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REGULAR ARTICLE

Growth and photosynthetic CO_2 responses of date palm plants to water availability

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ABSTRACT

Date palm is known to survive and withstand harsh environment, especially under scarce water availability and extreme dry conditions. Drought adaptation in plant species includes evolutionary consequences detectable at a wide range of morphological, genetic as well as physiological multifunctional responses. Although, significant researches have been reported dealing with water relations of date palms to agronomic traits and yield performance, yet, revealing the mechanism of date palm adaptation to drought needs adequate attention. In this study, the aim was to examine the growth adjustments and photosynthetic CO_2 (Carbon dioxide) responses of date palm plants to water availability. The experimental methodology included long-term irrigation treatments based on field capacity measures, evaluation of the biochemical gas exchange model and assessment of growth and photosynthetic performance. As results, a variety of morphological as well as physiological adjustments were observed to take place in response to water availability. Accelerated leaf senescence, reduced green area as well the balanced root: Shoot ratio were among the main morphological adjustments observed. Stomatal conductance (g_s) showed a slight decrease in response to increasing external supply of CO_2 from ambient to 1,500 ppm (part per million), while intercellular CO_2 (C_i) continued increasing up to the highest tested level. As consequences, the increasing CO_2 significantly ($P \leq 0.001$) increased the net photosynthetic rate of the intact leaves of date palm plants with significant ($P \leq 0.001$) gas-water interaction effect. Reduction of water by 50% of field capacity did not generate significant effect on the photosynthetic ability of the tested plants; this result also confirmed by the slight changes in the biochemical reaction indices. However, at 25% and 10% water availability changes in responses become more pronounced. On the other hand, the reduction of g_s by 30% at 10% water availability compared to 100% did not affect the increasing pattern of C_i/C_a ratio (intercellular CO_2 concentration/gas external supply ratio) of elevated CO_2 when compared to that of the ambient; an observation might indicate a non-absolute stomatal role among the determinants of photosynthetic capacity of date palms in response to water availability. The observed growth adjustments, the indexed changes in the photosynthetic biochemical reactions as well as the implications for date palm adaptation to drought are considered in the discussion.

Keywords: Biochemical model; drought adaptation; gas exchange; photosynthesis; plant growth adjustment

INTRODUCTION

Drought and its effect on plants is the most widespread and acute problem in the arid and semi-arid regions. Problems associated with drought are expected to rise due to global climate change and human impacts. Low water availability is a serious environmental factor that limits plant growth and photosynthesis (Munns, 2002; Lambers et al., 2008), however, plants are known to use different strategies to cope with, and these strategies are associated with a variety of adaptive traits. These traits are detectable through a wide range of different types of responses, such as minimizing water loss and maximizing water uptake or maintaining a large internal storage of water (Kummerow, 1980; Jones, 1980; Lambers et al., 2008). Tolerance to low tissue water potential involves osmotic adjustment (Morgan, 1984) that occurs by means of morphological or physiological modifications that reduce transpiration or increase absorption (Kramer, 1980). However, stomatal adjustment to water potential and carbon dioxide recycling during photosynthesis in water-stressed plants are considered as the main physiological mechanisms that have adaptive significance to water stress (Ludlow, 1980; Lambers et al., 2008).

Generally photosynthesis is co-limited by CO_2 diffusion through stomata pores and light-driven electron transport, which include the CO_2 supply and demand functions. The demand function is determined by the rate of processing CO_2 in the chloroplast (Lambers et al., 2008). Research reports that describe plants' responses to water availability and stress have pointed out that limiting CO_2 supply

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function (Chaves, 1991; Cronic, 2000) as well as changes in metabolic demand function (Flexas and Medrano, 2002) take place when plants subjected to water stress. Researchers reported different responses within plant species considering the main physiological target that limits the photosynthetic capacity of plants under water stress conditions (Flexas and Medrano, 2002; Flexas et al., 2004; Flexas et al., 2006; Lawlor and Tezara, 2009). The role of genotype combined to other environmental conditions is suggested to be a major factor that may lead to different kinds of responses observed among plant species (Lawlor and Tezara, 2009).

