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Crassulacean Acid Metabolism Permutation and Survival of Caralluma Species (Apocynaceae) in Arid Habitats

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Abstract. Several species of the stem succulent *Caralluma* (Apocynaceae) are abundant perennials in arid regions of the Arabian Peninsula. These arid regions have a short wet season with erratic rainfall and are characterized by harsh climatic conditions of high temperature, high evaporation and sand storms. Work presented in this paper aimed at investigating importance of Crassulacean Acid Metabolism (CAM) for survival of three *Caralluma* species in their natural habitat. Investigations involved studying stomatal characteristics, stomatal diffusive conductance, chlorophyll fluorescence, and CAM in three species of *Caralluma*, namely *C. acutangula* (Decne.) N.E.Br., *C. edulis* (Edgew.) Benth. ex Hook.f., and *C. subulata* (Forssk.) Decne. Microscopic examination revealed a pattern of stomatal characteristics typical of CAM plants in these three *Caralluma* species. Results showed that these three *Caralluma* species were obligate CAM plants exhibiting this mode of photosynthesis during both the wet and the dry seasons. Under protracted water stress during the long dry season very low values of stomatal diffusive conductance and dampening of CAM acidification-deacidification cycles denoted the tendency of these three *Caralluma* species to shift from the obligate CAM physiotype to CAM-idling mode. Chlorophyll fluorescence measurements indicated that protracted water stress induced a reduction in Photosystem II (PSII) antenna efficiency and quantum yield in the three studied *Caralluma* species. This reduction of PSII activity occurred in concomitance with a marked rise in non-photochemical quenching of chlorophyll fluorescence denoting operation of non-photochemical energy dissipating mechanisms known to be important for photoprotection of the photosynthetic apparatus.

Key words: Apocynaceae, Crassulacean Acid Metabolism (CAM), CAM-idling, *Caralluma*, chlorophyll fluorescence, diffusive conductance, stomata

Introduction

Plant survival in desert ecosystems is profoundly limited by water availability. Arid regions of the Arabian Peninsula are characterized by high temperature, high evaporation, scarce water, and erratic rainfall. In such arid habitats, leaf succulents reduce their transpirational surface area by seasonal partial leaf shedding (SAYED, 1996; SAYED, 1998; SAYED, 2001a; BOBICH & NORTH, 2009), whereas leafless stem succulents rely on ample water storage capacity, morphoanatomical features, and physiological adaptations (NOBEL, 1988; SAYED, 2001a; MASRAHI *et al*., 2012). Many desert succulents exhibit the CAM pathway of photosynthesis with its unique nocturnal carbon acquisition pattern and beneficial ecophysiological consequences including improved plant water economy (BORNALD *et al*., 2000; SAYED, 2001b; DODD *et al*., 2002; LÜTTGE, 2002). A large body of information exists in the literature on the importance of CAM in stem succulents of the Agavaceae and Cactaceae (NOBEL, 1988; LÜTTGE, 2004; LÜTTGE, 2008). However, very few studies

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have dealt with these aspects as survival mechanisms that enable members of the Apocynaceae to survive months of protracted water stress in their natural arid habitats (LANGE *et al*., 1975; WINTER *et al.* 1976; LANGE & ZUBER, 1977). Moreover, many species of the stem succulent *Caralluma* (Apocynaceae) inhabit arid regions of the Arabian Peninsula, of which *C. acutangula*, *C. edulis*, and *C. subulata* are abundant (COLLENETTE, 1999). The present paper aimed at describing the existence and possible permutation of CAM in these three *Caralluma* species by studying stomatal characteristics, stomatal diffusive conductance, and chlorenchyma diurnal acidity changes.

