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DIFFERENTIAL RESPONSE TO WATER DEFICIT STRESS AND SHADE OF TWO WHEAT (*TRITICUM DURUM* DESF.) CULTIVARS: GROWTH, WATER RELATIONS, OSMOLYTE ACCUMULATION AND PHOTOSYNTHETIC PIGMENTS

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Abstract

This study was conducted to investigate the effects of water deficit stress and shading on two wheat cultivars (*Triticum durum* Desf. cv Om Rabiaa and cv Maali). Comparison was based on growth, leaf water relations, photosynthetic pigments and the accumulation of organic solute. In both cultivars, water stress deficit significantly decreased total dry mass (TDM), leaf area (LA), water potential (Ψw), osmotic potential (Ψπ) and relative water content (RWC). Photosynthetic pigments, i.e. chlorophyll a (Chl a), chlorophyll b (Chl b) and total chlorophyll (Tot Chl), decreased while carotenoids (car) increased. Proline concentration increased significantly in water stressed plants under full light conditions while sugar accumulated more under shade conditions. In addition, shade improved leaf area, leaf water potential, and osmotic potential as well as alleviated the negative drought impact on photosynthesis performance. For the Maali cultivar, the reduction in RWC and its inability to achieve osmotic adjustment (OA) emphasize this cultivar's sensitivity to water deficit stress. For the Om Rabiaa cultivar, the ability to avoid relative tissue dehydration and preserve a higher RWC with a significant increase in OA in shade-treated plants were tolerance mechanisms enabling this cultivar to absorb water effectively and sustain normal growth and productivity under water stress conditions.

Key words: Drought, Osmotic adjustment, RWC, Shading, Wheat cultivar.

Introduction

Wheat (*Triticum durum* Desf.) is a staple food crop and the most widely distributed cereal crop in Tunisia (Ayed *et al*., 2017). In many rainfed agricultural areas, water stress deficit is a major constraint affecting cereal production and yield in arid and semi-arid regions (Sassi *et al*., 2012). Light, however, is considered a key physical factor controlling many biological processes including photosynthesis, transpiration, respiration, chlorophyll synthesis, photoperiodism and photomorphogenesis (Li *et al*., 2011). Drought and light are not independent either in space or in time and may cause a variety of plant responses which can be additive, synergistic or antagonistic. In semi-arid and arid environments, shading with lower levels of water deficit and cooler temperatures may be an intermediate solution for reducing plant water stress (Nicolas *et al.*, 2008), but it can also aggravate the growth of seedlings exposed to drought (Carneiro *et al*., 2015). Since water availability and light are often the main factors affecting productivity in dry regions, strategies to improve sustainable use of water and plant drought tolerance are of paramount interest (Dolferus, 2014). Drought intensity and length are also determining factors when studying the effects of water stress on plants. In this study, we examined the effect of light and water availability on the early development of two of the most common wheat cultivars in local production in Tunisia (Slama *et al*., 2005). Exploring the variability of plant water relations behavior would make it possible to select tolerant cultivars and provide a scientific basis for improving wheat yield in response to variations in environmental conditions. Plant water status equilibrates with soil water content through water potential, but internal ecophysiological processes allow for the maintenance of cell water content, as proline metabolism or the increase in soluble sugar concentration, impacting osmotic pressure (Anjum *et al*., 2011). In addition, reduced transpiration processes through stomatal closure under dry conditions might increase leaf temperature and affect photosystems, in turn reducing carbon assimilation (Embiale *et al*., 2016). How cultivars manage to adjust their water status under various climate conditions and how these adjustments impact their final carbon assimilation and productivity is needed for their scientifically-sound selection under peculiar cultivation practices. The objectives of this work were (1) to investigate the effects of water deficit stress and shade on the eco-physiological responses of two wheat cultivars and (2) to compare their ability to grow under different environmental conditions.

