Plant Water Relations, Stomatal Behavior, Photosynthetic Pigments and Anatomical Characteristics of *Solenostemma arghel* (Del.) Hayne under Hyper-arid Environmental Conditions

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Abstract: Plant water relations, transpiration, stomatal conductance, Chlorophyll *a-b* contents and anatomical characteristics of *Solenostemma arghel* (Del.) Hayne were studied under hyper-arid environmental stresses in homogenous 18-months-old potted plants in controlled environmental conditions. Mean predawn leaf water potential was higher than mean midday values and larger negative leaf water potentials was observed at midday water potentials were recorded at highest temperature level (40°C) and lowest soil moisture content (2% by weight). In general, diurnal range between predawn and associated midday water potential tends to increase in response to gradual soil moisture depletion. Maximum transpiration rate (7.57 μgm m^{-2} s^{-1}) and stomatal conductance (0.13 μmol s^{-1} m^{-2}) were achieved in *Solenostemma* plants at soil moisture content below field capacity (8%) and under high levels of temperature (40°C) and PPFD (2000 μmol s^{-1} m^{-2}). Chlorophyll *a* content exhibited more stability than Chlorophyll *b* in response to both higher temperature levels and gradual soil moisture depletion. Minimum Chl *a/b* ratio was observed at lowest soil moisture content (2%) and highest temperature level. Leaf anatomical characteristics exhibited multi-layered palisade mesophyll, mesophyll thickness was 326±28 μm and cuticle thickness was 2-5 μm. Highest trichome and stomatal frequencies were observed on abaxial leaf surface. In general, xylem vessels diameter was varied from 16-20 μm in leaf, 18-22 μm in green stem and 30-68 μm in fine roots. Revealing the physiological mechanisms, anatomical adaptations and ability to withstand hyper-arid environmental stresses is of great importance in reserving and restoring of *Solenostemma* and similar species.

Key words: Soil moisture · water potential · photosynthetic photon flux · transpiration · stomatal conductance · chlorophyll content · anatomical characteristics

INTRODUCTION

In South eastern desert a combination of drought, high temperature and irradiation imposing a complex of stress on seed germination, seedling establishment and plant survival. *Solenostemma arghel* (Del.) Hayne (Asclepediaceae) its distribution extended from central Africa to south of the Mediterranean, common in the south of Eastern Desert and Sinai, favoring rocky ground at the edge of wadi bed and grows in sandy soil withstanding long drought and high air temperature [1]. The presence of *Solenostemma* in such hyper-arid environmental conditions would involve physiological and anatomical adaptations that allow this species to survive and thrive under aridity condition stresses.

In previous studies, the effect of salinity on stomatal conductance and leaf water potential revealed that *Solenostemma* plant would increase their stomatal conductance and maintaining high negative leaf water potential at high levels of PPFD and salinity stress [2]. In another study on water use efficiency of *Solenostemma* under salinity stress we also found that, salinity stress had minor effect on transpiration rate and increasing its water use efficiency and placing this plant in group of saline tolerant plants [3]. In arid conditions, investigating the adaptation mechanisms of indigenous species is of great importance to understand their ecological success, growth condition and their suitability in restoration efforts [4, 5]. The qualification of plant and soil water status using plant water potential measurements is greatly accepted [6] and it considered as scale for characterization

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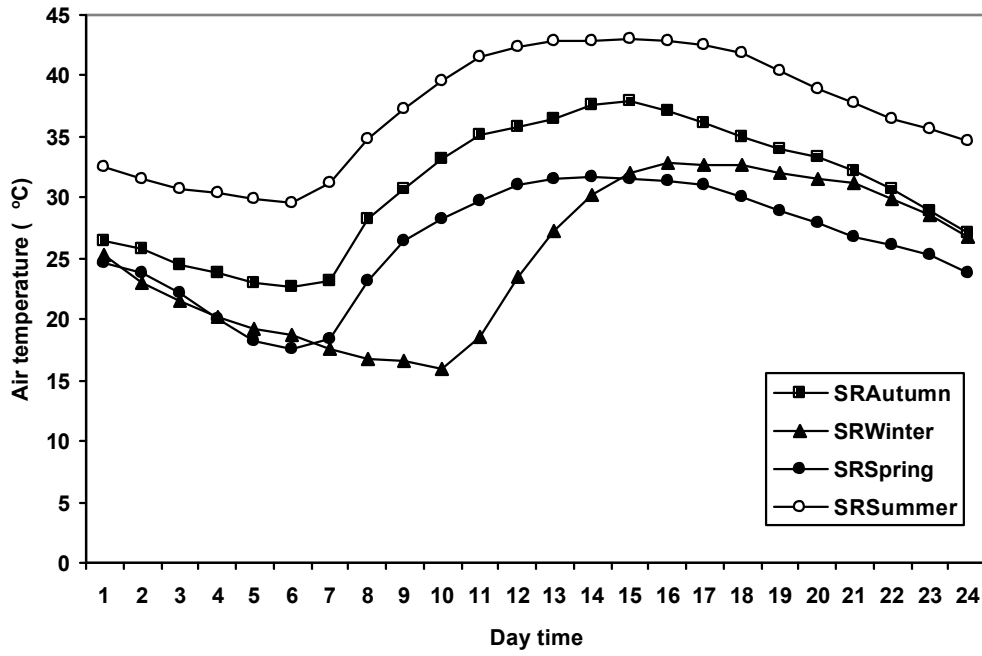
Fig. 1: Seasonal diurnal air temperature (°C) averages in Wadi Allaqi, South-Eastern Desert, Egypt (2001-2006)
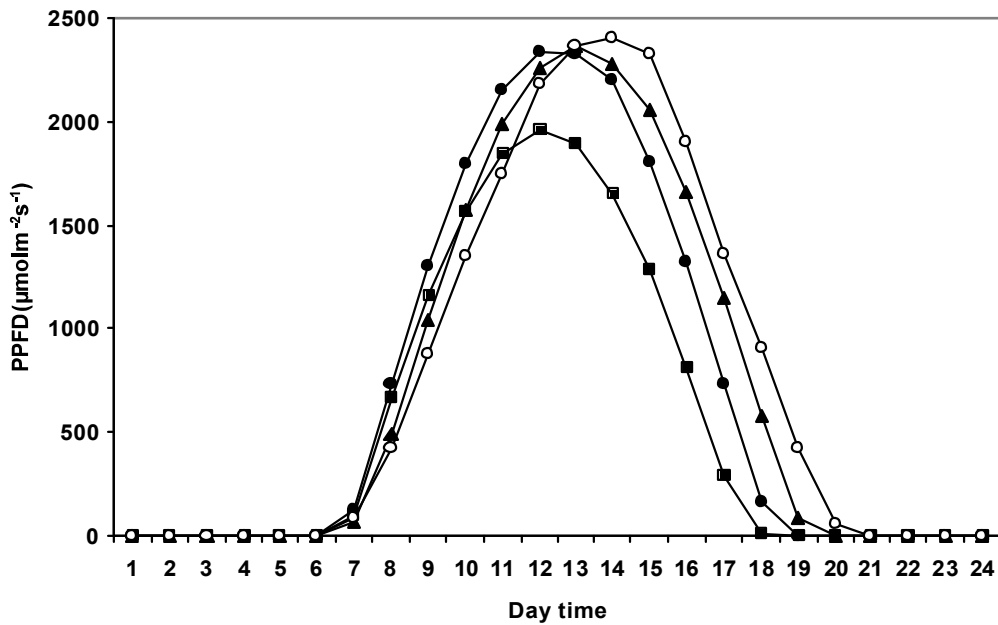