Furthermore, plants with the CAM pathway exhibit different CAM physiotypes including obligate CAM, facultative CAM, CAM-cycling, and CAM-idling (LÜTTGE, 2004; HERRERA, 2009). Of these modes, CAM-idling has early been recognized (OSMOND, 1978; TING, 1985; TING & SIPES, 1985), and is considered to be a very strong permutation of CAM (CUSHMAN, 2001; SAYED, 2001b; CUSHMAN & BORLAND, 2002; DODD *et al*., 2002; OSMOND *et al*., 2008). The CAM-idling mode is characterized by stomatal closure during the entire day and night, no net CO_2 uptake, and acidification fed by internal recycling of nocturnally re-fixed respiratory CO_2 (LÜTTGE, 2004; HERRERA, 2009). During Phase III of CAM that takes place behind closed stomata under high irradiance and high temperature, PSII can become over-energized (NIEWIADOMSKA & BORLAND, 2008), and CAM-idling is thought to invoke reduction of oxidative stress caused by this over-energization (LÜTTGE, 2002). It is thought that under such conditions, CAM-idling plays a photoprotective role by non-radiative excess energy dissipation via the xanthophyll cycle (TALLMAN *et al*., 1997; TALLMAN, 2004; HERRERA, 2009). Earlier studies suggested that operation of CAM coupled to the xanthophyll cycle was at the heart of a photoprotective mechanism operating under severe drought (TALLMAN *et al*., 1997; TALLMAN, 2004). In this context, chlorophyll fluorescence is a subtle reflection of primary reactions of photosynthesis and a useful non-invasive tool that helps reveal stress-induced changes in photosynthetic biophysical processes (BOLHAR-NORDENKAMPF & ÖQUIST, 1993; SAYED, 2003). Therefore, our work also involved using pulse amplitude modulated chlorophyll fluorescence technique to investigate the involvement of CAM-idling in alleviating water stress-induced effects on the photosynthetic machinery.

Materials and methods

Study Site. The study site - southwest of Saudi Arabia (17°19'N; 42°48'E) is characterized by sand-loam soil, high temperature, high irradiance, scarce water, erratic rainfall, and a climate influenced by a tropical maritime air mass (BROWN & JACKSON, 1979; MULLER, 1984; FISHER & MEMBERY, 1998). The wet season is a short three month period (June–August) associated with spells of strong sand storms that add to the harshness of the environment, and the long dry season extends over a period of nine months (MIDDLETON, 1986).

Climatic Conditions. Records of the past 40 years (1970-2010) of mean monthly maximum air temperature, precipitation, and evaporation were obtained cortsey the Ministry of Electricity and Water (Riyadh, Saudi Arabia). Soil temperature was monitored at depth of 10cm using a field digital thermometer (Kestrel 2000, Boothwyn, Philadelphia, USA).

Plant Material. The plant material used in this field study included mature plants of the stem succulents *C. acutangula* (Decne.) N.E.Br., *C. edulis* (Edgew.) Benth. ex Hook.f., and *C. subulata* (Forssk.) Decne.

Measurements. Stomatal density and the percentage of stem area occupied by stomata were determined in stem epidermal strips using an ocular micrometer at 400x mounted on research microscope (Accu-scope 3025 Ergo Tilting Microscope, Nikon, Kingston-Upon-Thames, Surrey, UK). Stomata and stomatal pore were treated as ellipse shape, and hence stomatal area and stomatal pore area were determined using the following equations:

Stomatal Size = π . Ls . Ws

where: Ls, and Ws are stomatal length, and maximum stomatal width, respectively.

Stomatal Pore Size = π . Lp . Wp

where: Lp, and Wp are stomatal pore length, and maximum stomatal pore width, respectively.

