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Ecophysiological performance of a threatened shrub under restored and natural conditions in a harsh tropical mountaintop environment

Silvana A. B. Castro[1*], Camila E. M. Sá[1], Fabiana A. Mourão[1], Heitor M. Duarte[2], G. Wilson Fernandes[1,3] and José P. Lemos-Filho[4]

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ABSTRACT
Ecophysiological responses of plants are useful for monitoring the success of ecological restoration projects that target species conservation. In this study we evaluated the ecophysiological traits of individuals of *Chamaecrista semaphora* from a natural population and from a site under restoration. Water potential and chlorophyll *a* fluorescence parameters were measured both in adult and young plants of the two populations. No difference in water potential was found between sites, but individuals in the restored site had higher water potential at predawn. Adults in the natural site presented lower daily values of potential quantum yield, indicating the occurrence of photoinhibition. Individuals in the restored site also presented higher maximum relative electron transport rate (ETR_{MAX}). No difference was found in leaf carbon isotope discrimination values ($\delta^{13}C$) between plants growing in restored and natural sites, suggesting similar water use efficiency. These results indicate that *C. semaphora* individuals in the restored site had similar or better photosynthetic and water economy performances than individuals at the natural site. Methodologies traditionally employed to assess stress response of plants, such as chlorophyll *a* fluorescence and procedures used to evaluate the efficiency of water use, allowed us to verify the success of restoration procedures using an endangered species.

Keywords: chlorophyll fluorescence, ecological restoration, endangered species, plant performance, rupestrian grasslands

Introduction

Rupestrian grassland, one of the physiognomies of the Cerrado biome (Savannah), is a mosaic of grassland types or habitats with scattered shrubs and trees growing among rocky outcrops at elevations between 900 m and 1200 m, mainly in the Espinhaço mountain range (Giulietti *et al*. 1997). This physiognomy is especially important for plant conservation programs because it includes most of the endangered plant species of the Cerrado (Giulietti *et al*. 1997; Fernandes *et al*. 2014). Soil erosion is easily seen in many places in the southern portion of the Espinhaço range (Serra do Cipó) due to mining activities and paving of dirt roads and highways (see Fernandes *et al*. 2014). These activities facilitate the introduction of invasive species, one of the greatest threats to the native flora of rupestrian grasslands (Barbosa *et al*. 2010; Fernandes *et al*. 2014; 2015). In view of this imminent threat, there is an urgent need to develop sound restoration procedures for rupestrian grasslands, preferably using endemic and endangered species. We argue that this strategy would

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[1] Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, 31270-901, Belo Horizonte, MG, Brazil
[2] Núcleo de Ecologia e Desenvolvimento Ambiental de Macaé, Universidade Federal do Rio de Janeiro, P.O. Box 119331, Rio de Janeiro, RJ, Brazil
[3] Department of Biology, Stanford University, Stanford CA 94040, USA
[4] Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, 31270-901, Belo Horizonte, MG, Brazil
* Corresponding author: silvana.abcastro@gmail.com

not only restore the unique ecological mechanisms and evolutionary processes present in such a tropical montane region, but could also serve as a barrier to biological invasion.

The environments of quartzitic rupestrian grasslands are characterized by the predominance of shallow acidic soils with low nutrient availability, high luminosity, and a seasonal climate with a well defined dry season (Ribeiro & Fernandes 2000; Fernandes *et al.* 2014). Due to these environmental characteristics, water deficit and excessive light could place limitations on photosynthetic performance, especially during the dry season when drought is a common phenomenon. The few field studies performed with rupestrian plant species indicate limitations in gas exchange during the dry season (e.g. Lemos-Filho & Mendonça-Filho 2000; Morales *et al.* 2015). A decline in stomatal conductance coupled with an osmotic adjustment in response to water stress was observed in an experimental study with *Lavoisiera campos-portoana*, an endemic species of rupestrian grasslands (França *et al.* 2012). Although Lüttge *et al.* (1998), Lemos-Filho & Mendonça-Filho (2000) recorded damage to photosystem II (PSII) in some species under excessive light in the natural environment of the rupestrian grassland, although no significant photoinhibition was observed in some species of Velloziaceae even during the dry season (Lüttge *et al.* 2007; Morales *et al.* 2014). The limited ecophysiological data, in contrast to the high species richness of rupestrian grasslands, indicates the need for additional study in order to identify strategies that can lead to the use of more species in restoration programs, as well as to understand their physiological behavior under the current scenario of climate change.