Materials and Methods

Plant material and experimental design: The experiment was done on two Tunisian wheat cultivars (*Triticum durum* Desf. cv Om Rabiaa and cv Maali). Seeds were sterilized in a solution of 20% sodium hypochlorite, washed with distilled water and germinated in peat. The seedlings obtained were irrigated with deionized water to soil field capacity (100% FC) and placed in culture chamber. The environmental conditions were a temperature of 23 ± 3°C, 16 h of light and 70-90 % relative humidity. At the third true leaf stage, plants of each cultivar were randomly assigned to two light treatments with two different levels of photosynthetic photon flux density (PPFD): 100% PPFD (600 µmol m^{-2} s^{-1}) and 33% PPFD (200 µmol m^{-2} s^{-1}) of full irradiance, hereafter, L (full light) and S (shade). Seedlings of each light treatment were randomly divided into three watering treatments, Ww (well watered treatment, 100 % FC), Wm (moderate water stress, 66 % FC) and Ws (severe water stress, 33% FC). The plants were irrigated with Hoagland nutrient solution at half strength and soil moisture was restored to 100, 66 or 33% FC at the time of regular weightings (every 2 days). Each treatment was done in triplicate. Treatments were maintained for two weeks, after which seedlings from each water x light combination were harvested.

Plant growth and water relations: Fresh weight (FW) of plant samples was determined upon harvesting and total dry matter (TDM) was obtained after oven drying at 70°C until a constant weight was reached. Total leaf area was measured with a Delta T Image Analysis System (Delta T Ltd, England, UK). Midday leaf water potential (Ψw) measurements were recorded between 12h 30 and 13h 30 in the third youngest fully expanded leaf using a Scholander pressure chamber (SKPM 1400; Skye instruments Ltd, England, UK). For measurements of osmotic potential (Ψπ), leaves were frozen with liquid N_2 before being pressed by a syringe then centrifuged. The osmolarity of the leaf sap was measured by the freezing point depression method using a Digimatic osmometer (OSMOMAT 3000, Gonotec, Berlin, Germany) and then converted from mosmoles kg^{-1} to MPa according to the Van't Hoff equation ($\Psi\pi$ = -n R T; where R is the universal gas constant, T is the temperature (K) and n is the osmolarity). Relative water content (RWC) was estimated using the following equation:

$$RWC (\%) = 100 \times (FW-DW) / (TW-DW),$$

where FW is the fresh weight determined after harvest, TW is the turgid weight obtained after soaking leaves in distilled water for 24 h at room temperature (20°C) and DW is the dry weight obtained after oven drying at 70°C until a constant weight was reached. Leaf osmotic adjustment (OA) was determined as the difference $\Psi\pi_0 RWC_0$ - $\Psi\pi RWC$, where $\Psi\pi_0 RWC_0$ is the product of [osmotic potential] x [osmotic volume] of unstressed plants and $\Psi\pi RWC$ is the product of [osmotic potential] x [osmotic volume] of leaves from stressed plants.

Analysis of chlorophyll and organic metabolites: Chlorophyll content was determined using the acetone method described by Lichtenthaler (1987). Proline colorimetric determination proceeded according to Bates *et al*., (1973) based on proline reaction with ninhydrin, using L proline as a standard. The content of total soluble carbohydrates was determined according to Mc Cready *et al*., (1950) and Staub (1963), using glucose as a standard.

Statistical analysis: The experiment was arranged in a randomized complete block design. All data were expressed as mean ± standard error (SD) and the means of the three replicates were compared using a one-way analysis of variance (ANOVA). Two and three-way ANOVA tests were performed using the General Linear Model procedure and the differences between treatments were compared using Duncan's multiple range test ($p \leq 0.05$). SPSS ver 20.0 software (SPSS statistics, Chicago, USA) was used for all statistical analysis.

