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Seed priming improved the physiological parameters, growth, and yield of durum wheat varieties under tillering and anthesis drought stress conditions

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Abstract

A pot experiment was carried out to investigate the impact of seed priming on some physiological parameters, growth, and yield components of four durum wheat varieties (Hourani, Umqais, Sham 1, and Maru 1) during both stages of tillering and anthesis drought. Four pre-sowing seed treatments (hydropriming with distilled water, osmopriming with PEG, osmopriming with 1.5% $CaCl_2$, and controls) were applied for 12 hours at 24 ºC. Drought was imposed at both stages by withholding water for 7 days and being compared with well-watered conditions. The experimental design was 4 x 4 x 3 factorial in a completely randomized design with three replicates for each treatment. During anthesis, seed priming significantly improved transpiration rate, total chlorophyll content, and relative water content (RWC) by 29%, 1.7%, and 3.5%, while drought suppressed these physiological parameters by 18.6%, 6.5%, and 12.1%, respectively, when compared with those during tillering. Osmopriming with PEG had significantly 35% higher transpiration rate and 4.9% higher RWC during anthesis stage than hydropriming treatment. Overall, osmopriming with either PEG or $CaCl_2$ significantly improved the growth and yield parameters of wheat when compared with hydropriming. The highest grain yield was significantly improved by 82.7% for var. Sham 1 when seeds were primed with PEG. However, var. Hourani had the highest reduction in grain yield (67.8%) under drought at anthesis stage. In conclusion, seed priming resulted in an increase in grain yield at both stages, with more substantial improvement observed under severe anthesis drought due to the enhanced physiological performance of wheat.

Keywords: Hydropriming; polyethylene glycol; relative water content; yield component; water stress.
Abbreviations: ANOVA_Analysis of variance; $CaCl_2$_Calcium chloride; D1_Drought at tillering; D2_Drought at anthesis; HI_Harvest index; Ψs_Osmotic potential; PEG_Polyethylene glycol; RWC_Relative water content; T_Transpiration rate; WW_Well-watered.

Introduction

Wheat is the third-most-growing cereal crop in the world after maize and rice. It is considered a main source of nutrition for an ever-increasing population as a staple food (Faisal et al., 2023), with a world annual production of 776.7 million tons in 2020/2021 (FAO, 2022). Durum wheat (*Triticum durum* L.) accounts for approximately 5% of the wheat produced globally (Kobata et al., 2018). However, durum wheat is among the most essential field crops grown under rainfed conditions in Jordan for ensuring food security at the national level. However, extreme climate changes and increased water scarcity challenge food security, which is further impaired due to the need to feed a growing population (Munaweera et al., 2022).

The main impact of climate change on crop production is due to changes in rainfall patterns and drought. Therefore, plant productivity and resistance to climatic stresses are currently the major topics of interest for sustainable agriculture (Saeed et al., 2022). Drought is a major environmental (abiotic) stress with adverse impacts on crop production (Kim et al., 2019). Drought has a negative impact on plants by disturbing many plant activities, including the carbon assimilation rate, decreased turgor, and changes in leaf gas exchange, thus causing a reduction in yield (Hussain et al., 2018). Water stress decreases chlorophyll content, which causes chlorosis and leads to a reduction in photosynthesis (Tyagi and Pandey, 2022). Drought also reduces leaf relative water content and stomatal conductance, which ultimately leads to reduced growth and biomass production (Caser et al., 2018). Moreover, drought stress can occur at any growth stage depending upon the frequency and duration of drought, and its effect varies with crop variety as well as with the local environmental conditions (Anjum et al., 2017). However, drought stress most commonly occurs after anthesis in wheat (Ru et al., 2022).

Many strategies are involved to generate plants that can withstand the stresses. Among these approaches is seed priming, which has been developed as a crucial method to produce drought-tolerant plants (Jisha et al., 2013; Hussein et al., 2017). Seed priming is quite simple and cost-effective, in which seeds are hydrated partially until the initiation of metabolic activities required for seed germination (Marthandan et al., 2020). It stimulates the physiological plant states by soaking the seeds in a natural and synthetic solution. This technique is classified into conventional methods (such as hydropriming, osmopriming, and priming with plant growth regulators) and advanced methods such as nano-priming (Waqas et al., 2019). However, the most common priming techniques include osmopriming by soaking seeds in osmotic solutions such as PEG, and hydropriming by soaking seeds in water (Paparella et al., 2015).

