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Response of Three Accessions of Jordanian *Aegilops crassa* Boiss. and Durum Wheat to Controlled Drought

Amal M. Harb* and Jamil N. Lahham

Department of Biological Sciences, Faculty of Science, Yarmouk Univeristy. Irbid, Jordan.

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Abstract

Drought is a major abiotic stress that is threatening the production and the survival of many crops such as cereals. The response of three *Aegilops crassa* accessions (C1, C2 and C3) that inhabit areas with different rates of rainfall and durum wheat to controlled drought (with soil moisture of 50% field capacity) was tested in terms of changes in: relative water content, chlorophyll content, chlorophyll fluorescence and biomass accumulation. At the end of drought treatment, a slightly significant decrease in relative water content (RWC) was shown in two *Ae. crassa* accessions (C2 and C3). RWC of C1 accession and durum wheat showed no change. In all *Aegilops* accessions and durum wheat, the effect of drought on chlorophyll content and chlorophyll fluorescence was minimal. A differential response to drought in terms of biomass accumulation was revealed. *Ae. crassa* C2 and C3 accessions that are adapted to semiarid and arid areas, respectively, showed no significant difference in their biomass under drought stress. The biomass of C1 accession that is adapted to well-watered area was significantly decreased. A highly significant decrease in biomass was also shown in durum wheat. Hence, C2 and C3 accessions of *Ae. crassa* are promising genetic sources for the genetic engineering of drought tolerant wheat plants. Future understanding the molecular basis of how drought-tolerant *Aegilops* species respond to drought stress, can be one of the approaches to improve drought tolerance in wheat.

Keywords: Controlled drought, *Ae. crassa*, durum wheat, biomass, acclimation.

1. Introduction

Being sessile, plants are susceptible to environmental changes. Drought is a major abiotic stress, which challenge crop production and plant survival. Large body of information has been gained from studies of abiotic stress in the model plants Arabidopsis and rice at physiological, biochemical and molecular levels (Ingram and Bartels, 1996; Bartels and Sunkar, 2005; Shinozaki and Yamaguchi-Shinozaki, 2007; Nakashima *et al.*, 2009). However, still a lot need to be learned about the complexity of plant interaction with the surrounding environment.

Drought can be chronic in semiarid and arid areas with low water availability, or random and unpredictable due to weather changes during the growing season. Drought problem is exacerbating, due to global warming and climate change, in addition to the increasing demands of water for many purposes including agriculture. Therefore, studying the response of crop plants to drought will enhance our understanding of this problem. In addition, the screening of natural variations is a promising approach to harness traits that fit the changing environments (Nevo and Chen, 2010).

Wild relatives of cultivated crops that are distributed in a wide climatic range are valuable genetic sources for the improvement of economic crop plants. *Aegilops* (goatgrass) belongs to Poaceae and is well known as the wild relative of wheat. Indeed, bread wheat (*Triticum aestivum*) resulted from the hybridization between wheat and *Aegilops* (Dvorak *et al.*, 1998; Hedge *et al.*, 2000; Faris *et al.*, 2002; Petersen *et al.*, 2006). Hence, *Aegilops* is considered as the progenitor of wheat. Twenty-three *Aegilops* species were identified (Kilian *et al.*, 2011). Eleven species are diploids and 12 are allopolyploids. *Aegilops* plants exist with different types of genomes: A, B, D and G (Kimber and Feldman, 1987). *Aegilops* species are distributed in southwestern Asia. *Aegilops* is considered as a Mediterranean plant (Hegde *et al.*, 2002). It was shown that *Aegilops* species inhabit warm areas with short winter and hot and dry summer (Baalbaki *et al.*, 2006).

Ae. crassa is distributed in different parts of Asia: Iran, Iraq, Afghanistan, Kazakhstan, Kyrgyzstan, Syria, Turkmenisatn, Usbekistan, Tajikistan, Turkey, Jordan and Lebanon (Kilian *et al.*, 2011). *Ae. crassa* is considered

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* Corresponding author. e-mail: harbhope78@gmail.com.

drought tolerant species because it grows in areas with 150 - 350 mm rainfall (Kilian *et al.,* 2011).