Results and Discussion

Water relations: Results showed that water stress led to a significant decrease in the leaf water potential (Ψw) of both cultivars. The reductions in Ψw were more severe under full light than those measured under shade (Table 1).Under full light conditions, Ψw was -1.23 MPa in control plants, while reaching -2.08 MPa and -2.23 MPa with severe water deficit stress in Om Rabiaa and Maali cultivars, respectively. Leaf Ψw responds to soil water deficit by adjusting its potential to soil water potential, illustrating the higher plant deficit in less watered experiments. Shaded conditions reduced potential evapotranspiration and in turn plant water demand and the resulting actual plant transpiration and soil water content (Bakhshy *et al.*, 2013). In turn, shading improved Ψw even at the highest water deficit stress, which increased to -1.72 MPa and -1.93 MPa in Om Rabiaa and Maali cultivars, respectively. Carneiro *et al.*, (2015) put forth the idea that the improved performance of shaded plants may also be related to better conditions both in terms of temperature and humidity. In addition, we showed a variation for drought tolerance between the two cultivars. Under full irradiance, relative water content (RWC) decreased significantly with increasing water deficit stress in the Maali cultivar and the Om Rabiaa cultivar preserved the highest RWC value suggesting the ability of this cultivar to avoid relative tissue dehydration. Reduced RWC under severe water stress was reported in other studies (Siddique *et al.*, 2000; Tasmina *et al.*, 2016; Mahmoud *et al.*, 2018). On the other hand, shading alleviated drought stress in the Om Rabiaa cultivar by conserving more water and maintaining a higher leaf RWC, as a consequence of reduced potential evapotranspiration (Cavatte *et al*., 2011). The analysis of variance revealed a significant effect on RWC between the two cultivars. This could be explained by differences between wheat cultivars in root performance to extract soil water and/or in the stomatal ability to control water loss through evaporative surfaces (Saeidi & Abdoli, 2015). We searched for ecophysiological mechanisms adjusting plant water status. Leaf osmotic potential (Ψπ) decreased significantly in the Om Rabiaa cultivar, whereas for the Maali cultivar, the reduction in Ψπ was not significant under full light conditions. Under shade conditions, reductions in Ψπ with increasing water stress deficit were greater in the Om Rabiaa than in the Maali cultivar. The greater ability of Om Rabiaa cultivar to decrease its osmotic potential is an adaptive mechanism that promotes maintenance of high tissue water content and tolerance to low water availability (Guo *et al.*, 2013). When drought stress level was high, active osmotic adjustment (OA) was triggered, thus helping maintain leaf turgor (Rodriguez *et al.*, 2012). Increased RWC in the Om Rabiaa cultivar was concomittent with a significant increase in leaf Osmotic adjustment (OA). In the Maali cultivar, there was no significant difference in OA in any of the stressed plants. Statistical analysis (Table 1) revealed that there were strong interactions in water potential, osmotic potential, relative water content and osmotic adjustment under different light intensities and cultivars. For the Maali cultivar, both the significant reduction in RWC and its inability to achieve osmotic adjustment emphasize this cultivar's sensitivity to water deficit stress. For the Om Rabiaa cultivar, the ability to avoid relative tissue dehydration and preserve a higher RWC with a significant increase in OA in shade-treated plants, confirmed the tolerance of this cultivar to water deficit stress.

Table 1. Interactive effects of light intensity and water status on leaf water relations in two wheat cultivars.

Treatment	Ψw (MPa)		Ψπ (MPa)		RWC (%)		OA (MPa)	
	Om Rabiaa	Maali	Om Rabiaa	Maali	Om Rabiaa	Maali	Om Rabiaa	Maali
LWw	-1,23 ± 0,21^{cd}	-1,23 ± 0,06^{d}	-2,45 ± 0,02^{c}	-2,53 ± 0,03^{a}	76,3 ± 1,60^{bc}	76,0 ± 1,20^{a}	-	-
LWm	-1,72 ± 0,13^{ab}	-1,75 ± 0,13^{bc}	-2,74 ± 0,05^{a}	-2,58 ± 0,02^{a}	74,2 ± 0,90^{c}	74,2 ± 0,50^{ab}	0,16 ± 0,06^{b}	0,09 ± 0,05^{a}
LWs	-2,08 ± 0,16^{a}	-2,23 ± 0,12^{a}	-2,71 ± 0,02^{a}	-2,55 ± 0,04^{a}	74,1 ± 0,50^{c}	71,6 ± 0,09^{b}	0,14 ± 0,05^{b}	0,01 ± 0,06^{a}
SWw	-1,10 ± 0,10^{d}	-1,13 ± 0,12^{d}	-2,30 ± 0,03^{d}	-2,26 ± 0,03^{c}	77,9 ± 1,07^{ab}	76,6 ± 1,10^{a}	-	-
SWm	-1,53 ± 0,06^{bc}	-1,53 ± 0,06^{c}	-2,54 ± 0,01^{b}	-2,31 ± 0,03^{c}	81,5 ± 0,90^{a}	76,0 ± 1,00^{a}	0,28 ± 0,04^{a}	0,02 ± 0,04^{a}
SWs	-1,72 ± 0,13^{ab}	-1,93 ± 0,06^{b}	-2,60 ± 0,03^{b}	-2,42 ± 0,04^{b}	81,4 ± 0,90^{a}	73,1 ± 1,00^{b}	0,28 ± 0,05^{a}	0,04 ± 0,02^{a}
C	*		***		***		***	
LI	***		***		***		*	
W	***		ns		**		ns	
C x LI	ns		ns		***		**	
C x W	ns		ns		**		ns	
LI x W	ns		**		ns		ns	
C x LI x W	ns		ns		ns		ns	