Improvement in grain yield of wheat followed by seed priming has been reported previously by many researchers. For example, Farooq et al. (2020) found that the maximum growth and grain yield were observed in wheat raised from seeds osmoprimed with $CaCl_2$. However, Toklu et al. (2015) indicated that PEG, KCl, and hydropriming were the most effective treatments to attain a higher grain yield of wheat among different priming agents. However, information is lacking regarding the yield and physiological performance of primed seed of wheat varieties in Jordan that were exposed to drought at either tillering or anthesis stage. Therefore, this study was conducted to investigate if the response of primed wheat seeds is differs when imposed under different growth stages of drought.

Results

The main effect of seed priming on some physiological measurements of wheat under tillering and anthesis drought

Analysis of variance (mean squares values) for the main and interaction effect of seed priming on some physiological measurements of wheat under drought conditions is present in Table S1. Different seed priming treatments significantly increased some physiological parameters of wheat varieties under drought conditions at tillering and anthesis stages when compared with the control (Table 1). For example, seed priming with polyethylene glycol (PEG) significantly ($p \leq 0.01$) increased transpiration rate (T) by 21.3% and 64.8%, SPAD by 9.8% and 14%, and relative water content (RWC) by 7.6% and 12.2% at the tillering and anthesis stages, respectively. However, PEG treatment had significantly higher RWC than distilled water (DW) treatment at the tillering stage, with significantly higher T and RWC at the anthesis stage. Drought at the end of Day 7 significantly reduced T by 30.1 % and 48.7%, SPAD by 16.4% and 22.9%, and RWC by 21.5% and 33.6% at the tillering and anthesis stages, respectively, when compared with drought at the beginning of Day 0 (Table 1). During the anthesis stage, vars. Maru 1 and Umqais had significantly the highest (17 µg cm^{-2} s^{-1}) and the lowest (11.7 µg cm^{-2} s^{-1}) T, respectively, among wheat varieties (Figure 1).

Interaction effects of seed priming and drought conditions on some physiological measurements of wheat

At the tillering stage, var. Hourani had significantly 43% higher T than controls when seeds were primed with DW, while the T of other wheat varieties was not significantly affected by DW treatment (Figure 2). At the anthesis stage, vars. Umqais and Hourani had significantly ($p \leq 0.05$) higher RWC than var. Sham 1 only during Day 7 of drought (Figure 3A). However, var. Maru 1 had significantly higher T than other wheat varieties only during Day 0 (Figure 3B). Controls

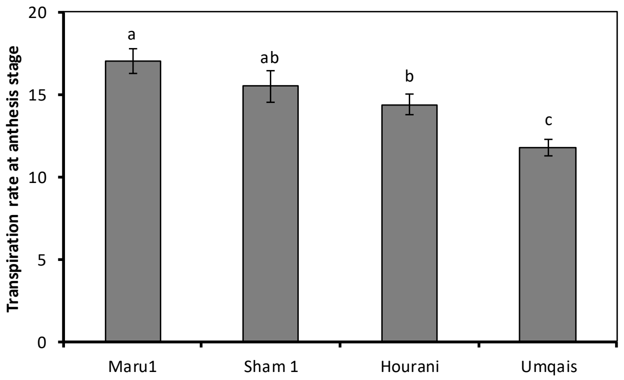

Fig 1. Effect of wheat varieties on transpiration rate (µg cm^{-2} s^{-1}) during the anthesis stage. Lines with the same letter are not significantly different at p< 0.05 using Tukey's test. Error bars show standard errors, n = 3.

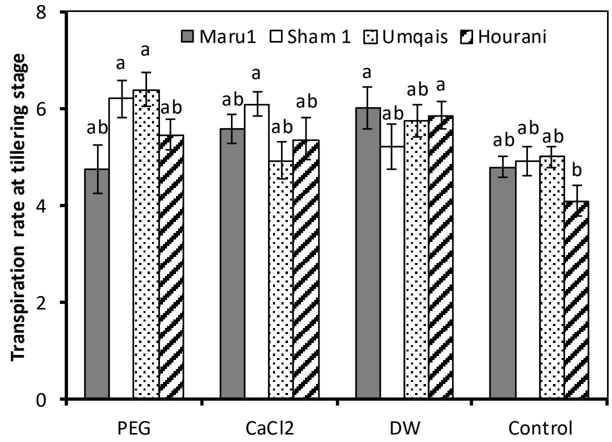

Fig 2. Interaction between wheat varieties and seed priming for transpiration rate (µg cm^{-2} s^{-1}) during the tillering stage. Lines with the same letter are not significantly different at p< 0.05 using Tukey's test. Error bars show standard errors, n = 3.

