We determined the seasonal ecophysiological performance under perennial plants and under high solar radiation for adult individuals from the ‘living rock’ cactus *Ariocarpus kotschoubeyanus*, which occurs equally under nurse plants and in open spaces. We evaluated the effective quantum yield of photosystem II (Φ_{PSII}) and the dissipation of thermal energy [non-photochemical quenching (NPQ)] thorough the year. The maximum apparent electron transport rate (ETR_{max}) and the saturating photosynthetically active photon flux density for PSII (PFD_{sat}) were also determined from rapid light curves. We found that although the Φ_{PSII} was higher in shaded sites under potential nurse plants than in exposed sites, all values were close to the optimal value of 0.83. The high Φ_{PSII} found for *A. kotschoubeyanus* plants suggests that they use a great proportion of the absorbed light for photosynthesis, under nurse plants as well as in open spaces. We also found higher NPQ values in exposed sites than in shaded ones but only in Autumn, thus reducing the risk of photoinhibition. In addition, the PFD_{sat} was higher in exposed sites than in shaded ones in Spring, Summer and Autumn, but in Winter there were no differences between treatments. We also found high saturating light levels for ETR (PFD_{sat} higher than 1378 μmol m^{-2} s^{-1}) in all seasons but in winter for shaded and non-shaded plants. Our findings indicate that *A. kotschoubeyanus* plants use a great proportion of the light that they absorb for photosynthesis. This high tolerance to high-light conditions could explain why *A. kotschoubeyanus* do not show preferences for protected sites under nurse plants.

**Key words:** Chihuahuan desert, chlorophyll fluorescence, endangered species, living rock cactus, nurse plants, stress tolerance

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Introduction

In response to harsh conditions, many species appear to be more tolerant under canopies of adult plants of other species which provide a less stressful micro-environment (Ellner and Shmida, 1981). This association has been called ‘nurse plant syndrome’ (Niering et al., 1963) or ‘nurse–protégé’ interaction (Cody, 1993). Cactaceae is a plant family in which many species grow primarily under nurse plants (Flores and Jurado, 2003). Relationships can vary between cactus species and environments and perhaps multiple causes could be involved in facilitation by nurse plants (Valiente-Banuet et al., 1991; Muro-Pérez et al., 2012). Thus, shade can be beneficial by reducing overheating, excessive transpiration and photoinhibition that plants growing in open areas may experience (Flores and Jurado, 2003; Pérez-Sánchez et al., 2015). However, shade may also represent a cost for the cacti in terms of photosynthetically active radiation because it could induce stress by limiting photosynthesis and arrest plant development (Kitajima and Fenner, 2000). Some cactus species, however, occur equally under nurse plants and in open spaces (Jurado et al., 2013), for which the mechanisms avoiding photoinhibition are unknown.

Photoinhibition is defined as any downregulation of the photosynthetic apparatus in response to excess light when more sugar is produced in leaves than can be utilized by the rest of the plant and/or more light energy is harvested than can be utilized by the chloroplasts for the fixation of carbon dioxide into sugars (Adams et al., 2013). Stress caused by drought or extreme temperatures increases the risk and severity of photoinhibition in arid environments (Valladares, 2004).

Ariocarpus kotschoubeyanus (Lem.) K. Schum (Cactaceae) is an especially protected species in the framework of the environmental laws and regulations of México (Semarnat, 2010), and as near threatened in the framework of the international regulations of IUCN (Gómez-Hinoostroza et al., 2013), as well and is listed under Appendix 1 of CITES (Sajeva et al., 2012). This species occurs equally under nurse plants and in open spaces at the southern part of its distribution (Suzán-Aspiri et al., 2011). It is unknown if this lack of micro-site preference occurs across the species’ entire climate range. Thus, we hypothesized that at the southern part of its distribution A. kotschoubeyanus performs better under nurse plants, showing higher maximum quantum yield of photosystem II (ΦPSII) and electron transport rate (ETR) values, under nurse plants than individuals under direct sunlight, but higher non-photochemical quenching (NPQ) in open spaces than under nurse plants in order to tolerate stress. We also hypothesized that the light level at which A. kotschoubeyanus PSII becomes saturated (PPFDsat) is related to acclimatization to the light environment in which the plants grew. Thus, if plants grow in open sites then they must show high saturating light levels for ETR during all year.