The stressful conditions of rupestrian grasslands can adversely affect the success of restoration of degraded areas. Generally neglected in restoration studies, the evaluation of ecophysiological traits can be useful in determining the success of a target plant species, as well as the efficiency of restoration procedures, since the physiological responses can provide more information about adaptation than the usual procedures based on population metrics (Cooke & Suski 2008). We evaluate ecophysiological traits related to water economy (water potential and leaf carbon isotope discrimination) and photosynthetic performance (through measures of chlorophyll *a* fluorescence) in adult and juvenile plants of *Chamaecrista semaphora* (Fabaceae). This woody legume is a micro-endemic species found adjacent to highway MG 10 (Silva & Dillenburg 2007), where it was propagated by seed and used in a pilot restoration program. We evaluated the same physiological traits of plants growing in this restored site with those of plants growing in a natural site. We addressed two main questions: 1) Do young and adult individual plants growing in the restored site exhibit water status and carbon isotope discrimination similar those of individuals in a natural site? 2) Is photosynthetic performance, assessed from chlorophyll *a* fluorescence measurements, similar between the two sites? Similar or better ecophysiological performance of plants of the restoration site compared to those of the natural site would indicate that the technique of using an endangered species in the restoration of a degraded area of rupestrian grassland was successful.

Materials and Methods

Study Area

The study was carried out during three consecutive days of the dry season (August of 2008) in two sites in rupestrian grasslands of Serra do Cipó (MG), southeastern Brazil. The sites included a natural site (19º16’47.5’’S-43º35’28.1’’W), and in a restored site (19º16’26.7’’S-43º35’41.7’’W) and at Vellozia Reserve. According to Köppen’s classification, the climate in the region corresponds to Cwb, tropical highlands, with well-defined wet and dry seasons. Mean annual precipitation reaches 1500 mm and mean annual temperature varies between 17.4 and 19.8°C (Madeira & Fernandes 1999).

The species and restoration procedures

Chamaecrista semaphora H. S. Irwin and Barneby (Fabaceae) (Fig. 1) is a perennial leguminous shrub endemic to the high altitude montane grasslands and rocky outcrops of Serra do Cipó, Minas Gerais, Brazil, where only two population patches exist separated ca. 4 km from each other (Madeira & Fernandes 1999; Silva & Dillenburg 2007). Due to its endemism and degree of threat, *C. semaphora* is included in the official list of endangered species of the state of Minas Gerais (http://www.biodiversitas.org.br).

In November 2002, fruits were collected just before their opening from 10 adult plants found within the study area. Seeds were mechanically treated and placed to germinate in 6 x 20 cm plastic bags filled with a substrate made of subsoil and organic substrate (1:1) with the addition of 6 g of dolomitic limestone and 2.8 g of NPK 4:14:8. Saplings were kept in a greenhouse covered by a 50% mesh for five months. Plants were irrigated daily in the morning for three months, at which time the saplings were exposed to sunlight while irrigation was gradually reduced. In July 2003, eight-month-old saplings of similar height, selected to form a more homogenous group, were transplanted to the pilot restoration site, an area of quartzite soil that had been subject to superficial soil and gravel removal. Saplings were planted in holes of 20 x 20 cm in which of 25g of dolomitic limestone and 0.5 L of cattle manure had been applied 60 days previously.

Figure 1. Adult individual of *Chamaecrista semaphora* growing on a quartzitic rocky outcrop in Serra do Cipó National Park, Brazil.

During the first two months after planting, the individual plants were irrigated using conventional sprinklers at 10-day intervals, after which the plants were subjected to natural conditions.

Ecophysiological measurements were taken of adult and young plants of the restored and natural sites at the end of dry season (August 2008). Five young and five adult individuals were randomly selected for ecophysiological measurements in the restored site, while four young and five adults were randomly selected from the natural site (quartzitic rocky outcrops). Adult individuals were identified by the presence of reproductive structures and were ca. 1.0 m high, while young individuals were between 0.4 and 0.5 m high. The two areas are approximately 1km apart along highway MG 010.

Environmental data

Sensors for the measurement of temperature, relative humidity and photosyntheticaly active photon flux density (PPFD), coupled to a Datalogger LI-COR Model LI-1400 (Li-Cor, Lincoln, Nebraska, USA), were installed in both sites. The vapor pressure deficit (VPD) was calculated using the measured temperature and relative humidity values. The instantaneous incident light on leaves was measured using a quantum sensor coupled to a LI-189 light meter (Li-Cor, Lincoln, Nebraska, USA). Leaf temperature was measured using a Ni-CrNi thermocouple of the leaf-clip holder model 2030-B (H. Walz, Effeltrich, Germany) pressed on the lower leaf surface.

Water status and carbon isotope composition

As an indicator of the water status of plants, the water potential was measured using a pressure chamber (PMS, Covalis, Oregon, USA). Measurements were taken before dawn (between 5h00m - 6h00m), in the morning (9h00m - 10h00m), at noon (11h30m - 12h30m), in the afternoon (14h30m - 15h30m), and at sunset (around 18h00m), in mature leaves collected from terminal branches of each individual plant.