Ψw — leaf water potential;Ψπ—osmotic potential; RWC — relative water content; OA — osmotic adjustment; C —cultivars; LI—light intensity; W—water. L—full light; S—shade; Ww—well-watered; Wm—moderate water stress; Ws—severe water stress. Data represent means ± standard error (SE) of three replicates. Different letters in each column in same cultivar indicate significant differences between the treatments at $p<0.05$. ns: no significant at the 0.05 level; *, **, ***, significant at $p<0.05$, $p<0.01$ and $p<0.001$, respectively

Table 3. Interactive effects of light intensity and water status on photosynthetic pigments contents in two wheat cultivars.

Treatment	Chl a [μg g^{-1} FW]		Chl b [μg g^{-1} FW]		Tot Chl [μg g^{-1} FW]		Car [μg g^{-1} FW]	
	Om Rabiaa	Maali	Om Rabiaa	Maali	Om Rabiaa	Maali	Om Rabiaa	Maali
LWw	1,77 ± 0,01^{b}	1,81 ± 0,05^{b}	0,69 ± 0,16^{b}	0,94 ± 0,10^{b}	2,46 ± 0,17^{bc}	2,75 ± 0,06^{b}	0,36 ± 0,01^{b}	0,44 ± 0,04^{a}
LWm	1,70 ± 0,03^{b}	1,75 ± 0,11^{bc}	0,74 ± 0,11^{ab}	0,84 ± 0,08^{bc}	2,44 ± 0,11^{bc}	2,59 ± 0,21^{bc}	0,43 ± 0,02^{ab}	0,46 ± 0,01^{a}
LWs	1,53 ± 0,09^{c}	1,49 ± 0,18^{c}	0,65 ± 0,08^{b}	0,71 ± 0,11^{c}	2,18 ± 0,17^{c}	2,19 ± 0,23^{c}	0,46 ± 0,04^{a}	0,48 ± 0,04^{a}
SWw	1,98 ± 0,07^{a}	2,13 ± 0,07^{a}	0,98 ± 0,11^{a}	1,18 ± 0,15^{a}	2,96 ± 0,07^{a}	3,30 ± 0,15^{a}	0,24 ± 0,04^{c}	0,25 ± 0,09^{c}
SWm	1,86 ± 0,06^{ab}	2,00 ± 0,10^{ab}	0,90 ± 0,03^{ab}	0,96 ± 0,06^{b}	2,76 ± 0,09^{ab}	2,96 ± 0,13^{ab}	0,36 ± 0,01^{b}	0,31 ± 0,02^{bc}
SWs	1,77 ± 0,06^{b}	1,99 ± 0,08^{ab}	0,86 ± 0,05^{ab}	0,88 ± 0,03^{bc}	2,64 ± 0,11^{ab}	2,88 ± 0,09^{ab}	0,40 ± 0,04^{ab}	0,38 ± 0,02^{ab}
C	**		***		***		ns	
LI	***		***		***		***	
W	***		***		***		***	
C x LI	*		ns		ns		*	
C x W	ns		*		ns		ns	
LI x W	ns		ns		ns		ns	
C x LI x W	ns		ns		ns		ns	

Chl a—chlorophyll a content; Chl b—chlorophyll b content; Tot Chl—total chlorophyll content; Car—carotenoïds content; Pro—proline content; SS—soluble sugar content ; C—cultivars; LI—light intensity; W—water. L—full light; S—shade; Ww—well-watered; Wm—moderate water stress; Ws—severe water stress. Data represent means ± standard error (SE) of three replicates. Different letters in each column in same cultivar indicate significant differences between the treatments at $p<0.05$. ns: no significant at the 0.05 level; *, **, ***, significant at $p<0.05$, $p<0.01$ and $p<0.001$, respectively

Table 2. Interactive effects of light intensity and water status on organic metabolites accumulation in two wheat cultivars.