had significantly lower SPAD values than other seed priming treatments only during Day 7 at either the tillering or anthesis (Figures 4A and 4C). Furthermore, controls had significantly lower RWC during the tillering stage than seed priming with $CaCl_2$ and DW only during Day 7 (Figure 4B). However, seed priming with PEG had significantly ($p \leq 0.01$) higher RWC than DW only during Day 7 at the anthesis stage (Figure 4D).

The main effect of seed priming on wheat growth and yield components

Analysis of variance showing the main and interaction effect of seed priming on growth and yield parameters of wheat under drought conditions is indicated in Table S2. Seed priming had significantly enhanced all measured growth and yield parameters (Table 2). For instance, seed priming with PEG significantly increased head number/plant (HN), grain number/plant (GN), 1000-grain weight/plant (1000-GW), and grain weight/plant (GW) by 20%, 39.4%, 12.9%, and 51.2%, respectively, when compared with controls. Additionally, PEG and $CaCl_2$ treatments had significantly higher tiller number/plant (TN), HN, 1000-GW, GW, and dry matter weight/ plant (DMW) than DW treatment. However,

Table 1. Mean values of transpiration rate (T), total chlorophyll content by SPAD, and relative water content (RWC) for seed priming treatments and for the beginning of drought (Day 0) and end of drought (Day 7) at tillering and anthesis stages averaged across wheat varieties.

	Tillering			Anthesis		
Priming treatments	T ($\mu g\ cm^{-2}\ s^{-1}$)	SPAD	RWC (%)	T ($\mu g\ cm^{-2}\ s^{-1}$)	SPAD	RWC (%)
PEG	5.7 a	57.5 a	84.7 a	17.8 a	54.4 a	79.9 a
$CaCl_2$	5.5 a	57.3 a	83.3 ab	16.9 a	52.8 a	77.7 ab
DW	5.7 a	57.5 a	82.4 b	13.2 b	52.3 a	76.2 b
Control	4.7 b	52.4 b	78.7 c	10.8 c	47.7 b	71.2 c
Standard error	0.25	1.37	0.86	0.73	1.1	1.23
HSD (0.05)	0.66	3.62	2.26	1.9	2.91	3.24
Drought						
Day 0	6.4 a	61.2 a	92.2 a	19.4 a	58.5 a	91.6 a
Day 7	4.4 b	51.2 b	72.4 b	9.9 b	45.1 b	60.9 b
Standard error	0.18	0.97	0.61	0.52	0.78	0.87
HSD (0.05)	0.35	1.94	1.21	1.04	1.56	1.73

PEG_Polyethylene glycol; $CaCl_2$_Calcium chloride; DW_Distilled Water; HSD_honestly significant difference at $p< 0.05$ probability level using Tukey's test. Different letters within the same columns indicate significant differences.

Table 2. The main effects of seed priming treatments on tiller number/plant (TN), head number/plant (HN), grain number/plant (GN), 1000-grain weight/plant (TGW), grain weight/plant (GW), dry matter weight/plant (DMW), and harvest index (HI) averaged across drought conditions and wheat varieties.

Priming treatments	TN	HN	GN	TGW (g)	GW (g)	DMW (g)	HI
PEG	11.4 a	10.8 a	449.1 a	40.3 a	18.6 a	19.9 a	0.47 a
$CaCl_2$	11.5 a	10.7 a	426.4 b	40.0 a	17.8 a	20.0 a	0.45 ab
DW	10.6 b	9.9 b	380.9 c	38.8 b	15.4 b	18.1 b	0.44 b
Control	9.7 c	9.0 c	322.1 d	35.7 c	12.3 c	16.3 c	0.40 c
Standard error	0.26	0.23	8.02	0.46	0.31	0.47	0.06
HSD (0.05)	0.67	0.61	20.97	1.21	0.82	1.24	0.018

PEG_Polyethylene glycol; $CaCl_2$_Calcium chloride; DW_Distilled Water; HSD_honestly significant difference at $p< 0.05$ probability level using Tukey's test. Different letters within the same columns indicate significant differences.

PEG treatment had significantly more GN than other treatments.