In order to compare the long time performance of plants in relation to water stress, leaf carbon isotope discrimination was evaluated. For this purpose, mature leaves from four adult and four young individuals from each site were used for the carbon stable isotope composition ($\delta^{13}C$) analysis. Samples were dried in a forced-air circulating oven at 50 °C and ground. The material was placed in a cryogenic mill (Freezer/Mill 6750 Certiprep, Metuchen, NJ, USA) for 3 minutes at maximum rotation. Samples were analyzed with a Delta-S mass spectrometer (Finnigan MAT, Bremen, Germany) using 50 μg of leaf. Data are presented in the delta notation (δ‰) $\delta = \{(Rsample/Rstandard) - 1\} \times 1000$, where: Rsample and Rstandard are the isotope ratio ($^{13}C/^{12}C$) of the sample and standard (Pee Dee belemnite).

Pigments contents and photosynthetic performance

Mature, healthy sun-exposed leaf samples were collected for analysis of photosynthetic pigments. Leaf discs of known area (0.5 cm^2) were used for pigment extraction using 80% acetone. Chlorophyll and carotenoid contents were quantified using equations described by Lichtenthaler & Wellburn (1983).

Photosynthetic performance was evaluated by chlorophyll fluorescence measurements using a Pulse-Amplitude-Modulation fluorometer, Mini-PAM (H. Walz, Effeltrich, Germany) equipped with a 2030-B leaf-clip holder (Bilger *et al.* 1995). The potential quantum yield of PSII was calculated as Fv/Fm ($Fv = Fm – F_0$), measured at predawn and during the day after 30 minutes of adaptation to darkness. Fv is the variable fluorescence of a leaf adapted to darkness, Fm is the maximum fluorescence of a leaf adapted to darkness after the saturating light pulse and F_0 is the basal level of fluorescence production by leaves adapted to darkness. The effective quantum yield of photosystem II (PSII) (ΔF/Fm') was calculated as (Fm'- F)/Fm' (Genty *et al.* 1989), where F is the fluorescence produced by samples adapted to light and Fm' is the maximum fluorescence production obtained by sample exposure to a saturating light pulse in addition to the environmental light. Non-photochemical quenching (NPQ) was obtained according Bilger & Björkman (1990) as NPQ = (Fm - Fm')/Fm'. The measurements were done just before the evaluation of the plant's water potential. During measurements, care was taken to maintain constant environmental conditions such as foliar angle and shade. Also, in the morning, light response curves were obtained using the Mini-PAM internal program where the actinic light increases by eight steps every 30 seconds in pre-programmed light levels. Apparent electron transport rates (ETR) were calculated as 0.5 x ΔF/Fm' x PPFD. This calculation assumes an equal partitioning of excitation energy between the two photosystems (Genty *et al.* 1990). The PPFD incidence was measured with the quantum micro sensor of the leaf-clip holder calibrated of the against a LI-COR sensor model 190 (Li-Cor, Lincoln, Nebraska, USA). Light dependence of ETR and ΔF/Fm' were used to extract the cardinal points according Rascher *et al.* (2000). The extracted points were: ETR at light saturation (ETR_{Max}); PPFD at 90% and 50% of ETR_{Max} ($PPFD_{90\%}$, $PPFD_{50\%}$); ΔF/Fm' at ETR_{Max} ($\Delta F/Fm'_{Sat}$) and ΔF/Fm' at 50% of ETR_{Max} ($\Delta F/Fm'_{50\%}$).