Treatment	Pro [µmol g^{-1} FW]		SS [µmol g^{-1} DW]	
	Om Rabiaa	Maali	Om Rabiaa	Maali
LWw	0,29 ± $0,08^{bc}$	0,37 ± $0,04^{b}$	1679 ± 159^{d}	2270 ± 25^{b}
LWm	0,41 ± $0,04^{ab}$	0,42 ± $0,01^{b}$	1837 ± 94^{cd}	2309 ± 99^{b}
LWs	0,42 ± $0,05^{a}$	0,53 ± $0,02^{a}$	2278 ± 93^{ab}	2378 ± 58^{b}
SWw	0,21 ± $0,03^{c}$	0,13 ± $0,01^{c}$	2167 ± 25^{bc}	1667 ± 69^{c}
SWm	0,21 ± $0,02^{c}$	0,17 ± $0,04^{c}$	2242 ± 201^{b}	2267 ± 71^{b}
SWs	0,20 ± $0,01^{c}$	0,20 ± $0,04^{c}$	2644 ± 96^{a}	2672 ± 99^{a}
C	***		**	
LI	***		ns	
W	**		***	
C x LI	***		***	
C x W	**		ns	
LI x W	ns		*	
C x LI x W	ns		***	

Pro—proline content; SS—soluble sugar content; C—cultivars; LI—light intensity; W—water. L—full light; S—shade; Ww—well-watered; Wm—moderate water stress; Ws—severe water stress. Data represent means ± standard error (SE) of three replicates. Different letters in each column in same cultivar indicate significant differences between the treatments at $p<0.05$. ns: no significant at the 0.05 level; *, **, ***, significant at $p<0.05$, $p<0.01$ and $p<0.001$, respectively

Proline and soluble sugar accumulation: Ecophysiological adjustments in plant water status could be attributed to either proline metabolism or changes in soluble sugar concentration, modifying the RWC/ Ψw relationship and Ψπ. Table 2 shows that leaf proline (Pro) concentration increased significantly with increasing water deficit stress in both cultivars under full irradiance. In well watered plants, Pro concentration was higher in the Maali than in the Om Rabiaa cultivar. An increase in proline would lower the osmotic potential in the cells, thus helping maintain turgor under water stress (Ghobadi *et al.*, 2013). The same results have been found for other plant species (Li *et al.*, 2011; Kwon &Woo, 2016). Under shade conditions, proline accumulation was markedly reduced in both cultivars. This could be explained by the fact that shaded plants exposed to water stress have probably not yet reached the threshold of stress which triggers the overexpression of the genes responsible for the biosynthesis of proline (Cavatte *et al*., 2011). Therefore, the decrease of osmotic potential in shaded plants with no increase in proline content in both cultivars suggest that there are other metabolites implicated in osmotic adjustment. Our results showed an increase in soluble sugar (SS) content under water deficit stress for both cultivars under full iradiance, while SS increased only for the Om Rabiaa cultivar under shade conditions. This indicates that sugars could help regulate and maintain physiological process activity within the plant in a water-stress environment by raising the osmotic potential of the cells. Our results agreed with those of Farooq *et al*., (2009) who reported an increase in leaf SS concentrations under water deficit with a large variability among plants. The three-way ANOVA revealed that there was a significant difference in proline under different water deficit stresses and light intensities and a strong interaction in soluble sugars between the cultivar and water regime. A significant two-way interaction was observed on proline and soluble sugar content between the light intensities and three-way interactions among the cultivars, light and water only for SS.