Fig. 2: Seasonal diurnal photosynthetic photon flux density (μmol s^{-1} m^{-2}) averages in Wadi Allaqi, South-Eastern desert, Egypt (2001-2006)

of species and their habitats [5]. Some desert plant species native to Egyptian Mediterranean area exhibited different growth and productivity which attributed mainly to qualitative and quantitative changes in photosynthetic pigments [7, 8]. Xylem vessels density and size could be considered as good criteria for drought conditions [9, 11]. Anatomical adaptations to xeric environments which considered as xeromorphic characteristics, may occur in leaves, stem and roots [12].

In Egypt, as in the majority of arid lands, the survival of desert plants depends on their capacity to maintain a favorable balance between water uptake and water loss under conditions of severe climatic and atmospheric drought [13]. *Solenostemma* are valued highly for its traditional medicine [14-17] and many author focused on *Solenostemma* chemical constituents [18-27]. Seasonal diurnal averages of air temperature (Fig. 1) and photosynthetic photon flux density (Fig. 2) were measured in Wadi Allaqi, Southeastern Egyptian Desert. (2001-2006) courtesy of Unit of Environmental Studies and Development, South Valley University, Aswan, Egypt, using Meteorological Station with integrated Data Acquisition Unit (Model 457 Met One Instrument, Inc., Oregon, USA). Both maximum average of diurnal air temperature (43°C) and photosynthetic photon flux density (2400 μmol s^{-1} m^{-2}) were recorded in summer and around midday (1200-1600 h).

The aim of the present investigation was to evaluate the variations in responses of *Solenostemma* plant water relations, stomatal behavior in term of transpiration rate, stomatal conductance and photosynthetic pigment contents to hyper-arid environmental prevailing conditions, which could reveal some drought avoidance mechanisms of *Solenostemma*. In addition examining of *Solenostemma* anatomical characteristics and adaptations roles in such stresses tolerance.

MATERIALS AND METHODS

Seeds of *Solenostemma* were collected from Wadi Allaqi, Southeastern Egyptian desert in May 2005. Seeds were sown directly into pots of 30 cm in diameter and 20 cm deep with four 1.5 mm-holes at the bottom. Soil used in the experiment was clay: sand (1:2). Soil characteristics and water release curve was obtained using the filter paper method [28, 29].

Two to three seeds were planted in each pot, after seedling establishment, seedlings were thinned to one plant in each pot.

Pots were watered with tap water with no addition of nutrient; watering regime was maintained at 9% by soil weight. Plants were kept in controlled environmental conditions at constant temperature 30±°C, photosynthetic photon flux density (400-700 μmol s^{-1} m^{-2}) photoperiod of 12:12 L: D cycle and relative humidity (20±5%).

Homogenous 18-months-old plants were used in this experiment. The experimental design was completely randomized with two fixed factors: gradual soil moisture depletion (short-term), soil moisture was adjusted to field capacity (9%) and then allowed to gradual dryness to reach 2% (2% below wilting point based on soil water release curve). Soil moisture monitored gravimetrically. 3 sets of 6 plants each were selected to impose temperature differences factor at three levels (20, 30 and 40°C).

Leaf water potential measurements of *Solenostemma* were taken twice a day, at midday (1200-1430 h) and then followed by predawn (0300-0530 h). Measurements were taken at 9, 8, 7, 6, 5, 4, 3 and 2% of soil moisture contents and at 20, 30 and 40°C.

Using pressure Chamber (Soil Moisture Equipment Crop., Model 3005) [30]. Fully developed leaves were carefully cut off with scissors and measurements of leaf water potential were carried out in one randomly selected plant from six randomly selected replicates [31].