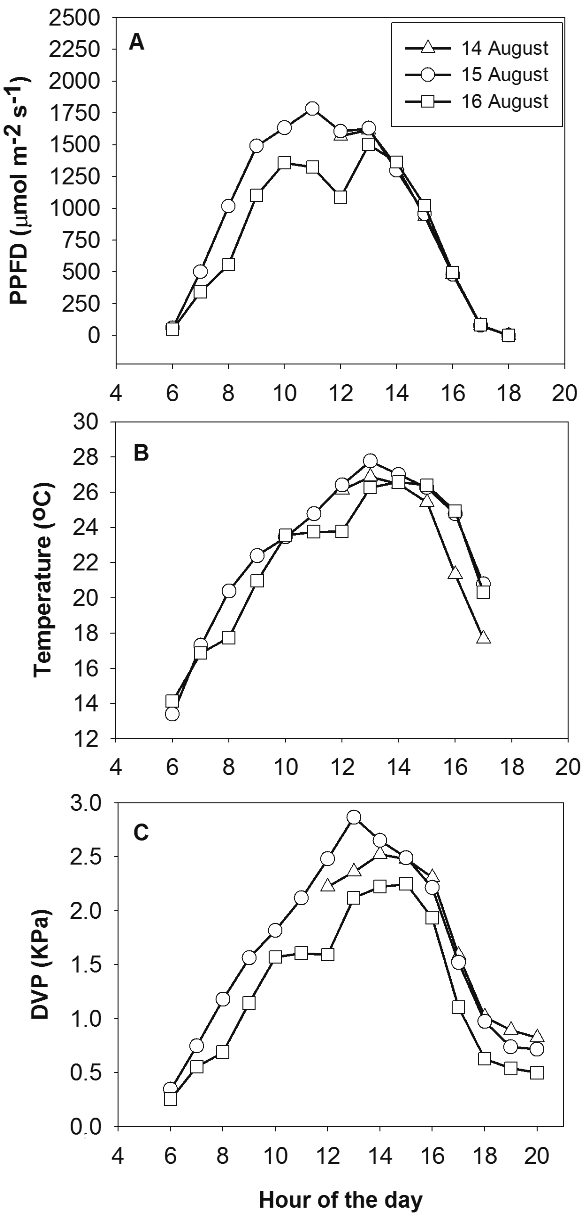

Figure 2. Daily course of photosynthetically active photon flux density-PPFD (A), air temperature (B), and Vapour Pressure Deficit-DVP (C) during the ecophysiological measurements.

Statistical analysis

After testing for normality, a one-way Analysis of Variance (ANOVA) followed by a Tukey test were used to compare adult and young individuals growing in the natural and the restored site. The t-test was used to compare the water potential, Fv/Fm and ΔF/Fm' values of each measurement during the day between restored and natural sites. NPQ data were analysed using a Kruskal-Wallis test. Statistical analyses were carried out using the software packages GraphPad Prism 5.0 and Sigma Plot 10.0.

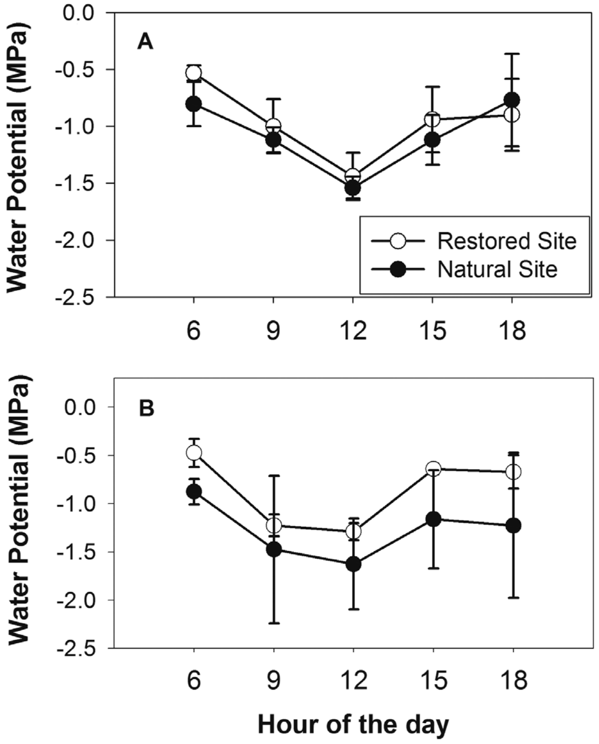

Figure 3. Daily course of the water potential (Ψw) of adult (A) and young individuals (B) of *Chamaecrista semaphora* growing in the natural (filled symbols) and restored (open symbols) sites. Data expressed as mean ± SE of five replicates each of young and adults of the restored site, and four replicates of young and five replicates of adults of the natural site.