Stomatal diffusive conductance and pulse amplitude modulated chlorophyll fluorescence were measured in intact stem using a porometer (AP4, Delta-T Devices, Cambridge, UK), and a chlorophyll fluorescence monitoring system (FMS2, Hansatech Instruments, Norfolk, UK), respectively. Measured chlorophyll fluorescence parameters included Fv/Fm, and Φ PSII, reflecting the efficiency of PSII antenna and the quantum yield of PSII, respectively (BOLHAR-NORDENKAMPF & ÖQUIST, 1993; SAYED, 2003). The value qNP reflecting non-photosynthetic quenching of chlorophyll fluorescence was calculated using standard fluorescence nomenclature (BUSCHMANN, 1999; SAYED, 2003) and the equation:

qNP = (Fm-Fm') / (Fm-Fo)

where:

Fo minimal fluorescence level emitted by antenna chlorophyll molecules,

Fm maximal fluorescence level emitted when all PSII traps become closed,

Fm' light-adapted fluorescence maximum.

Chlorenchyma was separated along parts of the stem length and cell sap was extracted by grinding a known weight of tissue. Cell sap was then expressed through two layers of muslin and diurnal changes in cell sap titratable acidity were determined (OSMOND *et al.*, 1991).

Statistical analyses. All experiments were routinely repeated in samples taken from ten different individuals and the standard deviation was calculated using SPSS v.11.5 software.

Results

Climatic records of the study site indicated that the dry season is a long nine months period and the wet season is a short three months period (Fig. 1).

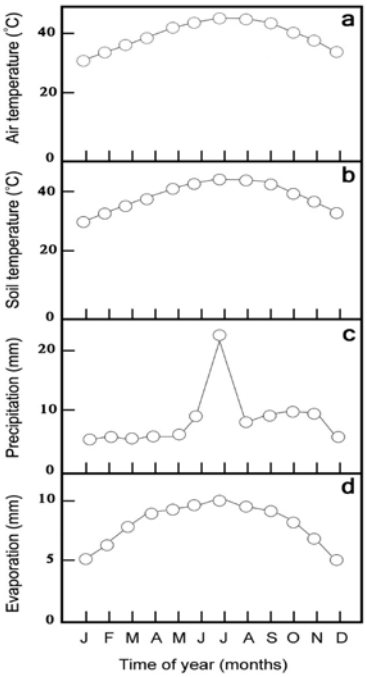

Fig. 1. Climatic records (1970-2010) of the study site.

During the wet season air temperature, soil temperature, and evaporation markedly increase (Fig. 1a, b, d). Climatic records also showed that the total annual rainfall at the study site was in the order of 100 mm occurring mainly during the period June–August (Fig. 1c). Microscopic examination of stomatal characteristics of *C. acutangula*, *C. edulis*, and *C. subulata* were performed on stem epidermal strips and stomatal density, stomatal size, stomatal pore size, and the area of stem occupied by stomata are given in Table 1.

Measurements of stomatal diffusive conductance during the wet season indicated that *C. acutangula*, *C. edulis*, and *C. subulata* exhibited high night-time values in the range of 40-50 mmol m^{-2} s^{-1}), and low day-time values in the range of 5-10 mmol m^{-2} s^{-1} (Fig. 2). On the other hand, measurements during the dry season indicated that *C. acutangula*, *C. edulis*, and *C. subulata* exhibited very low values of stomatal diffusive conductance in the range of 3-5 mmol m^{-2} s^{-1} during both night and day (Fig. 2).

Table 1. Stomatal characteristics of the three studied *Caralluma* species (mean ± standard deviation, n = 10).

Species	Stomatal Density (stomata mm^{-2})	Stomatal Size (µm^2)	Stomatal Pore Size (µm)	Area of Stem Occupied by Stomata (%)
C. acutangula	26 ± 3	829 ± 5	6.0 ± 2	1.4 ± 0.3
C. edulis	25 ± 5	818 ± 2	7.2 ± 1	1.6 ± 0.2
C. subulata	30 ± 8	887 ± 4	6.9 ± 1	1.9 ± 0.4

Table 2. Chlorophyll fluorescence parameters in the three studied *Caralluma* species measured during the wet and the dry seasons (mean ± standard deviation, n = 10).