Measurements of transpiration rate and stomatal conductance of *Solenostemma* fully developed and expanded leaf (six measurements replicates were recorded at each treatment level) were taken at different temperature (20°C, 30°C and 40°C), soil moisture contents (9, 8, 7, 6, 5, 4, 3 and 2%) and PPFD ranged from 0 to 2000 μ mol s^{-1} m^{-2}, using Steady State Porometer (LI-COR 1600, LI-COR, NE, USA). Porometry is well-established method to estimate transpiration and stomatal conductance [32, 33]. Light source was (6V-30W) tungsten lamp light intensity was varied by power supply (Model Olympus, TGHM, Japan).

Chlorophyll a and b was extracted in 8% chilled acetone from 1gm of homogenized fresh leaves at each treatments level (soil moisture content and temperature). The transparent supernatant was thin filtered and completed to 10 ml with 80% acetone. Chlorophyll a and b were determined spectrophotometrically (Spectronic 601, Milton Roy) at wavelength 663 and 645 nm, respectively [34].

Three individuals of *Solenostemma* were selected randomly and examined for determining the overall anatomical structural plane and quantitative measurements. Leaf, green stem and fine root fresh sample

were collected and preserved in 70% aqueous ethanol and were sectioned on a rotary microtome. Sections were stained with 0.05% toluidine blue (pH 4.4) for two minutes, rinsed with water, dyed and mounted [35]. Photographs of section were taken using Leitz Deplane photomicroscope and direct measurements of T.S using stage micrometer.

Fresh strips of both abaxial and adaxial leaf surfaces and stained with 50% water soluble safranine and light microscopy examined stomatal and trichomes characteristics.

Differences of leaf water potential in response to gradual soil moisture depletion and temperature differences were examined using a two-way analysis of variance; water potential values of midday and predawn at each temperature level were subjected to paired t-test [36].

Significance of changes in transpiration rate and stomatal conductance in response to differences in soil moisture content, temperature and PPFD, as well as interaction among factors were estimated from Three-Way analysis of variance.

Differences in Chl *a*, Chl *b* and Chl *a/b* ratio in response to different levels of soil moisture contents and temperature were examined using Two-Way analysis of variance and parson correlation coefficient was used to examine the correlation between the two factors and Chlorophyll *a* and *b* contents.

For anatomical characteristics measurements, numerical values are means ± standard error.

All the above mentioned statistical data analysis were carried out using Minitab Statistical program [37].

RESULTS

The predawn, midday and diurnal range of leaf water potential is shown in Table 1. From Two-way analysis of variance, significant changes in predawn, midday and diurnal range of leaf water potential (MPa) of *S. arghel* were attributed to both temperature differences and gradual soil moisture depletion.

In general, mean predawn leaf water potential was higher than mean midday values and larger negative leaf water potentials were attained at midday. At high level of soil moisture content (9%) highest predawn water potentials (-065, -07 and -0.01 MPa) were reached at 20, 30 and 40°C, respectively. On other hand both larger negative predawn and midday water potentials (-2.25 and 2.91MPa, respectively), were recorded at lowest level of soil moisture content (2%) in *Solenostemma* plants kept at 40°C.

Table 1: Leaf water potential (Mean ± SE) of *Solenostemma arghel* at different temperatures and under gradual soil moisture depletion

Temperature (C°)	Soil moisture content (% by wt.)	Water potentials (Mpa)		
		Predawn	Midday	Diurnal range
20	9	-0.65±0.03	-0.75±0.01	0.10±0.03
	8	-0.70±0.08	-0.81±0.01	0.11±0.02
	7	-0.76±0.02	-0.87±0.01	0.11±0.01
	6	-0.80±0.02	-0.91±0.03	0.11±0.02
	5	-0.90±0.01	-1.05±0.01	0.15±0.01
	4	-0.95±0.02	-1.19±0.03	0.15±0.04
	3	-1.25±0.02	-1.44±0.02	0.18±0.02
	2	-1.30±0.02	-1.66±0.02	0.36±0.03
30	9	-0.70±0.01	-0.81±0.03	0.11±0.05
	8	-0.75±0.03	-0.89±0.01	0.14±0.04
	7	-0.81±0.01	-0.95±0.02	0.14±0.01
	6	-0.90±0.02	-1.13±0.03	0.23±0.04
	5	-1.00±0.08	-1.25±0.01	0.25±0.09
	4	-1.02±0.05	-1.35±0.01	0.33±0.05
	3	-1.15±0.01	-1.56±0.01	0.40±0.02
	2	-1.24±0.02	-1.69±0.02	0.46±0.02
40	9	-1.01±0.07	-1.13±0.06	0.12±0.09
	8	-1.07±0.09	-1.24±0.08	0.17±0.05
	7	-1.03±0.02	-1.50±0.02	0.20±0.02
	6	-1.50±0.01	-1.75±0.01	0.25±0.01
	5	-1.55±0.01	-1.85±0.02	0.30±0.03
	4	-1.95±0.01	-2.45±0.03	0.50±0.04
	3	-2.14±0.03	-2.78±0.01	0.63±0.04
	2	-2.25±0.01	-2.91±0.01	0.66±0.01

The paired t-test and confidence interval of mean differences for predawn and midday water potential showed significance differences were T= 10.42; P<0.0001, T= 10.8; P<0.0001 and T= 9.68; P<0.0001 at 20, 30 and 40°C respectively. While, diurnal range between predawn and associated midday water potentials tend to increase in response to gradual soil moisture depletion varied from 0.1 to 0.36 MPa at 20°C, 0.11 to 0.46 MPa at 30°C and from 0.12 to 0.66 MPa at 40°C.

Transpiration and stomatal conductance of *Solenostemma* (Fig. 3a-c and Fig. 4a-c) in response to gradual soil moisture depletion, temperature differences and increments of photosynthetic photon flux density (PPFD).