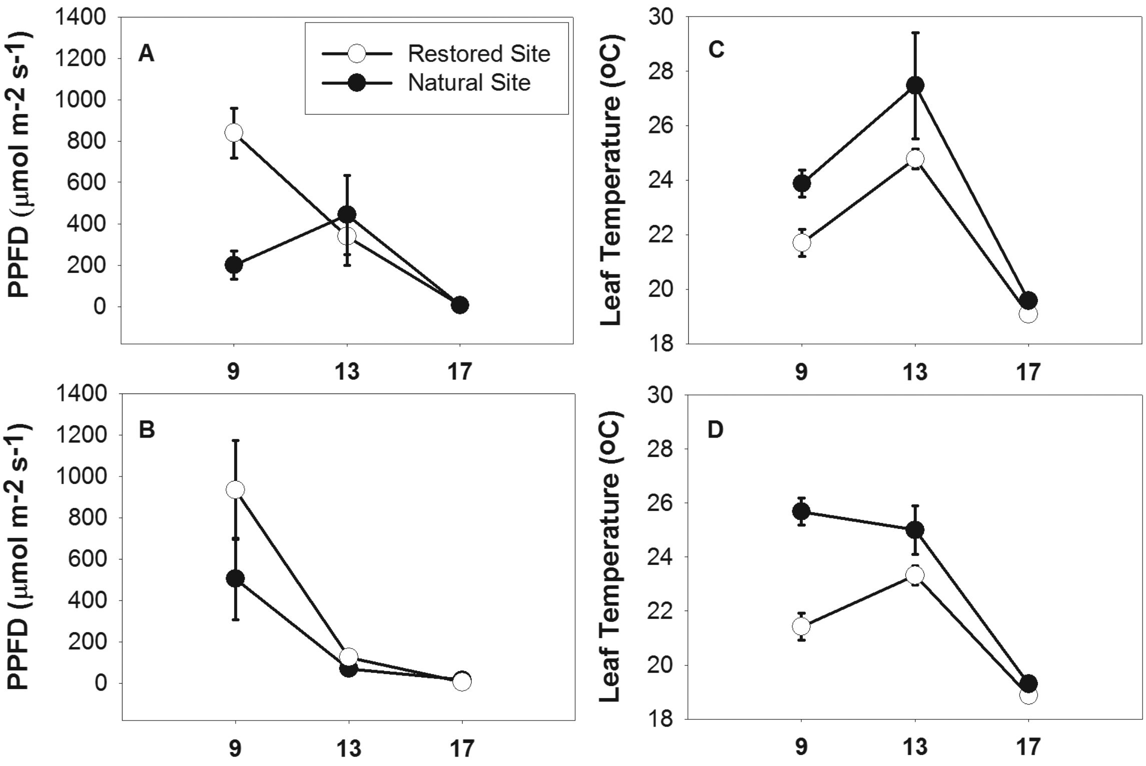

Figure 4. Diurnal course of photosynthetically active photon flux density (PPFD) incident on the leaf blade of young (A) and adult (B) individuals, and leaf temperature in young (C) in adult (D) individuals of *Chamaecrista semaphora* growing in the natural (filled symbols) and restored (open symbols) sites. Data expressed as mean ± SE of five replicates each of young and adults of the restored site, and four replicates of young and five replicates of adults of the natural site.

Results

Environmental conditions were similar in the two sites for the three days when the chlorophyll fluorescence measurements were made so the data were grouped into a single curve (Fig. 2). The maximum PPFD was 1785 μmol m^{-2} s^{-1}, the temperature varied from 13°C to a maximum of 28°C at 1PM, when the higher VPD values were recorded (between 2 and 2.8 KPa).

Young and adult individuals in the restored site had water potential values (Ψ_w) similar to those of individuals in the natural site at midday (Fig. 3A-B). However, predawn measurements of adult individuals showed a significant difference between restored (mean Ψ_w = -0.53 ± 0.06 MPa) and natural sites (mean Ψ_w = -0.80 ± 0.19) (t-test = 2.996, df = 7, p = 0.0172; Fig. 3A). Such a difference was also found between young individuals of the restored site (mean Ψ_w = -0.847 ± 0.085 MPa) and the natural site (mean Ψ_w = -1.195 ± 0.093 MPa) (t-test = 3.649 df = 7, p = 0.0082; Fig. 3B).

The incident light on the leaf blade was higher during the morning in adults in the restored and natural site (Fig. 4A-B), except for juvenile *C. semaphora* in the natural site (Fig. 4A). The leaf incident PPFD decreased at midday and remained low during the evening as compared with the morning values. Leaf temperature in the morning and midday was higher in individuals inhabiting the natural site (Fig. 4C-D), with values ca. 2-4°C higher than air temperature (Fig. 2B).

Individuals from both the restored and natural site had quantum potential yield (Fv/Fm) values ca. 0.8 at predawn (Fig. 5A-B). A decline of Fv/Fm was observed in all indi-

