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Photosynthetic adaptation and survival strategy of *Duvalia velutina* in an extremely arid environment

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Abstract

Leafless *Duvalia velutina* Lavranos (Apocynaceae) is an arido-active stem succulent common in the arid region southwest of the Arabian Peninsula. This region is characterized by a short wet season with erratic rainfall and a long dry season with high temperature and high irradiance. We investigated the survival strategy of *D. velutina* by studying nurse association, gas exchange, and chlorophyll fluorescence. Results showed that *D. velutina* exhibited the strict nurse association with shade for protection against heat and high irradiance. Results also showed that *D. velutina* is an obligate CAM plant with ample physiotypic plasticity involving a shift to CAM-idling under prolonged drought. Chlorophyll fluorescence measurements revealed water stress-induced reduction of PSII activity occurring in concomitance with a marked rise of nonphotochemical quenching and chlorenchyma anthocyanin content. These results reflected photoprotective capacity involving nonradiative excess energy dissipation and antioxidative attributes. We concluded that the complex survival strategy of *D. velutina* in its natural arid habitat includes a multifaceted interplay of nurse association, physiotypic plasticity, and photoprotective mechanisms.

Additional key words: chlorophyll fluorescence; CAM; CAM-idling; drought; *Duvalia velutina*; nurse association; photoprotection.

Introduction

Arid regions southwest of the Arabian Peninsula are characterized by high temperature, high evaporation, high irradiance, scarce water, and erratic rainfall (Fisher and Membery 1998). In such inimical habitats, arido-active-stem succulents exhibit biotic nurse association with a nurse plant for protection from heat and high irradiance (Padilla and Pugnaire 2006, Larrea-Alcázar *et al.* 2008, Pérez-Sánchez *et al.* 2013, Valiente-Banuet and Verdu 2013). Association also occurs with a non-living nurse, such as rocks, and is known as abiotic nurse association (Reyes-Olivas *et al.* 2002, Peters *et al.* 2008, Rojas-Sandoval and Meléndez-Ackerman 2013). Our field observations indicated that *D. velutina* does not grow in exposed places and tends to associate with phanerophytes and large basaltic rocks commonly found in the area. Therefore, we studied the nurse association as a possible part of *D. velutina* survival strategy in its natural arid habitat.

Desert stem succulents also rely on high water storage capacity, morpho-anatomical traits, and physiological adaptations (Sayed 2001a). These physiological adaptations include the CAM pathway of photosynthesis for its nocturnal CO_2 uptake which improves plant water economy (Sayed 2001b, Masrahi *et al.* 2011, Masrahi *et al.* 2012a,b; Al-Turki *et al.* 2014). Therefore, our work also involved investigating existence and modifications of CAM in *D. velutina* by studying diurnal and seasonal changes in gas exchange and chlorenchyma titratable acidity. The CAM pathway includes several physiotypes, namely, obligate CAM, facultative CAM, CAM-cycling, and CAM-idling. Of these physiotypes, obligate CAM means strictly exhibiting CAM, while facultative CAM involves shifting carbon metabolism to CAM in response to environmental stress (Lüttge 2004). In CAM-cycling, stomata close during the night with nocturnal refixation of respiratory CO_2 and open during the day with CO_2 uptake and the Calvin cycle in operation together with assimilation of CO_2 remobilized from nocturnally stored organic acid (Lüttge 2004). In CAM-idling, stomata close day and night with no net CO_2 uptake and nocturnal refixation of respiratory CO_2 (Lüttge 2010).