Materials and methods

Study site

The study site includes one population of A. kotschoubeyanus located in Tolimán, Querétaro, México (latitude 20°52’N; longitude −99°57’ W; 1 200 msnm) at the southern part of the Chihuahua desert. This area has an annual temperature of 19.2°C and an annual precipitation of 361.4 mm (CONAGUA, 2016). Its vegetation type is thorny xerophilous scrub (González-Medrano, 2012).

Studied species

Ariocarpus kotschoubeyanus (Lem.) K. Schum (Cactaceae) is a globose-depressed cactus that grows in the Chihuahuan Desert from western Coahuila through Querétaro; it can reach 7 cm in diameter (Pilbeam and Weightman, 2006). This species is called ‘living rock cactus’, like all Ariocarpus species (Glass and Foster, 1974). As other Ariocarpus, this species presents triangular flattened tubercles and is usually found semi-buried during periods of drought (Bravo-Hollis and Sánchez-Mejorada, 1991; Anderson, 2001). Populations of A. kotschoubeyanus are threatened due to increased agriculture and livestock areas, urban expansion, residue deposits and overexploitation for medicinal or ornamental purposes (Anderson et al., 1994; Oldfield, 1997).

Micro-environmental measurements

Photon flux density (PFD) and temperature were registered at midday using a portable pulse amplitude modulation fluorometer (Mini-PAM; H. Walz, Effeltrich, Germany). PFD was measured with a micro-quantum sensor (0.5 mm diameter), and temperature was evaluated with the aid of a NiCr-Ni thermocouple, both measurements were done at the photosynthetic surface of the stem (de la Rosa-Manzano et al., 2016). Measurements were conducted under nurse plants and in open sunlight during periods of full sunlight. All measurements were performed once in each season (Autumn 2011, and Winter, Spring, and Summer 2012).

Chlorophyll fluorescence of A. kotschoubeyanus in open species and under nurse plants

We selected A. kotschoubeyanus adult plants of 3–6 cm diameter and without damaged tubercles. Karwinskia humboldtiana (Schult.) Zucc. (Rhamnaceae), a common species in the study area, was chosen as nurse plant. Thus, A. kotschoubeyanus plants under K. humboldtiana individuals (one cactus per nurse plant, n = 6) and six A. kotschoubeyanus plants in exposed sites (n = 6) were selected. Shaded plants were under the densest part of the shrub canopy, near the stem of the nurse plant. The exposed plants were not shaded by nearby shrubs or rocks.
The effective quantum efficiency of photosystem II (ΦPSII), the ETR, and the NPQ in exposed plants (n = 6) and under the more frequent nurse plant found (n = 6), were measured after acclimation in darkness for 20 min once each year season. All measures were performed once by each season using a portable fluorometer (Mini-PAM, Walz, Effeltrich, Germany). The Mini-PAM was equipped with a leaf-clip holder (2030-B; Walz), where the optic fibre was inserted; the distance between the optic fiber and the surface stem was ~12 mm, with an angle of 60° relative to the upper surface of the stem.

The light source was a halogen lamp inside the instrument. The intensity of actinic light was increased every 10 s for 2 min. Photosynthetic PFD and temperature data were used to estimate a series of variables related to the photosynthetic performance of plants located under nurse plants and outside them. Chlorophyll fluorescence measurements were carried out at noon (between 12:00 and 14:00 h), when plants faced the maximum daily temperature. The effective quantum efficiency of photosystem II (ΦPSII) was estimated as (F′m - F0)/F′m, where F0 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). The values for ΦPSII oscillate between 0.80 and 0.83 if environmental stress is negligible for plants, but these values decreased with increasing environmental stress (Maxwell and Johnson, 2000).