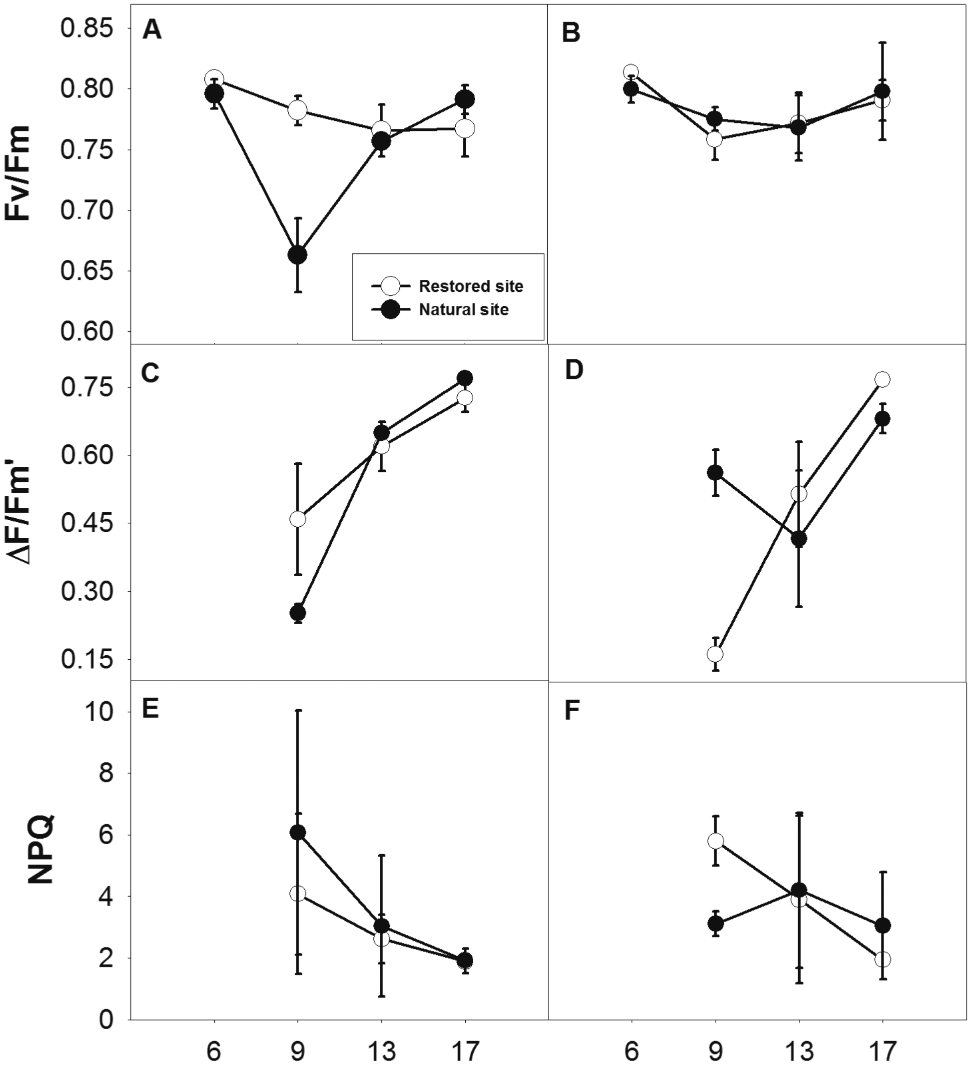

Figure 5. Potential quantum yield (Fv/Fm), effective quantum yield (ΔF/Fm') and non-photochemical quenching (NPQ) throughout the day of adult (A, C and E) and young (B, D and F) individuals of *Chamaecrista semaphora* growing in the natural (filled symbols) and restored (open symbols) sites. Data expressed as mean ± SE of five replicates each of young and adults of the restored site, and four replicates of young and five replicates of adults of the natural site.

Table 1. Chlorophyll fluorescence parameters extracted from light dependence curves of adults and young individuals of *Chamaecrista semaphora* in natural and restored site. ETR_{Max} (maximum apparent electron transport rates); $\text{PPFD}_{90\%}$, and $\text{PPFD}_{50\%}$ (Photosynthetic photon flux density at 90% and 50% of ETR_{Max}); $\Delta F/Fm'_{\text{sat}}$ ($\Delta F/Fm'$ at ETR_{Max}) and $\Delta F/Fm'_{50\%}$ ($\Delta F/Fm'$ at 50% of ETR_{Max}). Data expressed as mean ± SE of five replicates to young and adults in restored site, and four replicates to young and five adults in natural site.

	Adults		Young	
	Restored Site	Natural Site	Restored Site	Natural Site
ETR$_{\text{Max}}$	110.80±38 b	84.50±30 b	164.20±19 a	77.50±21 b
PPFD$_{90\%}$	712.50±177 b	524±256 b	1040±293 a	490.80±105 b
PPFD$_{50\%}$	215±52 b	160±26 b	343 ±26 a	152±28 b
ΔF/Fm'$_{\text{Sat}}$	0.34±0.04 a	0.38±0.08 a	0.36±0.05 a	0.35±0.09 a
ΔF/Fm'$_{50\%}$	0.57±0.07 a	0.60±0.07 a	0.54±0.05 a	0.56±0.07 a

[a] Different letters indicate significant differences between means (One-way ANOVA followed by Tukey test, $p < 0.05$).