At all stages of their development, plants are exposed to different environmental stresses. Both the developmental stage and the severity of drought were found to play crucial role in plant response to stress (Blum *et al.,* 1980; Harb *et al.,* 2010). No correlation was found between the response of wheat grains and the photosynthesizing seedling when exposing these stages to osmotic stress induced by polyethylene glycol (PEG) (Blum *et al.,* 1980). Therefore, one cannot extrapolate results about stress response from one developmental stage to another, which necessitates independent studies of stress response for each developmental stage.

The performance of *Aegilops* species under soil drought were evaluated in different areas (Farooq and Azam, 2001; Baalbaki *et al.,* 2006; Colmer *et al.,* 2006). Response of some Lebanese *Aegilops* species and accessions to drought was tested; *Ae. geniculata* and *Ae. markgrafii* were found to be the most drought tolerant species (Baalbaki *et al.,* 2006). In another study, utilizing gas exchange parameters (photosynthesis and stomatal conductance) to evaluate drought tolerance in some Hungarian *Aegilops* species indicated that *Ae. tauschi* and *Ae. speltoides* were shown to be drought tolerant. These two species showed high stomatal conductance and CO_2 fixation at low water potential, which was measured in terms of plant relative water content (RWC) (Molnar *et al.,* 2004). Biochemical evaluation of drought response of two accessions of *Ae. biuncialis* revealed different strategies of drought tolerance (Czovek *et al.,* 2006). All previous studies demonstrate the potential of *Aegilops* species and accessions as rich reservoir for stress resistance genes towards wheat improvement (Schneider *et al.,* 2008). Indeed, screening *Aegilops* plants for abiotic stress resistance is the first step in the mining process for stress responsive genes towards the improvement of wheat for high yield under stress conditions.

In the present study, acclimation efficiency of *Ae. crassa* accessions collected from areas that differ in the rate of rainfall under controlled drought compared to that of durum wheat was tested. Acclimation efficiency was evaluated in terms of biomass accumulation at the end of drought treatment.

2. Materials and Methods

2.1. Plant Material

Grains of three *Ae. crassa* accessions were collected from areas with different rainfall rate in Jordan during the summer of 2011 (Table 1). One accession (C1) is grown in area that is considered well-watered with rainfall 300 - 600 mm. The second one (C2) is grown in a semiarid area with rainfall 150 - 300 mm. The third accession (C3) is grown in an arid area with rainfall 50 - 200 mm. Grains were harvested and properly stored. In addition, grains of durum wheat (*Triticum durum* Desf. cv. Haurani 27) were provided by the National Center for Agriculture Research and Extension (NCARE)/Jordan.

2.2. Plant Growth Conditions

Grains of *Ae. crassa* and durum wheat were surface sterilized by 5% Chlorox and washed with distilled water for several times. Sterile grains were kept in 9 cm plates on wet filter paper. Plates were wrapped with aluminum foil and kept for 5 days at 4ºC for dormancy breakage. After that, grains were kept to germinate at 25ºC. After 2 days of germination, seedlings were transferred to pots of capacity of 150 g filled with soil mix of 1:1:2 (loam: peatmoss: sand). Seedlings were kept to grow under six white fluorescent lamps for 16 hrs and temperature of 20 ± 2ºC.