Moreover, carbon metabolism *via* CAM takes place in four consecutive phases of which Phase I takes place

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Abbreviations: C_i – intercellular CO_2 concentration; Chl – chlorophyll; F_v/F_m – maximal photochemical efficiency of PSII antenna; g_s – stomatal conductance; NPQ – nonphotochemical quenching; P_N – photosynthetic rate; Φ_{PSII} – PSII quantum yield.

during the night, whereas Phase II, Phase III, and Phase IV take place during the day (Lüttge 2004). During Phase III, decarboxylation of nocturnally stored organic acid generates CO_2 with internal partial pressure high enough to initiate stomatal closure. Since Phase III takes place under closed stomata and high irradiance, PSII may become over-energized (Niewiadomska and Borland 2008, Lüttge 2010). Under such conditions, plants invoke photoprotection by nonradiative excess energy dissipation *via* the xanthophyll cycle (Horton and Ruban 2005, Murchie and Niyogi 2011). We studied chlorophyll (Chl) fluorescence quenching to elucidate photoprotective mechanisms operating in *D. velutina*. Furthermore, our field observations indicated that *D. velutina* stem develops a red colour during the dry season. In this context, anthocyanins were reported to have photoprotective and antioxidative properties under conditions of high irradiance (Gould 2004). Therefore, our work also included studying anthocyanin accumulation to envisage other mechanisms involved in mitigation of stress-induced effects on photosynthetic machinery.

Materials and methods

The study site, southwest of the Arabian Peninsula (17°19'N – 42°48'E), is characterized by sand-loam soil, high temperature, high irradiance, scarce water, and erratic rainfall (Fisher and Membery 1998). Long term records (1975–2010) of mean monthly air temperature and precipitation (Ministry of Electricity and Water, Riyadh, Saudi Arabia) were used to construct climagram of the study site (Fig. 1). Daytime changes in air temperature and PPFD were measured during the dry season using field digital thermometer (*Kestrel 2000*, Boothwyn, Philadelphia, USA), and PAR/LAI ceptometer (*AccuPar LP-80*, *Decagon Devices*, Pullman, USA), respectively. Mature *D. velutina* plants were used as plant material.

Nurse association was assessed by randomly setting up sixty quadrats (25 m^2 each) and constructing contingency tables in which presence/absence of *D. velutina* and nurse was determined (Kent 2012). The association was tested by determining frequency of joint occurrence (F) of *D. velutina* and nurse using the equation:

F = (number of quadrats with joint occurrence/total number of quadrats) × 100

Assessment of frequency of *D. velutina* occurrence in exposed and shaded places was also carried out. Significance of association was tested by determining Chi square (χ^2) and applying single factor analysis of variance (*ANOVA*) and the least significant differences. Association was considered significant if χ^2 value at 0.05 level exceeds 3.84 (Kent 2012). Nature of association as being positive or negative was assessed by calculating standardized residuals (SR) using the equation: $SR = O - E/\sqrt{E}$, where O is observed frequency and E expected frequency. Association was considered positive if the value of SR was greater than two (López *et al*. 2007).

Existence of CAM was investigated by determining diurnal and seasonal changes in gas exchange and chlorenchyma cell sap acidity. Gas exchange was measured using portable open system infrared gas analyzer (*Lci-SD*, *ADC Bioscientific*, Hertfordshire, UK). Measured gas-exchange parameters included photosynthetic rate (P_N), stomatal conductance (g_s), and substomatal intercellular CO_2 concentration (C_i). Chlorenchyma cell sap was extracted by grinding a known mass of tissue in distilled water, filtering cell sap through two layers of muslin, and determining titratable acidity using 0.01N NaOH and phenolphthalein as indicator (Osmond *et al*. 1991).

Pulse amplitude modulated Chl fluorescence was studied using a fluorometer (*FMS2*, *Hansatech*, Norfolk, UK) and standard nomenclature (Sayed 2003, Govindjee 2004, Kalaji *et al.* 2012). Measured Chl fluorescence parameters included maximal efficiency of PSII antenna (F_v/F_m), and PSII quantum yield (Φ_{PSII}) (Baker 2008). Chl fluorescence measurements were carried out in 15-min dark-adapted *D. velutina* stems using dark-adaptation plastic clips (*Hansatech Instruments*, Norfolk, UK), a moderate modulating light intensity (MOD level 2 set by instrument hardware), and a saturating actinic light intensity of 3,000 μmol(photon) m^{-2} s^{-1}.

Nonphotochemical quenching of Chl fluorescence was assessed by calculating the value NPQ using the equation $NPQ = (F_m/F_m') - 1$, where F_m is maximal fluorescence emitted, when all PSII traps become closed, and F_m' is light-adapted fluorescence maximum (Backer 2008, Kalaji *et al*. 2014) .