The ETR across the electron chain of chloroplasts was estimated as ETR = ΦPSII × PFD × 0.84 × 0.5, where ΦPSII is the effective quantum yield of photosystem II, PFD is the photosynthetic PFD 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).

Finally, we calculated the NPQ efficiency. This variable was calculated as NPQ = (Fv - Fm)/Fm, where Fv is the basal chlorophyll fluorescence emitted by cacti at darkness, and Fm 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 high NPQ values are expected with increasing levels of environmental stress (Maxwell and Johnson, 2000; Aragón-Gastélum et al., 2014).

In order to evaluate the level of light at which photosystem II is saturated (PFDsat) (Rascher et al., 2000; Hernández and Briones-Villarreal, 2007), rapid light curves (RLC) for chlorophyll fluorescence were produced. Light curves allow to deduce cardinal points which are quantitative physiological indicators of intrinsic photosynthetic capacity (Lüttge and Scarano, 2007), such as the maximum apparent ETR (ETRmax) and the saturating photosynthetically active PFD for PSII (PFDsat).

For each species, the data for ΦPSII and ETR against PFD were adjusted according to the statistical models proposed by Rascher et al. (2000). With the adjusted ETR vs. PFD curve, the cardinal points were determined: ETRmax and saturating photosynthetically active PFD for PSII (PFDsat), determined to 0.9 of ETRmax. The RLC were produced using two scales of the Mini-PAM light curve program to obtain a sequence of 0, 255, 399, 590, 807, 1184, 1587 and 2372 μmol of PFD m−2 s−1. These RLC were obtained in exposed plants (n = 6) and under the more frequent nurse plant found (n = 6), once each year season.

**Statistical analysis**

Factorial ANOVAs for repeated measurements were carried out for ΦPSII, NPQ and ETRmax, as well as for temperature and photosynthetic PFD, using micro-environment as factor. There were two micro-environment levels (under nurse plant an under direct sunlight) and four season levels (Spring, Summer, Autumn and Winter). Tukey tests were used to detect different means. Analyses were carried out using STATISTICA (8) with α = 0.05. Data were transformed, if required to comply with the assumption of normal distribution (Sokal and Rohlf, 1995).

**Results**

**Micro-environmental measurements**

The photosynthetic PFD was affected by the micro-environment (F1,10 = 667.69; P < 0.00001), the season (F3,30 = 188.08; P < 0.00001) and the interaction micro-environment X season (F1,30 = 72.16; P < 0.00001). The PFD was lower under shaded sites nurse plants than in exposed sites at all seasons except for Winter (Fig. 1a–d). Higher typical daily PFD in open spaces was found in Spring than in Summer, as well as in Summer than in Autumn. The lowest PFD was found in Winter (Fig. 1a–d).

Temperature was affected by the micro-environment (F1,10 = 93.37; P < 0.00001), the season (F3,30 = 4276.58; P < 0.00001) and the interaction micro-environment X season was significant (F3,30 = 31.71; P < 0.00001). The temperature was lower under nurse plants than in exposed sites at Summer and Autumn. The lowest temperature was found in Winter in both nurse plants and open spaces (Fig. 1e–h).

**Chlorophyll fluorescence of A. kotschubeyanus in open species and under potential nurse plants**

The effective quantum yield of photosystem II (ΦPSII) was affected by micro-environment (F1,10 = 9.89; P = 0.01), but not by the season (F1,30 = 1.40; P = 0.26), or by the
micro-environment × season interaction ($F_{3,30} = 1.68; P = 0.192$). In average for all seasons, the $\Phi_{\text{PSII}}$ was higher in shaded sites under potential nurse plants (0.80 ± 0.01) than in exposed sites (0.75 ± 0.03).