2.3. Drought Treatment

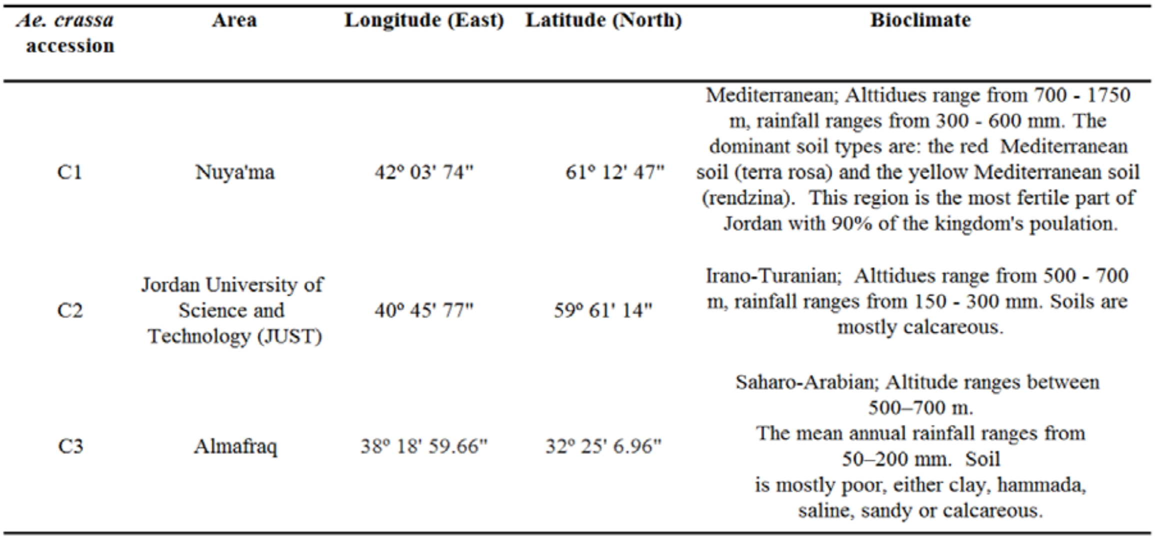
At 2-leaf stage, plants were grouped into 8 plants of the control (well-watered 100% Field capacity (FC)) and 8 plants of the drought-treated (50% FC). Watering was withheld for the drought treated group. Soil water moisture was monitored until it reached 50% FC. After that, pots were weighed daily and soil water content was adjusted to final weight based on calculation using EXCEL software. Final weight that gives 50% FC was calculated as follows:

FC = (Wet soil wt - Dry soil wt)/ (Dry soil wt - pot wt)*100

50% FC = 0.5 * FC

Wt of soil and pot at 50% FC = ((1 + 50 % FC)* Dry soil wt) - (50% FC * pot wt)) (Harb *et al.*, 2010)

Table 1. Areas of collection of *Ae. crassa* with their geographic location and bioclimate



Ae. crassa accession	Area	Longitude (East)	Latitude (North)	Bioclimate
C1	Nuya'ma	42º 03' 74"	61º 12' 47"	Mediterranean; Alttidues range from 700 - 1750 m, rainfall ranges from 300 - 600 mm. The dominant soil types are: the red Mediterranean soil (terra rosa) and the yellow Mediterranean soil (rendzina). This region is the most fertile part of Jordan with 90% of the kingdom's poulation.
C2	Jordan University of Science and Technology (JUST)	40º 45' 77"	59º 61' 14"	Irano-Turanian; Alttidues range from 500 - 700 m, rainfall ranges from 150 - 300 mm. Soils are mostly calcareous.
C3	Almafraq	38º 18' 59.66"	32º 25' 6.96"	Saharo-Arabian; Altitude ranges between 500–700 m. The mean annual rainfall ranges from 50–200 mm. Soil is mostly poor, either clay, hammada, saline, sandy or calcareous.

2.4. Determination of Relative Water Content (RWC)

After 10 days of 50% FC drought treatment, segments of the third fully expanded leaves of 6 drought-treated and 6 well-watered plants were taken and their fresh weight (FW) was measured. After that, they were soaked in water and kept in water at 4ºC for 16 hrs. After soaking, segments were weighed to determine their turgid weight (TW). Then, segments were dried at 80ºC for 2 days and their dry weights (DW) were measured. RWC was calculated as follows:

RWC% = (FW- DW)/ (TW - DW)*100

2.5. Determination of Cut Leaf Water Loss (CLWL)

After 10 days of 50% FC drought treatment, the second leaves were excised from 6 drought-treated and 6 well-watered plants, and their fresh weight was measured. Leaves were kept to dehydrate under growth room conditions (Temperature of 20 ± 2ºC) for 2 hrs and then their weight was measured. Dry weight was measured after drying plant samples in oven at 80ºC for 2 days. CLWL was calculated as follows:

CLWL% = (W0-Wt)/ (W0-Wd)*100

W0: Initial weight (fresh weight)

Wt: Weight after dehydration period (2 hrs in this experiment)