Anthocyanin pigment content was determined in chlorenchyma cells by grinding a known mass of tissue in ice-cold 10% methanolic HCl (0.1% HCl, v/v), determining absorbance at 530 and 653 nm (*UV-Vis1800* spectrophotometer, *Shimadzu*, Kyoto, Japan) and calculating anthocyanin content as $A_{530} - 0.24\ A_{653}$ using an extinction coefficient of 30,000 L mol^{-1} cm^{-1} (Murray and Hackett 1991). Experiments were carried out during the dry season in May and then during October to ensure full recovery of plants after the rain. All experiments were routinely repeated (five replicates) in samples taken from different individual plants (five induviduals) and the standard error was calculated.

Results

The climagram based on long-term climatic records reflected aridity of the study site with a nine-month-long dry season, a very short wet season (June-August), and total annual rainfall of about 150 mm (Fig. 1). Monitoring daily changes in air temperature and PPFD during the dry season indicated that these parameters can attain high midday values of 45°C, and 2,250 μmol(photon) m^{-2} s^{-1}, respectively (Table 1). Measurement of midday irradiance during the dry season in exposed places and in shade under canopy of *Acacia tortilis* indicated that PPFD was 2,250 and 220 μmol m^{-2} s^{-1}, respectively.

Field observations indicated that *D. velutina* did not occur on exposed places and tended to associate with nurse plants (*Acacia tortilis*, *Capparis decidua*, *Commiphora quadricincta*) and with large rocks, commonly found at the study site. Assessment of this association with contingency table analysis using Chi square and standardized residuals revealed lack of significant association of *D. velutina* with any particular nurse (Table 2). However, determination of frequency of occurrence of *D. velutina* in relation to shade availability indicated that this plant strictly occurred at places where sufficient shade occurred (Table 2).

Gas exchange measurements during the wet season indicated an early morning peak with increased P_N and g_s and decreased C_i (Fig. 2*A*–*C*). This early morning peak was followed by a marked decline of P_N and g_s and increased C_i towards midday. During mid-afternoon, P_N and g_s peaked again, while C_i decreased. Towards the end of the light period, g_s markedly increased, while P_N and C_i showed a sharp decline. Night-time measurements showed significantly increased g_s (Fig. 2*B*) and negative P_N values of about 1 μmol m^{-2} s^{-1} (not shown in Fig. 2). Gas exchange measurements during the dry season indicated very low values of P_N and g_s and persistently high values of C_i in the range of 700–800 μmol(CO_2)mol^{-1} (Fig. 2*A*–*C*). Determination of chlorenchyma cell sap titratable acidity indicated low day-time acidity and high night-time acidity with marked diurnal acidity oscillation during the wet season and considerably dampened oscillation during the dry season (Fig. 2*D*).

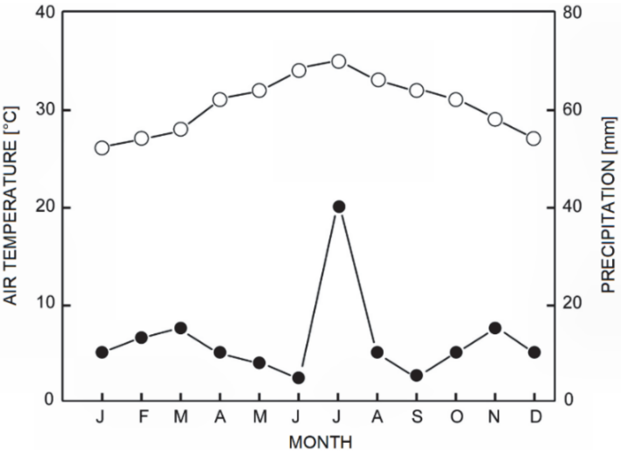

Fig. 1. Climagram of the study site. Air temperature – *open circles*, precipitation – *closed circles*.

Table 1. Daytime changes in air temperature and PPFD at the study site during the dry season.