From three-way analysis of variance, transpiration rate changed significantly due to gradual soil depletion (F= 39.7 and P<0.0001), PPFD (F= 280.96 and P<0.0001) and temperature (F= 139.08 and P<0.0001). Also, significant changes in transpiration could be attributed to the combination of the above mentioned three factors (F= 56.57 and P<0.0001).
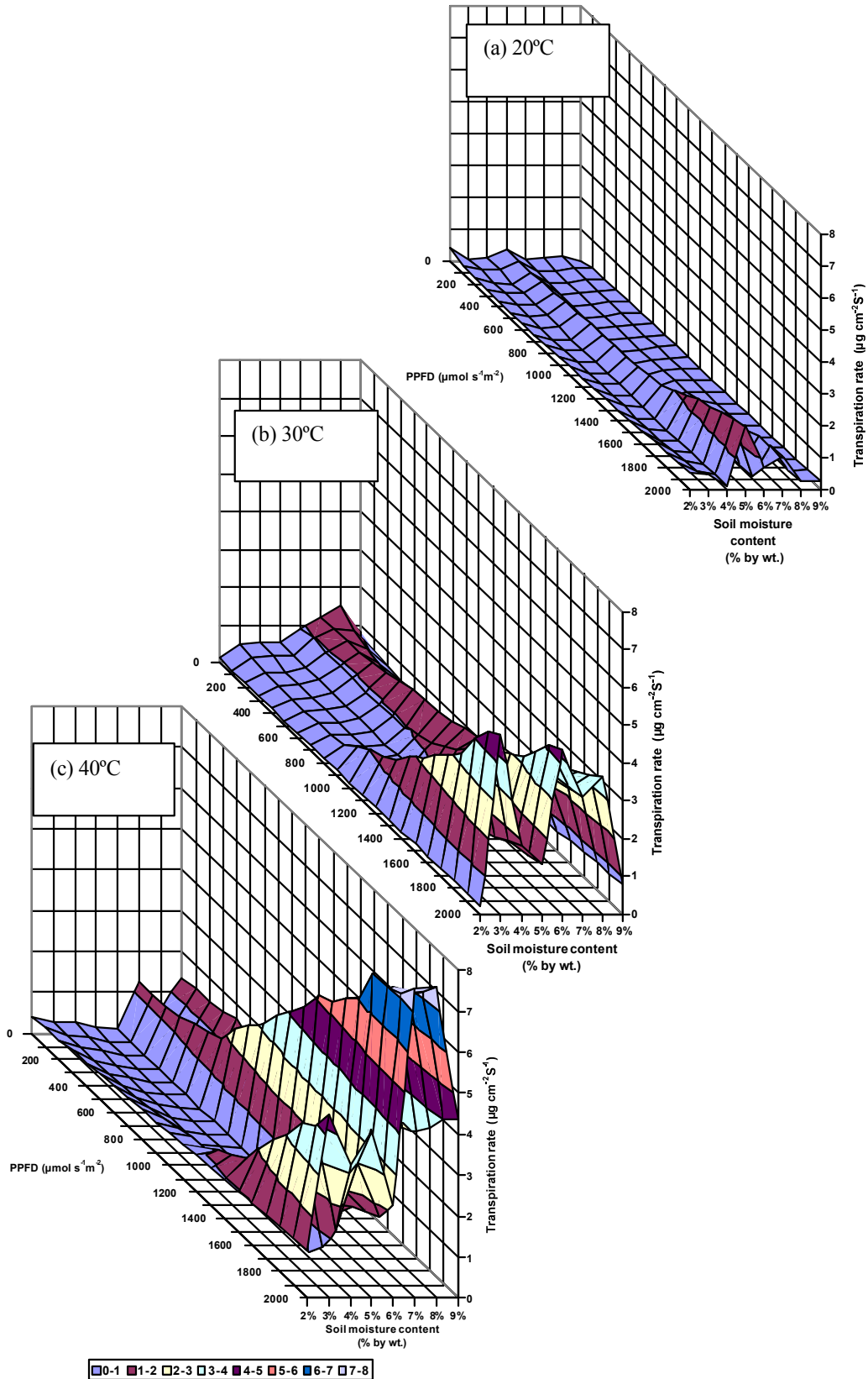
Fig. 3: Transpiration rate (µgcm⁻²s⁻¹) of *Solenostemma* at different temperatures (a) 20ºC; (b) 30ºC; (c) 40ºC, photosynthetic photon flux densities (PPFD) and gradual soil moisture depletion
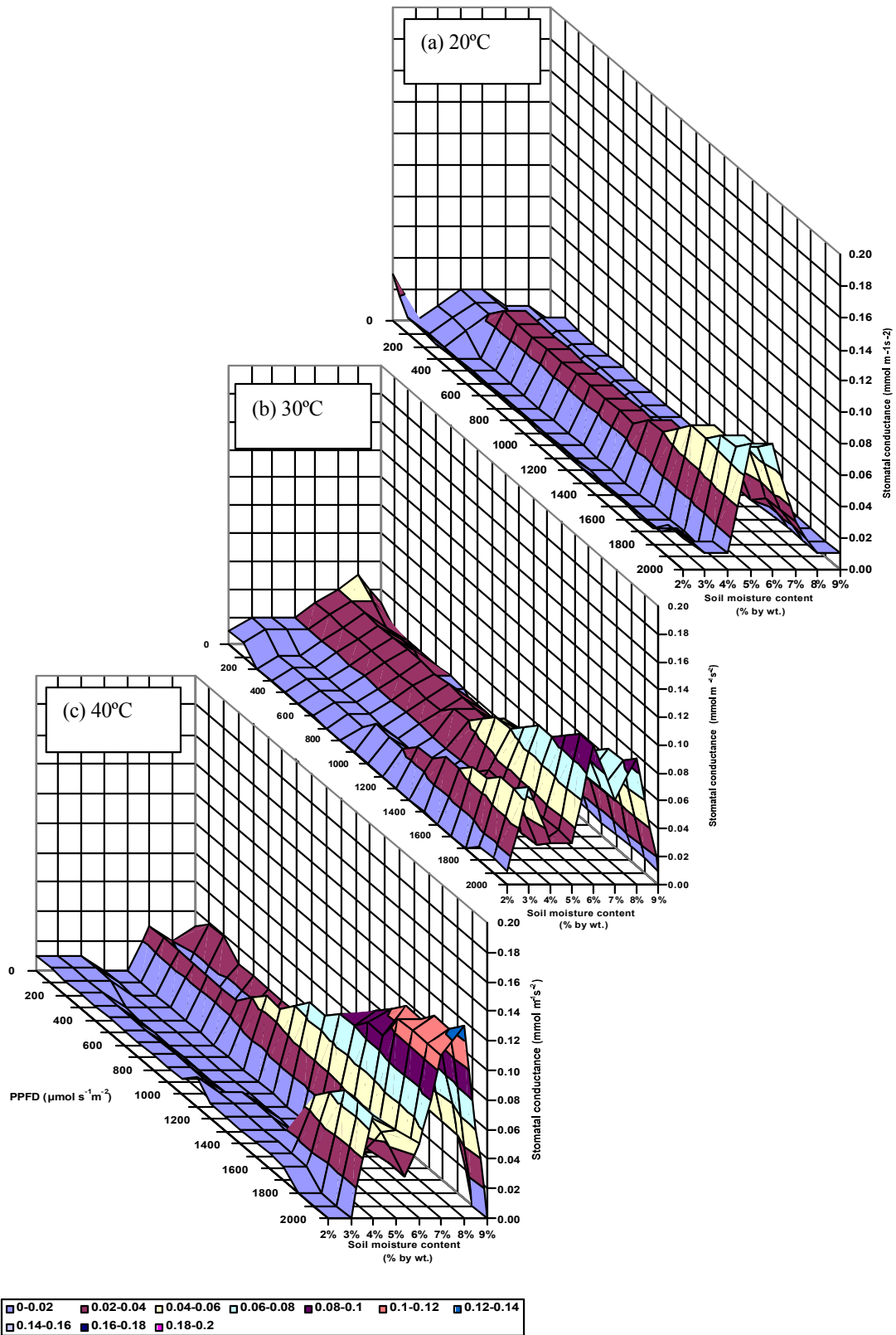
Legend:
☐ 0-0.02 ■ 0.02-0.04 ☐ 0.04-0.06 ☐ 0.06-0.08 ■ 0.08-0.1 ■ 0.1-0.12 ■ 0.12-0.14
☐ 0.14-0.16 ■ 0.16-0.18 ■ 0.18-0.2