Interaction effects of seed priming and drought conditions on wheat growth and yield components

Varieties of Maru 1 and Sham 1 did not significantly differ for GW when seeds were primed with PEG, $CaCl_2$, and DW, while var. Sham 1 had a significantly lower GW than var. Maru 1 when seeds were not primed (Figure 5A). In addition, vars. Maru 1 and Sham 1 had significantly higher 1000-GW than other wheat varieties when seeds were primed with PEG and $CaCl_2$. However, wheat varieties had no significant effect on 1000-GW under unprimed seeds (Figure 5B). Varieties of Maru 1 and Sham 1 had significantly higher harvest index (HI) than other wheat varieties when seeds were primed with PEG, while var. Maru 1 had significantly higher HI than other varieties when seeds were not primed (Figure 5C). Variety Maru 1 had significantly higher TN and HN than var. Hourani under well-watered (WW) conditions, but the effect was not significant at either tillering drought (D1) or anthesis drought (D2) conditions (Figures 6A and 6B). Under WW conditions, both vars. Maru 1 and Sham 1 had significantly higher GN than other wheat varieties, while var. Maru 1 had significantly higher GN than other wheat varieties at D1 (Figure 6C). Both vars. Maru 1 and Sham 1 had significantly higher 1000-GW and GW than other wheat varieties under WW and D2 conditions, but var. Maru 1 had significantly higher 1000-GW and GW than other wheat varieties at D1 (Figures 6D and 6E). Variety Maru 1 had significantly higher DMW than var. Umqais at WW, and vice

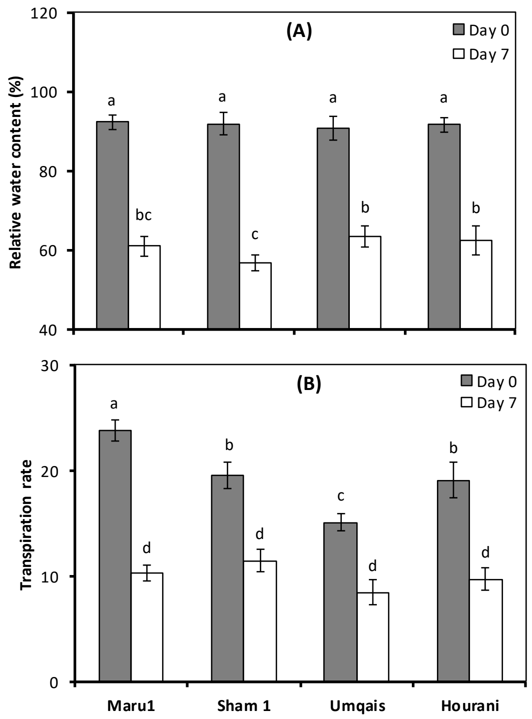

Fig 3. Interaction between drought and wheat varieties for relative water content (A) and transpiration rate (B) during the anthesis stage. Lines with the same letter are not significantly different at $p< 0.05$ using Tukey's test. Error bars show standard errors, n = 3.