Parameter	Time of day 06:00	08:00	10:00	12:00	14:00	16:00	18:00
Air temperature [°C]	36	39	41	45	43	41	36
PPFD [μmol m^{-1} s^{-1}]	500	1,500	2,000	2,250	2,225	2,100	200

Table 2. Association of *D. velutina* with phanerophytes, rocks, and shade. Association is significant if χ^2 exceeds 3.84, and positive if SR is greater than 2. (SR – standardized residuals, F – frequency of joint occurrence,* – significant association).

Nurse	Parameter			Association
	χ^2	SR	F [%]	type
Acacia ehrenbergiana	0.01	0.19	46	–
Acacia tortilis	0.30	– 0.04	56	–
Capparis decidua	2.06	0.16	5	–
Commiphora quadricincta	2.06	0.16	5	–
Rocks	3.39	– 0.97	5	–
Exposed microhabitat			0	–
Shaded microhabitat			85^*	+

Table 3. Seasonal changes in efficiency of PSII antenna (F_v/F_m), PSII quantum yield (Φ_{PSII}), nonphotochemical quenching (NPQ), and chlorenchyma anthocyanin content of *D. velutina* (mean ± SE, *n* = 5).

Parameter	Season	
	Wet	Dry
F_v/F_m	0.85± 0.10	0.75± 0.24
Φ_{PSII}	0.85± 0.28	0.75 ± 0.15
NPQ	0.06 ± 0.003	0.45 ± 0.05
Anthocyanin [μg g^{-1}(DM)]	25 ± 4.5	95 ± 8.5

Chl fluorescence measurements during the dry season showed pronounced reduction of the values of F_v/F_m and Φ_{PSII} compared to those measured during the wet season (Table 3). This reduction of F_v/F_m and Φ_{PSII} during the dry season occurred in concomitance with markedly increased values of NPQ and the chlorenchyma anthocyanin content (Table 3).

Discussion

The climagram based on long-term climatic records reflected aridity of the study site (Fig. 1). Climagrams with precipitation line beneath that of temperature and low total annual rainfall are typical of arid zones (Middleton and Thomas 1997, Mainguet and Reimer 1998, Le Houérou 2003). Monitoring daytime changes in air temperature and PPFD during the dry season revealed that these parameters can attain high values that add to the harshness of the environment (Table 1). However, midday PPFD measured in the shade under canopy of *A. tortilis* was reduced to 10% of that measured at exposed places. This pronounced PPFD reduction indicated the suficient amount of shade provided by nurse plants at the study site.

Our field observations indicated that *D. velutina* did not occur at the exposed places but was rather associated with phanerophytes growing at the study site. This biotic nurse association was attributed to establishment of succulent seedlings under canopies of desert phanerophytes, where nutrients are more available (Flores and Jurado 2003, Méndez *et al.* 2004, Armas and Pugnaire 2005, Padilla and Pugnaire 2006, Suzán-Azpiri and Sosa 2006, Ren *et al.* 2008). However, our results indicated that nurse plant canopies created shaded microhabitats with considerably reduced irradiance (Table 2), and contingency table analysis revealed lack of preference of association of *D. velutina* with any particular nurse plant (Table 2). Recent studies indicated that association of desert succulent seedlings with nurse phanerophytes was mainly attributed to shade provided by nurse plants for protection against overheating and photoinhibition during seedling establishment (Martínez-Berdeja and Valverde 2008, Masrahi *et al.* 2011, 2012a; Pérez-Sánchez *et al.* 2013, Valiente-Banuet *et al.* 2013). Desert succulents are also known to exhibit the abiotic nurse association with rocks that can hold moisture for long periods after rain and provide moist microhabitats suitable for seedling establishment (Reyes-Olivas *et al.* 2002, Peters *et al.* 2008, Rojas-Sandoval and Meléndez-Ackerman 2013). However, our data revealed that the association of *D. velutina* with rocks also was not significant (Table 2). Therefore, frequency of occurrence was calculated to assess the general association of *D. velutina* with shade regardless of the nurse providing this shade. Calculated frequency of occurrence was 85% and 0% for shaded microhabitats and exposed places, respectively (Table 2). This noticeable difference in the association indicated that *D. velutina* tended to strictly associate with shade regardless of the nurse providing this shade. This association appears to result in enhanced seedling establishment not only due to nutrients and moisture availability, but mainly for protection against heat and high irradiance. Similar results with desert succulents have previously been reported (Masrahi *et al.* 2011, 2012a).

