons but increased in warm seasons. Although minimum temperature showed similar values between OTC and control plots, they were lower in autumn (≥ 7.2 °C) and winter (≥ 1.9 °C), than in spring (≥ 12.57 °C) and summer (≥ 8.63 °C).

3.2. Environmental variables

The total rainfall during our study period was 382.6 mm, mean ET and GPFD were 4.3 ± 0.09 mm and 1576.5 ± 21.9 µmol m^{-2} s^{-1}, respectively. Seasonal variations in these variables were found; in all cases, higher values were recorded during spring and summer (ET: $F_{(3, 361)} = 30.462$, $P < 0.001$; GPFD: $F_{(3, 361)} = 11.012$, $P < 0.001$, and rainfall, $F_{(3, 361)} = 10.401$, $P = 0.015$) than in autumn and winter (Table 2).

Table 1

Seasonal changes (mean $\pm$ standard error) in two induced warming treatments (OTC = Open top chamber vs Control plots) in the study area between June 1st 2013 and May 31st 2014.

Variables	Mean temperature (°C)		Maximum temperature (°C)		Relative Humidity (%)		PFD (µmol m^{-2} s^{-1})	
Treatment/ Season	OTC	Control plot	OTC	Control plot	OTC	Control plot	OTC	Control plot
Summer	23.0 ± 0.2^a	21.2 ± 0.1^b	38.4 ± 0.6^a	32.8 ± 0.3^b	67.3 ± 0.4^a	70.8 ± 0.3^b	1326.7 ± 24.5^a	1351.6 ± 43.6^a
Autumn	17.7 ± 0.1^a	16.1 ± 0.2^b	35.3 ± 0.5^a	28.5 ± 1.52^b	73.9 ± 0.6^a	74.8 ± 1.4^a	1387.5 ± 50.0^a	1351.6 ± 22.2^a
Winter	14.8 ± 0.3^a	13.5 ± 0.3^b	33.4 ± 0.6^a	28.1 ± 0.7^b	66.7 ± 1.4^a	65.8 ± 1.2^a	1529.5 ± 62.5^a	1565.0 ± 42.6^a
Spring	23.0 ± 0.3^a	21.1 ± 0.2^b	42.0 ± 0.9^a	35.9 ± 0.2^b	53.9 ± 1.4^a	56.5 ± 0.6^a	1717.5 ± 36.9^a	1660.4 ± 36.4^a

*Different letters indicate significant differences between treatments ($P < 0.05$).

*PFD = Photon flux density.

3.3. Ecophysiological variables

The photosynthetic performance of *E. platyacanthus* showed variations throughout the year. Nevertheless, these fluctuations did not affect the survival rate in this species, which was 100% in both OTCs and control plots. The quantum yield of photosystem II (Φ_{PSII}) was low during summer in OTCs but increased in autumn and winter and decreased again in spring. Significant differences were only found for summer, in that Φ_{PSII} values were lower under induced warming than in the control ($F_{(3, 894)}$ = 5.189, P < 0.001; Fig. 2a).

The electron transport rate (ETR) values were lower under warming than in the control plot only during summer. ETR values under warming decreased in summer but increased in the other seasons ($F_{(3, 894)}$ = 4.735, P = 0.002; Fig. 2b).

3.4. Generalized canonical correlation

The generalized canonical correlation revealed that there was only one canonical variate. The eigenvalue (2.17; Wilks' λ = 1.35; P < 0.0001, n = 1440) represents most of the variance of the first canonical variable (Table 3). In addition, this eigenvalue showed that two of three sets of variables are highly correlated. Thus, a strong influence between the environment and the micro-environments, and the micro-environment and the cactus ecophysiology were found, but the influence of the environment on ecophysiology was low (Fig. 3). The eigenvector elements (e_1 = 0.538 environment; 0.515 ecophysiology; 0.666 micro-environment) showed that the ecophysiological set had the lowest value. However, all sets had the same importance within the canonical correlation.

Table 3 shows the correlations between the original variables and the canonical variates within sets. These correlation coefficients corroborated that effective quantum yield of photosystem II (Φ_{PSII}) and electron transport rate (ETR) were highly correlated with ecophysiological (their first canonical) variate, which means that these variables were important in the resolution of the canonical variate. Evapotranspiration (ET) and global photon flux density (GPFD) were highly correlated with the environment. Finally, relative humidity (RH) and photon flux density (PFD) were highly correlated with micro-environment.