Species	Chlorophyll Fluorescence Parameters					
	Fv/Fm		ΦPSII		qNP	
	Wet	Dry	Wet	Dry	Wet	Dry
C. acutangula	0.84 ± 0.1	0.78 ± 0.2	0.83 ± 0.1	0.69 ± 0.3	0.02 ± 0.005	0.06 ± 0.008
C. edulis	0.83 ± 0.3	0.74 ± 0.1	0.83 ± 0.4	0.75 ± 0.4	0.01 ± 0.003	0.05 ± 0.005
C. subulata	0.78 ± 0.5	0.67 ± 0.4	0.82 ± 0.5	0.69 ± 0.1	0.01 ± 0.001	0.04 ± 0.003

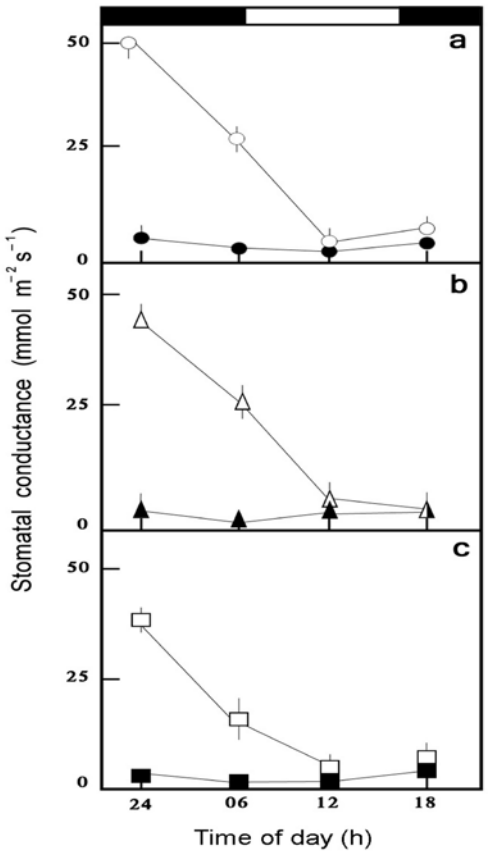

Fig. 2. Diurnal changes (white colour - wet season; black colour - dry season) in stomatal conductance of *C. acutangula* (a), *C. edulis* (b), and *C. subulata* (c). (mean ± standard deviation, n = 10).

Determinations of chlorenchyma cell sap titratable acidity during the wet season indicated that *C. acutangula*, *C. edulis*, and *C. subulata* exhibited diurnal acidity changes (Fig. 3). These changes in chlorenchyma cell sap titratable acidity were markedly dampened during the dry season (Fig. 3). Comparison of chlorophyll fluorescence parameters measured during the wet and the dry seasons indicated that water stress-induced effects in the three studied *Caralluma* species included 10-15% reduction in the value of the parameters Fv/Fm, and ΦPSII occurring in concomitance with a marked increase in the value of the parameter qNP (Table 2).

Discussion

Harsh environmental conditions represent a formidable challenge for plant survival in desert arid habitats. Climatic records reflected the extreme aridity prevailing at the study site manifested by a nine-month-long dry season and a short wet season characterized by scarce water availability, and increased temperature and evaporation (Fig. 1). In such arid habitats, arido-active stem succulents survive periods of protracted drought due to morpho-anatomical and physiological adaptations

that enable them to tolerate harsh environmental conditions (NOBEL, 1988; SAYED, 2001a; SAYED, 2001b; MASRAHI *et al*. 2011; MASRAHI *et al*. 2012). Microscopic studies indicated that *C. acutangula*, *C. edulis*, and *C. subulata* exhibit low values of stomatal density, stomatal size, stomatal pore size, and area of stem occupied by stomata (Table 1). These stomatal features have repeatedly been recognized as characteristic of plants exhibiting the CAM pathway (TING, 1987; HERRERA & CUBEROS, 1990, WILLMER & FRICKER, 1996; CROXDALE, 2000).

