



Differential tolerance of native and invasive tree seedlings from arid African deserts to drought and shade

A.M. Abbas^{a,1}, A.E. Rubio-Casal^b, A. De Cires^b, B.J. Grewell^c, J.M. Castillo^{b,*}

^a Department of Biology, Faculty of Science, King Khalid University, 61413 Abha, Saudi Arabia

^b Department of Plant Biology and Ecology, University of Seville, Av. Reina Mercedes, s/n.-41012 Sevilla, Spain

^c USDA-ARS Invasive Species and Pollinator Health Research Unit, Department of Plant Sciences MS-4, University of California, Davis, California, USA

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ABSTRACT

Efforts to understand why some species become successful invaders and why some habitats are more at risk from invasive species is an important research focus in invasion ecology. With current global climate change, evaluation of the effects of shade and drought on cohabiting native and invasive species from extreme ecosystems is especially important. *Acacia tortilis* subsp. *raddiana* is a tree taxon native to arid African deserts. *Prosopis glandulosa*, native to the southwestern United States and Mexico, is invading African arid and semiarid regions that are habitat for *A. t.* subsp. *raddiana*. The aim of this study was to evaluate and compare the tolerance and responses of the seedlings of these two tree species to shade, water stress and their interactions. We measured and recorded growth rates and morphological, biochemical and physiological plant traits under two radiation and two water treatments in greenhouse conditions. Radiation intensity was a stronger driver of the performance of both species than water availability. Beyond the independent effects of shade and drought, the interactions of these factors yielded synergistic effects on seedlings of both tree species, affecting key plant traits. The seedlings of *A. t.* subsp. *raddiana* were able to implement important shifts in key functional traits in response to altering abiotic stress conditions, behaving as a stress-tolerant species that is well-adapted to the habitat it occupies in hot arid African deserts. In contrast, the fast-growing seedlings of *P. glandulosa* were stress-avoiding. The alien *P. glandulosa* seedlings were highly sensitive to water and shade stress. Moreover, they were particularly sensitive to drought in shade conditions. However, although alien *P. glandulosa* seedlings were exposed to high stress levels, they were able to avoid permanent damage to their photosynthetic apparatus by mechanisms such as increasing energy dissipation by heat emission and by adjusting the relative allocation of resources to above- and below-ground structures. Our results are useful for conservation planning and restoration of invaded hyperarid ecosystems.

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1. Introduction

An important research challenge in plant invasion ecology has been devoted to understanding why some species become successful invaders and why some habitats are easier to invade than others (Hamilton et al., 2005; Richardson and Pysek, 2006). Plant communities in physiologically stressful environments have been reported to be less invaded by alien species than those in less stressful conditions (Rejmánek et al., 2013; Zefferman et al., 2015). However, a wide diversity of plant types have invaded arid ecosystems of Africa, and within these environments alien plants are spreading exponentially (Milton

and Dean, 2010). With current global warming trends, improved understanding of how native species and alien invaders perform under extreme abiotic stress is especially important for conservation management.

It has long been considered that successful invasive plants have advantageous functional traits that support their invasiveness (Rejmanek and Richardson, 1996). Among those plant traits promoting invasiveness are high capacity for dispersion and growth (high competitive ability) and high phenotypic plasticity in response to changing environments (Drenovsky et al., 2012). Most ecosystems include multiple co-occurring invasive and native plant species, yet ecological studies and management strategies typically focus on single invader species (D'Antonio et al., 2017). While both biotic and abiotic factors influence the invasibility of a particular habitat (Guo et al., 2015), the exact role of biotic factors is debated and under-studied (Fridley et al., 2007). Traits and impacts of both invasive species and native plants interact within ecological communities, influence both invasiveness and

* Corresponding author at: Department of Plant Biology and Ecology, University of Seville, Apartado 1095, 41080 Sevilla, Spain.

E-mail address: manucas@us.es (J.M. Castillo).

¹ Permanent address: Department of Botany and Microbiology, Faculty of Science, South Valley University 83523 Qena, Egypt.

invasion resistance, and can be key drivers of invasive plant abundance (Scharfy et al., 2011; Mouillot et al., 2007). While understanding of plant traits that support the invasiveness of alien species has advanced, a functional trait response framework can be useful for evaluating ecological impacts of invaders (Drenovsky et al., 2012). In addition, this framework may help to understand complex biotic and abiotic interactions between native and naturalized species to support restoration of invaded ecosystems (Drenovsky et al., 2012).

With current global climate change, the range of invasive plant species may expand or contract as air temperatures, drought and evapotranspiration demand increase in some areas. Furthermore, global warming and atmospheric CO₂ enrichment are expected to differentially affect particular plant species (Liu et al., 2017). In this global context, the effects of abiotic stresses on plant invasions are especially important in extreme ecosystems such as hot, hyperarid deserts (Abatzoglou and Kolden, 2011). It is therefore important to predict and to control plant invasions into arid lands, and to improve our understanding of how water and light availability influence alien and native species. During the establishment stage of an alien species into novel environmental conditions when vulnerability to abiotic stresses can be high (Horton and Clark, 2001), the invader can benefit from increased levels of abiotic resources such as space, light, nutrients and water (Alpert et al., 2000; Davis et al., 2000; Stohlgren et al., 2001; Daehler, 2003). A high degree of environmental variation and complex spatial mosaics of limiting resources can occur where native and invasive species coexist, and the plants themselves and through interspecific interactions can impact and change local conditions.

The vast Sahara desert ecosystem includes Gebel Elba National Park in southeastern Egypt. This site provides an ideal model system for addressing native and invasive plant responses to extreme heat and aridity (Abd El-Ghani et al., 2017). Desert and savannah ecosystems of arid and semiarid Africa are characterized by a scattered, isolated spatial pattern of drought-tolerant species of shrubs and trees. The isolated trees in open canopy “scattered tree ecosystems” (sensu Manning et al., 2006) in many landscapes worldwide have been characterized as ecosystem engineers and keystone structures given their dramatic influences and long-lasting legacies on interacting organisms and local environments (Manning et al., 2006; Stahlheber et al., 2015). Busso et al. (2013) included tolerance to shading and water stress among those plant responses promoting successful invasions in dry rangelands in Argentina, but evaluation of the effects of shade and water stress and their interaction on cohabiting native and invasive species in arid ecosystems are rare (e.g. Schumacher et al., 2008; Gonzalez-Munoz et al., 2014).

Two perennial deciduous trees from the Fabaceae, subfamily Mimosoideae, are the focus of our study. *Acacia tortilis* (Forssk.) subsp. *raddiana* (Savi) Brenan, native to arid African deserts, and *Prosopis glandulosa* Torr., an invasive neophyte tree that is recognized by the IUCN as one of the world’s 100 most invasive species (ICUN Global Invasive Species Database, 2018). In arid Africa and the Middle East, *Acacia tortilis* is considered a keystone species that mediates the dynamics of vegetation through interspecific interactions (Aronson et al., 1993). *Acacia tortilis* subsp. *raddiana* provides crucial ecosystem services in African savannah ecosystems, including soil nutrient enrichment, high quality forage for livestock and wildlife, and wood and food products for humans (Felker, 1981). This native mesquite can also provide important ecological functions when used as a biotool for restoration of degraded ecosystems (Noumi et al., 2015). Exotic stands of *Prosopis* have invaded over 6 million ha of South Africa (Shackleton et al., 2017), including large areas of dry seasonal and ephemeral watercourses and alluvial plains (Richardson and van Wilgen, 2004). An ecological impact of the widespread replacement of native *Acacia*-dominated communities by invasive *Prosopis* spp. has been major alteration of bird habitats, leading to loss of raptors and reduced plant and bird species richness and diversity (Dean et al., 2002).

Prosopis glandulosa is a phreatophyte (Oliveira et al., 2017) native to southwestern United States and northern Mexico that was intentionally introduced to several countries, including southeast Egypt during the late 80s for agro-forestry, animal fodder and fuel uses (Fagg and Steward, 1994). *Prosopis glandulosa* has naturalized and become a problematic tree in wildlands because of its invasive behavior (Abbas et al., 2016). Recently, *P. juliflora* was also recorded as an invasive alien *Prosopis* spp. in Egypt (Abd El Halim and Azer, 2015), though elsewhere this morphologically similar species is a non-accepted synonym for *P. glandulosa* (Integrated Taxonomic Information System, ITIS, and Global Biodiversity Information Facility, GBIF). The spread of *P. glandulosa* in Egypt has resulted in interactions with *A. t.* subsp. *raddiana* (Aref et al., 2013; Kebbas et al., 2015).

Understanding the environmental conditions influencing the recruitment ability and success of co-occurring native and invasive alien species can inform management actions to achieve conservation goals. Water and light are among the key abiotic resources conditioning seedling establishment. The aim of this study was to evaluate and compare the tolerance and responses of tree seedlings of the native *Acacia tortilis* subsp. *raddiana* and seedlings of the invasive tree *Prosopis glandulosa* to shade, water stress and their interactions. With this aim, we measured and recorded growth rates and morphological, biochemical and physiological plant traits for both species under two radiation and two water treatments in controlled greenhouse conditions. We hypothesized that invasive *P. glandulosa* would be less tolerant to abiotic stress, particularly to the combination of shade and water stress, than the native *A. t.* subsp. *raddiana*.