Gas-exchange measurements in *D. velutina* during the wet season revealed a pattern typical of CAM plants (Fig. 2*A–C*). The early morning peak of CO_2 uptake reflected operation of Phase II of CAM, followed by midday stomatal closure reflecting onset of Phase III of CAM. Stomata then reopened in mid-afternoon with a peak of CO_2 uptake characteristic of Phase IV of CAM. The sharp decline of P_N recorded late in the afternoon was due to decreased irradiance and onset of the dark period (Fig. 2*A*). Negative values of P_N, low values of C_i, and high values of g_s are characteristic of night-time Phase I of CAM. Operation of CAM in *D. velutina* manifested by gas-exchange results was supported by observed diurnal oscillations of chlorenchyma cell sap titratable acidity (Fig. 2*D*). Oscillation of cell sap titratable acidity during both wet and dry seasons denoted that *D. velutina* exhibited obligate CAM. Prolonged drought represents a serious challenge for survival of arido-active-desert stem succulents which exhibit CAM to improve their water economy. Nocturnal CO_2 uptake and daytime stomatal closure characteristic of CAM allow avoidance of gas exchange, when environmental conditions favour transpirational water loss, and enhance plant water economy (Sayed 2001b, Lüttge 2004). However, during the long dry season, *D. velutina* exhibited very low values of gas exchange parameters (Fig. 2*A–C*) and markedly dampened diurnal oscillation of chlorenchyma titratable acidity (Fig. 2*D*). These results indicated that *D. velutina* shifted from CAM to CAM-idling in response to prolonged drought. The CAM-idling mode is a modification of CAM that greatly enhances plant water economy by stomatal closure during day and night and sustaining cell sap acidity oscillations by nocturnal re-fixation of respiratory CO_2 (Sayed 2001b, Lüttge 2010, Borland *et al.* 2011). Similar drought-initiated CAM-idling shift has previously been reported in other desert stem succulents (Masrahi *et al.* 2011, Masrahi *et al.* 2012a,b, Al-Turki *et al.* 2014).

Chl fluorescence measurements in *D. velutina* during the dry seasons indicated reduction of F_v/F_m and Φ_{PSII} (Table 3) reflecting reduced efficiency of PSII antenna and PSII quantum yield, respectively (Adams and Demmig-Adams 2004, Baker 2008). This reduction of PSII activity during the dry season is not surprising in view of the prevailing severe drought and high midday air temperature and PPFD (Table 1). Reduction of PSII activity in CAM plants was attributed to an over-energized PSII during Phase III of CAM operating behind closed stomata under