Impacts on photosynthetic pigments: Table 3 shows that under different light intensities, water deficit stress induced a significant decrease in chlorophyll a (Chla) and an increase in carotenoids (Car) in the Om Rabiaa cultivar. For the Maali cultivar, increasing water deficit stress significantly decreased Chl a, Chl b and total chlorophyll (Tot Chl) under full light conditions and increased Car under shade conditions. The decrease in chlorophyll content could be caused by the impaired structure of chloroplasts or the chlorophyll biosynthesis pathway while increased carotenoid content could be due to the protectant role of this pigment against reactive oxygen species (Saeidi & Abdoli, 2015). Similar effects have been observed in *Triticum aestivum* seedlings (Guo *et al.*, 2013) and tomato seedlings (Wang *et al.*, 2018). On the other hand, we showed that shading increased chlorophyll, decreased carotenoid and alleviated the negative impact of drought on photosynthetic pigment content. Statistical analysis showed that there was significant effect (p≤0.05) of light intensity and water status on all photosynthetic pigments. It also showed that, except for carotenoids, there was a significant difference between cultivars. No significant three-way interaction was observed on photosynthetic pigments for the cultivars or based on light intensity. The results of this experiment are in accordance with the data of Zhang *et al*. (2016).

Impacts on carbon assimilation and final plant growth: Table 4 shows that total dry mass (TDM) of both Om Rabiaa and Maali cultivars decreased significantly in water stress conditions under the different light intensities. In full light conditions, the Om Rabiaa cultivar showed the lowest reduction in TDM when compared to its control. The maximum biomass reduction recorded under severe water stress (33% of field capacity) was 50% for the Maali cultivar whereas it did not exceed 30% for the Om Rabiaa cultivar. Being able to maintain growth and productivity under stress conditions highlighted the tolerance of the Om Rabiaa cultivar to water deficit stress (Dolferus, 2014). Under shade conditions, lower TDM, even in well-watered cultivars could be caused by reduced light availability (Abraham *et al.*, 2014). The effects of water stress on straw length (SL) were not significant for either cultivar in full light conditions. However, in shade conditions, SL was significantly decreased compared to values recorded in full light. On the other hand, results showed that the reduction of leaf area (LA) under full light conditions was greater in the Om Rabiaa cultivar. The reductions taken down were 50% and 40% for the Om Rabiaa and Maali cultivars, respectively. The higher capacity of Om Rabiaa cultivar to reduce its leaf area may be an adaptive mechanism to water deficit stress (Kwon &Woo, 2016). Under shade conditions, the LA was remarkably improved for both cultivars. Increased LA under shade conditions has been reported in other plant species (Diaz-Perez, 2013; Abraham *et al.*, 2014; Zhang *et al.*, 2016). Our results showed that the Om Rabiaa cultivar could grow adequately under water deficit and a low level of light by increasing its specific leaf area, thereby maximizing the carbon gain per unit of leaf mass. The three-way ANOVA revealed that there was a significant difference among TDM, SL and LA under different water conditions, light intensities and cultivars (Table 4). Moreover, there were significant two-way interactions in TDM, SL and LA between the cultivars, light and water. In addition, a significant three-way interaction was observed among these factors.

Table 4. Interactive effects of light intensity and water status on growth parameters in two wheat cultivars.

Treatment	TDM (g)		SL (cm)		LA (cm^2)	
	Om Rabia	Maali	Om Rabia	Maali	Om Rabia	Maali
LWw	$0,141 \pm 0,004^a$	$0,246\pm 0,011^a$	$18,33 \pm 0,57^a$	$28,16 \pm 1,60^a$	$12,31 \pm 0,77^b$	$12,60 \pm 0,40^b$
LWm	$0,129 \pm 0,002^a$	$0,190 \pm 0,003^b$	$16,50 \pm 0,50^a$	$28,66 \pm 1,52^a$	$7,19 \pm 0,66^c$	$12,44 \pm 0,54^b$
LWs	$0,099 \pm 0,014^b$	$0,126 \pm 0,007^c$	$17,66 \pm 0,57^a$	$26,00 \pm 0,86^{ab}$	$6,33 \pm 0,58^c$	$7,67 \pm 0,32^c$
SWw	$0,132 \pm 0,004^a$	$0,180 \pm 0,022^b$	$12,00 \pm 1,00^b$	$24,00 \pm 1,00^{bc}$	$15,01 \pm 0,77^a$	$14,28 \pm 0,40^a$
SWm	$0,121 \pm 0,007^a$	$0,134 \pm 0,022^c$	$11,50 \pm 0,87^b$	$22,00 \pm 1,00^c$	$13,44 \pm 0,62^{ab}$	$13,79 \pm 0,54^{ab}$
SWs	$0,092 \pm 0,013^b$	$0,117 \pm 0,013^c$	$11,83 \pm 0,76^b$	$21,66 \pm 0,76^c$	$12,63\pm 0,71^b$	$13,24 \pm 0,94^{ab}$
C	***		***		***	
LI	***		***		***	
W	***		***		***	
C x LI	***		*		***	
C x W	***		**		***	
LI x W	**		**		***	
C x LI x W	*		***		***	