2. Materials and methods

2.1. Experimental design

Fruits of the invasive tree *Prosopis glandulosa* and the native tree *Acacia tortilis* subsp. *raddiana* were collected from multiple mature individuals chosen randomly in July 2016 in Wadi Merakwan, Gebel Elba National Park, Southeast Egypt (22°14'2" N–36°36'30" E). Gebel Elba National Park has an arid climate, with desert like precipitation. The Eastern Desert region invaded by *Prosopis* receives rainfall at 50–100 mm y⁻¹ with constant high air temperatures that average ca. 32 °C. Further descriptions of the site are reported by Abd El-Ghani and Abdel-Khalik (2006) and Al-Gohary (2008). Collected seeds were stored in dry and dark conditions at 25 °C until the beginning of the experiment in the greenhouse facilities of the University of Seville (37°21'42" N–5°59'15" W). Air temperature and relative humidity (RH) in the greenhouse were 25 ± 2 °C and 40 ± 10% during the experiment. In September 2016, seeds of both species were placed for germination in plastic pots (7.5 cm diameter × 11.5 cm deep) containing 1.5 l of soil with a similar texture (55% sand) and pH (ca. 8.5) to soil at the collection site in Gebel Elba National Park. Seedlings were exposed from the beginning of the experiment to two radiation treatments: full sunlight (FR; maximum photosynthetic photon flux density (PPFD) of 1200 μmol m⁻² s⁻¹ at midday) and a shaded treatment of 20% sunlight (LR). Irradiance was controlled with neutral shade cloth (Hummert International, Earth City, MO, USA). The FR treatment represented field conditions at open areas and the LR treatment mimicked light conditions under the canopy of trees colonized by *P. glandulosa* and *A. tortilis* in the Gebel Elba National Park (Ahmed M. Abbas personal observation). Additionally, seedlings were subjected from germination to two irrigation treatments: a control treatment without water limitation (W) where 30 ml of water was applied to pots every day, and a drought treatment (D) had 30 ml of water applied to pots once a week. Plant responses to treatments were measured and recorded during November 2016. Response measures included growth, biomass production and allocation, leaf tissue chemistry, and photosynthetic traits.

2.2. Plant morphology, growth and survival

Initial biomass (DW) was recorded for randomly chosen seedlings of each species 8 days after final germination ($n = 10$ for *P. glandulosa* and $n = 5$ for *A. tortilis*). At the end of the experiment, maximum plant height (cm), the width at the base of the main shoot (mm), the number of leaves and the occupied soil area by the canopy (cm^2) were recorded for every seedling of both species. Then, plants were removed from the pots, carefully washed and divided in three biomass fractions (leaves, stems and roots) that were dried in a forced-air oven (80°C for 48 h) and their DW was recorded ($n = 3$ – 10 seedlings). The raw data were used to calculate below-ground biomass (BGB): above-ground biomass (AGB) ratio, and the relative growth rate ($\text{RGR} = \ln(\text{DW at the end}) - \ln(\text{DW at the beginning}) / \text{duration of experiment}$) for every treatment and both species (Richter et al., 2014).

Leaf area (cm^2) was recorded for one leaf of each seedling using a Hewlett-Packard Scan Jet 6200C desktop scanner (Hewlett-Packard, Cupertino, CA) with HP Precision Scan Pro (version 1.1, images scanned at 300 dpi) software, and its DW was also recorded. Specific Leaf Area (SLA; in $\text{cm}^2 \text{g}^{-1}$) was calculated as the ratio between the leaf area and the leaf biomass (DW) (Garnier et al., 2001). The total leaf area for every seedling was calculated as product between the SLA and the total leaf biomass of all its leaves. The Leaf Area Index (LAI; $\text{m}^2 \text{m}^{-2}$) was calculated for every seedling as the ratio between the total leaf

area of all its leaves and the occupied area by its canopy (Garnier et al., 2001). Seedling survival was recorded weekly for both species and survival rate (percentage of seedling still alive) was calculated at the end of the experiment.

2.3. Leaf water traits

Leaf water content (WC) and leaf relative water content (RWC) were determined for adult leaves ($n = 3$ – 5 leaves of each randomly chosen seedling per treatment). Leaf samples were collected and transported as soon as possible to the laboratory in sealed plastic bags in an insulated cooler for fresh weight (FW) determination. Samples were hydrated in distilled water for 24 h and the turgid weight (TW) was also recorded. Dry weight (DW) was obtained by dehydrating the leaf samples at 80°C for 48 h to constant weight. Following Castillo et al. (2007), LWC and LRWC were calculated as:

$$\text{WC}(\%) = \frac{(\text{FW} - \text{DW})}{\text{FW}} * 100$$

$$\text{RWC}(\%) = \frac{(\text{FW} - \text{DW})}{(\text{TW} - \text{DW})} * 100$$

Table 1
General Linear Models with species (S), radiation (R) treatment (equivalent to full and 20% sunlight) and water (W) treatment (well-watered control and drought) as fixed factors, and their corresponding factor interactions, for morphological, biochemical and physiological traits of the invasive tree *Prosopis glandulosa* and the native African tree *Acacia tortilis* subspecies *raddiana*.

Plant traits	Species (S)		Radiation (R)		S × R		Water (W)		S × W		R × W		S × R × W	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Plant height (cm)	ns		ns		ns		51.35	<0.0001	ns		ns		ns	
Shoot width (mm)	15.55	<0.0001	42.91	<0.0001	12.40	<0.001	41.02	<0.0001	3.40	0.07	16.90	<0.0001	ns	
Leaves #	6.00	<0.01	13.32	<0.001	ns		32.23	<0.0001	ns		ns		5.60	<0.01
Occupied area (cm^2)	59.72	<0.0001	ns		ns		22.51	<0.0001	ns		ns		ns	
Specific Leaf Area* ($\text{cm}^2 \text{g}^{-1}$)	7.25	<0.05	4.72	<0.05	5.29	<0.05	ns		15.71	<0.001	8.86	<0.01	16.28	<0.001
Leaf Area Index* ($\text{m}^2 \text{m}^{-2}$)	9.38	<0.01	7.30	<0.05	ns		ns		ns		ns		ns	
Root: shoot ratio*	16.80	<0.0001	5.60	<0.05	ns		5.50	<0.05	5.57	<0.05	ns		ns	
Relative Growth Rate (g day^{-1})	ns		108.27	<0.0001	30.66	<0.0001	8.16	<0.01	5.16	<0.05	ns		ns	
Leaf water content (%)	7.6	<0.05	28.5	<0.0001	ns		ns		4.87	<0.05	ns		ns	
Leaf relative water content (%)	4.4	<0.05	ns		ns		ns		9.8	<0.005	ns		ns	
Chl a* ($\text{mg g}^{-1} \text{DW}$)	16.55	<0.0001	124.14	<0.0001	ns		14.13	<0.001	10.81	<0.005	15.01	<0.001	ns	
Chl b* ($\text{mg g}^{-1} \text{DW}$)	53.79	<0.0001	61.12	<0.0001	ns		5.63	<0.05	4.02	<0.05	ns		3.08	0.09
Car* ($\text{mg g}^{-1} \text{DW}$)	27.73	<0.0001	155.98	<0.0001	ns		14.58	<0.001	10.88	<0.005	16.60	<0.0001	ns	
Car: Chl (a + b)*	ns		6.12	<0.05	ns		ns		ns		8.46	<0.01	ns	
Chl a: Chl b*	11.26	<0.005	8.32	<0.01	ns		4.64	<0.05	ns		16.67	<0.0001	ns	
Free proline content ($\mu\text{g g}^{-1} \text{DW}$)	7.31	<0.05	40.72	<0.0001	ns		5.51	<0.05	ns		8.00	<0.01	ns	
F_v/f_m at predawn	ns		ns		ns		ns		ns		ns		ns	
F_0 at predawn (r.u.f.)	ns		ns		ns		ns		ns		ns		ns	
F_m at predawn (r.u.f.)	ns		ns		ns		ns		ns		ns		ns	
F_v at predawn (r.u.f.)	ns		4.30	<0.05	ns		ns		ns		ns		ns	
Φ_{PSII} at predawn	ns		ns		ns		ns		0.17	0.07	3.10	0.09	ns	
NPQ at predawn	ns		ns		ns		2.70	<0.05	ns		ns		9.20	<0.001
F_v/f_m at midday	4.50	<0.05	ns		ns		ns		ns		ns		ns	
F_0 at midday (r.u.f.)	4.70	<0.05	ns		ns		5.00	<0.05	ns		7.00	<0.01	ns	
F_m at midday (r.u.f.)	ns		ns		ns		4.80	<0.05	ns		7.40	<0.01	ns	
F_v at midday (r.u.f.)	ns		ns		5.00	<0.05	ns		ns		ns		ns	
Φ_{PSII} at midday	ns		ns		7.00	<0.05	ns		ns		ns		ns	
NPQ at midday	4.63	<0.05	ns		ns		9.00	<0.01	ns		ns		ns	
Max net photosynthesis rate ($\mu\text{mol O}_2 \text{m}^{-2} \text{s}^{-1}$)	13.10	<0.005	ns		ns		12.72	<0.005	ns		5.45	<0.05	ns	
Net photosynthesis rate ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)	ns		25.50	<0.0001	ns		ns		3.99	0.07	9.29	<0.01	–	
Stomatal conductance* ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)	ns		10.57	<0.01	ns		8.31	<0.05	ns		ns		–	
Water use efficiency ($\mu\text{mol CO}_2 \text{mmol H}_2\text{O}^{-1}$)	8.42	<0.05	ns		ns		12.22	<0.005	ns		ns		–	
Intercellular CO_2 conc. (μmol)	ns		43.96	<0.0001	6.10	<0.05	11.56	<0.005	6.44	<0.05	17.38	<0.001	–	
Dark respiration rate ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)	4.61	<0.05	ns		ns		49.23	<0.0001	4.27	0.06	ns		–	
Light compensation point* ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$)	ns		ns		ns		ns		ns		ns		–	

DW, dry weight; r.u.f., relative unit of fluorescence.

* Data series transformed using square root function. ns, not significant.

2.4. Leaf tissue biochemistry

2.4.1. Photosynthetic pigments

Leaf samples for photosynthetic pigments were collected during midday (n = 6 leaves of different seedlings chosen at random per treatment for *Prosopis*; n = 3–4 leaves per treatments for *Acacia*). Chlorophyll (Chl) a, Chl b and carotenoids (carotenes and xanthophylls, Car) were extracted using 0.1 g of fresh material in 5 mL of 80% aqueous acetone (n = 3–6 leaves of different seedlings chosen at random per treatment and species). After filtering, 0.5 ml of the suspension was diluted with a further 2 ml of acetone, and pigments concentrations were determined with a Hitachi U-2001 spectrophotometer (Hitachi Ltd., Tokyo, Japan) using three wavelengths (663.2, 646.8 and 470.0 nm). Contents of pigments (mg g⁻¹ DW) were obtained through calculation

(Lichtenthaler, 1987). The ratios Chl (a + b):Car and Chl a:b were also calculated.