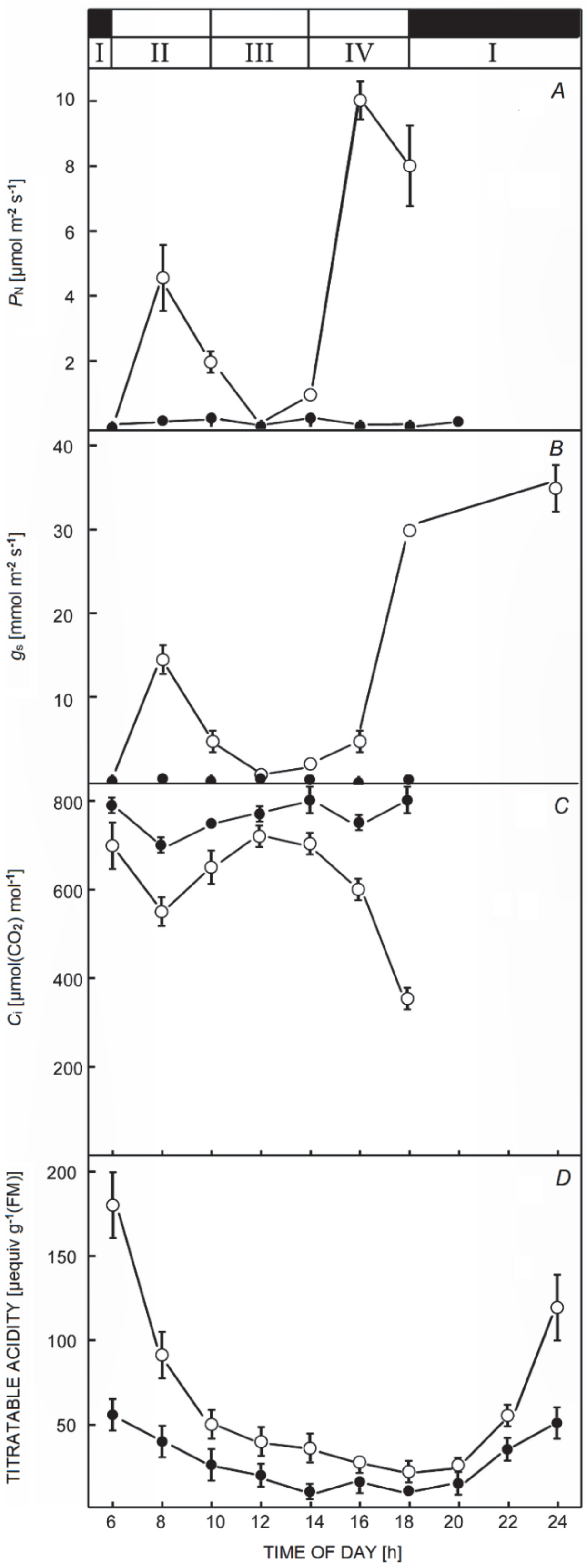

Fig. 2. Diurnal and seasonal changes in gas exchange and cell sap titratable acidity of *D. velutina* photosynthetic rate (*A*), stomatal conductance (*B*), substomatal CO$_2$ concentration (*C*), titratable acidity (*D*), measured during the wet season (*open circles*) and the dry season (*closed circles*). P_N – net photosynthetic rate; g_s – stomatal conductance; C_i – intercellular CO2 concentration. Mean ± SE, *n* = 5.

high temperature and high irradiance (Niewiadomska and Borland 2008, Lüttge 2010). However, our observed reduction in PSII activity occurred in concomitance with increased NPQ (Table 3). Increased NPQ under stress conditions occurs due to operation of nonphotochemical excess energy dissipation (Kalaji *et al*. 2014). Strong correlation exists between xanthophyll cycle pigments and increased nonphotochemical quenching of Chl fluorescence. As photoinhibitory high irradiance diminishes PSII capacity to process absorbed light, increased zeaxanthin and antheraxanthin contents enable to dissipate excess excitation energy as heat (Murchie and Niyogi 2011). Our results also showed a considerable rise in anthocyanin content during the dry season suggesting its involvement in photoprotection (Table 3). Several reports in the literature implicated cell vacuole anthocyanin in conferring photoprotection by absorbing high energy quanta and protecting chloroplasts from photoinhibitory high irradiance (Gould *et al*. 2002, Manetas *et al*. 2002, Close and Beadle 2003, Gould 2004, Adams *et al*. 2006, Liakopoulos *et al*. 2006). Anthocyanin has also been shown to mitigate photooxidative injury by scavenging reactive oxygen species formed during Phase III of CAM (Steyn *et al*. 2002, Neill and Gould 2003, Nagata *et al*. 2003).

It can be concluded that survival strategy of *D. velutina* in its extremely arid habitat involved facilitation of seedling establishment by the strict association with shade of biotic or abiotic nurses. This strategy also included a concerted combination of physiological adaptations involving obligate CAM, physiotypic plasticity allowing CAM-idling shift to improve water economy, and mitigating oxidative stress by photoprotective nonradiative excess energy dissipation and increased anthocyanin content.

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