Fig. 4: Stomatal conductance (mmol m^{-2}s^{-1}) of *Solenostemma* at different temperatures (a) 20ºC; (b) 30ºC; (c) 40ºC, photosynthetic photon flux densities (PPFD) and gradual soil moisture depletion
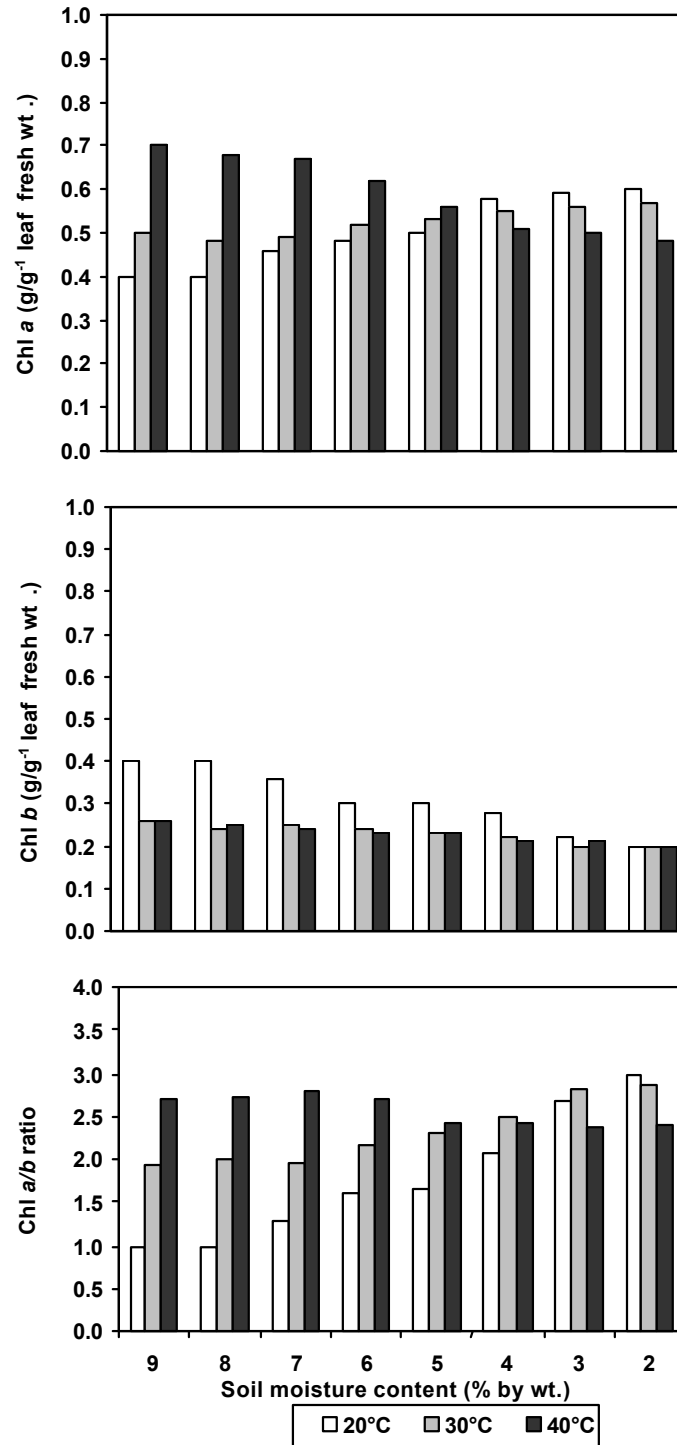
Fig. 5: Chlorophyll Content (Chl) *a* and *b*, and Chl *a/b* ratio of *Solenostemma* at different temperatures (20º, 30º and 40ºC), and under gradual soil moisture depletion