2.4.2. Proline

Free proline content in leaf tissue was determined using 0.5 g of plant material (n = 4 leaves of different seedlings chosen at random per treatment and species) that was homogenized in 10 ml of 3% aqueous sulfosalicylic acid and the homogenate filtered through Whatman filter paper. 2 ml of filtrate reacted with 2 ml acidic ninhydrin and 2 ml of glacial acetic acid in a test tube for 1 h at 100 °C, and the reaction terminated in an ice bath. The reaction mixture was extracted with 4 ml toluene, mixed vigorously with a test tube stirrer for 20 s. The chromophore containing toluene was aspirated from the aqueous phase, warmed to room temperature and the absorbance read at 520 nm

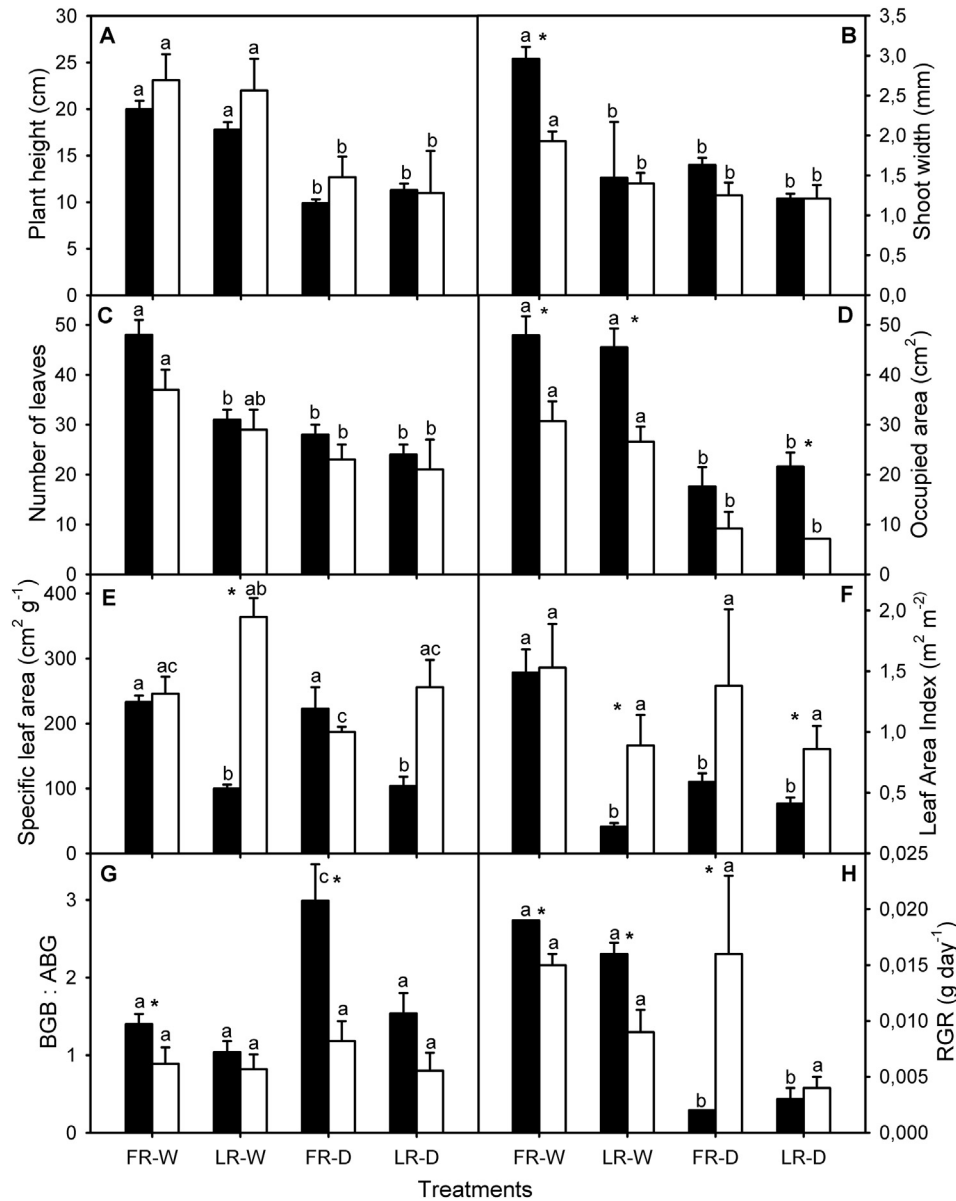


Fig. 1. Plant height (cm) (A), main shoot width (mm) (B), number of leaves (C), occupied area by the canopy (cm²) (D), specific leaf area (cm² g⁻¹) (E), leaf area index (m² m⁻²) (F), below-ground biomass (BGB): above-ground biomass (AGB) ratio (G) and relative growth rate (g day⁻¹) (H) for seedlings of *Prosopis glandulosa* (filled bars) and *Acacia tortilis subsp. raddiana* (open bars) exposed to two radiation treatments (FR, 100% sunlight; LR, 20% sunlight) and two water treatments (W, control; D, drought). Values are mean ± SE. Different letters indicate significant differences between treatment combinations for the same species (ANOVA, P < .05; Tukey's test, P < .05) and asterisks indicate significant differences between species for the same treatment combination (Student t-test, P < .05).

using toluene for a blank. Contents of proline ($\mu\text{g g}^{-1}$ DW) were obtained through calculation (Bates et al., 1973).

2.5. Photosynthetic trait responses

2.5.1. Chlorophyll fluorescence

Chl fluorescence parameters were recorded at predawn (13 °C air temperature and 62% RH) and at midday (25 °C and 58% RH) at the radiation flux of each radiation treatment. Fluorescence was measured in the adaxial leaf surface of the youngest fully developed leaf of randomly chosen stems ($n = 3\text{--}10$ plants per treatment; one leaf per plant) using a portable modulated fluorimeter (FMS-2, Hansatech Instruments Ltd., King's Lynn, UK). Leaves were adapted to dark conditions for 30 min using leaf clips. The minimal fluorescence level in the dark-adapted state (F_0) was measured using a modulate pulse [PPFD $< 0.05 \mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ for 1.8 μs] too small to induce significant physiological changes (Schreiber et al., 1986). The data recorded were averages taken over a 1.6-s period. Maximal fluorescence (F_m) was measured after applying a saturating actinic light pulse of 15,000 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ for 0.7 s and the value of F_m was recorded as the highest average of two consecutive points. Variable fluorescence ($F_v = F_m - F_0$) and maximum quantum efficiency of Photosystem II (PSII) photochemistry (F_v/f_m) were calculated. Light-adapted chlorophyll fluorescence parameters were recorded at the same leaf sections after acclimating plants to ambient light conditions. Steady-state fluorescence yield (F_s) was recorded at ambient light conditions and the maximum fluorescence yield (F_m') was recorded after a saturating actinic light pulse of 15,000 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ for 0.7 s. Combining light- and dark-adapted states fluorescence parameters, the following were calculated: quantum yield of PSII [$\Phi_{\text{PSII}} = (F_m' - F_s)/F_m'$], and non-photochemical quenching [$\text{NPQ} = (F_m - F_m')/F_m'$] (Bolh ar-Nordenkamp and  quist, 1993).

2.5.2. Gas exchange

Maximum net photosynthesis rate at a CO_2 saturated atmosphere (P_{max}) was measured as O_2 evolution using a LD2 Hansatech leaf chamber with a gas phase O_2 electrode at 25 °C ($n = 3$ leaves per treatment and 4 measurements in each leaf). A buffer of 1 M carbonate/bicarbonate (pH 9.0) was used to provide a CO_2 saturated atmosphere. Irradiance (1100 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$) was provided by a Hansatech source LS2. PPFD was measured using an integrating quantum sensor cell (Li-Cor, 190 SB).

Foliar gas exchange was also recorded at natural conditions (27 °C, 55% RH and 410 ppm CO_2) using an infrared gas analyzer (IRGA) in an open circuit (ADC BioScientific Ltd., LCPro, Herts, England). Measurements were recorded for the youngest fully developed leaf of randomly chosen stems at 1100, 850, 650, 400, 200, 90, 45 and 0 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ ($n = 3$ light curves per treatment). It was not possible to obtain these data for *A. tortilis* under drought in the shade because its leaves were too small for IRGA measurements (Rubio-Casal et al., 2010). Vapor pressure deficit was held at a constant range from 1.0 to 1.3 kPa. The photosynthetic response of the leaves to PPFD was modeled by a rectangular hyperbola quadratic equation presented by Marino et al. (2010), where the light compensation point (LCP) and the dark respiration rate (R_D) were estimated from axis intercepts. Net photosynthetic rate (P_{net}), stomatal conductance (G_s) and intercellular CO_2 concentration (C_i) were calculated for light saturation conditions according to von Caemmerer and Farquhar (1981). Intrinsic water-use efficiency (WUE_i) was calculated as the ratio between P_{net} and G_s (Moutinho-Pereira et al., 2004).

2.6. Statistical analysis

Analyses were carried out using SPSS release 12.0 (SPSS Inc.). Deviations were calculated as Standard Error (SE). The α level of significance was $p < .05$ for all tests. Homogeneity of variance and normality of raw data series were tested with the Levene test and the

Kolmogorov–Smirnov test, respectively. When homogeneity of variance between groups was not found, data were transformed using \sqrt{x} function. General Linear Model (GLM) with species, light and water treatments as fixed factors was used to analyze differences in every plant trait between tree species to drought and shade. When significant differences were found for the interaction between the species factor and any abiotic factor for a given plant trait, one-way analyses of variance (ANOVA) was carried out comparing its four treatment combinations coupled with Tukey's as post-hoc test. Differences between species for each treatment combination were analyzed using Student t-test for independent samples. Principal Components Analysis (PCA) was performed for both species independently to analyze the relationships between plant traits and to reduce the number of variables, analyzing the correlation matrix with 25 maximum iterations for convergence without rotation to extract independent PC factors with eigenvalues > 1 . Linear regression analyses were used to characterize the relationships between PCA factors of each species with light and water treatments.