Wd: Dry weight

2.6. Chlorophyll Quantification

Samples from the third fully expanded leaves of 5 drought-treated and 5 well-watered plants were used for the quantification of chlorophyll after 10 days of 50% FC drought treatment. Chlorophyll (Chl) was extracted in 80% acetone solution. Absorbance was determined at 663 nm and 645 nm and Chl a, Chl b and total Chl were calculated as shown in the following equations:

mg Chl a/ g fresh tissue wt = (12.7*A663 - 2.69 *A645)* V/1000 * wt

mg Chl b/ g fresh tissue wt = (22.9*A645 - 4.68*A663)* V/1000 * wt

mg total Chl / g fresh tissue wt = (20.2*A645 + 8.02 *A663)* V/1000 * wt

V: final volume of 80% acetone used in the extraction of chlorophyll.

2.7. Chlorophyll Fluorescence Measurements

The quantum efficiency of photosystem II (YII) was determined using OS1p chlorophyll fluorometer (Opti-Science, USA). Measurements were made on the youngest fully expanded leaves of the well-watered control and the drought-treated (50% FC) plants. YII was measured for 8 plants per treatment per accession.

2.8. Fresh Weight and Dry Weight Determination

After 10 days of 50% FC drought treatment, 3 – 8 plants of the treated and the control groups were harvested and their fresh weight was measured. After that, they were kept into an oven to dry at 80ºC for 2 days and their dry weights were measured.

2.9. Statistical Analysis

All data were analyzed by Student's - T test. Differences with *p*-value less than 0.05 were considered significant.

3. Results

3.1. Changes in Relative Water Content in Response to Drought

The effect of drought treatment (Fig. 1) on the water status of plants in terms of relative water content (RWC) was diagramed. No significant differences occurred in RWC between the drought-treated and the well-watered control in each of *Ae. crassa* accession C1 and durum wheat (*P* = 0.3 and 0.6, respectively) (Fig. 2A). However, a significant decrease (*P*=0.04) in RWC was shown in leaves of C2 and C3 of *Ae. crassa* accessions (Fig. 2A).

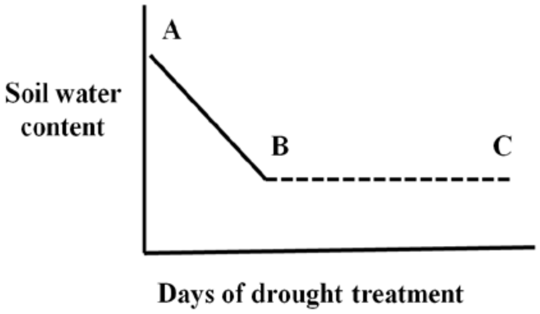


Figure 1. Schematic illustration of the drought treatment. A. Watering was withheld at two true leaf stages. B. Soil water content reached 50% of field capacity (FC). Then, pots were weighed daily and their weights were adjusted to keep soil water content 50% FC for 10 days. C. Drought treatment was terminated and plants were harvested for the physiological, biochemical and morphological analyses.

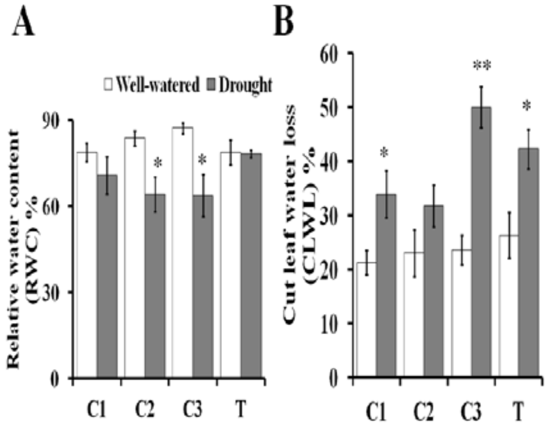


Figure 2. Physiological response of plants to drought. A. Relative water content (RWC) of *Ae. crassa* accessions (C1, C2 and C3) and durum wheat (T) under drought compared to the well-watered control. B. Cut leaf water loss (CLWL) of *Ae. crassa* accessions (C1, C2 and C3) and durum wheat (T) under drought compared to the well-watered control. * represents significant difference ≤ 0.05 and ** represents significant difference ≤ 0.01.