On the other hand, also significant changes in stomatal conductance could be due to combination of imposed soil drought, different temperature and PPFD (F= 4.522 and P<0.0001).

Lowest transpiration rate (2.02 μ gm m^{-2} S^{-1}) was recorded in plants kept at 20°C (Fig. 3a) 5% soil moisture content (S.M.C) and at highest levels of PPFD (2000 μmol s^{-1}m^{-2}). At the same conditions minimum stomatal conductance (0.08μmol s^{-1}m^{-2}) was recorded (Fig. 4a).

On the other hand, as temperature increased to 30°C (Fig. 3b), transpiration rate was increased gradually to reach and two peaks were observed at high PPFD range (1000-2000 μ mol s^{-1} m^{-2}), first peak (4.32 μgm m^{-2}s^{-1}) accompanied with maximum stomatal conductance (0.10 μmol s^{-1} m^{-2}), (Fig. 4b). While, second peak was observed as soil moisture content dropped to 3% and transpiration rate was 4.32 μgm m^{-2} s^{-})$. Highest transpiration rate was achieved in *Solenostemma* plant kept at 40°C (Fig. 3c).

The transpiration rate increased in response to both gradual soil moisture depletion (8-7%) and high levels of photosynthetic photon flux density (1400-2000 μmol s^{-1}m^{-2}). Stomatal conductance was ranged from 0.11 to 0.13μmol s^{-1}m^{-2}) (Fig. 4c).

The imposed drought treatment caused decrement in both transpiration rate and stomatal conductance (figures 3c and 4c). As soil moisture content reached 3%, maximum transpiration rate (4.48μgm m^{-2}s^{-1}), while stomatal conductance was 0.0 μmol s^{-1}m^{-2} at 2000 μmol s^{-1}m^{-2} (PPFD) and at 2% soil moisture content lowest transpiration rate and stomatal conductance (1.16 μgm m^{-2} s^{-1} and 0.0 μmol s^{-1}m^{-2}) were observed at highest PPFD level (2000 μmol s^{-1}m^{-2}).

Figure 5 Shows Chlorophyll content Chl *a* and *b* and Chl *a/b* ratio of *Solenostemma* at different temperature and under gradual soil moisture depletion.

From Two-way analysis of variance Chl *a* content showed no significant changes in response to either temperature differences nor gradual soil moisture depletion. While, Chl *b* contents of *Solenostemma* exhibited significant changes attributed to both temperature differences and gradual soil moisture content were, F= 15.57; P<0.0001 and F= 4.34; P<0.0001, respectively. Otherwise, Chl *a/b* ratio significantly changed in response to temperature differences only were F= 4.94 and P<0.05.

Also, Pearson correlation coefficient revealed that, Chl *a* content low significant correlation with temperature differences only (P<0.05). Otherwise, both Chl *b* and Chl *a/b* ratio showed high significant correlation with both temperature differences and gradual soil moisture depletion (P<0.01).

Chl *a* content of *Solenostemma* leaves showed more stability in response to imposed drought treatment at 20°C and 30°C. It showed slight increment in response to gradual soil moisture depletion, ranged from 0.4 to 0.6 g g^{-1} leaf fresh weight at 20°C and from 0.5 to 0.57 g g^{-1} leaf fresh weight at 30°C.

Otherwise, in *Solenostemma* plants kept at 40°C Chl *a* content was 0.7 g g^{-1} leaf fresh weight at 9% (S.M.C) and decreased in response to soil dryness reaching 0.48g g^{-1} leaf fresh weight at 2% (S.M.C). Chl *b* content exhibited less stability than Chl *a* content in response to both temperature differences and gradual soil moisture depletion. Highest Chl *a* content (0.40g g^{-1} leaf fresh weight) was recorded in plants maintained at 8 and 9% of soil moisture content at 20°C and it gradually increased in response to drought reaching 0.2 g g^{-1} leaf fresh weight at lowest level of soil moisture (2%).

As temperature increased (30 and 40°C), Chl *b* contents tends to decrease even at high levels of soil moisture contents ranged from 0.26g g^{-1} leaf fresh weight at 9% (S.M.C) to 0.26g g^{-1} leaf fresh weight at 2% (S.M.C).

In general, as a result of Chl *a* showing more stability than Chl *b* in response to both temperature differences and imposed drought treatment, Chl *a/b* ratio gave more recognizable changes. Highest Chl *a/b* ratio (30 and 2.85 g g^{-1} leaf fresh weight) were recorded in plants kept at 20°C and 30°C, respectively, under lowest levels of soil moisture content (2%).

Otherwise, as temperature raised to 40°C, Chl *a/b* ratio tends to decrease ranged from 2.69g g^{-1} leaf fresh weight at 9% (S.M.C) to 2.40g g^{-1} leaf fresh weight at 2% (S.M.C).