Changes in the biochemical demand function can be estimated by studying the relationship between the assimilation rate of CO_2 in leaves (A) and the CO_2 concentration in the intercellular space (C_i), as demonstrated by the biochemical gas exchange model of Farquhar et al. (1980). This model has become a common tool for estimating photosynthetic biochemical parameters of the intact leaf under a wide range of experimental conditions, including abiotic stresses (Flexas and Medrano, 2002; Lawlor and Cronic, 2002; Lambers et al., 2008). According to this model, in C_3 plants, carboxylation rates are limited by one of the following three processes: (1) the amount, activity and kinetics of Rubisco (Ribulose 1, 5-biphosphate carboxylase-oxygenase, (2) the RuBP (Ribulose 1, 5-biphosphate) regeneration supported by electron transport and (3) triose- phosphate utilization (TPU; Von caemmerer and Farquhar, 1981; Sharkey, 1985; Harley and Sharkey, 1991; Harley et al., 1992).

The cultivation of date palm (*Phoenix dactylifera* L.) constitutes one of the most successful agricultural activities in arid and semi-arid regions. Adaptation of date palm to water shortage is expected as it was one of the first fruit trees distributed and taken into cultivation in naturally dry lands. Date palm has a thick waxy cuticle, spines may constitute 1/5 - 1/4 of the pinnately compound leaf (depending on cultivar) and an efficient insulation of the growing point. On the other hand, trees successfully cultivated across a wide range of soil types are able to trap water in rapidly draining soil by their deep network of roots. These traits are examples of features that contribute to reduced evaporation and maximized water uptake, and are considered important in the adaptation of date palm to drought, salinity and high temperature (Nixon, 1951; Martin, 1992; Wickens, 1998; Zaid and de Wet, 2002; Ramoliya and Pandey, 2003; Djibril et al., 2005). On the other hand, wide range of variation at genetic as well as phenotypic traits was observed among date palm cultivars (Elshibli and Korpelainen, 2009a, 2009b), which can reveal also variation in adaptability to drought. However, most of research related to date palm's response to water availability has concentrated on the effects on yield performance and productivity. The main objective of undertaking this work was to examine the growth adjustments and photosynthetic CO_2 (Carbon dioxide) responses of date palm plants to water availability. The effect of genetic background at half-sib level of cultivar was also considered.

MATERIALS AND METHODS

Plant material and experimental design

Seeds of five date palm cultivars (half-sibs) were collected from two locations in the Northern State of Sudan. Initially, 100 seeds per cultivar were randomly collected. The cultivars Gondaila, Barakawi and Bitamoda were collected from the Nori Horticultural Orchard in Nori (18º32' 45" N; 31º54' 15" E), and Mishrig Wad Laggai (Laggai) and Mishrig Wad Khateeb (Khateeb) were collected from a farmer's orchard in Elbaoga (18º17' 45" N; 33º54' 30" E). Twenty seeds per cultivar were grown for germination in pure sand soil in an incubator for two months under temperature condition of 27ºC. Seedlings were individually transferred to plastic pots (2 L) filled with sand and peat (White Sphagnum Peat, H 1-3 von post) in a 1:2 by volume ratio. Seedlings were grown in the greenhouse at 27±2ºC, relative humidity about 65%, and photoperiod maintained at 12 h d^{-1} photoperiod, 800 $\mu mol\ m^{-2}\ s^{-1}$ light intensity.

Prior to experimentation, uniform, healthy, one-year- old plants of each cultivar were transferred to bigger plastic pots (7 L) containing a mixture of fertilized peat (White Sphagnum Peat, H 1-3 von post) and sand (3:1 by volume). Before the start of the water stress treatments, the plants were watered twice per week to field capacity. Plants were equally fertilized at different intervals during the growth experiment with N-P-K-ratio of 8-4-14. The water experimentation phase started in early May, 2006. A randomized complete block design with two factors consisting of five cultivars and four watering regimes (10%, 25%, 50% and 100% field capacity) was established. Each treatment was replicated four times. Plants were weighed and watered twice a week in the morning to compensate for water loss at each treatment. The pots were enclosed in plastic bags at soil level to minimize evaporation from the soil surface. To avoid errors due to possible differences in growth conditions in the greenhouse, the plants were circulated once every 2-3 weeks.