3.2. The Effect of Drought Pretreatment on the Cut Leaf Water Loss under Dehydration

To test the effect of controlled drought pretreatment on water loss under dehydration, The cut leaf water loss (CLWL) was determined for all accessions under two treatments (drought and well-watered). *Ae. crassa* accession C1 and durum wheat plants that were drought-treated have significantly higher water loss than the well-watered control (*P* =0.04 and 0.02, respectively) (Fig. 2B). Drought-treated plants of *Ae. crassa* accession C3 showed a highly significant water loss compared to the well-watered (*P* = 0.0007) (Fig. 2B). No significant change in CLWL appeared in *Ae. crassa* accession C2 (*P* = 0.2) (Fig. 2B).

3.3. Chlorophyll Content in Response to Drought

It is known that chlorophyll quantity decreases under drought treatment and this effect is correlated with the severity of drought. To test the effect of controlled moderate drought on chlorophyll quantity, chlorophyll content of the drought-treated and the well-watered plants was determined. For all *Ae. crassa* accessions and durum wheat, no significant differences in chlorophyll a and b and the total chlorophyll content between the drought-treated and the well-watered were shown (Table 2).

Table 2. Chlorophyll a, b and total chlorophyll content (µg/ g fresh weight) of *Ae. crassa* accessions (C1, C2 and C3) and durum wheat under drought compared to the well-watered control.

Plant	Control			Drought		
Genotype *Ae. Crassa*	Chl a	Chl b	Total Chl	Chl a	Chl b	Total Chl
C1	2.35 ± 0.53	1.41 ± 0.30	3.75 ± 0.82	2.23 ± 0.64	1.33 ± 0.42	3.55 ± 1.06
C2	1.98 ± 0.81	1.42 ± 0.60	2.10 ± 0.70	1.88 ± 0.16	1.33 ± 0.18	3.21 ± 0.31
C3	2.37 ± 0.54	1.24 ± 0.23	3.61 ± 0.78	1.41 ± 0.24	0.74 ± 0.12	2.16 ± 0.34
T. durum	2.00 ± 0.24	1.33 ± 0.30	3.33 ± 0.45	3.10 ± 0.80	1.45 ± 0.33	3.44 ± 0.33

Values are the means ± standard error (n = 4 – 5).

3.4. The Effect of Drought on Chlorophyll Fluorescence

Under drought stress, the efficiency of photosystem II (PSII) is decreased depending on the nature and the severity of drought treatment. Therefore, the quantum efficiency of PSII (YII) of the drought-treated and the well-watered plants was measured. For all accessions, there was no significant difference in YII between the drought-treated and the well-watered control (Fig. 3). However, under drought stress YII of *Ae. crassa* accession C3 was significantly higher than that of C1 accession and durum wheat (*P* = 0.02 and 0.04, respectively) (Fig. 3).

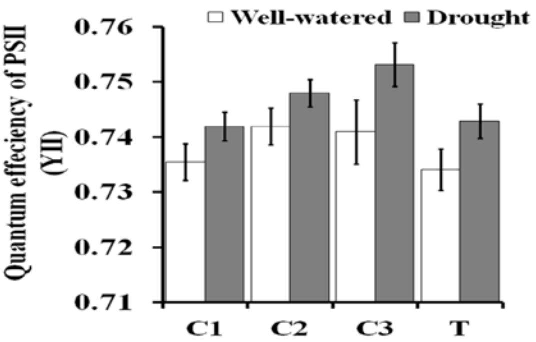


Figure 3. The effect of drought on the quantum efficiency of PSII (YII) of *Ae. crassa* accessions (C1, C2 and C3) and durum wheat (T) under drought compared to the well-watered control.

3.5. Changes in Fresh and Dry Weight under Drought

The outcome of drought stress will be manifested as a change in plant's biomass. Therefore, fresh and dry weights of plants were measured for the drought-treated and the well-watered plants. Both fresh weight and dry weight of *Ae. crassa* accession C1 were significantly reduced (*P*= 0.01 and 0.03, respectively). For C2 accession, the reduction in fresh weight in response to drought was highly significant, whereas no significant change was shown in the dry weight (*P*= 0.009 and 0.12, respectively). Plants of C3 accession showed no significant change in fresh and dry weight (*P*= 0.1 and 0.2, respectively). In durum wheat, the reduction in fresh and dry weight was highly significant in the drought-treated plants compared to the well-watered ones (*P*= 0.01 and 0.0008, respectively) (Fig. 4).