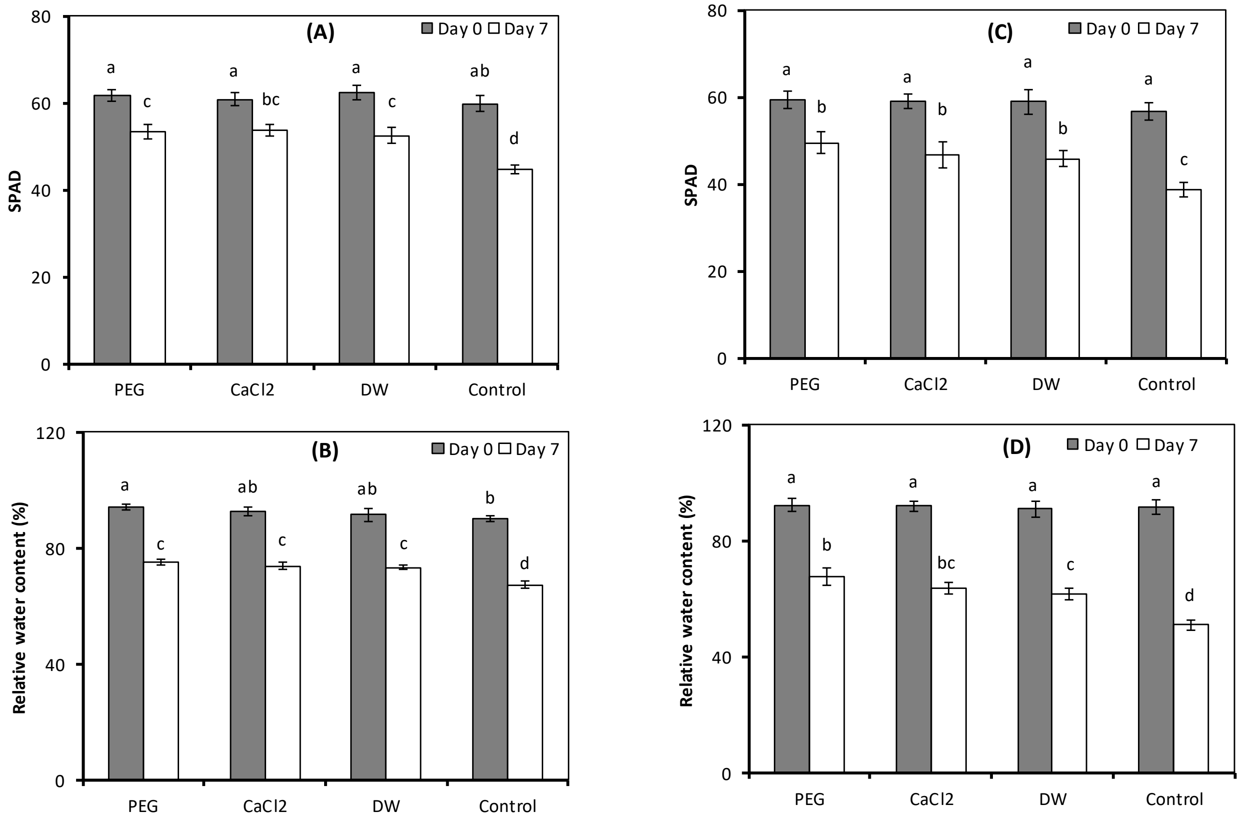

Fig 4. Interaction between drought and seed priming for SPAD and relative water content during tillering (A and B, respectively) and for SPAD and relative water content during anthesis (C and D, respectively). Lines with the same letter are not significantly different at p< 0.05 using Tukey's test. Error bars show standard errors, n = 3.

versa at D2 (Figure 6F). Varieties of Maru 1 and Sham 1 had significantly higher HI than other wheat varieties at WW, while var. Maru 1 had significantly higher HI than other wheat varieties at D2 (Figure 6G). Seed priming with PEG and $CaCl_2$ had significantly higher GN and GW than those primed with DW at either WW or D1, while PEG treatment had significantly higher GN and GW than other treatments at D2 (Figures 7A and 7C). Seed priming with PEG had significantly higher 1000-GW and HI than DW at D2, although both treatments were not significantly different at WW and D1 (Figures 7B and 7D).

Discussion

In this study, seed priming was highly effective in improving the physiological parameters of wheat under drought conditions at either the tillering or anthesis stages. Similarly, Abdolahi et al. (2018) found that seed priming increased transpiration rates and SPAD values at different growth stages of wheat. It was indicated that $CaCl_2$ and PEG priming treatments significantly increased leaf total chlorophyll and RWC in wheat, rice, and sorghum under drought conditions (Faisal et al., 2023; Hussain et al., 2017; Zhang et al., 2015). Our results demonstrated that osmopriming was more effective than hydropriming as it improved RWC and transpiration rate under anthesis drought. These results are consistent with the study by Tabassum et al. (2018). Osmopriming by $CaCl_2$ had the potential to regulate cell membrane rigidity, and to alleviate the contrasting effects of abiotic stresses (Hepler, 2005). Meanwhile, osmopriming with PEG had the potential to strengthen the antioxidant system, and to increase osmotic adjustment, resulting in better stress tolerance (Zhang et al., 2015).