Plate (1) exhibits the detailed anatomical characteristics of leaf (A and B1, B2), stem (C-D) and root (E-F) of *Solenostemma* plants.

Plate 1-A shows detailed leaf anatomical features. Cuticle was approximately 2-5 μm thick. Cutin deposited only on the outer wall of epidermal cells. Variability in size and shape of epidermal cells caused undulation of leaf surface. Approximate cell dimension were 14-20 μm thick and 16-18 μm long. Stomata evenly distributed over leaf surface (Plate B1-B2) and they present on both abaxial and ad axial leaf surfaces. Leaf anatomical characteristics (Plate B1 abaxial, B2 ad axial) revealed that abaxial leaf surface have higher stomatal frequency (56±2.36 mm^{-2}) in comparison with ad axial leaf surface (23±1.4mm^{-2}) also highest trichome frequency (26±1.37mm^{-2}) was observed on the abaxial leaf surface while lowest trichome
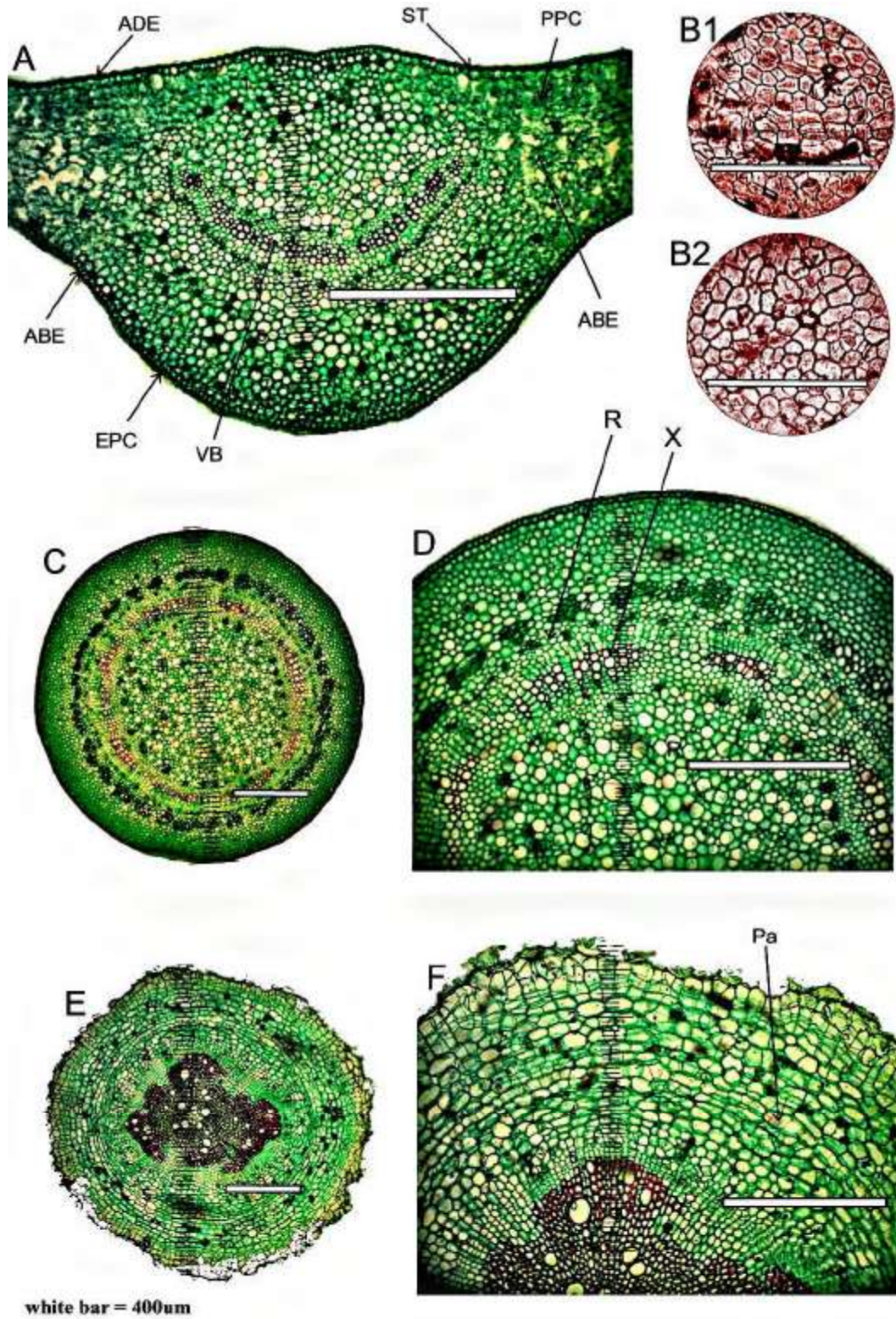
Plate 1: Detailed structure light microscopy of *Solenostemma*' leaf (A) with palisade parenchyma cells (PPC); spongy parenchyma cells (EPC); vascular bundle (VB); adaxial epidermis (ADE); abaxial epidermis (ABE); stomata (ST), (B1) abaxial leaf surface stems (B2) adaxial leaf surface, stems (C and D) with ray (R); xylem vessels (X) and roots (E and F) with passage cells (Pa)

frequency ($15 \pm 0.92 mm^{-2}$) recorded on the adaxial leaf surface, trichome length was $209 \pm 2 \mu m$ on both abaxial and adaxial leaf surface and larger stomatal length ($38.15 \pm 0.12 \mu m$) and width ($26.24 \pm 0.19 \mu m$) were observed on abaxial leaf surface, while, smaller stomatal length ($31.41 \pm 0.8 \mu m$) and width ($21.23 \pm 0.17 \mu m$) were observed on ad axial leaf surface.