3.5. Canonical discriminant analysis

Our two discriminant functions accounted for 100% of the data set total variation, contributing significantly to the separation between treatments (Wilks' λ = 0.042; P < 0.0001, n = 1440). The first function (eigenvalue of 0.955; P < 0.0001) explained 95.8% of the total variation and the second one (eigenvalue of 0.060; P < 0.0001) explained 5.8%. The redundancy value was 0.23.

The classificatory discriminant analysis showed that centroids of each group were significantly different (P < 0.0001). ETR, $\Phi_{PSII,}$ PFD, and temperature were the variables that most contributed to centroid separation between treatments (Fig. 4). All observations were correctly classified for both treatments and seasons. The responses in both OTCs and control plots showed a high variability in summer, but autumn, winter, and spring all seem to have a positive linear trend (Fig. 5).

4. Discussion

We found seasonal variations in photosynthetic responses in five years-old individuals of *E. platyacanthus*. The Φ_{PSII} values were lower during summer in OTCs than in control plots but increased in autumn and winter and decreased again in spring in both treatments. The ETR values were low during summer in OTCs and in control plots but increased in autumn to spring in both treatments. Thus, our hypothesis that photosynthetic responses and survival would be adversely affected due to the increased temperature stress by induced climatic warming through the different seasons of the year was partially confirmed, because we found fluctuations in photosynthetic responses but not in survival.

Thus, although photosynthetic responses were impacted, there is no indication that this had a negative impact for the plants. A long-term study over multiple years could give a different result, whether that may be from acclimation (e.g. Kumarathunge et al., 2019) or seen as a consistent decline that impacts survival.

Most climate models indicate that mean temperature for drylands ecosystems worldwide will increase by 1–3 °C by the late twenty-first century (IPCC et al., 2013). The 1.6 °C increases in mean daily air temperature during our study period was within these predictions. Particularly, global change projections for Chihuahuan Desert indicate an increase by 1–2 °C during summer by 2030 (June–September; Magaña et al., 2004). Our results showed a similar temperature increase (1.6 °C). These findings agree with

Table 2

Seasonal changes in abiotic variables registered by the meteorological station of Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP) between June 1st 2013 and May 31st 2014.

Variable/Season	*GPFD (μmol m^{-2} s^{-1}) mean ± S.E.	*ET (mm) mean ± S.E.	Rainfall (mm) total ± S.E
Summer	1597.44 ± 45.95[b]	4.73 ± 0.17[b]	103.4 ± 0.30[a]
Autumn	1427. 96 ± 37.72[c]	3.36 ± 0.11[c]	87.9 ± 0.31[b]
Winter	1515.49 ± 49.09[b,c]	3.81 ± 0.17[c]	83.6 ± 0.43[b]
Spring	1757. 90 ± 34.09[a]	5.42 ± 0.18[a]	107.7 ± 0.41[a]

*Different letters indicate significant differences between seasons (P < 0.05).

*GPFD = Global photon flux density.
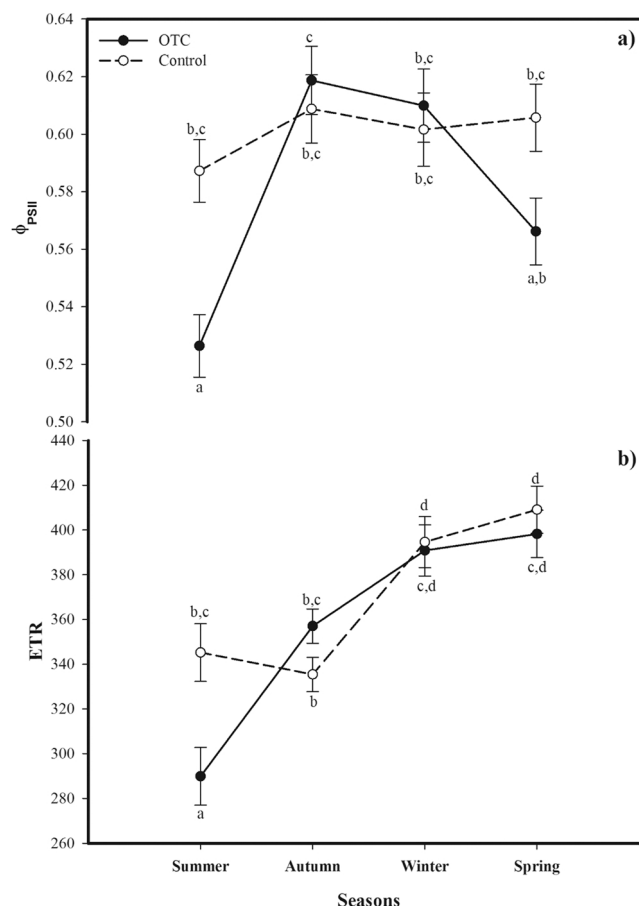
*ET = Evapotranspiration.