Drought significantly reduced the transpiration rate, total chlorophyll content, and RWC of wheat varieties at both growth stages, with higher reductions at the anthesis stage. Similar results were obtained by Wasaya et al. (2021); Aldahadha et al. (2019); and Chowdhury et al. (2021). Our results indicated that the reduction in wheat transpiration at anthesis drought was approximately 19% lower than those at tillering drought. This may be due to the higher water uptake of larger root biomass at anthesis time (Abdolahi et al., 2018; Aldahadha et al., 2019). Therefore, the soil water supply is more rapidly exhausted during anthesis drought (Morgan, 1977). Nikolaeva et al. (2010) found that the chlorophyll content decreased by 13–15% only after a 7-day drought period. Abdelkader et al. (2007) documented the decrease in chlorophyll content as one of the most important limiting factors for plant photosynthetic activity under drought conditions. A higher reduction in RWC during anthesis drought may be due to higher transpiration rates, which was similar to a study on wheat reported by Aldahadha et al. (2019). Our results also demonstrated that wheat varieties responded differently to RWC at the end of the drought (Day 7) of anthesis. Varieties Umqais and Hourani retained maximum RWC in stress treatments. Varietal differences in RWC may be due to variation in their genetic ability to absorb water in the existing rooting zone (Siddique et al., 2000).

Seed priming improved growth and yield parameters of wheat varieties under different drought conditions, with superiority of the osmopriming by PEG. The maximum increase in grain yield was recorded for var. Sham 1 when seeds were primed with PEG, while the minimum increase was documented for var. Hourani when seeds were primed with DW. This increase in grain yield may be due to the fundamental role of seed priming in improving some physiological attributes of wheat. Besides, osmoprimed seeds imbibed more water, which enabled better stand establishment (Farooq et al., 2015). In the present study, seed priming interacted differently with grain yield under various drought conditions. The improvement of grain yield by seed priming was greater at anthesis drought than at tillering drought. Therefore, these results confirmed a better performance of seed-primed plants at later stages (anthesis) of growth when exposed to a similar duration of drought. In other words, seed priming enhanced drought tolerance at anthesis in wheat through a higher improvement in tissue water status and total chlorophyll content. Thus, photosynthesis may be induced by priming through the rapid recovery from stress and complete restoration of photosynthesis function (Aswathi et al., 2022). Many researchers have used various seed priming treatments for improving the growth and yield-related traits in wheat under abiotic stresses (Jafar et al., 2012; Meena et al., 2013; Tabassum et al., 2018). The increase in harvest indices by seed priming was due to enhanced dry matter partitioning towards spikelets (Faisal et al., 2023).

Usually, yield and yield attribute traits of wheat varieties were decreased when the drought was imposed, with greater impact under the anthesis stage. The lowest decrease in grain yield was for var. Maru 1 at tillering drought, whereas the highest reduction was for var. Hourani at anthesis drought. A decline in growth and metabolic activities leads to a reduction in agronomic and yield attributes under water stress (Hussain et al., 2018). Drought occurring during the reproductive phase caused a larger decrease in grain weight and number per plant and in the number of tillers and heads per plant (Aldahadha et al., 2019; Agrawal et al., 2021). A higher reduction in grain yield parameters under anthesis drought might be due to less retention of RWC, reflecting fewer metabolic activities (Clarke and McCaig, 1982). A decline in the number of grains may be explained by a lower number of spikelets per spike and spike length under drought. Consequently, the flowering stage was found to be the most sensitive to water stress. Furthermore, drought at either the vegetative or flowering stages substantially reduced the total biomass of wheat. Similar results were achieved by Blum (2005) and Bavita et al. (2015). Declined 1000-grain weight was described by Plaut et al. (2004) under water stress at the anthesis stage due to less efficient uptake of nutrients and restricted photosynthetic translation within the plant, which accelerated maturity and produced shriveled kernels. Reduced yield and yield components under drought might be due to a decrease in chlorophyll contents as well as photosynthetic parameters including stomatal conductance and transpiration rate (Wasaya et al., 2021).