Table 2. Mean values of pigment and Carbon isotopic composition ($\delta^{13}C$) in leaves of adults and young individuals of *Chamaecrista semaphora* in natural and restored areas. Data expressed as mean ± SE of five replicates to young and adults in restored site, and four replicates to young and five adults in natural site.

	Adults		Young	
	Restored Site	Natural Site	Restored Site	Natural Site
Chlorophyll Total (μg/cm^2)	87.0±20.6 ab	117±27.5 a	90.8±13 ab	72.7±22 b
Ratio Chlorophyll a/b	4.4±0.5 a	3.7±0.1 a	3.5±1 a	3.9± 0.4 a
Carotenoids (μg/cm^2)	27.2±4.6 a	32.8±7 a	26.5±8 a	22±5 a
Cholorophyll/Carotenoids	0.31±0.03 a	0.28±0.01a	0.29±0.07 a	0.31±0.03 a
$\delta^{13}C$	29.5±0.4a	29.6±1.2a	28.7±0.8 a	29.8±0.3 a

[a] Different letters indicate significant differences between means (One-way ANOVA followed by Tukey test, $p < 0.05$).

viduals in the morning, although the decline was sharper for adult individuals of the natural site (t-test = 3.628, df = 8, $p = 0.0067$; Fig. 5A). Reduction in Fv/Fm values was also observed in young individuals but no statistically significant differences were detected between sites (Fig. 5B). Low values of effective quantum yield of PSII (ΔF/Fm') were observed during the morning and these values increased during the day (Fig. 5C). The ΔF/Fm' values at morning were significantly lower for the adult individuals of the natural site (t-test= 3.177, df = 7, $p = 0.0155$; Fig. 5C). However, young individuals of the natural site had higher ΔF/Fm' values (t-test = 6.904, df = 7, $p = 0.0002$; Fig. 5D). This result can be explained by the lower incident light in the morning on the leaves of young plants growing in the natural site (Fig. 4C). The NPQ values were very similar between sites (Fig. 5E-F), except during the morning when young individuals of the restored site had higher values (Kruskal-Wallis Test H= 5.000, $p = 0.025$; Fig. 5F).

The analysis of light dependence curves indicates significant differences in ETR_{Max}, $\text{PPFD}_{90\%,}$ and $\text{PPFD}_{50\%}$ of adult and young individuals (Tab. 1). Young individuals of the restored site had higher ETR_{Max} values followed by adult individuals of the restored site ($F_{3,16} = 9.266$, $p = 0.015$). They also presented higher values of $\text{PPFD}_{90\%}$ ($F_{3,16} = 5.682$, $p = 0.0104$), and $\text{PPFD}_{50\%}$ ($F_{3,16} = 9.693$, $p = 0.0013$). However, no statistically significant differences for $\Delta F/Fm'_{\text{Sat}}$ ($F_{3,16} = 0.1917$, $p = 0.900$) and $\Delta F/Fm'_{50\%}$ ($F_{3,16} = 0.6175$, $p = 0.6159$) were found.

Regarding leaf pigments, there were significant differences in total chlorophyll ($F_{3,18} = 3.426$, $p = 0.0446$; Tab. 2), with lower values being recorded for young individuals of the natural site. There were no statistically significant differences in carotenoid content, chlorophyll a/b ratio, and carotenoids/total chlorophyll ratio. Leaf carbon isotope compositions ($\delta^{13}C$) did not differ statistically between individuals of the natural and restored sites ($F_{3,15} = 1.708$, $p = 0.2183$; Tab. 2).

Discussion

Individuals of *C. semaphora* growing in the restored site presented similar or better photosynthetic and water economy performances in comparison to individuals growing in the natural site. Improvements to the physical properties and fertility of the soil and the provisioning of irrigation after planting may have improved habitat quality and thus environmental conditions at the restored site, hence resulting in higher plant physiological performance. These conditions may have been retained even over the years since the beginning of the experiment. The favorable response to stressor factors indicated by the high values of predawn water potential and high values of ETR_{MAX} are in accordance with the visible success of *C. semaphora* individuals in the restored site. At the restored site, plants produced viable seeds that resulted in vigorous young individuals who settled around the parent plants.

A recent study with *Vellozia gigantea* in the same region led by Morales *et al.* (2014) reported that differences in leaf contents of tocopherols and tocotrienols depend on plant size. However, the authors did not find differences in Fv/Fm values or in stomata conductance between taller and smaller individuals. In another study taking into account plant size, Lüttge *et al.* (2007) verified that taller species of Velloziaceae had higher intrinsic photosynthetic capacity as revealed by chlorophyll fluorescence parameters extracted from light curves. Our data for *C. semaphora* indicate that plant size does not affect most of the evaluated physiological traits. There were no statistically significant differences in pigment contents and $\delta^{13}C$ values, as well as no differences for most of the chlorophyll fluorescence parameters extracted from light dependence curves, between adult and young individuals growing in the restored or natural site.