3. Results

Prosopis glandulosa and *Acacia tortilis* subsp. *raddiana* showed contrasted responses to drought, shade and the combination of both abiotic factors. Significant interactions between both stress factors were recorded for foliar contents of pigments and proline, net photosynthesis rate (both P and P_{max}), shoot width and SLA for both species (GLM, radiation \times water treatment, $P < .05$). However, only the number of leaves per seedling and SLA traits had a significant interaction between both stress factors and the species (GLM, species \times radiation \times water treatment, $P < .05$) (Table 1).

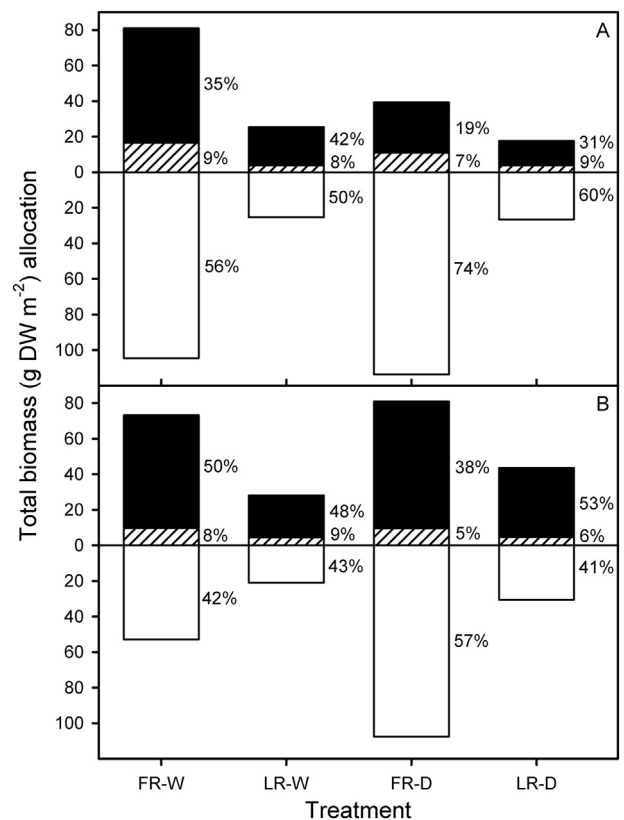


Fig. 2. Allocation of biomass production (g DW m^{-2}) to roots (open bar), shoot (striped bar) and leaves (black-filled bar) for seedlings of *Prosopis glandulosa* (A) and *Acacia tortilis* subsp. *raddiana* (B) exposed to two radiation treatments (FR, 100% sunlight; LR, 20% sunlight) and two water treatments (W, control; D, drought). The percentages for every plant fraction in relation to the total biomass are indicated.

3.1. Plant morphology, biomass, relative growth rate and mortality

Plant height decreased by ca. 45% under drought for both species, irrespective of the radiation intensity (Fig. 1A). The width of the main shoot of both species also decreased ca. 45% under drought in comparison to well-watered conditions at full sunlight, and in the shade in relation to full sunlight without drought. *Prosopis glandulosa* presented 45% wider shoots than *A. tortilis* without drought at full sunlight (t-test, $t = 5.099$, $df = 15$, $P < .0001$; Fig. 1B). The number of leaves per seedling was lower with than without drought at full sunlight for both species, and in the shade than under full sunlight without drought for *P. glandulosa* (Fig. 1C). The canopy of *Prosopis* occupied between 36 and 67% more soil surface than that of the *Acacia* in every treatment combination (t-test, $P < .05$), except under drought at full sunlight (t-test, $P > .05$). Both species occupied much less (between –53 and –73%) area under drought (Fig. 1D). The SLA of *P. glandulosa* decreased by ca. 55%

in the shade, independently of the water treatment, whereas the SLA of *A. t. subsp. raddiana* was ca. 30% higher in the shade than at full sunlight. *Acacia tortilis* subsp. *raddiana* showed more than 59% higher SLA than *P. glandulosa* in the shade (Fig. 1E). The LAI decreased in the shade without drought and under drought at full sunlight for *P. glandulosa* in comparison with full sunlight and water control conditions, respectively. *Acacia tortilis* subsp. *raddiana* more than doubled the LAI of *P. glandulosa* in the shade with and without drought (t-test, $P < .005$; Fig. 1F; Table 1).

Prosopis glandulosa showed its highest AGB without drought at full sunlight, whereas the highest values of AGB for *A. t. subsp. raddiana* were recorded with and without drought also at full sunlight. The lowest AGB were recorded under drought in the shade for *P. glandulosa* and without drought in the shade for *A. t. subsp. raddiana* (Fig. 2). The maximum BGB was recorded under drought at full sunlight for both species and the lowest BGB were always recorded in the shade (Fig. 2). BGB:

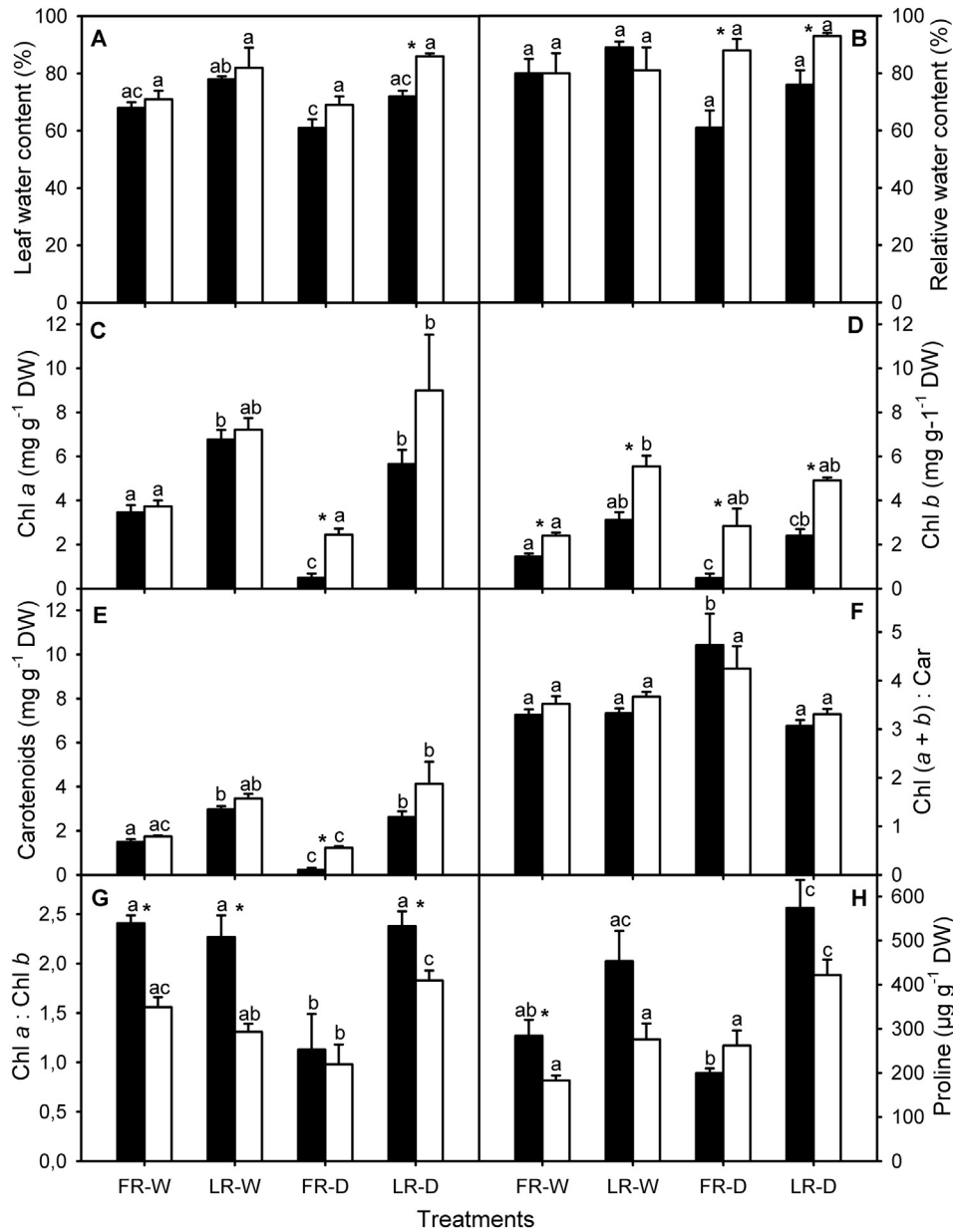


Fig. 3. Leaf water content (%) (A), relative water content (%) (B), photosynthetic pigment concentrations (mg g⁻¹ DW) and ratios (C–G), and free proline content (μg g⁻¹ DW) (F) for seedlings of *Prosopis glandulosa* (filled bars) and *Acacia tortilis* subsp. *raddiana* (open bars) exposed to two radiation treatments (FR, 100% sunlight; LR, 20% sunlight) and two water treatments (W, control; D, drought). Values are mean ± SE. Different letters indicate significant differences between treatment combinations for the same species (ANOVA, $P < .05$; Tukey's test, $P < .05$) and asterisks indicate significant differences between species for the same treatment combination (Student t-test, $P < .05$).

AGB ratio decreased in the shade under drought and increased under drought at full sunlight for *P. glandulosa*, whereas none significant differences between treatments were recorded for *A. t. subsp. raddiana*. *Prosopis glandulosa* showed higher BGB:AGB ratio than for *A. t. subsp. raddiana* at full sunlight (t-test, $P < .05$; Fig. 1G; Table 1).

RGR tended to be lower in the shade than at full sunlight without drought. *Prosopis glandulosa* showed higher RGR without than with drought, presenting higher RGR than *A. tortilis* without drought. On the contrary, *A. t. subsp. raddiana* showed higher RGR than *P. glandulosa* under drought at full sunlight (t-test, $P < .05$; Fig. 1H; Table 1). Sixteen percent of *P. glandulosa* and 75% of *A. t. subsp. raddiana* seedlings survived until the end of the experiment under drought at full sunlight, and 90% of the seedlings of *P. glandulosa* and 100% of *A. t. subsp. raddiana* survived under drought in the shade. Every seedling of both species survived without drought until the end of the experiment.