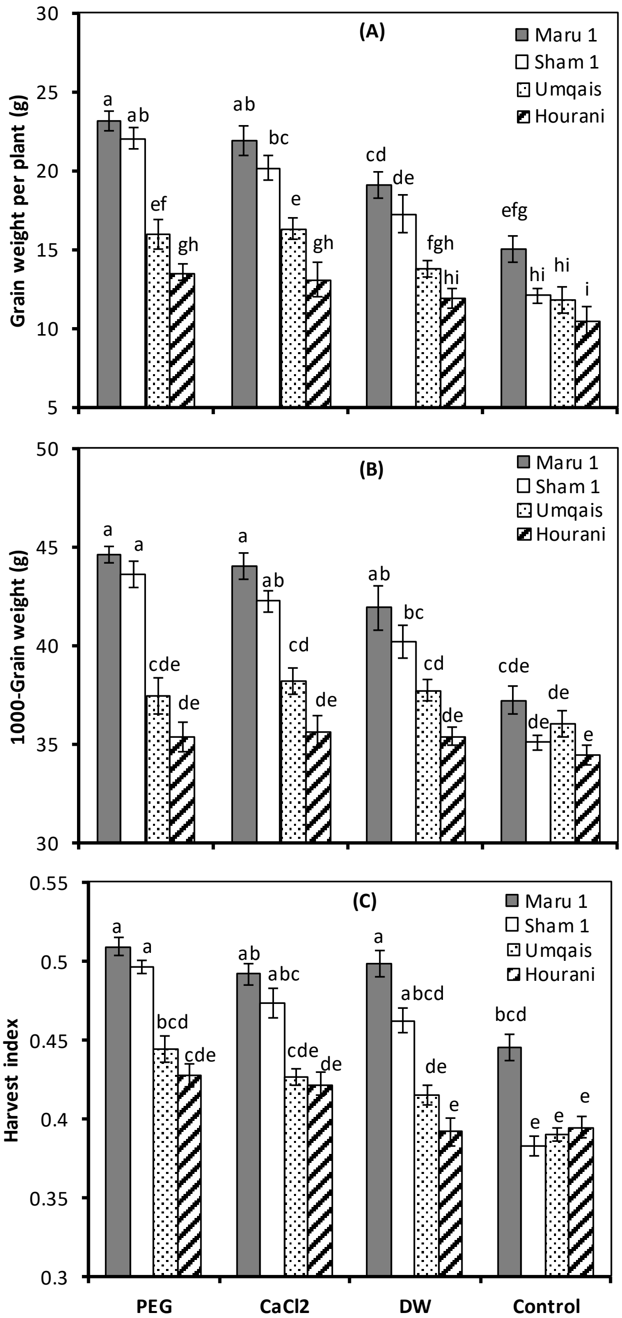

Fig 5. Interaction between wheat varieties and seed priming for grain weight per plant (A), 1000-grain weight per plant (B), and harvest index (C). Lines with the same letter are not significantly different at p< 0.05 using Tukey's test. Error bars show standard errors, n = 3.

Materials and Methods

Plant material

Four durum wheat (*Triticum durum* L.) varieties were supplied by Mushagar Agricultural Research Center, Madaba, Jordan. Maru1 (pedigree: ACS323/Stojocri-3ACSAD-D-(1998)-8515-IZ7-IZ3-IZ1-IZ0) is an improved variety which was released recently and registered in 2019-2020. Hourani (pedigree: landrace) is an old variety which was released in 1976 and is known as a drought-tolerant variety (Almeselmani et al. 2013). Variety Sham 1 (pedigree: 'Waha = plc's'-ruff's'X gta's'-rtte) was released in 1988, while var. Umqais (pedigree: Um Rabi 5) was released in 2004 (Allozi and AlRawashdeh, 2014). These wheat varieties are among the most cultivated in Jordan.

Seed priming treatments

Methods of seed priming have been described in detail by Khan (1992). In the laboratory of the National Agricultural Research Centre (NARC), wheat seeds from four varieties were surface sterilized with a 5% sodium hypochlorite solution for 10 minutes, followed by three rinses with distilled water, and dried. Wheat seeds were primed for 12