The water potential (Ψ_w) at predawn observed for adult and young *C. semaphora* plants in the restored site were higher than those recorded for plants growing in the natural site (Fig. 3). The values of Ψ_w at predawn and midday were very close to the values described for Cerrado trees during the dry season (Goldstein *et al.* 2008; Rossatto *et al*. 2013a; b). However, these values are higher than those obtained for some non-desiccation tolerant species of the rupestrian grassland during the dry season at predawn and midday (approximately -1.0 MPa and -1.8 MPa), respectively (Alcantara *et al.* 2015). These values were also higher than those described for two out of three woody species from a granitic rock outcrop (Silva & Dillenburg 2007). The higher values of Ψ_w mainly at predawn for plants of the restoration site may be a consequence of the improvement in soil conditions due to the addition of manure, which increased water availability. In contrast, the natural site has a thin layer of soil in rock crevices with low water retention capacity.

Plants exhibit several mechanisms to control water loss is situations of water stress. Stomata regulation is one of the most critical responses to water stress. A low stomata conductance and a low ratio of intercellular to ambient CO_2 can result in low isotope discrimination in relation to the atmospheric CO_2 and consequently promote higher $\delta^{13}C$ values (Farquhar & Hubick. 1989). Even though the individuals from the restored site exhibited higher values of predawn Ψ_w as compared to individuals from the natural site, there was no difference for the $\delta^{13}C$ values between individuals from the two sites. According to Ehleringer & Cooper (1988), $\delta^{13}C$ values allow an integrated long-term estimation of the intrinsic water use efficiency (WUE). This explains why *C. semaphora* plants inhabiting the site under restoration showed similar WUE to those from the natural site.

The quantum potential yield values (Fv/Fm) recorded during predawn indicates the absence of chronic damage to PSII (Björkman & Demmig 1987) in plants of both sites. The lowest Fv/Fm and ΔF/Fm' values and the highest NPQ values were recorded at morning, notably for adult individuals growing in the natural environment with a midday recovery (Fig. 5). These results can be explained by the vertical tilt angle of the leaves of *C. semaphora* (Fig. 1), which result in more incident light during in the morning (Fig. 4A). In vertical leaves a smaller fraction of leaf surface area is exposed to the sun at midday and light interception is reduced, thereby avoiding excess irradiance and, thus, photoinhibition (Valladares & Niinemets 2007). This reversible photoinhibition process was consistently observed in several species of the Brazilian Cerrado (Mattos 1998; Franco & Lüttge 2002). Non-photochemical processes for energy dispersion in the PSII act as mechanisms to reduce photoinhibition during a period of higher light intensity. The NPQ values recorded in *C. semaphora* were higher than those found by Franco *et al.* (2007) for some Cerrado plant species, but similar to those reported by Mattos *et al.* (1997) at noon for species in coastal sandy areas (Restinga) and rock outcrops in Brazil. The recovery of Fv/Fm values during the afternoon and the absence of chronic photoinhibition are indicative of the effectiveness of mechanisms that dissipate excess light in plants growing in both sites. The favorable performance of adult and young plants in the restored site detected by fluorescence measurements was confirmed by chlorophyll pigment data. There was no difference in pigments between adult individuals in the restored site and the natural site, but young individuals from the restored site had higher total chlorophyll as compared to their counterpart of the natural site.

The results of the photosynthetic parameters assessed from light response curves reveals that adult and young individuals from the restored site had higher values of ETR_{MAX} and $PPFD_{90\%}$ as compared to those from the natural site. In a study comparing smaller and taller Velloziaceae species, Lüttge *et al.* (2007) attributed the high values of ETR_{MAX} and $PPFD_{90\%}$ found in taller species to the minor frequency of shading of the rosettes due to the height of the plants. In the present study, the differences of ETR_{MAX} and $PPFD_{90\%}$ between plants grown in the natural and restored sites could also be attributed to differences in the light environment. Adult and young *C. semaphora* individuals in the restored site would be subject to less shading than the plants of the natural environment. Their sunny environment notwithstanding, adult and young individuals in the restored site had less variation in leaf and air temperatures. In the natural site on the other hand, individuals had leaf temperature values 2-4°C above the air temperature. A higher transpiration rate will result in a cooler leaf; hence the higher values of leaf temperature could be interpreted as a consequence of a more stressful environment in the natural rocky outcrops that limits transpiration. In summary, these ecophysiological data reported in this study indicate that the restoration process favored positive photosynthetic performance of the endangered species *C. semaphora,* enabling its establishment, survival and reproduction.

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