Fig. 2. Seasonal variations of induced warming on photosynthetic performance of young plants of *Echinocactus platyacanthus*, in open top-chambers (OTC; black line) and control plots (dotted line). a), effective quantum yield of photosystem II (Φ_{PSII}) and b) electron transport rate (ETR). The mean comparison was made within the dates only. Different letters indicate significant differences between treatments (P < 0.005).

Table 3
Results from: A) The first canonical variates vector to examine the relationships between more than two sets of variables, to measure the intensity of the relationships and to delineate strategies of simple canonical correlation by pairs of canonical variates; B) Canonical variables derived from generalized canonical correlation; and C) Correlation between original and canonical variables within groups.

Set	Original Variables	A) Canonical Variates	B) Canonical variates	C) Canonical variates
Ecophysiology	Effective quantum yield of photosystem II (Φ_{PSII})	-0.643	-0.625	-0.879
	Electron transport rate (ETR)	0.990	0.548	0.820
Environment	Rainfall	-0.212	-0.245	0.157
	Evapotranspiration (ET)	-0.016	0.989	1.039
	Global photon flux density (GPFD)	0.357	0.547	0.017
	Temperature	-0.038	0.565	0.329
Micro-environment	Relative humidity (RH)	-0.030	-0.773	-0.452
	Photon flux density (PFD)	0.996	0.747	0.619

previous studies in the study area (Aragón-Gastélum et al., 2014, 2017, 2018, 2020).

Increased temperature within OTCs were expected to also affect survival of *E. platyacanthus*. Nevertheless, we found 100% survival in both OTCs and control plots, which agree with findings for young cacti of *E. platyacanthus* in a four-month period under drought/high temperature conditions (Aragón-Gastélum et al., 2014), but is contrary to findings for southern African quartz-field succulents, 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 (Musil et al., 2005). Similarly, the survival and growth of seedlings from *Tillandsia recurvata*, a bromeliad epiphyte native to semiarid ecosystems of America, were more affected within OTCs than in controls (Pérez-Noyola et al., 2020).