Mesophyll and vascular tissue: mesophyll thickness ($326 \pm 28 \mu m$). Below the upper epidermis, the palisade mesophyll was multi-layered (2-3 cells long) representing approximately one third of the leaf thickness. Below the palisade tissue was spongy mesophyll layer followed by single less distinct and thinner layer of palisade tissue. The main vein ran along the leaf section (Plate 1-A). Associated with large vascular bundles, which in turn enclosed with paranchymatous tissue containing druses crystals. Xylem vessels diameter ranged from 16 to 20 μm).

The epidermis of young shoot was slightly papillose (Plate C-D), with no stomata present. Beneath epidermis the cortex comprised a layers of varied size paranchymatous cells characterized by presence of druses crystals, ended by a layer of endodermis suberised cells. Beneath the endodermis was a sclerenchymatous sheath immediately exterior to the vascular tissue of metabolism (which contain druses shaped crystals). The vascular cambium of discrete bundles of xylem vessels (Plate 1-C). There were parenchyma rays through both phloem and xylem tissues. Diameter of xylem vessels of secondary xylem was ranged 18-22μm. Primary xylem was embedded in the outer paranchymatous cells of pith. Pith comprised almost half of stem area and composed of different size of paranchymatous.

Anatomy of fine roots (Plate 1.E-F) showed that outer surface of *Solenostemma* roots was composed of multilayered periderm, which comprised of several layers of thin-walled cork cells followed by a relatively thin layer of parenchyma cortex. Beneath cortex was a layer of suberized endodermal cells associated with passage cells (Plate 1. F). Passage cells were present in the endodermis and parenchyma rays (8-14 cells wise) projected from cortex through to the stele. The central section of vascular cylinder was occupied by sclerenchyma, protoxylem and large metaxylem vessels (30-68μm in diameter) in a polyarch arrangement.

DISCUSSION

The hyper-arid environmental conditions imposed different types of stress including drought, high temperatures and irradiation. Leaf water potentials were measured at midday and predawn in *Solenostemma* plant

under gradual soil moisture condition revealed its ability to develop suction force to extract water from soil [5-38]. Highest mean predawn leaf water potential were observed in *Solenostemma* plants at soil moisture content equal to field capacity (9%) at all levels of temperatures, which could be due to increased internal resistance. While larger negative leaf water potentials were achieved at midday indicates that, the need to provide additional water to the foliage is demanding [39]. Similar results were observed in previous work on *Solenostemma* under salinity stress [2]. Low osmotic potential at leaf water relations considered as a potential gradient for water uptake and turger maintenance during soil drying [40].

In water stressed plants both soil moisture and high radiation have an accumulative effect on plant water relation, lowering leaf water potential, leaf stomatal conductance and gas exchange via stomata [41].

The highest transpiration rate and stomatal conductance which were observed in *Solenostemma* at soil moisture less than field capacity. At low level of soil moisture content, an high temperature level (40%), the water potential of *Solenostemma* decreased as the water balance in plant become more negative as a result of insufficient water uptake to cope with required transpiration [42]. In herbaceous laboratory-sized plants, the transpiration-induced tension is dominant driving force which help in water ascent [43].

Maximum transpiration rate was recorded in *Leptadenia pyrotechnica* which grow in Egyptian desert during summer midday [44].

Diurnal range of leaf water potential in *Solenostemma* revealed their great ability to recover to its predawn values which in turn proved their drought-adaptation. The normal range of water potential is generally large in drought-adapted species [45].

The stability of Chl *a* content in *Solenostemma* leaves under combined stress of drought and high temperature confirmed the fact that Chl *a* considered a major stress tolerant constituent of photosynthetic pigment in some desert plants [46]. While, decrement in Chl *a/b* ratio in response to gradual soil moisture depletion and high temperature (40°C) revealed the adaptation of desert plants to withstand drought and high temperature as a result of decreased Chl a/b ratio balanced by increased Chlorophyll a stability to heat stress [47].

Solenostemma small leave, with thick cuticle, multilayered palisade cells and small but more abundant stomata on abaxial leaf surface could be considered as structural feature of the drought adapted leaf of xerophytes which have been related to the whole plant physiology and adaptability [48]. Small and thick leaves

with multilayered mesophyll are considered to characterize sun species [49, 50].

Amphistomaty and leaf compartmentation of *Solenostemma* was repeatedly evaluated by many authors concerning leaf xeromorphy [51,52] as it shortens the distance of CO_2 diffusion to mesophyll cells [50].

Mesophyll compartmentalization of *Solenostemma* leave is suggested to protect the leaf against water stress [53]. Multilayered palisade tissue is also believed to increase CO2 absorbing surface of the mesophyll [54].

Green-stemmed *Solenostemma* showed similar convergent stem anatomy to Mediterranean shrub *Calicotome villosa* which exhibits well-developed cuticle, sclerenchyma and chlorenchyma and delayed periderm formation [55]. Also, the presences of high number of small grouped vessels in the wood of stem maximizing the safety of the hydraulic system [56].

The larger diameter of xylem vessels in fine roots of *Solenostemma* in comparison with that of leaf and stem is proved to keep consistently hydraulic conductance [57].

In desert perennial C_3 subshrub *Encelia farinose* high transpiration rate and low water potential occurred due to short path length along the leaves, large number of xylem elements in the stems and large xylem lumen diameters in roots [58].

In conclusion, *Solenostemma* behave as a water spender as a result of its high capability of keeping a hydraulic equilibrium between water uptake and loss by mean of physiological and anatomical adaptations to avoid the stress, which could help in understanding the mechanisms of stress tolerance in similar desert species.

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