3.2. Leaf tissue biochemistry

Leaf WC tended to be higher in the shade than at full sunlight for both species. *Acacia tortilis subsp. raddiana* showed ca. 15% higher leaf WC and between 18 and 31% higher RWC than *P. glandulosa* under drought (t-test, $P < .05$) (Fig. 3A,B; Table 1).

Both species produced more than double photosynthetic pigment concentrations in the shade than they produced in full sunlight (Fig. 3C,D,E). The ratio Chl ($a + b$):Car of *P. glandulosa* decreased by

ca. 30% and the ratio Chl $a:b$ increased by ca. 50% for both species in the shade under drought (Fig. 3F,G). *Prosopis glandulosa* showed a marked drop in pigment concentrations under drought in relation to water control conditions; this trend was specially marked ($>75%$) at full sunlight where *P. glandulosa* presented lower [Chl a] than *A. t. subsp. raddiana* (t-test, $t = -6.982$, $df = 7$, $P < .0001$). For *A. t. subsp. raddiana*, [Chl a] and [Car], but not [Chl b], decreased by ca. 30% under drought at full sunlight, but these pigments concentrations remained constant in the shade (Fig. 3C,D,E). The ratio Chl ($a + b$):Car of *P. glandulosa* increased more than 15% and the ratio Chl $a:b$ decreased more than 35% for both species under drought in relation to water control conditions at full sunlight, but not in the shade (Fig. 3F,G). In general, *P. glandulosa* had lower [Chl b] content and higher Chl $a:b$ ratio without drought than *A. t. subsp. raddiana* (Fig. 3D,G). Photosynthetic pigment concentrations for *P. glandulosa* were lower than those of *A. tortilis* under drought (t-test, $P < .05$) (Fig. 3C,D,E) (Table 1).

Prosopis glandulosa showed ca. 37% higher free proline content than *A. t. subsp. raddiana* without drought at full sunlight (t-test, $t = 2.636$, $df = 6$, $P < .05$). The proline content was ca. 35% higher in the shade than at full sunlight, both with and without drought, for both species. *Acacia tortilis subsp. raddiana* increased its proline content by ca. 33% when exposed to drought in relation to water control conditions, particularly in the shade; this response was absent in *P. glandulosa* (Fig. 3H) (Table 1).

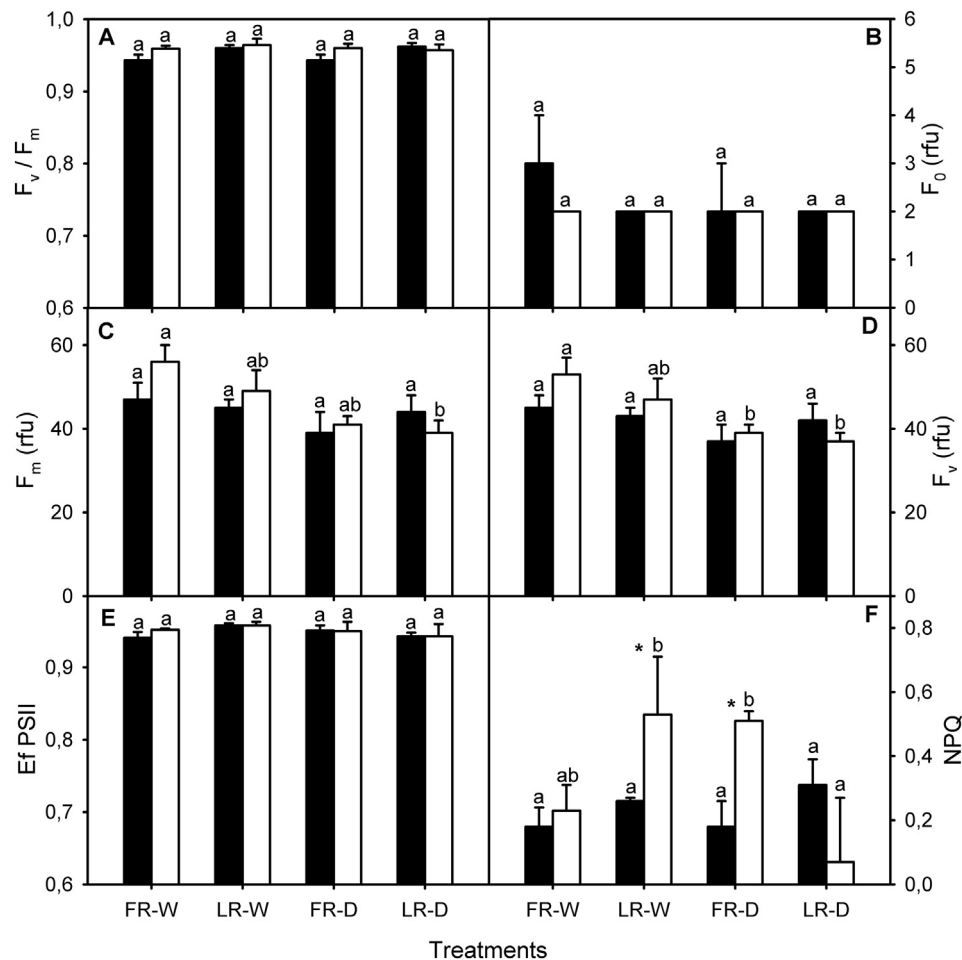


Fig. 4. Basal fluorescence (F_0) (in relative fluorescence units, rfu) (A), maximal fluorescence (F_m) (rfu) (B), variable fluorescence (F_v) (rfu) (C), maximum quantum efficiency of Photosystem II (PSII) photochemistry (F_v/f_m) (D), quantum efficiency of PSII (Φ_{PSII}) (E), and non-photochemical quenching (NPQ) (F) at predawn for seedlings of *Prosopis glandulosa* (filled bars) and *Acacia tortilis subsp. raddiana* (open bars) exposed to two radiation treatments (FR, 100% sunlight; LR, 20% sunlight) and two water treatments (W, control; D, drought). Values are mean \pm SE. Different letters indicate significant differences between treatment combinations for the same species (ANOVA, $P < .05$; Tukey's test, $P < .05$) and asterisks indicate significant differences between species for the same treatment combination (Student t-test, $P < .05$).

3.3. Photosynthetic trait responses

3.3.1. Chlorophyll fluorescence

At predawn, *A. t.* subsp. *raddiana* showed higher NPQ with than without drought at full sunlight and at full sunlight than in the shade under drought, while *P. glandulosa* kept constant values. NPQ for *A. t.* subsp. *raddiana* more than doubled that of *P. glandulosa* in the shade without drought and at full sunlight under drought (t-test, $P < .05$; Fig. 4F; Table 1).

At midday, F_v/fm was always higher than 0.900 with no significant differences between species. However, *A. t.* subsp. *raddiana* tended to have a higher F_v/fm than *P. glandulosa* at full sunlight (Fig. 5A). F_0 , F_m , F_v were generally lower for *A. t.* subsp. *raddiana* than for *P. glandulosa* (Fig. 5B,C,D). Both species tended to have higher F_m and F_v values in the shade than at full sunlight under drought, but not under the control for water conditions (Fig. 5C,D). On the other hand, *P. glandulosa* had lower Φ_{PSII} at full sunlight than in the shade without drought, while *A. t.* subsp. *raddiana* kept similar Φ_{PSII} under different radiations (Fig. 5A, E; Table 1).

3.3.2. Gas exchange

Acacia tortilis had ca. 40% higher P_{max} than *P. glandulosa* under drought. P_{max} of *P. glandulosa* dropped (–36%) in the shade at water control conditions and with drought at full sunlight (–54%), whereas the *A. tortilis* had a similar P_{max} for every treatment (Fig. 6A). The net photosynthesis rates (P_{net}) of *A. t.* subsp. *raddiana* seedlings were ca.

45% lower in the shade than at full sunlight, without showing significant differences between water treatments. *Prosopis glandulosa* had lower P_{net} in the shade under drought, coinciding its highest Ci and a non-significant decrease in Gs (Fig. 6B,C,E). Gs was ca. 20% higher and WUE was lower for *A. t.* subsp. *raddiana* than for *P. glandulosa* in the shade without drought (t-test, $P < .05$) (Fig. 6C,D). Both species presented higher R_D with than without drought, presenting *P. glandulosa* 52% higher R_D than *A. t.* subsp. *raddiana* under drought (t-test, $t = -2.683$, $df = 4$, $P = .055$) (Fig. 6F) (Table 1).

3.4. Relationships between plant traits and abiotic stress factors

Seven factors from the PCA explained 94.7% of the variance for seedling response traits of *P. glandulosa* to environmental stress factors (Table 2). The first factor PC1-Pj explained 35.6% of the variance and was positively correlated with radiation intensity ($r = 0.980$, $P < .0001$, $n = 12$) and with AGB (shoot biomass and width), LAI (and the number of leaves), occupied soil surface, BGB, P and RGR. This first factor was negatively correlated with the pigment concentrations, water and proline, F_v/fm at predawn and Φ_{PSII} at midday (Table 2). The second factor (PC2-Pj; explaining 15.7% of the variance) was positively correlated with the irrigation amount ($r = 0.785$, $P < .005$, $n = 12$) and with plant height and R_D , and negatively with SLA, BGB:AGB ratio, and F_0 , F_m and F_v at midday (Table 2).

Nine factors in the PCA explained 97.1% of the variance in traits responses of *A. t.* subsp. *raddiana* to environmental stresses (Table 3).