Φ_{PSII} and ETR are involved in electron transfer via PSII (Maxwell and Johnson, 2000; Baker and Rosenqvist, 2004) and concomitant
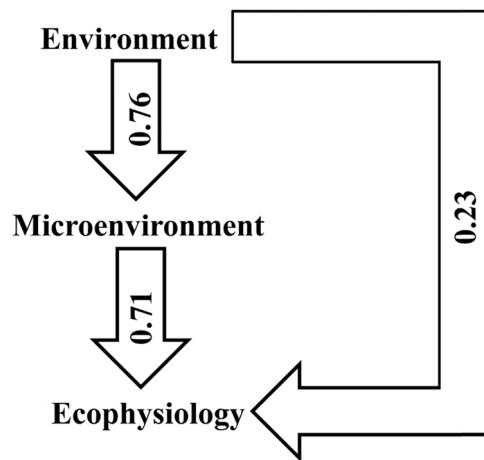
Fig. 3. Proposed model derived from the correlation matrix between the canonical variables. It indicates a high correlation between induced warming (micro-environment) and ecophysiology responses in young plants of *E. platyacanthus*.
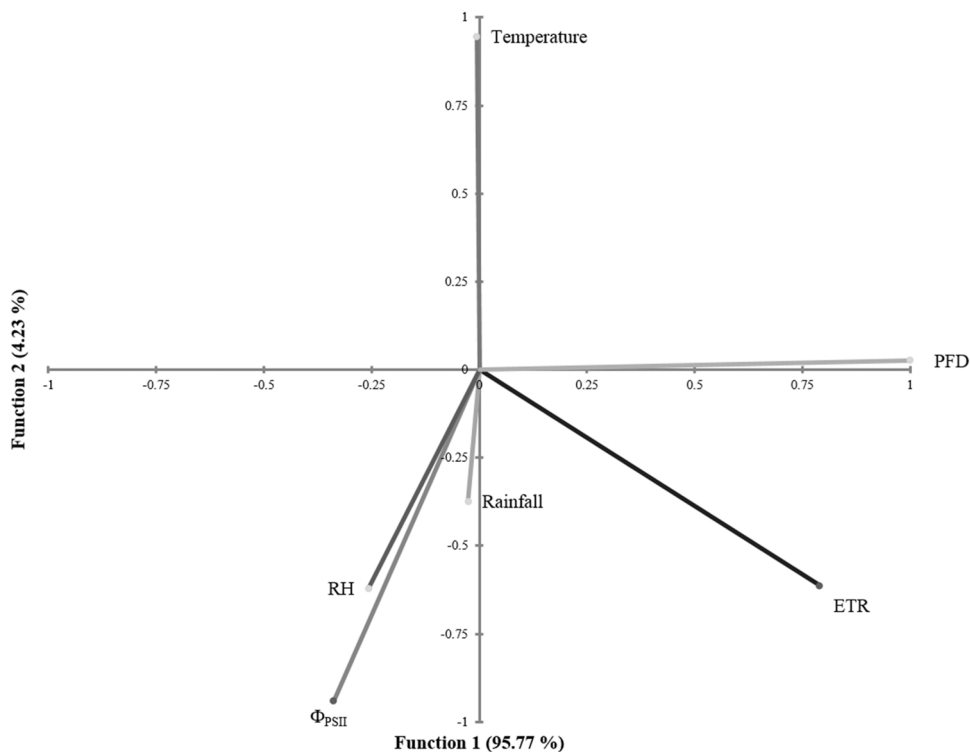

Fig. 4. Correlations between the variables and their canonical variates. PFD = photon flux density, ETR = electron transport rate, Φ_{PSII} = effective quantum yield of photosystem II, and RH = relative humidity.

plants' ability to assimilate CO_2 (Kakani et al., 2008). Thus, they are used as indicators of plants' photosynthetic performance (Maxwell and Johnson, 2000); however, there is little information about photosynthetic performance of cactus species and/ or succulent species under global warming scenarios.

In the same study area, using similar OTC scheme, and during a period of three months, Aragón-Gastélum et al. (2014) documented (from January to April) a decrease in photosynthetic performance [maximum quantum efficiency of photosystem II (F_v/F_m), Φ_{PSII} and ETR] in five years-old individuals of *E. platyacanthus*. In our study, this species showed a similar decline in the Φ_{PSII} values at the same period but higher ETR values for OTCs and control plots, which could be attributed by an alleviation of the stress condition promoted in the previous rainy season (June and October; Medina-García et al., 2005) until the end of the experiment.