Gas-exchange measurements

Gas exchange measurements were carried out using CIRAS2 portable photosynthesis measurement system (PP Systems, Hitchin, Hertfordshire, UK) during early October 2006. Leaf temperature was adjusted to 25ºC. Light intensity was adjusted to above plant light saturation capacity at 1,000 µmol m^{-2} s^{-1}, provided by Tungsten Halogen light source. For each of the four tested plants in each treatment CIRAS2 was set to provide five observations per measurement per each level of external supply of CO2. Net photosynthesis and other parameters were measured from the upper fully expanded leaf of each plant. Sampled leaves within each plant were always of the same age and similar position. The A:C_i measurements started at a CO_2 concentration close to ambient (350 ppm) and continued down to 50 ppm through four steps, increased back to 350 ppm, after which the leaf was allowed to acclimate for five minutes, and then up again to about 1,500 ppm in four steps. At each step, gas exchange variables were recorded after achieving steady-state conditions (240 s and 180 s for stabilizing and recording, respectively).

The photosynthetic curves plotted against intercellular CO_2 concentration (A/Ci curves) were analysed to estimate the maximum rate of RUBP carboxylation (V_{max}) and the maximum rate of electron transport (J_{max}), which in turn drives RUBP regeneration. V_{max} and J_{max} were together estimated by applying the A-Ci data to the model proposed by Farquhar et al. (1980), and subsequently modified (von Caemmerer and Farquhar, 1981; Sharkey, 1985; Harley and Sharkey, 1991; Harley et al., 1992) using Photosynthesis Assistant software (Dundee Scientific, Dundee, Scotland, version 1.2 2007), where the best fit was solved by minimizing the parameters to produce a minimum sum of squares for the difference between experimental and model data.

Statistical analyses

Analysis of variance (ANOVA) was used to analyse the morphological adjustments (traits in Table 1) that take place in response to water treatments, and as affected by cultivar and their interactions.

ANOVA was also used to analyse the effects of the tested cultivars, amount of irrigation water and external supply of C_a on photosynthesis and photosynthetic parameters; stomatal conductance (g_s) and C_i. A stomatal limitation index (Sage, 1994; Drake et al., 1997) was estimated by calculating the C_i/C_a ratios across all water treatments. Two-way ANOVA was performed to test the interaction effect of water availability and C_a on photosynthesis. Comparisons between means were conducted by Duncan test, except for the external supply of C_a, where Bonferroni adjustments method for multiple comparisons was used (Chan, 2003). ANOVA was also used to test the differences among the photosynthetic biochemical parameters (V_{max} and J_{max}) of date palm plants in response to irrigation water, where three replications were considered. Logarithmic transformation was applied to the data of the photosynthetic parameter C_i which enabled the run of ANOVA under the normal distribution of the variable. Pearson's correlations were also performed for some variables. All tests for descriptive statistics and data exploration were performed using SPSS 15.0 (SPSS Inc., Chicago, IL, USA).

Table 1: The significance of the effect of different treatments (water, cultivar and their interactions) on morphological traits of the studied plants

Morphological trait	ANOVA P		
	Water treatments	Cultivar	Cultivar×water interaction
Plant height (m)	<0.001	n.s*	< 0.01
Root fresh weight (g)	<0.001	n.s	n.s
Shoot fresh weight (g)	<0.001	n.s	n.s
Root dry weight (g)	<0.05	n.s	< 0.05
Shoot dry weight (g)	<0.001	n.s	n.s
No. of green leaves	<0.001	n.s	n.s
No. of dry leaves	<0.001	n.s	n.s
No. of pinnae	<0.001	n.s	n.s
Root/shoot ratio	n.s.	n.s	n.s
Total biomass (g)	<0.001	n.s	n.s