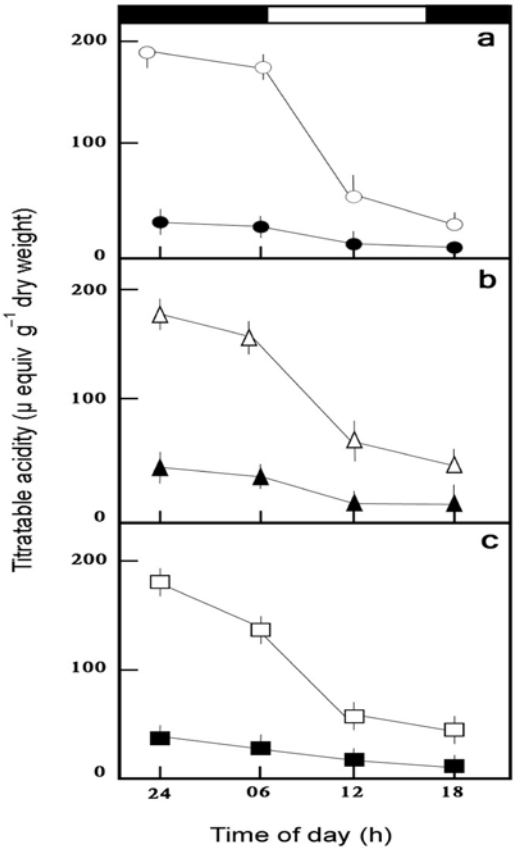

Fig. 3. Diurnal changes (white colour - wet season; black colour - dry season) in chlorenchyma cell sap titratable acidity of *C. acutangula* (a), *C. edulis* (b), and *C. subulata* (c). (mean ± standard deviation, n = 10).

During the wet season, *C. acutangula*, *C. edulis*, and *C. subulata* exhibited values of stomatal diffusive conductance that were high during the night and low during the day (Fig. 2) revealing stomatal behavior typical of plants with the CAM pathway (NOBEL, 1988; SAYED, 2001b; LÜTTGE, 2004; HERRERA, 2009). Determination of stem chlorenchyma cell sap titratable acidity during both the wet and the dry seasons indicated the occurrence of diurnal acidification-deacidification cycles denoting the operation of obligate CAM in the three investigated *Caralluma* species. Obligate CAM has previously been shown in some *Caralluma* species (LANGE *et al*., 1975; WINTER *et al.* 1976, LANGE & ZUBER, 1977; MASRAHI *et al*., 2011; MASRAHI *et al*., 2012). Nocturnal CO_2 uptake and daytime stomatal closure associated with CAM imply avoidance of gas exchange when environmental conditions favor transpirational water loss and enhanced plant water economy (WINTER & SMITH, 1996; BORLAND *et al*., 2000; SAYED, 2001b; LÜTTGE, 2002; LÜTTGE, 2004; SCHULZE *et al*., 2005; LÜTTGE, 2008; HERRERA, 2009). However, during the dry season, the three investigated *Caralluma* species exhibited very low values of stomatal diffusive conductance during the entire day and night (Fig. 2) and markedly dampened diurnal oscillation of chlorenchyma cell sap titratable acidity (Fig. 3). These results indicated that the three investigated *Caralluma* species shifted from the obligate CAM physiotype to CAM-idling in response to protracted water stress. The CAM-idling mode is a strong permutation of CAM that greatly enhances plant water economy by stomatal closure during the entire day and night and sustaining diurnal fluctuations in cell sap titratable acidity by nocturnally re-fixed respiratory CO_2 (SAYED, 2001b; DODD *et al*., 2002; LÜTTGE, 2002; NOBEL & DE LA BARRERA, 2002; LÜTTGE, 2004; LÜTTGE, 2007; HERRERA, 2009).