In addition, Aragón-Gastélum et al. (2020) also documented decrease in the Φ_{PSII} and ETR values (from October to December) in
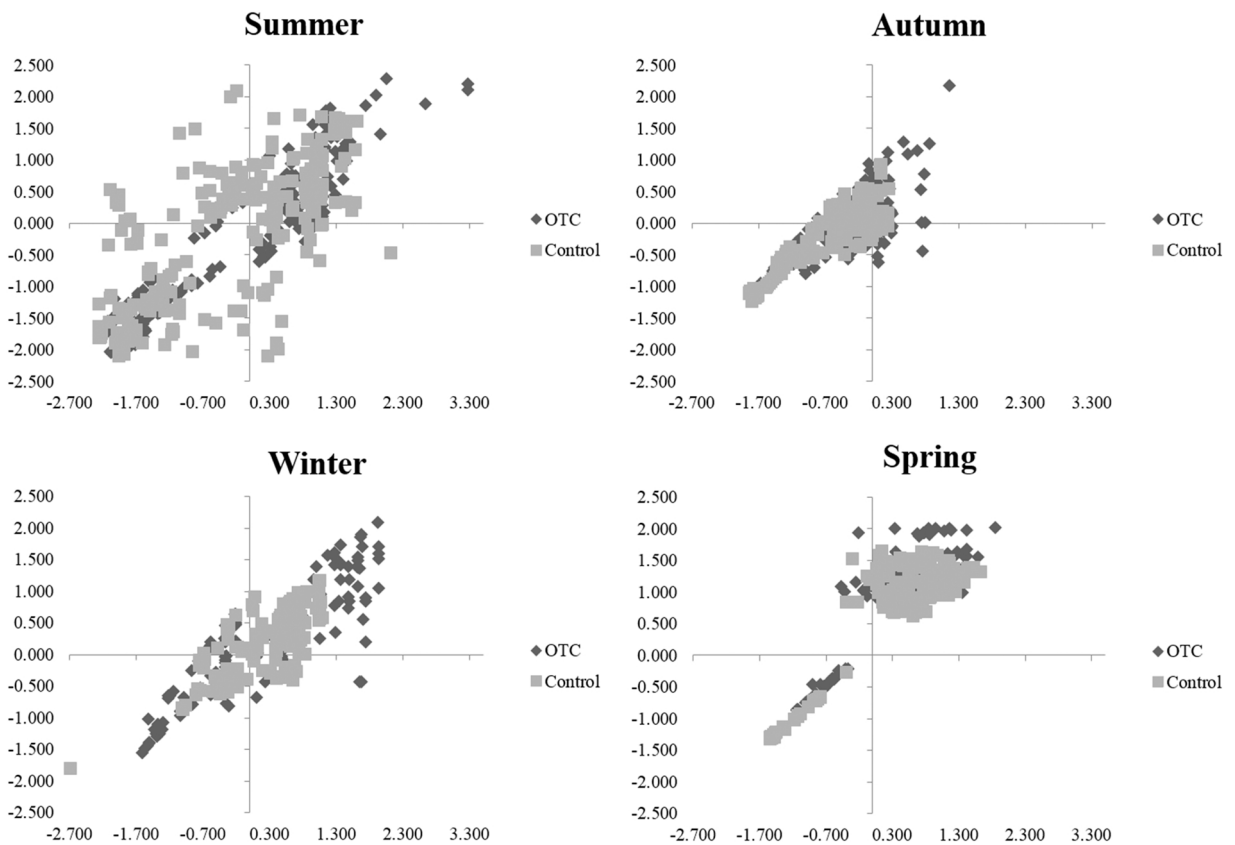
Fig. 5. Scatterplot showing the canonical correlation between centroids of the first pair of canonical variates and lineal tendency line between treatments [open top-chambers plots (OTC) and control plots] and seasons.

two-years-old plants and five-years-old plants of *Agave angustifolia* subsp. *tequilana*. Also, Musil et al. (2009) found a decline in both photochemical efficiency and ETR for the succulent *Cephalophyllum spissum*, a South African succulent species. Our ETR findings are contrary to both works and denote a high tolerance of *E. platyacanthus* to stress conditions.

Despite the fact that a wide variation was observed due to the interaction of several sets of variables, the canonical correlation analysis showed a strongest influence between environmental (rainfall, evapotranspiration and global solar radiation) and microenvironmental (temperature, relative humidity and photosynthetic photon flux density) variables, as well as between microenvironmental and ecophysiological (Φ_{PSII} and ETR) ones, which suggest that the young individuals of *E. platyacanthus* depend on the microenvironment to survive. These correlations between climate and microclimate variables and their influence in ecophysiological traits have been found in species of both tropical forest (Yáñez-Espinosa et al., 2006) and arid environments (Delgado-Sánchez et al., 2013). Our study is the first focusing on the potential impact of climate warming throughout all seasons of the year in performance photosynthetic of young individuals in cactus species, which simultaneously analyzed several sets of variables.