*n.s: Not significant

RESULTS

Growth and morphology

Water treatments greatly affected the performance of the tested plants and most of the tested traits showed significant adjustment to water availability (Table 1). The reduction in growth traits was visible mainly at water levels of 25% and/or 10% of FC (Fig. 1). The increase in the number of dry leaves is negatively correlated to the number of green leaves, which mean dry leaves are not replaced by new leaves in the same rate. Although there was no significant differences in growth performance among cultivars, cultivar-water interaction effect was observed for plant height ($p \leq 0.01$) and root dry weight ($p \leq 0.05$) (Table 1).

Photosynthesis and gas exchange

Stomatal conductance was significantly ($P \leq 0.001$) affected by water availability mainly at 25% and 10% FC. Stomatal conductance, showed only a slight decrease in response to increasing external supply of C_a from 350 ppm to 1,500 ppm at each water level including 25% and 10% FC (Fig. 2a). The pattern of C_i concentration continued increasing up to the higher tested level of C_a (Fig. 2b) and resulted in higher C_i/C_a ratios at elevated levels of C_a than at ambient C_a (350 ppm). The mean C_i/C_a ratios at 350 ppm were 0.3 at 100% FC and 0.4 at 50% FC, with approximately equal amounts of photosynthesis (5.2 µmol$m^{-2}s^{-1}$). Consequently, the increasing C_a significantly ($p \leq 0.001$) increased the net photosynthesis of the intact leaves of date palm plants (Fig. 3), with a significant gas-water interaction effect ($p \leq 0.001$). However, the amount of irrigation water significantly ($p \leq 0.001$) affected the photosynthetic

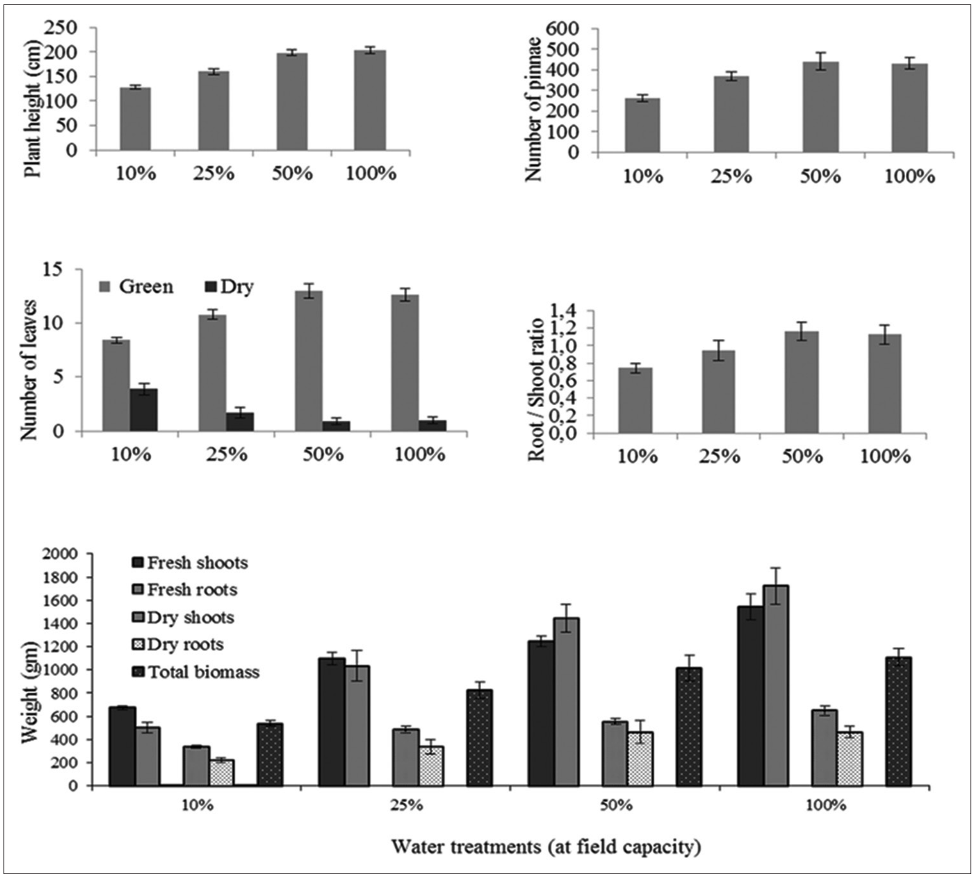

Fig 1. Morphological adjustments in date palm plants to water availability. Values are means ± SE.