TDM—total dry mass; SL—straw length; LA—leaf area; C—cultivars; LI—light intensity; W—water. L—full light; S—shade; Ww—well-watered; Wm—moderate water stress; Ws—severe water stress. Data represent means ± standard error (SE) of three replicates. Different letters in each column in same cultivar indicate significant differences between the treatments at $p<0.05$. *, **, ***, significant at $p<0.05$, $p<0.01$ and $p<0.001$, respectively

Conclusions

Responses to water deficit stress were variable in the two wheat cultivars. The Om Rabiaa cultivar clearly exhibited a stronger ability to resist stress caused by drought than did the Maali cultivar. The ability to maintain a higher RWC and the increase in osmotic adjustment and leaf area in the shade-treated plants might be efficient mechanisms in stress conditions, enabling Om Rabiaa cultivar to absorb water effectively and sustain normal growth and productivity under water stress conditions. Thus, the Om Rabiaa cultivar is more suitable for cultivation in shaded semi-arid farming systems.

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References

Abraham, E.M., A.P. Kyriazopoulos, Z.M. Parissi, P. Kostopoulou, M. Karatassiou, K. Anjalanidou and C. Katsouta. 2014. Growth, dry matter production, phenotypic plasticity and nutritive value of three natural populations of *Dactylis glomerata* L. under various shading treatments. *Agroforest. Syst*., 88: 287-299.

Anjum, S., A. Anjum, X. Xie, L. Wang, M.F. Saleem, C. Man and W. Lei. 2011. Morphological, physiological and biochemical responses of plants to drought stress. *Afr. J. Agri. Res*., 6: 2026-2032.

Ayed, S., M. Rezgui, A. Othmani, M. Rezgui, H. Trad, A. Jaime, T. Silva, M. Ben Younes, H. Ben Salah and M. Kharrat. 2017. Response of *Tunisian durum* (*Triticum durum* ssp.) and bread (*Triticum aestivum* L.) wheats to water stress. *Agrociencia*, 51: 13-26.

Bakhshy, J., K. Ghassemi–Golezani, S. Zehtab-Salmasi and M. Moghaddam. 2013. Effects of water deficit and shading on morphology and grain yield of soybean (*Glycine max* L.). *Tech. J. Engin & App Sci*., 3(1): 39-43.

Bates L. S., R.P. Waldren and I.D. Teare. 1973. Rapid determination of the free proline in water stress studies. *Plant Soil*, 39: 205-208.

Carneiro, I.C.S., E.G. Pereira and J.P. Souza. 2015. Combined effects of low light and water stress on *Jatropha curcas* L. promotes shoot growth and morphological adjustment. *Acta Bot. Bras*., 29: 467-472.

Cavatte C., A.G. Oliveira, E. Morais, C.V. Martins, M.V.P. Sanglard and M. Damatta. 2011. Could shading reduce the negative impacts of drought on Coffee? *Physiol. Plant.*, 144: 111-122.

Diaz-Perez, J.C. 2013. Bell Pepper (*Capsicum annum* L.) crop as affected by shade level: Microenvironnement, plant growth, leaf gas exchange and leaf mineral nutrient concentration. *Hort. Sci.*, 48 (2): 175-182.

Dolferus, R. 2014. To grow or not to grow: A stressful decision for plants. *Plant Sci.*, 229: 247-261.