Nobel (2010) suggests that desert succulents have high tolerance to water and temperature stress. Furthermore, different development phases of cactus species such as adult (Smith et al., 1984; Arroyo-Pérez et al., 2017), young (Aragón-Gastélum et al., 2014), and seedlings (Nobel, 1984) are tolerant to high temperatures. However, tolerance of cactus seedlings to high temperatures increases with age (Nobel, 1984). The high survival of five years-old individuals of *E. platyacanthus* under induced warming and in control plots documented here support this premise, because two-year-old seedlings from *E. platyacanthus*, in addition of *Stenocactus coptonogonus* and *Ferocactus histrix*, appear be not tolerant because they suffered an extremely high mortality in a similar scenario of induced warming (Aragón-Gastélum et al., 2017).

Many young cactus seedlings are not tolerant to high temperatures because cactus seedling establishment occurs at higher frequency under nurse plants, and shade provided by these plants can reduce overheating, excessive transpiration, and photoinhibition (Flores and Jurado, 2003; Pérez-Sánchez et al., 2015). In addition, Ureta et al. (2012) suggested that the most widespread species would be less affected by climate change, proposing that past selection on plasticity might allow them to survive under variable conditions. *E. platyacanthus*, is a most widespread distribution cactus species (Jiménez-Sierra et al., 2007), which might also partially explain its high tolerance under future global warming projections.

Induced warming increases abiotic stress on several succulent plants (Musil et al., 2005, 2009; Aragón-Gastélum et al., 2014, 2017, 2018, 2020; Pérez-Noyola et al., 2020). However, physiologically these species have diverse adaptive, avoidance, or acclimation or tolerance mechanisms to cope with stress caused by high temperatures (Hasanuzzaman et al., 2013), and they can trigger changes in

both physiological and molecular responses to persist (Chen et al., 2006).

Increases in the Φ_{PSII} values during autumn and winter as well as in the ETR values from autumn to spring of the *E. platyacanthus* individuals within OTCs suggest a buffer to low temperature (with concomitant lower PFD values) by micro-climate (OTC plots), which improved the photosynthetic response of *E. platyacanthus* (even maintained high ETR values until the end of the experiment). Therefore, it is possible that this micro-environment allows the maintenance of the thermal threshold as well as tolerating the effect of low temperature in this species.

Our findings suggest a high tolerance in terms of photosynthetic performance of *E. platyacanthus* under an induced global warming scenario. Using similar OTC design, this species forms a soil seed bank and concomitant cycling inter-seasonal dormancy/germination associated with seasonal changes (Aragón-Gastélum et al., 2018). Based in these physiological mechanisms and taking some considerations, *E. platyacanthus* could cope well under climate change predicted. However, because plants in our experiments received water in the rainfall season, the combined effect of warming and drought remains to be tested.

Nevertheless, to promote effective conservation strategies in *E. platyacanthus*, it is important to point out the severe anthropogenic pressures due to overexploitation for food and ornamental purposes that this species is subject at present (Jiménez-Sierra et al., 2007). Thus, efforts to the conservation of *E. platyacanthus* (like other cactus species) could focus on establish a strict legal framework to limit species illegal trade (Bárcenas, 2006; Carrillo-Angeles et al., 2016), the creation of more conservation areas and promote initiatives for the sustainable use of this natural resource (Carrillo-Angeles et al., 2016). An eco-evolutionary approach to assess the effect of anthropogenic disturbance on the genetic diversity of the *E. platyacanthus* populations should also be explored.

5. Conclusions

We found a strongest correlation between micro-environmental and ecophysiological variables, which support the premise that the young individuals of *E. platyacanthus* (like many other cactus species) depend on the microenvironment to survive. After a continuous year under induced warming, five-year individuals of *E. platyacanthus* showed a decrease in the Φ_{PSII} values during summer inside OTCs, but an increase in autumn and winter in both treatments. The ETR values were lower during the summer in OTCs than in control plots but remained high from autumn to spring in both OTCs and control plots. The *E. platyacanthus* survival was not affected, which reflects the extraordinary tolerance of this species to high temperatures under an induced global warming scenario. Our study acquires substantial importance because it provides novel data to better understand the potential impact of global warming in desert plants, specifically in endangered cactus species, utilizing a physiologic approach. These results can help to refine population persistence models and conservation for this or related species.

CRediT authorship contribution statement

JLAG and JF conceived and designed the study. JLAG and CS carried out the measurements in the field. JLAG, LYE and JERA analyzed data. All authors contributed to the writing of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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