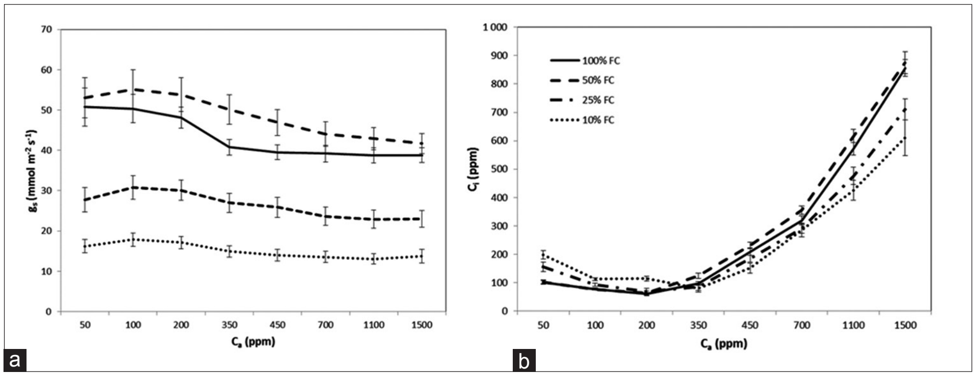

Fig 2. Combined effect of external supply of CO$_2$ (C_a) and water treatments on a) stomatal conductance (g_s) and b) substomatal CO$_2$ concentration (C_i). Water treatments measured at field capacity (FC). Values are means ± SE.

capacity of the plants (Fig. 4). Water supply at 25% and 10% FC significantly decreased photosynthesis ($p \leq 001$; Duncan test) compared to other treatments. Yet, there was no significant mean difference in photosynthesis at water FC of 100% and 50%. Changing water availability resulted in significant ($p \leq 0001$) changes in stomatal conductance among cultivars (Fig. 4) including significant cultivar-water interaction effect on photosynthesis ($P \leq 0001$).

The A/C_i curves of the four levels of water supply are presented in Fig. 5. At 100% (Fig. 5a) and 50% FC (Fig. 5b), the photosynthetic rate of the tested plants was clearly limited by RUBP regeneration. The inflection point ($C_{i\text{—inflection}}$), the Ci value where the Rubisco- and electron transport-limited portion of the curve intersects, increased as water stress increased. The increase in the $C_{i\text{—inflection}}$ reached high levels of C_i equaling around 85 Pa at 25% FC (Fig. 5c). At 25% and 10% FC (Fig. 5d), photosynthesis was found strongly driven by RUBP carboxylation. V_{max} and J_{max} were highest at 100% FC (Fig. 6). Reducing water availability to 25% and 10% FC tended to reduce both parameters, although the reduction was more pronounced

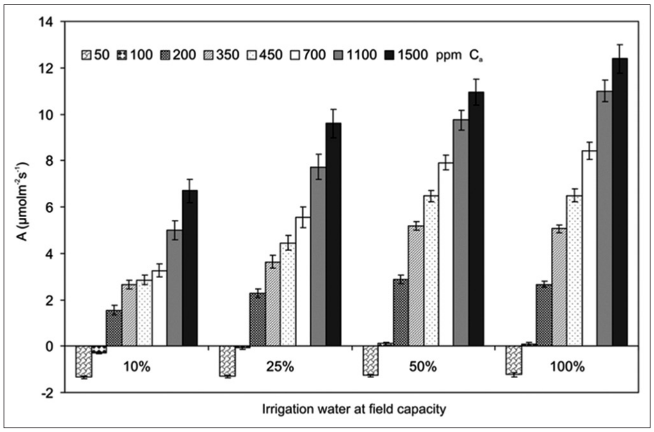

Fig 3. Combined effect of water treatments and external C_a supply on mean photosynthesis (A). Values are means ± SE (n=20). The overall values of photosynthesis are significantly different at each level of C_a (Bonferroni adjustments, $p < 0.05$).