Embiale, A., M. Hussein, A. Husen, S. Sahile and K. Mohammed. 2016. Differential sensitivity of *Pisumsativum* L. cultivars to water-deficit stress: changes in growth, water status, chlorophyll fluorescence and gas exchange attributes. *J. Agron*., 15: 47- 57.

Farooq, M., A. Wahid, N. Kobayashi, D. Fujita and S.M.A. Basra. 2009. Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev*., 29: 185-212.

Ghobadi, M., S. Taherabdi, M.E. Ghobadi, G.R. Mohammadi and S. Jelali-Honarmand. 2013. Antioxidant capacity photosynthetic characteristics and water relations of Sunflower. *Ind. Crops Prod*., 50: 29-38.

Guo, R., W.P. Hao, D.Z. Gong, X.L. Zhong and F.X. Gu. 2013. Effects of water stress on germination and growth of wheat, photosynthetic efficiency and accumulation of metabolites. In: INTECH (Eds), *Soil Processes and Current Trends in Quality Assessment*. *Open Sci.*, pp. 367-380.

Kwon, M.Y. and S.Y. Woo. 2016. Plants' responses to drought and shade environments. *Afr. J. Biotechnol*., 15: 29-31.

Li, Y., H. Zhao, B. Duan. H. Korpelainen and C. Li. 2011. Effect of drought and ABA on growth, photosynthesis and antioxidant system of *Cotinuscoggygria* seedlings under two different light conditions. *Environ. Exp. Bot.*, 71: 107-113.

Lichtenthaler, H.K. 1987. Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. In: (Eds.): Douce, R. and Packer, L. *Methods Enzymol*., pp. 350-382.

Mahmoud, E.A., M.A. Hassanin, T.I. Borham and E.I.R. Emara. 2018. Tolerance of some sugar beet varieties to water stress. *Agric. Water Manag.*, 201: 144-151.

Mc Cready, R.M., J. Guggolz, V. Silviera and H.S. Owens. 1950. Determination of starch and amylose in vegetables. *Anal. Chem.*, 22: 1156-1158.

Nicolas, E., V.L. Barradas, M.F. Ortuno, A. Navarro, A. Torrecillas and J.J. Alarcon. 2008. Environmental and stomatal control of transpiration, canopy conductance and decoupling coefficient in young lemon trees under shading net. *Environ. Exp. Bot*., 63: 200-206.

Rodriguez, P., C.D. Mellisho, W. Conejero, Z.N. Cruz, M.F. Ortuno, A. Galindo and A. Torrecillas. 2012. Plant water relations of leaves of Pomegranate trees under different irrigation conditions. *Environ. Exp. Bot*., 177: 19-24.

Saeidi, M. and M. Abdoli. 2015. Effect of drought stress during grain filling on yield and its components, gas exchange variables and some physiological traits of wheat cultivars. *J. Agr. Sci. Tech.***,** 17: 893-898.

Sassi, K., G. Abid, L. Jemni, B. Dridi-Al Mohandes and M. Boubaker. 2012. Etude comparative de six variétés de blédur (*Triticum durum* Desf.) vis-à-vis du stress hydrique. *J. Anim. Plant Sci.*, 15: 2157-2170.

Siddique, B.M.R., A. Hamid and M.S. Islam. 2000. Drought stress effect on water relation of wheat. *Bot. Bull. Acad. Sinica*, 41: 35-39.

Slama, A., M. Ben Salem, M. Ben Naceur and E. Zid. 2005. Les céréales en Tunisie: production, effet de la sécheresse etmécanismes de résistance. *Sécheresse*, 16(3): 225-229.

Tasmina, T., A.R. Khan, A. Karim, N. Akter and R. Islam. 2016. Physiological changes of wheat varieties under water deficit condition. *Bangladesh Agron. J.*, 19: 105-114.

Wang, S., K. Zhuang, S. Zhang, M. Yang, F. Kong and Q. Meng. 2018. Overexpression of a Tomato carotenoid έ-hydroxylase gene (SILUT1) improved the drought tolerance of transgenic Tobacco. *Plant Physiol. Biochem*., 70: 235-245.

Zhang, J., J. Liu, C. Yang, S. Du and W. Yang. 2016. Photosynthetic performance of Soybean plants to water deficit under high and low light intensity. *S. Afr. J. Bot*., 105: 279-287.

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