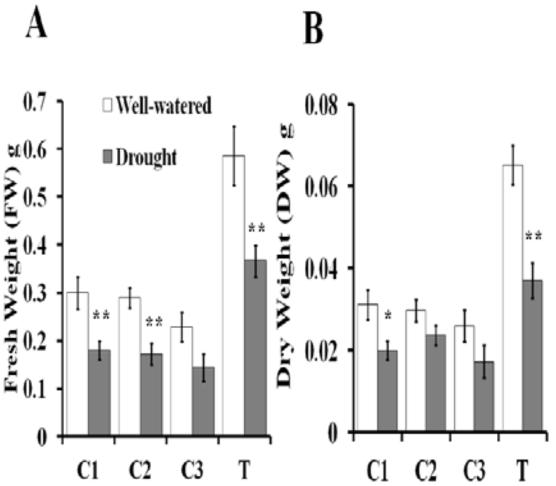


Figure 4. The effect of drought on plants growth. A. Fresh weight (FW) in grams of *Ae. crassa* accessions (C1, C2 and C3) and durum wheat (T) under drought compared to the well-watered control . B. Dry weight (DW) in grams of *Ae. crassa* accessions (C1, C2 and C3) and durum wheat (T) under drought compared to the well-watered control. * represents significant difference ≤ 0.05 and ** represents significant difference ≤ 0.01.

Discussion

Plant water status is a good indicator of plant performance under drought stress. In two maize hybrids, progressive drought for 9 days resulted in a significant decrease in RWC of the two hybrids (Medici *et al*., 2003). In four bread wheat cultivars, rainfed plants showed reduced RWC compared to the irrigated control (Sarker *et al*., 1999). In *Aegilops* and wheat, severe drought resulted in a significant reduction in RWC (Molnar *et al*., 2004; Keyvan, 2010). In one accession of *Ae. bicornis* adapted to area with rainfall of 75-275 mm, progressive drought resulted in slow decrease in RWC, which led to a fast stomatal closure and reduction of photosynthetic efficiency (Dulai *et al*., 2006). In the latter study, two other *Aegilops* species adapted to arid regions (*Ae. tauschii* and *Ae. speltoides)* showed differential response to progressive drought in terms of change in RWC. Their RWC was drastically decreased, but they kept high stomatal conductance even at 70% RWC. In the present study, *Aegilops* and wheat plants showed differential response to controlled moderate drought. Two *Ae. crassa* accessions C2 and C3 slightly decreased their RWC under moderate drought, whereas C1 accession and durum wheat showed no change in their RWC. Reduction of RWC under drought stress could be drought tolerance strategy to alleviate the detrimental effect of drought on plant's growth (Price *et al*., 2002). Reduction of RWC increases the internal osmotic potential, and consequently protects plants against water loss. This is consistent with the strategy adopted by one accession of *Ae. biuncialis* that inhabits areas with 550 mm annual rainfall (Molnar *et al*., 2004). In this accession of *Ae. biuncialis*, the reduction in RWC did not affect its performance under mild and severe osmotic stress. Indeed, it showed a better performance under stress conditions in terms of CO_2 assimilation and biomass compared to accessions adapted to areas with high rainfall rate. Moreover, progressive drought under greenhouse conditions resulted in the reduction of the RWC of this accession without affecting its yield (Molnar *et al*., 2004).

The response of plants to dehydration can be by reducing water loss through stomatal closure to avoid the detrimental effects of dehydration, or by tolerating low internal water content because of fast water loss (Levitt, 1980). In this study, CLWL of *Ae. crassa* accession C1 and C3 and durum wheat was significantly increased in the drought-treated plants compared to the well-watered ones. This is inconsistent with a study in natural accessions of *Arabidopsis* as for many accessions no change in CLWL between the two treatments was shown while other accessions reduced their CLWL under drought treatment as a strategy to avoid drought stress (Bouchabke *et al*., 2008).