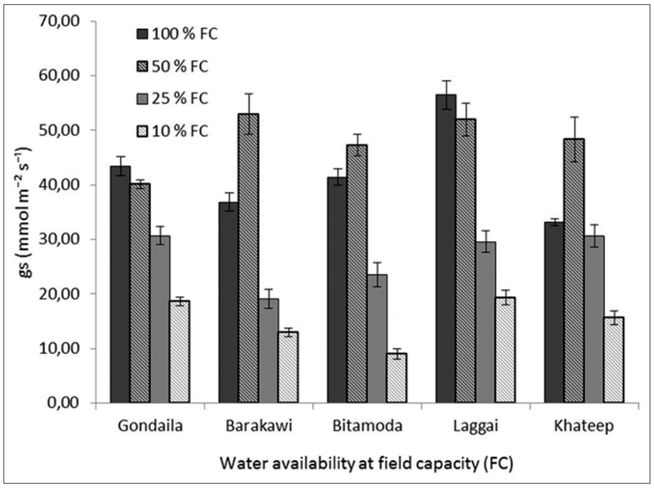

Fig 4. Stomatal conductance (gs) responses as affected by water availability and cultivar background. Values are means ± SE.

in V_{max} compared to J_{max}. A strong correlation was observed between J_{max} and V_{max} ($r^2 = 0.871$; $p \leq 0.01$, Pearson correlation), as also in a linear regression relationship ($r^2 = 0.884$) across all water treatments.

DISCUSSION

Growth and morphology

Reduced irrigation water in the tested date palm plants resulted in multiple changes in plant growth and morphology, the changes being most pronounced at 10% and/or 25% of field capacity (Fig. 1). The observed increase in the number of dry leaves – which are not replaced by new leaves in the growth rate - indicated one of the drought adaptive mechanisms, accelerated leaf senescence, which contributes to plant survival under drought stress and allows remobilization of nutrients from senescing leaves to young leaves; thus reduction in water loss at the whole plant level is achieved (Munne-Bosch and Alergre, 2004) in combination with the reduced number of green leaves and leaflets. It is worth mentioning that dead or senescent leaves of date palm trees are not shed and do not drop on their own, but are removed under cultivation. The normal lifespan of date palm leaves ranges from 3 to 7 years, depending on the variety, age and environmental conditions (Zaid and de Wet, 2002). The non-significant changes in the root: Shoot ratio, on the other hand, indicates the balanced carbohydrate allocation among the adjusted green top and roots of the tested plants (Harris, 1992).

Photosynthesis and gas exchange

For ambient C_a (350 ppm), the C_i/C_a ratio for the studied date palm plants, across all water treatments, was lower than the expected values of C_i/C_a ratio for C_3 plant species (Wong et al., 1979; Drake et al., 1998). As there is no available previous similar data for date palms in general, this result needs to be validated, especially under natural conditions of date palm culture. The values of C_i/C_a ratios of some plant species have been found to vary greatly between different growth conditions, for example, field versus greenhouse (Bunce, 2005). However, date palms may possess a specific strategy for gas exchange and photosynthetic metabolism, perhaps as it is a monocotyledonous desert tree.