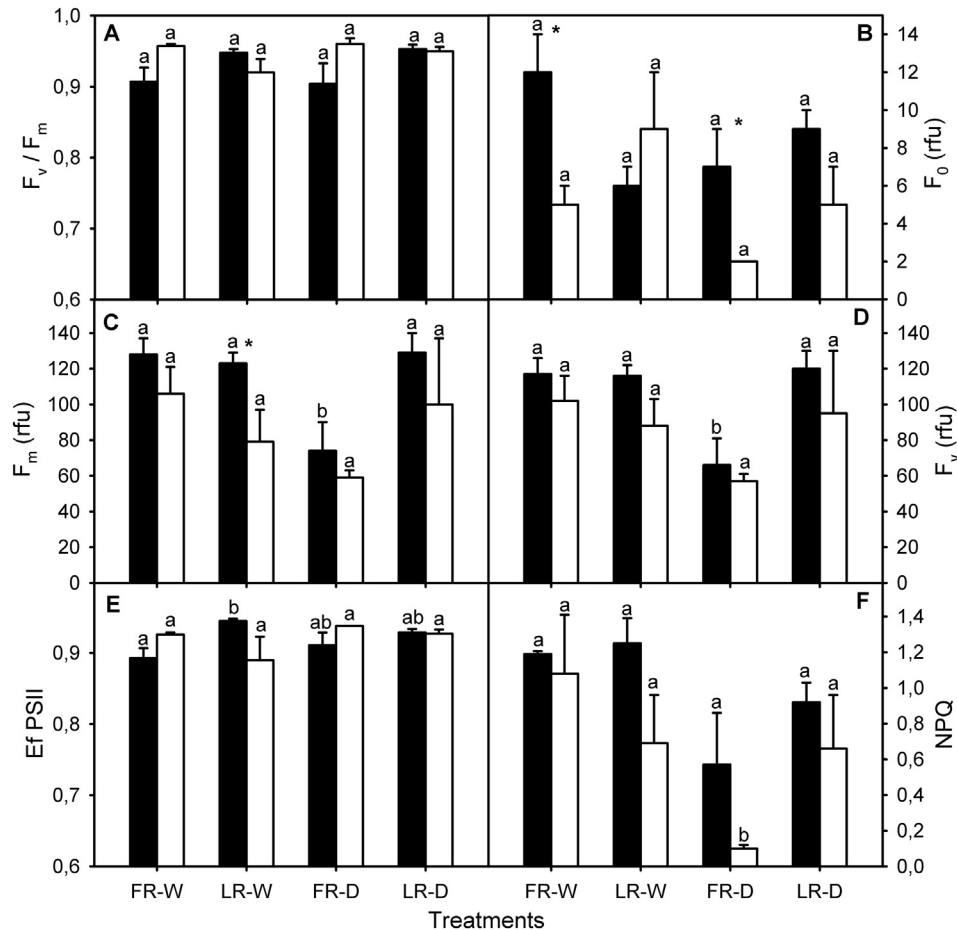


Fig. 5. Basal fluorescence (F_0) (in relative fluorescence units, rfu) (A), maximal fluorescence (F_m) (rfu) (B), variable fluorescence (F_v) (rfu) (C), maximum quantum efficiency of Photosystem II (PSII) photochemistry (F_v/fm) (D), quantum efficiency of PSII (Φ_{PSII}) (E), and non-photochemical quenching (NPQ) (F) at midday for seedlings of *Prosopis glandulosa* (filled bars) and *Acacia tortilis* subsp. *raddiana* (open bars) exposed to two radiation treatments (FR, 100% sunlight; LR, 20% sunlight) and two water treatments (W, control; D, drought). Values are mean \pm SE. Different letters indicate significant differences between treatment combinations for the same species (ANOVA, $P < .05$; Tukey's test, $P < .05$) and asterisks indicate significant differences between species for the same treatment combination (Student t-test, $P < .05$).

The first factor (PC1-At; explaining 25.2% of the variance) was positively correlated with the radiation intensity ($r = 0.866$, $P < .0001$, $n = 12$) and with AGB (shoot and leaf biomass), LAI, BGB, BGB:AGB ratio and P, and negatively with the content of water, Chl *a* and Car and SLA (Table 3). The second factor (PC2-At; explaining 16.1% of the variance) was positively correlated with the irrigation amount ($r = 0.751$, $P < .01$, $n = 12$) and with occupied soil area, Gs, R_D , and F_m and F_v at pre-dawn and negatively with WUE and Chl ($a + b$):Car ratio (Table 3). The third factor (PC3-At; explaining 11.7% of the variance) was also positively correlated with the irrigation amount ($r = 0.605$, $P < .05$, $n = 12$) and with F_0 at predawn (Table 3).

4. Discussion

The native African tree *Acacia tortilis* subsp. *raddiana* and the invasive tree *Prosopis glandulosa* showed contrasted responses to shade and water stress and their interaction. Without any experimentally

imposed abiotic stress, the seedlings of *P. glandulosa* grew more robust (wider shoots) and more rapidly above-ground (vertically and horizontally) and invested far more resources in below-ground biomass at this critical seedling stage than *A. t.* subsp. *raddiana*. The rapid below-ground development of the seedlings of *P. glandulosa* could enable the alien species access to deeper humid soil layers or phreatic zones before experiencing severe drought. This functional trait characteristic of phreatophytes has been previously associated with high invasive capacity in desert areas (Horton and Clark, 2001). Moreover, the configuration of the PSII of *P. glandulosa* in favorable conditions likely supported more efficient radiation capture and utilization (higher Chl *a*:*b* ratio due to lower Chl *b* content) than that of *A. t.* subsp. *raddiana* (Terashima and Hikosaka, 1995).

Overall, radiation intensity, and probably radiation quality (Sheerin and Hiltbrunner, 2017), were stronger drivers of the performance of both species than water availability as they explained most of the recorded variance in plant traits. Free proline content tended to be higher

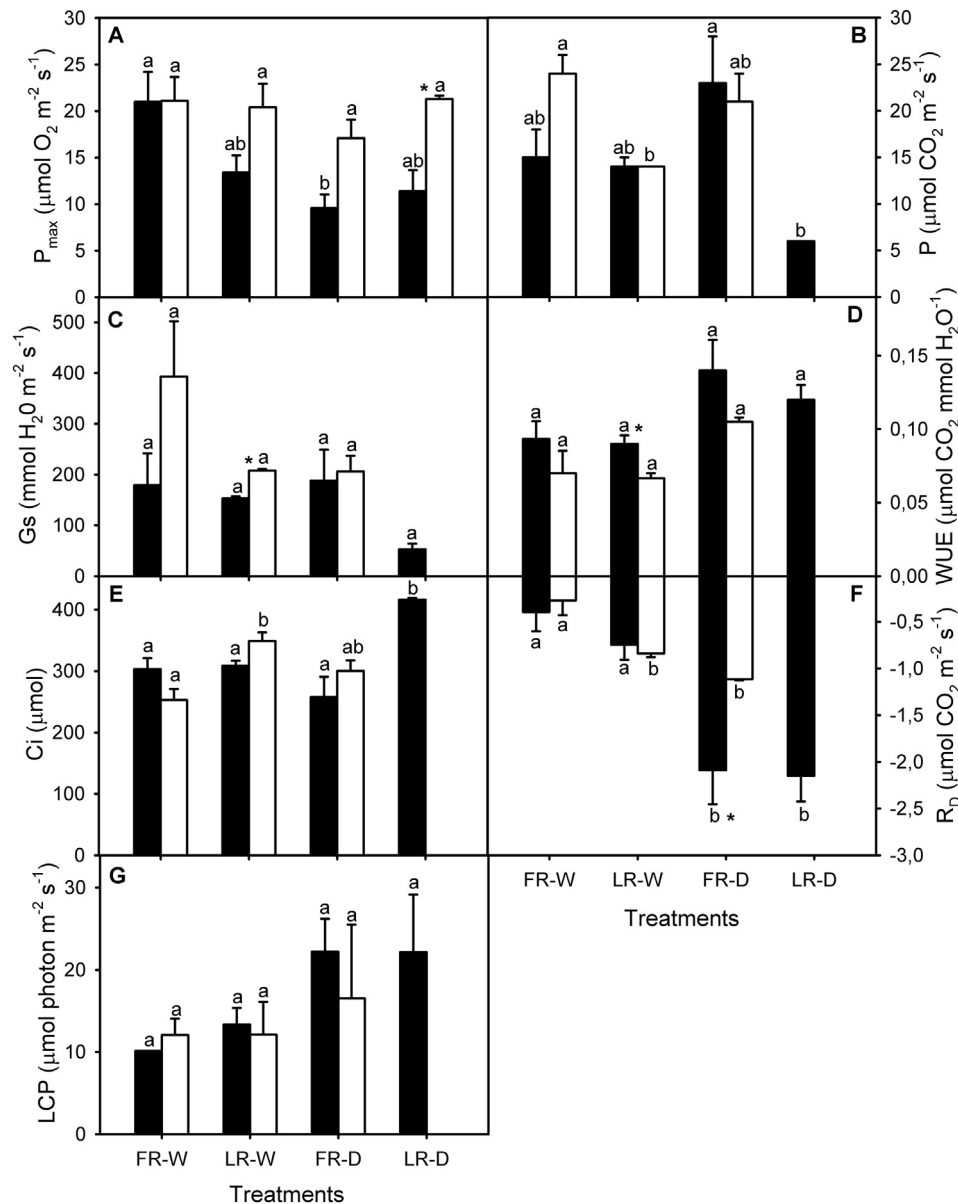


Fig. 6. Maximum net photosynthesis rate (P_{max}) ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$), net photosynthesis rate (P) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), water use efficiency ($\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$), intercellular CO_2 concentration ($\mu\text{mol CO}_2$), dark respiration rate (R_D) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and light compensation point (LCP) ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) for seedlings of *Prosopis glandulosa* (filled bars) and *Acacia tortilis* subsp. *raddiana* (open bars) exposed to two radiation treatments (FR, 100% sunlight; LR, 20% sunlight) and two water treatments (W, control; D, drought). Values are mean \pm SE. Different letters indicate significant differences between treatment combinations for the same species (ANOVA, $P < .05$; Tukey's test, $P < .05$) and asterisks indicate significant differences between species for the same treatment combination (Student t-test, $P < .05$).