NPQ values were affected by the season ($F_{3,30} = 6.34; P = 0.001$), and by the micro-environment × season interaction ($F_{3,30} = 3.22; P = 0.032$), but not by the micro-environment ($F_{1,10} = 3.46; P = 0.07$). We found higher NPQ values in exposed sites than in shaded ones only in Autumn (1.76 ± 0.41 SE vs. 0.60 ± 0.07, respectively; Fig. 1i). No significant differences in the NPQ values between treatments were found in the other seasons, but in general it was lower in Winter (Fig. 1i–l).

The ETR$_{\text{max}}$ was affected by the season ($F_{3,30} = 13.67; P < 0.00001$) and by the micro-environment ($F_{1,10} = 5.65; P = 0.038$), but not by the interaction micro-environment × season ($F_{3,10} = 0.49; P = 0.68$; Fig. 2). $A.\ kotschoubeyanus$ had lower values in Winter (28.61 ± 6.11) than in Spring (156.87 ± 21.72), Summer (113.70 ± 13.07) and Autumn (160.62 ± 18.76); as well as lower ETR$_{\text{max}}$ values in exposed sites (99.15 ± 14.16) than under nurse plants (130.75 ± 16.49).

The saturated photosynthetic PFD (PFD$_{\text{sat}}$) was affected by season ($F_{3,30} = 20.55; P < 0.00001$), and by the micro-environment × season interaction ($F_{3,30} = 3.09; P = 0.04$; Fig. 2), but not by the micro-environment ($F_{1,10} = 3.07; P = 0.11$). In general, PFD$_{\text{sat}}$ was higher in Spring, Summer and Autumn than in Winter. In addition, PFD$_{\text{sat}}$ was higher in exposed sites than in shaded ones in Spring, Summer and Autumn, but in Winter there were no differences between treatments (Fig. 2).

**Discussion**

Cacti have been subjected to intensive exploitation due to their great value, mainly as ornamental plants, thus their populations have been drastically affected due to illegal collection and habitat destruction (Anderson et al., 1994; Sajeva et al., 2012). As suggested by Brussard (1991), the collection of basic life-history information, including the influence of environmental factors on development, can be very useful in the conservation of rare species such as $A.\ kotschoubeyanus$. Similarly, Wikelski and Cook (2006) suggested that, for conservation strategies to be successful, it is important to understand the physiological responses of
To their changing environments. More recently, Cooke et al. (2013) mentioned that physiological tools and knowledge are especially useful for developing cause and effect relationships, and for identifying the optimal range of habitats and stressor thresholds for different organisms. Thus, by knowing the ecophysiological responses in the different micro-environments where these species occur, we can better understand the micro-environment to properly manage this and other endangered cacti.

Measurements of light–response curves lead to a deeper insight into characteristic parameters of an investigated plant, which are not related to the momentary ambient light conditions, but rather to the ontogeny of a photosynthetic shoot and to the range of physiological plasticity of a plant. Therefore the so-called cardinal points of light–response curves are highly interesting in ecophysiological research (Rascher et al., 2000).

We hypothesized that although A. kotschoubeyanus shows lower ΦPSII and ETR values under direct sunlight than under nurse plants, it shows higher NPQ values under direct sunlight in order to tolerate stress. Our hypothesis was supported in that we found higher ΦPSII and ETRmax in shaded sites under potential nurse plants than in exposed sites, although all values were close to the optimal value of 0.83 (Maxwell and Johnson, 2000). Our ΦPSII values (0.80 ± 0.01 for plants under nurse plants and 0.75 ± 0.03 for plants in exposed sites) appear to be higher than those found for other cacti (Hernández-González and Briones Villarreal, 2007; Badano et al., 2016). These high ΦPSII values suggest that A. kotschoubeyanus plants use a great proportion of the light that they absorb for photosynthesis, such under nurse plants as in open spaces.