The reduction of g_s by 30% at 10% FC compared to 100% did not affect the increasing pattern of C_i/C_a ratio of elevated CO_2 when compared to that of 350 ppm. Apart from the g_s effect, the increase in C_i/C_a might resulted from CO_2 that evolves from leaves due to the maintenance of light respiration (Haupt-Herting and Fock, 2002; Lawlor and Tezara, 2009), as a result of inhibition of photosynthetic metabolism affected directly by water stress (Farquhar et al., 1982; Lawlor and Tezara, 2009). Although photosynthesis was lower at 25% and 10% FC when compared to other treatments, the continuous increase in C_i (Fig. 2b) was accompanied by a comparable increase in photosynthesis (Fig. 3), which confirms the non-absolute stomatal inhibition of photosynthesis (Drake et al., 1997; Tezara et al., 1999; Haupt-Herting and Fock, 2002). The non-absolute stomatal limitation and utilization of both kinds of limitations tactic in response to water stress was reported in different plant species (Pankovic et al., 1999; Lawlor, 2002; Tezara et al., 2002, 2003) and have been considered as a strategy allowing drought-stressed plants to escape photo-damage by down-regulating photosynthesis (Pankovic et al., 1999; Maroco et al., 2002). Some researchers have suggested that the continuous increase in photosynthesis with C_i may also include partial re-assimilation of the evolved photo-respiratory CO_2, which is considered to maintain the carbon flux and the enzymatic substrate turnover, and enables the plants

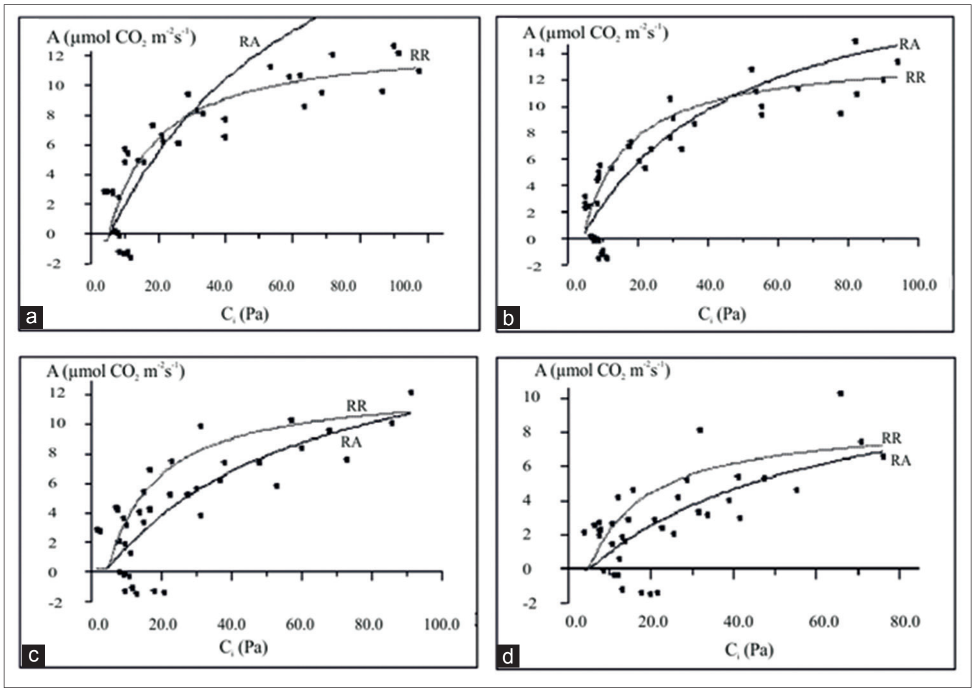

Fig 5. Response curve patterns of photosynthesis (A) in µmolm^{-2}s^{-1} versus C_i in Pascal (Pa) of the tested date palm plants as affected by different water levels; (a) 100%, (b) 50%, (c) 25% and (d) 10% field capacity. Biochemical factors RR assigned for RUBP regeneration and RA for Rubisco activity.