in shaded leaves than in leaves of seedlings grown in the high radiation for both species. This suggests that proline is a solute marker of shade stress that may alleviate oxidative damage (Fu et al., 2014). Proline has been recognized as a multi-functional molecule, protecting cells from damage by acting as both an osmotic agent and a radical scavenger, and providing a supply of energy to drive growth once the stress is relieved (Kavi Kishor and Sreenivasulu, 2013). Seedlings of both studied tree species established in low radiation conditions grew slower, and accumulated less AGB and BGB. These shaded seedlings also exhibited diminished photosynthesis rates coinciding with partial stomatal enclosure, especially under drought, that could be mediated by the concentration of free abscisic acid (ABA) within the cytosol (Haworth et al., 2018). The failure of the seedlings of both species to fully acclimate to low radiation intensity was also reflected at their canopy level, since neither responded with increased allocation to leaf area (measured as LAI) to intercept more radiation as has been reported for species well-acclimated to shade (Carrión-Tacuri et al., 2011). This structural limitation was partially compensated by the production of higher contents of photosynthetic pigments to absorb more radiation. Beyond these common inter-specific responses, the native *A. t.* subsp. *raddiana* seedlings appear to have traits that convey greater and more efficient tolerance to shade stress than *P. glandulosa*. The *Acacia* was able to acclimate to the low radiation environment by producing thinner leaves (high SLA), possibly allowing for greater utilization of available light (Droste et al., 2010), whereas the SLA of *P. glandulosa* decreased markedly in the shade. Moreover, the BGB:AGB ratio of *P. glandulosa* decreased in the shade, particularly under drought, and this response has been

described as shade avoidance (Page et al., 2011). In contrast, *A. tortilis* BGB:AGB response did not vary between shade and full sun radiation treatments. Additionally, only *P. glandulosa* had lower Φ_{PSII} and P_{max} (but not lower P_{net}) in shade compared to full sunlight, which indicates the invasive seedlings had photosynthetic limitations that may have been due to the inactivation of photosystems (Maxwell and Johnson, 2000) and changes in the concentration of Rubisco, the main enzyme in photosynthesis (Galmes et al., 2013). In fact, *P. glandulosa* tended to accumulate more proline than *A. tortilis*, especially in the shade, denoting higher stress levels.

While shade stress shaped the recorded plant responses to the greatest extent, drought also provoked significant stress response signals in both invasive and native tree seedlings, even causing mortality of some seedlings of both species. As in the case of the plants suffering shade stress, higher maintenance costs and biomass allocation adjustments resulted in less robust seedlings of both species established under drought. The seedlings with limited access to water were shorter than those in control treatments that received more water. In this sense, both species partially folded their leaflets in response to drought, thereby intercepting less radiation, and they produced more BGB, allowing them greater potential access to soil water (Chuyong and Acidri, 2017). The amount of water consumed and the soil depth where that water is extracted vary depending on the tree species and their age (Liu et al., 2018). Both species presented also higher R_D under drought that has been described as an indicator of water stress in relation to increasing maintaining costs (Xia et al., 2017). Although both species responded negatively to the imposed water stress, this

Table 2

Factor loadings (PC) of the individual variables obtained by a Principal Component Analysis (PCA) on traits of the invasive tree *Prosopis glandulosa* from Southeast Egypt exposed to different water and light treatments in a greenhouse experiment.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Relative growth rate	0.966	-0.170	-0.002	+0.002	-0.008	+0.109	+0.026
Below-ground biomass (BGB)	0.943	-0.201	-0.041	+0.012	+0.083	-0.122	+0.050
Shoot biomass	0.906	-0.103	+0.036	-0.143	-0.146	+0.079	+0.121
Carotenoids	-0.855	+0.287	+0.329	+0.047	+0.157	-0.076	-0.052
Chlorophyll <i>b</i>	-0.826	+0.342	+0.122	+0.066	+0.103	+0.286	-0.139
Chlorophyll <i>a</i>	-0.820	+0.340	+0.327	+0.102	+0.149	-0.051	-0.216
Above-ground biomass (AGB)	0.816	+0.355	-0.082	-0.325	+0.101	+0.115	-0.066
Leaf area index	0.773	-0.049	+0.140	-0.441	+0.327	-0.103	-0.104
Shoot width	0.762	+0.036	+0.561	-0.200	-0.068	+0.030	+0.103
Free proline	-0.745	-0.269	+0.229	+0.085	+0.325	+0.061	+0.290
F_v/f_m (predawn)	-0.729	-0.193	-0.003	+0.078	-0.526	+0.113	+0.133
Leaf biomass	0.719	+0.467	-0.111	-0.354	+0.170	+0.115	-0.120
Intercellular CO ₂ concentration	-0.713	-0.393	+0.282	-0.338	+0.348	+0.121	-0.090
Number of leaves per seedling	0.683	+0.068	+0.560	+0.253	+0.164	+0.132	+0.165
Leaf water content	-0.678	+0.285	+0.410	+0.228	-0.027	+0.438	+0.121
Net photosynthesis	0.668	+0.176	-0.334	+0.404	-0.475	-0.120	+0.088
Occupied area	0.664	+0.278	+0.594	-0.217	-0.040	+0.234	-0.129
Φ_{PSII} (midday)	-0.654	+0.536	-0.173	+0.317	+0.166	+0.139	+0.241
Stomatal conductance	0.623	+0.198	-0.015	+0.593	-0.454	-0.097	+0.048
Specific leaf area	-0.091	-0.864	+0.230	-0.069	+0.269	-0.207	+0.220
BGB: AGB ratio	+0.249	-0.773	-0.003	+0.299	+0.094	-0.282	+0.231
F_0 (midday)	+0.392	-0.734	+0.466	+0.105	-0.010	+0.172	-0.037
Plant height	+0.384	+0.674	+0.612	-0.029	-0.102	+0.060	-0.005
F_m (midday)	-0.064	-0.672	+0.591	+0.372	+0.048	+0.148	-0.083
F_v/f_m (midday)	-0.631	+0.662	-0.208	+0.180	+0.012	-0.136	-0.008
Dark respiration rate	+0.396	+0.652	+0.557	+0.126	-0.013	-0.104	+0.189
F_v (midday)	-0.136	-0.637	+0.589	+0.402	+0.056	+0.139	-0.088
NPQ (predawn)	-0.416	+0.012	-0.632	-0.019	+0.472	+0.098	+0.380
Water use efficiency	-0.078	-0.350	-0.607	-0.508	-0.017	+0.328	+0.308
Leaf relative water content	-0.498	+0.139	+0.504	-0.253	-0.097	+0.480	+0.140
F_0 (predawn)	+0.425	+0.107	-0.367	+0.738	+0.302	+0.048	-0.008
F_m (predawn)	+0.325	+0.126	-0.376	+0.707	+0.443	+0.035	-0.064
F_v (predawn)	+0.311	+0.127	-0.374	+0.697	+0.455	+0.033	-0.069
NPQ (midday)	+0.271	-0.146	+0.433	+0.601	-0.110	+0.472	-0.105
Φ_{PSII} (predawn)	-0.492	-0.041	+0.164	+0.296	-0.732	-0.080	+0.232
Maximum net photosynthesis	+0.415	+0.307	+0.475	+0.015	+0.638	+0.159	+0.222
Chlorophyll (<i>a</i> + <i>b</i>): Carotenoids	+0.316	-0.058	-0.554	+0.017	-0.086	+0.751	-0.097
Chlorophyll <i>a</i> : Chlorophyll <i>b</i>	-0.362	+0.134	+0.563	+0.079	-0.661	+0.172	-0.184
Light Compensation Point	-0.302	-0.477	-0.359	+0.068	-0.016	+0.182	-0.629

Correlations between the PCA and plant traits with factor loadings > ± 0.600 are marked in bold.

stress more greatly impacted the alien *P. glandulosa* seedlings. These invasive seedlings had lower leaf WC, and especially much lower RWC, than native *A. t. subsp. raddiana* (RWC: ca. 60% vs 90% at full sunlight), which revealed the poor water status of *P. glandulosa* (Porporato et al., 2001). In this context, the lower drought tolerance of *P. glandulosa* was reflected overall on diminished growth and AGB accumulation. This seems to be related to high maintenance costs (high R_D) yielding a decrease in P_{max} at full sunlight that may be also related to the down-regulation of the activation state of Rubisco (Galmes et al., 2013) as previously reported for this species (Shirke and Pathre, 2004). Moreover, there was a marked decrease in content of photosynthetic pigments in *P. glandulosa* seedlings subjected to drought at full sunlight. This has been described as an adaptive photoprotection mechanism to intercept less radiation during periods of limited photosynthetic capacity (Castillo et al., 2007). In contrast with *P. glandulosa* seedlings, seedlings of native *A. tortilis* exhibited drought-tolerance. They were able to produce smaller leaves with higher leaf mass by lowering SLA (e.g. as reported for other *Acacia* species; Shadwell and February, 2017). The native seedlings were also able to increase energy dissipation by heat emission, as reflected in higher NPQ values at pre-dawn in full sunlight. Hamerlynck and Huxman (2009) have described this type of response as a photoprotective mechanism of drought-tolerant desert evergreen trees. The RWC of native *A. t. subsp. raddiana* was always higher than 80%. This acclimation capacity improved the water economy of native *A. t. subsp. raddiana* under drought, allowing it to function in a great extent independently of the water status of soil. This response resulted in higher seedling survivorship rates for

the native species than seedlings of alien *P. glandulosa*. Aref et al. (2013) and Kebbas et al. (2015) have described *A. t. subsp. raddiana* as being well adapted to drought, being able to acclimate its seedling anatomy and to protect its photosynthetic machinery under water stress. The high survivorship of *A. t. subsp. raddiana* (>70%) even under conditions of drought and full radiation would allow it to colonize stressful arid areas before other plant species whose colonization and survivorship may be facilitated by this native tree (Ludwig et al., 1993).