The effect of drought on plant photosynthesis can be shown as a decrease of CO_2 diffusion due to stomatal closure, or by impeding metabolites regeneration during photosynthesis (Prasad *et al*., 2008). Chlorophyll fluorescence as a method of evaluation of plants response to drought stress is well known (Sayed, 2003). It was used for the evaluation of the performance of many crops: barley, oat, rice, sorghum and maize under different environmental stresses including drought (Sayed, 2003). Drought stress that led to RWC of 40% had no effect on dark and light adapted PSII activity in tomato and potato plants (Havaux, 1992). In two accessions of *Ae. biuncialis*, osmotic stress of -1.8 MPa resulted in a significant decrease in the quantum efficiency of PSII (YII) (Molnar *et al*., 2004). This decrease in YII did not affect the biomass of these accessions, whereas for the third accession the biomass was decreased without any change in its YII. In this study moderate controlled drought did not affect the quantum efficiency of PSII, but a significant increase in YII was shown in *Ae. crassa* accession C3 under drought compared to durum wheat. This might suggest a mechanism adopted by this accession to keep almost normal growth under drought stress.

Environmental stresses such as drought affect chlorophyll synthesis and consequently chlorophyll content in plants. In a study on 157 accessions of *Ae. geniculata*, some accessions reduced their chlorophyll content when exposed to drought stress in the field (Zaharieva *et al*., 2001). This was explained as a mechanism to alleviate the negative effect of high energy from sunlight. Moreover, a positive correlation was found between chlorophyll content and plant biomass (Zaharieva *et al*., 2001). Drought-treated plants of the three *Ae. crassa* accessions (C1, C2 and C3) and durum wheat showed no change in Chl a, Chl b and total chlorophyll content compared to the well-watered plants. This suggests that the drought treatment was not severe enough to inhibit chlorophyll synthesis. Indeed, exposing different cultivars of durum wheat to severe drought under field conditions resulted in the reduction of their chlorophyll content (Talebi, 2011). Moreover, progressive drought for 7 days led to a decrease in chlorophyll content of three cultivars of bread wheat (Nikolaeva *et al*., 2010). The effect of drought on chlorophyll content was found to be developmental stage dependent (Keyvan, 2010). In bread wheat, drought imposed at earlier reproductive stage resulted in higher decrease of chlorophyll content compared to that imposed at later stages (Keyvan, 2010).

Plant growth occurs by two processes: cell division and cell expansion. It was found that cell expansion is more sensitive to drought stress than cell division (Prasad *et al*., 2008). Cell division and cell expansion are sensitive to mild drought before any noticeable change in photosynthesis (Prasad *et al*., 2008). In plants, the effect of drought is manifested as a reduction in biomass. In different *Aegilops* species, two levels of drought stress (moderate and severe) resulted in a significant reduction in biomass (Baalbaki *et al*., 2006).

Different drought regimes: progressive and controlled moderate drought showed differential morphological, physiological, biochemical and molecular changes in *Arabidopsis* plants (Harb *et al*., 2010). Multiphasic effect was shown when *Arabidopsis* plants were exposed to controlled moderate drought (Harb *et al*., 2010). At early priming phase, most of the physiological, biochemical and molecular changes take place. This phase is followed by intermediate phase during which plants are preparing to acclimatize to drought stress. At late acclimation stage, plants reach new homeostasis and are acclimated to drought stress. In this study, *Ae. crassa* accessions and durum wheat were exposed to controlled moderate drought. At the end of drought treatment, morphological, physiological and biochemical parameters were evaluated. This phase might be the same as the late acclimation phase shown in *Arabidopsis*, at which plants are already acclimated to drought stress with new homeostasis. At this phase a few physiological, biochemical and molecular changes can be captured compared to the early priming phase. This might explain the minimal effect of drought treatment on RWC, chlorophyll content and chlorophyll fluorescence. The effect of drought on biomass is accumulative, so a substantial change in biomass will be shown at the end of drought treatment.

The two accessions of *Ae. crassa* (C2 and C3) are naturally adapted to semiarid and arid habitats, respectively. This may explain the minimum effect of drought stress obtained on these accessions compared to C1 accession that is adapted to well-watered habitat and durum wheat. Therefore, *Ae. crassa* C2 and C3 accessions are promising genetic sources for the genetic engineering of drought tolerant wheat plants.

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