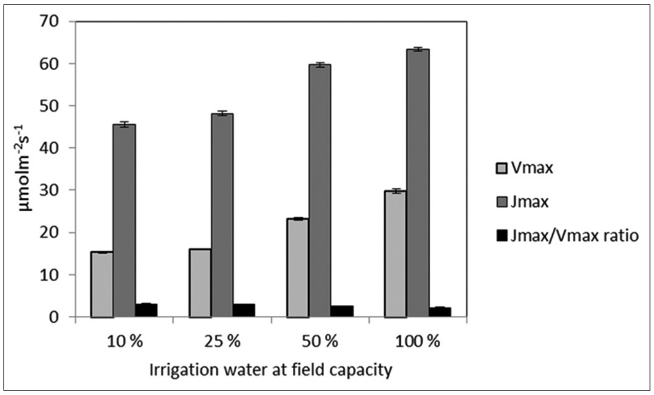

Fig 6. Responses of date palm plants to different water levels in terms of V_{max}, J_{max} and J_{max}/V_{max} ratio. Values are means ± SE.

to recover rabidly after re-watering (Haupt-Herting and Fock, 2002).

Metabolic impairement at water scarcity was apparent in the reduced V_{max} and J_{max} (Fig. 6). The changes in V_{max} and J_{max} resulted in an increasing J_{max}/V_{max} ratio, coupled with a shift in the $Ci_{inflection}$ of A/Ci curve to higher CO_2 concentrations (Fig. 5). This situation indicated that as water stress increases, the photosynthetic rate of date palm plants tends to be more dependent on CO_2 concentration (Bernacchi and Morgan, 2005; Onoda et al., 2005). Therefore, a greater stimulation of photosynthesis was observed with increasing CO_2 supply function, with water interaction effect. Manter and Kerrigan (2004) have observed in some woody plant species that when light is saturating, the actual rates of CO_2 assimilation are limited by the amount, activity and kinetics of Rubisco more often than electron transport rates, a situation detected when $C_i < C_{i—inflection}$. The differences observed in A/Ci responses of date palm plants at water level of 10% FC compared to non-stressed plants suggest a strategic shift from RUBP regeneration limitation (100% and 50% FC) to RUBP carboxylation limitation, however, some other factors may also play a role at limiting Rubisco activation (Manter and Kerrigan, 2004). The changes in the J_{max}/V_{max} ratio observed in this study were within the range of values reported by Wullschleger (1993), V_{max} from 6 to 194 µmol m^{-2} s^{-1}, and J_{max} from 17 to 372 µmol m^{-2} s^{-1} across 109 plant species with a strong correlation between these two parameters. According to Onoda et al. (2005), this relationship can be linearly presented across a range of woody plant species with $r^2=0.827$. Compared to our results $r^2=0.884$ across different water treatments, indicating that CO_2 assimilation is regulated in a coordinated manner by these two processes (Wullschleger, 1993).

The cultivar-water interaction effect in photosynthesis and in some growth parameters (Table 1) may indicate a stronger role among cultivars if the full sip conditions proposed. Although weak genetic differentiation was observed within Sudanese date palm cultivars at molecular bases including the four tested ones (Elshibli and Korpelainen, 2008), yet significant genetic differentiation was apparent when these cultivars grouped at phenotype level (Elshibli and

Korpelainen, 2009b). Generally, the unrevealed genetic bases of date palm cultivars or genotypes regarding the distinct growth and fruit traits point out that lots of research work need to be considered.

CONCLUSION

The morphological adjustments to water availability that was observed in this study can be further considered for heritability analysis to confirm their role as adaptive traits in response to drought condition. On the other hand, the revealed adjustments of biochemical reactions in the studied date palm plants can be featured mainly by the non-absolute stomatal limitation. Research that consider less water availability than the tested levels, higher levels of photosynthetic CO_2 enrichment as well as evaluation of date palm performance under long-term CO_{2-}elevated environments may add valuable knowledge regarding date palm adaptation to drought and many other related climate change issues. Experimentation under natural field conditions including water stress levels will validate and confirm the findings in our greenhouse study. The findings in this study also enrich research questions regarding the role of the existing range of date palm genotypes in response to challenging environmental conditions.

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Author contributions

S. E. designed and conducted all of the experiment, performed data collection and partial analysis and prepared the whole manuscript. E. M. E. involved intensively in data management and analysis and supported application of the data to the biochemical model. H. K. supervised the research and reviewed the manuscript.

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