Comparison of chlorophyll fluorescence parameters measured during the wet and the dry seasons in the three studied *Caralluma* species indicated that drought resulted in reduction of Fv/Fm and ΦPSII (Table 2) denoting reduction of the efficiency of PSII antenna, and PSII quantum yield, respectively (BUSCHMANN, 1999; SAYED, 2003). Similar reduction of PSII activity manifested by reduction of Fv/Fm and ΦPSII has been shown for the CAM plant *Clusia minor* under protracted drought

(MATTOS *et al*., 1999). Reduction of PSII activity under such conditions was attributed to over-energization of PSII during Phase III of CAM that takes place behind closed stomata and under high irradiance and high temperature (MATTOS *et al*., 1999; NIEWIADOMSKA & BORLAND, 2008). However, our observed reduction in PSII activity occurred in concomitance with a markedly increased qNP (Table 2) denoting increased non-photochemical quenching of chlorophyll fluorescence and hence increased non-photochemical excess energy dissipation (BUSCHMANN, 1999; SAYED, 2003). Similar observation of increased qNP was reported in *Clusia minor* performing CAM-idling (LÜTTGE, 2007). Increased non-photochemical energy dissipation under protracted drought was attributed to a relationship between zeaxanthin, a precursor of abscisic acid, and CAM-idling. Inhibition of zeaxanthin accumulation in guard cells of CAM-performing *Mesembryanthemum crystallinum* was suggested to prevent stomatal opening in response to light (TALLMAN *et al*., 1997). Daytime decarboxylation and high rate of respiration due to high temperature implies high intercellular CO_2 concentration that ensures daytime stomatal closure by favouring Calvin cycle activity in guard cell chloroplasts, consumption of NADPH, and prevention of destruction of endogenous guard cell abscisic acid (TALLMAN, 2004). It was also suggested that CAM-idling plays a role in photoprotection by non-radiative excess energy dissipation via the xanthophyll cycle (ROBINSON & OSMOND, 1994; TALLMAN *et al*., 1997; TALLMAN, 2004; HERRERA, 2009). The CAM-idling mode is thought to result in reduction of oxidative stress by processing reactive oxygen species that appear when PSII becomes over-energized during Phase III and hence confer photoprotection under protracted drought (LÜTTGE, 2007; NIEWIADOMSKA & BORLAND, 2008). Similar views on photoprotection associated with CAM were shown upon comparing performance of *Mesembryanthemum crystallinum* plants in the C_3-mode of photosynthesis with those performing CAM. The CAM-performing *M. crystallinum* plants exposed to oxidative conditions of high ozone concentrations showed no signs of oxidative damage in contrast to plants in the C_3-mode which showed necrosis and reduction in Fv/Fm (HURST *et al*., 2004). Moreover, when the CAM-less *M. crystallinum* mutant and the wild type were subjected to salinity, the activities of several isoforms of the enzyme CuZn-superoxide dismutase, used as markers for the production of reactive oxygen species, increased in both genotypes. However, this increase was larger in the mutant indicating a smaller oxidative load in the wild type (BORLAND *et al*., 2006). More recent studies indicated that photoprotection in CAM plants under protracted drought can be attributed to up-regulation of the antioxidative response enzyme CuZn-superoxide dismutase (SILVERA *et al*., 2010).

Conclusions

It can be concluded that the three studied stem succulents *C. acutangula*, *C. edulis*, and *C. sublata* exhibited stomatal characteristics typical of CAM plants. Occurrence of CAM during both the wet and the dry seasons indicated that the three studied *Caralluma* species are obligate CAM plants. The observed low stomatal diffusive conductance during the entire day and night combined with dampened acidification-deacidification cycles indicated that these three species shift from the obligate CAM physiotype to CAM-idling in response to protracted drought during the long dry season. Moreover, under protracted drought, PSII activity in these three *Caralluma* species was slightly reduced due at least in part to oxidative stress during CAM-idling. However, this oxidative stress appears to be somewhat alleviated by operation of photoprotective non-radiative excess energy dissipation as reflected by increased non-photochemical quenching of chlorophyll fluorescence.

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