Higher ΦPSII values in shaded sites compared to exposed sites have also been found for cactus seedlings by Hernández-González and Briones-Villarreal (2007). These authors found that the ΦPSII of 1-week old Pachycereus weberi and Escontria chiotilla seedlings was higher in the shade than in high-light. Pérez-Sánchez et al. (2015) also found that ΦPSII values of seedlings from seven succulent species, four cacti (Echinocactus platyacanthus, Ferocactus histrix, Myrtillocactus geometrizans and Stenocactus coptonogonus) and three Asparagaceae (Agave lechuguilla, Agave salmiana and Yucca filifera) were greater under nurse plants than in open spaces.

Hernández-González and Briones-Villarreal (2007) also found similar values of ΦPSII in the seedlings and adults of Stenocereus stellatus, M. geometrizans and Ferocactus recurvus (ΦPSII = 0.61 on average), even though the PFD was >2000 μmol m⁻² s⁻¹ in the field and 1500 or 750 μmol m⁻² s⁻¹ under high-light or shade. In contrast, adult plants of P. weberi and E. chiotilla had high ΦPSII (0.68 on average) in the field, while their seedlings had lower (ΦPSII = 0.52 on average) in the shade.

The ΦPSII has also been analysed for adult individuals of Cylindropuntia leptocaulis (Cactaceae) located under the

Figure 2: Rapid light curves determined from the maximum apparent electron transport rate (ETRmax) and the saturating photosynthetically active photon flux density for PSII (PFD), by adjusting an exponential function using the Sigma Plot Program. Data are means ± SE, n = 6. For PFDsat, different letters represent significant differences between the interaction micro-environment × season (P < 0.05). For ETRmax, this interaction was not significantly affected (P > 0.05).
canopy of *Larrea tridentata* and in open sites (Badano et al., 2016). In this study, at 15:00 h higher \( \Phi_{PSI} \) in shaded sites under nurse plants than in exposed sites was found.

We expected higher NPQ in open spaces than under nurse plants to tolerate stress and thus reduce the risk of photoinhibition (Adams et al., 1987; Barker and Adams, 1997; Barker et al., 1998; Aragón-Gastélum et al., 2014), but NPQ values were similar in exposed sites and under nurse plants in all seasons but Autumn, in which higher NPQ values were found in exposed sites than in shaded ones. Similarly, the NPQ values for cactus seedlings in high-light and shade were generally low, and differences were not statistically significant (Hernández-González and Briones-Villarreal, 2007). The \( \Phi_{PSI} \) values close to the optimal and similar NPQ values between plants in open sites and under nurse plants are findings helping to explain why *A. kotschoubeyanus* does not show association with nurse plants (Suzán-Azpíri et al., 2011).

Because high ETR values indicate increased photosynthetic performance in plants (Ritchie and Bunthawin, 2010; Aragón-Gastélum et al., 2014; Pérez-Sánchez et al., 2015), we also hypothesized that *A. kotschoubeyanus* shows high saturating light levels for ETR during all year. This hypothesis was supported in that we found high saturating light levels for ETR (PFD<sub>sat</sub> higher than 1378 \( \mu \text{mol} \text{m}^{-2} \text{s}^{-1} \) in both under nurse plants and in exposed sites) in most seasons, but in Winter where ETR becomes saturated at lower flux densities of light (PFD<sub>sat</sub> = 351.71 \( \mu \text{mol} \text{m}^{-2} \text{s}^{-1} \) in exposed sites and 776.68 \( \mu \text{mol} \text{m}^{-2} \text{s}^{-1} \) under nurse plants). Low ETR values in Winter coincided with low NPQ values. These high saturating light levels for ETR suggest high tolerance to high-light conditions could also explain that *A. kotschoubeyanus* does not show preferences by protected sites under nurse plants (Suzán-Azpíri et al., 2011).

### Conclusions

Our work provided strong evidence about how the cactus *A. kotschoubeyanus* tolerates the high-light intensities occurring in its habitat. This is the first study evaluating physiological performance for adult cacti under perennial species and under high solar radiation. Our findings give us a better understanding of the mechanisms that cacti use to survive under environmental stresses, which can be useful for conservation and management practices of this species and other endangered cacti.

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