Beyond the independent effects of shade and drought, the interactions of these factors yielded synergistic effects on seedlings of both tree species, affecting key plant traits. Some effects of drought were specially marked at full sunlight, under which the above-mentioned decreases in shoot width and leaf RWC were greater, and survival rates were lowest for both species. Additionally, the combination of drought and full sunlight induced drops in the Chl *a:b* ratio and F_m and F_v at midday for both species that did not occur in seedlings grown in the shade, denoting poorer energy transmission in the photosynthetic apparatus (Terashima and Hikosaka, 1995; Hamerlynck and Huxman, 2009). This response may be explained by higher evaporative demand and evapotranspiration rates for seedlings grown in full sunlight that would accentuate the effects of water limitation stress. On the other hand, the combination of drought and shade also yielded specific plant reactions. Thus, the Chl (*a + b*):Car ratio was lower for *P. glandulosa* and NPQ at midday was higher for *A. t. subsp. raddiana* in the shade than at full sunlight only under drought, reflecting an increase in energy dissipation by heat emission (Bolh ar-Nordenkamp and  quist, 1993). In fact, alien *P. glandulosa* had the lowest photosynthesis

Table 3
Factor loadings (PC) of the individual variables obtained by a Principal Component Analysis (PCA) on traits of the native tree *Acacia tortilis subsp. raddiana* from Southeast Egypt exposed to different water and light treatments in a greenhouse experiment.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Below-ground biomass (BGB)	+0.812	-0.207	-0.086	-0.249	+0.407	-0.182	+0.046	+0.091	-0.003
Above-ground biomass (AGB)	+0.772	-0.302	-0.038	-0.298	+0.331	+0.081	+0.179	-0.265	+0.023
Net photosynthesis	+0.755	+0.144	-0.530	+0.068	+0.219	-0.098	-0.121	+0.002	+0.008
Leaf biomass	+0.716	-0.388	-0.038	-0.308	+0.317	+0.028	+0.169	-0.328	-0.039
Carotenoids	-0.714	-0.022	+0.055	+0.238	+0.595	+0.084	-0.085	-0.124	+0.211
Leaf water content	-0.711	-0.101	+0.135	+0.400	+0.226	-0.110	+0.413	-0.045	-0.015
Leaf relative water content	-0.700	-0.520	-0.076	-0.206	-0.208	+0.365	+0.093	-0.035	-0.038
Shoot biomass	+0.680	+0.344	-0.017	-0.082	+0.239	+0.337	+0.136	+0.225	+0.366
BG:AGB ratio	+0.677	+0.140	-0.244	+0.116	+0.268	-0.184	-0.232	+0.434	-0.150
Chlorophyll <i>a</i>	-0.676	-0.026	+0.051	+0.273	+0.605	+0.137	-0.084	-0.112	+0.239
Intercellular CO ₂ concentration	-0.650	-0.323	+0.547	-0.050	-0.149	+0.164	+0.208	+0.018	-0.010
Specific Leaf Area	-0.604	+0.105	+0.575	+0.032	+0.235	+0.120	+0.102	+0.164	-0.365
Leaf area index	+0.470	-0.331	+0.238	-0.420	+0.396	+0.278	+0.214	-0.268	-0.264
Water use efficiency	+0.144	-0.773	-0.164	-0.141	-0.333	+0.329	+0.064	+0.123	-0.088
Dark respiration rate	+0.048	+0.695	-0.017	+0.258	+0.124	+0.037	-0.237	-0.163	-0.541
F_m (predawn)	+0.381	+0.679	+0.412	+0.154	+0.149	-0.075	+0.395	+0.123	+0.017
F_v (predawn)	+0.377	+0.668	+0.423	+0.185	+0.129	-0.085	+0.403	+0.104	+0.028
Occupied area	-0.154	+0.668	+0.586	-0.245	-0.241	+0.141	-0.196	-0.015	-0.080
Stomatal conductance	+0.466	+0.637	-0.315	+0.236	+0.289	-0.284	-0.081	-0.021	+0.208
Chlorophyll (<i>a + b</i>): Carotenoids	+0.517	-0.615	+0.269	-0.288	+0.209	-0.147	+0.043	+0.165	+0.077
NPQ (midday)	-0.164	+0.591	-0.386	-0.339	+0.145	+0.056	+0.539	-0.053	+0.146
Chlorophyll <i>a</i> : Chlorophyll <i>b</i>	-0.392	+0.518	-0.347	+0.349	+0.149	+0.357	+0.129	-0.361	+0.101
F_0 (predawn)	-0.122	+0.176	+0.610	+0.057	+0.398	-0.313	+0.218	+0.432	-0.214
NPQ (predawn)	+0.429	-0.324	+0.513	+0.130	-0.279	-0.445	+0.120	+0.268	+0.189
F_0 (midday)	-0.518	+0.222	-0.077	-0.737	-0.090	-0.306	-0.012	+0.021	+0.137
F_v/fm (midday)	+0.488	-0.057	-0.159	+0.711	-0.117	+0.313	+0.219	-0.002	-0.229
Φ_{PSII} (midday)	+0.451	-0.241	-0.190	+0.690	0.150	+0.274	+0.203	+0.135	-0.260
Light compensation point	-0.087	-0.106	-0.110	+0.635	-0.578	-0.040	-0.040	+0.215	+0.352
F_v/fm (predawn)	+0.151	+0.121	+0.306	+0.572	-0.390	-0.144	+0.353	-0.355	+0.174
F_m (midday)	-0.400	+0.376	-0.441	-0.524	-0.162	-0.115	+0.408	+0.068	-0.080
F_v (midday)	-0.370	+0.383	-0.472	-0.478	-0.165	-0.086	+0.447	+0.071	-0.105
Chlorophyll <i>b</i>	-0.558	-0.265	+0.318	+0.096	+0.650	-0.130	-0.081	+0.008	+0.203
Free proline	-0.487	-0.265	-0.481	+0.105	+0.623	+0.117	+0.169	+0.034	-0.002
Number of leaves per seedling	-0.419	-0.049	-0.349	+0.160	+0.537	+0.327	-0.182	+0.480	+0.023
Shoot width	+0.411	+0.432	+0.206	+0.013	-0.313	+0.641	-0.140	-0.243	+0.055
Plant height	-0.056	+0.320	+0.501	-0.367	+0.081	+0.613	-0.195	+0.254	+0.084
Relative growth rate	+0.468	+0.488	+0.196	-0.329	+0.098	+0.515	-0.175	+0.174	+0.221
Maximum net photosynthesis	-0.366	+0.492	-0.101	-0.043	+0.106	-0.474	-0.510	-0.255	-0.161
Φ_{PSII} (predawn)	+0.363	-0.158	+0.553	-0.007	+0.373	-0.167	-0.091	-0.592	+0.099

Correlations between the PCA and plant traits with factor loadings $\geq \pm 0.600$ are marked in bold.

rates and the lowest biomass production when shade and water stresses were combined. This may reflect its ability to partially cope with drought by adjusting the relative allocation of resources to above- and below-ground structures under high light. However, Schumacher et al. (2008) suggested this strategy is not effective when both light and water resources are limiting, because opposite responses in traits such as BGB:AGB ratio can result in an intermediate and not optimum phenotype in response to the combined stress treatments (Visser et al., 2016).

The invasion of alien species such as *P. glandulosa* may benefit from an increase in rainfall in hyperarid habitats as a result of climatic change (Dukes and Mooney, 1999). However, factors influencing how climate change may affect the dynamics of invasion by *Prosopis* species in Africa are numerous, complex and poorly understood (Richardson et al., 2000; Richardson and van Wilgen, 2004). In view of our results, the seedlings of the native tree *A. t.* subsp. *raddiana* are able to implement important shifts in key functional traits in response to changing abiotic stress conditions. Our results provide support for why the native species is stress-tolerant and well-adapted to the habitat it occupies in hot arid African deserts. Thus, its phenotypic plasticity in response to environmental stress allows the native seedlings to establish under drought conditions and under the canopy of other plant species. Some invasive species have also been shown to successfully invade new habitat due to high phenotypic plasticity that has been described as a Jack-and-Master strategy (e.g. Richards et al., 2006; Castillo et al., 2018). In contrast to native *A. t.* subsp. *raddiana* and highly plastic invasive species, seedlings of the invasive tree *P. glandulosa* did not demonstrate an ability to adjust to environmental stress conditions that would broadly facilitate its recruitment into novel environments. In view of our results, the alien *Prosopis* seedlings are stress-avoiding and fast-growing (sensu Oliveira et al., 2014). Consequently, for successful establishment, the seeds of alien *P. glandulosa* invading arid desert environments need to be dispersed into specific microenvironments where extreme abiotic stress can be avoided. In this sense, the dispersal of *P. glandulosa* seeds by camels, as well as moderate soil burial, in unvegetated areas may provide the moisture and the nutrients necessary for its germination and establishment (Abbas et al., 2018a, 2018b). In Egypt, *P. glandulosa* spreads along commercial routes into new areas of invasion, coinciding with ephemeral riverbeds (Abbas, pers. obs.). In East Africa, it generally establishes and begins its invasive spread on deep soils with high water availability (Meroni et al., 2017). The alien seedlings can successfully establish in these microenvironments due to their early allocation to rapid and strong root growth (Yoda et al., 2015) enabling access to humid soil layers. Even short periods of drought can cause high seedling mortality of desert trees that are very sensitive to water stress (Tian et al., 2014), as we have documented in this study. However, while *P. glandulosa* was highly sensitive to water and shade stress, and particularly to their interaction, seedlings were able to avoid permanent damage to their photosynthetic apparatus (F_v/f_m was always higher than 0.900), allowing them to resume more normal gas exchange processes if and when they experience pulses of water availability (Milchunas and Lauenroth, 1995; Yoda et al., 2015). They can also be opportunistic in response to sudden increased light availability due to a disturbance-generated gap or shade removal.

The establishment stage in the life cycle of a species can be the most critical aspect of its invasiveness. For this reason, our focus on the seedling stage of native and alien trees provides information that can be applied to management strategies to prevent invasive spread. Once established, growth and spread beyond the seedling stage can respond differently to environmental conditions. In contrast to the low stress tolerance during seedling establishment, adult trees of *P. glandulosa* can tolerate abiotic stress in environments with reduced water availability and high light (Oliveira et al., 2014). This is likely because critical foliar gas exchange in the adult trees are not reliant on shallow soil water content critical to seedlings, because the mature deep-rooted trees can tap water from phreatic levels (Tezara et al., 1998).

Our results are useful for conservation planning and restoration of invaded hyperarid ecosystems. Disturbances and alterations leading to the formation of microenvironments with diminished abiotic stress, such as opening gaps in native vegetation and creating humid and nutrient-rich patches (i.e. due to camel endozoochory), should be avoided to prevent the invasion of *P. glandulosa* though limiting its seedling establishment. Moreover, the conservation of adult *A. t.* subsp. *raddiana* trees and augmentative restoration plantings of seeds or seedlings may provide a valuable biotool to promote invasion resistance through establishment of shade to limit the invasion of *P. glandulosa*.

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