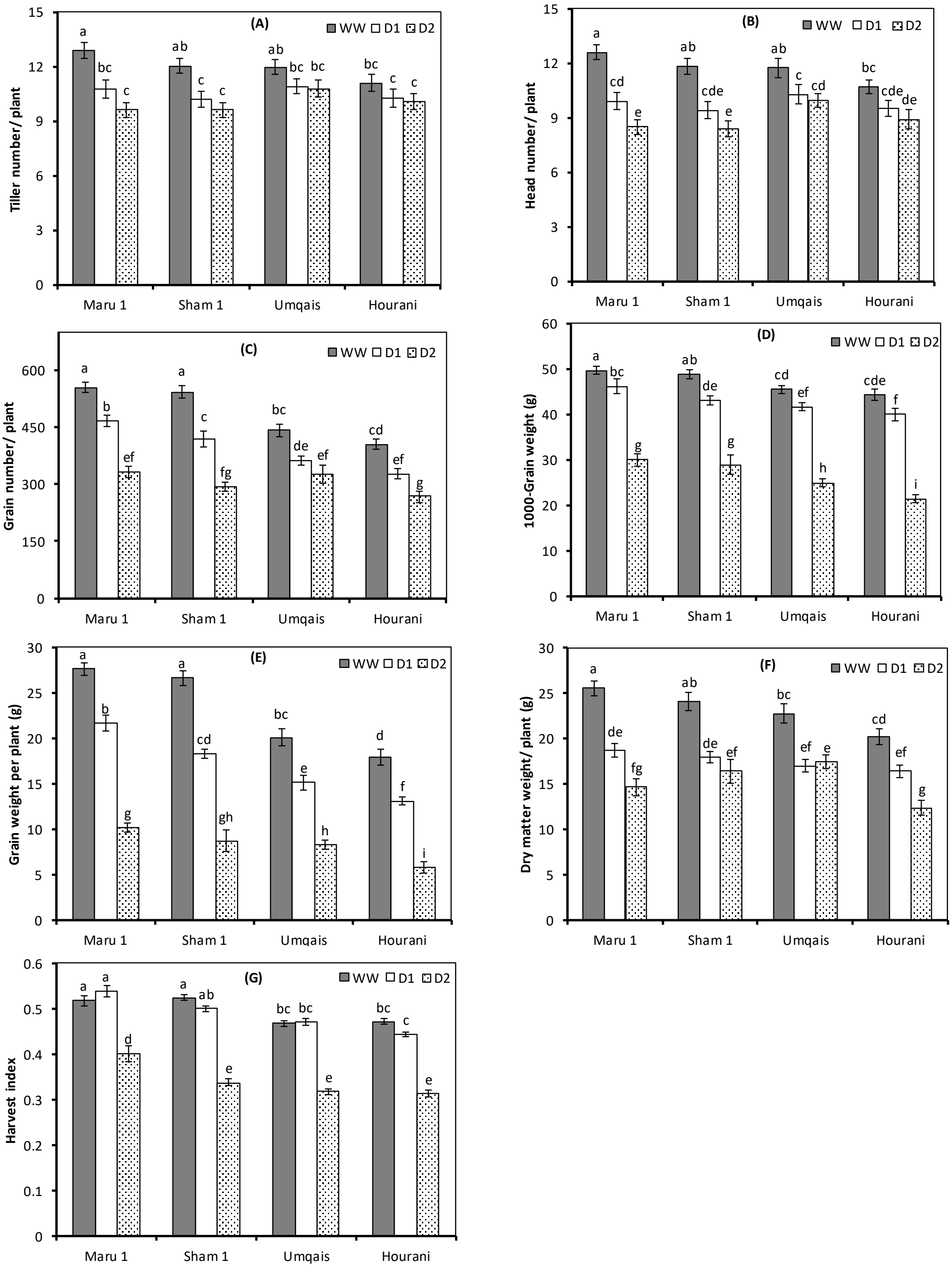

Fig 6. Interaction between wheat varieties and drought conditions for tiller number per plant (A), head number per plant (B), grain number per plant (C), 1000-grain weight (D), grain weight per plant (E), dry matter weight per plant (F), and harvest index (G). Lines with the same letter are not significantly different at p< 0.05 using Tukey's test. Error bars show standard errors, n = 3.

hours at 24 ºC with the following agents: hydropriming with distilled water, osmopriming with polyethylene glycol (PEG6000; Merck, Germany) at an osmotic potential (*Ψs*) of -1.2 MPa, and osmopriming with a 1.5% $CaCl_2$ solution. Untreated seeds were used as the non-primed (control) treatment. Seed priming was performed by placing seeds on Petri dishes containing a double-layered filter paper (Whatman No. 2) moistened with a 20 mL priming solution. For osmopriming treatments, seeds were soaked in aerated solutions with low water potential. However, aeration was not provided for submerged hydropriming seeds. After priming, seeds were dried near their original weight with forced air under shade, and then stored at 5 ºC until sowing.

Growth conditions, soil preparation, and seed sowing

A pot experiment was conducted in a glasshouse at NARC. The temperature in the glasshouse was controlled at 25/15 ºC (day/night). The relative humidity (RH) within the glasshouse was maintained at approximately 60%. The photoperiod (natural light) was 12 hours on average over the course of the experiment. One hundred and forty-four pots (27 cm diameter × 27 cm height) were used for this experiment, and each pot was filled with 4 kg of clay soil mixed with peat (1:1) (v/v). Diammonium phosphate (18% N and 46% P_2O_5) fertilizer was applied to the soil mixture at 10 g m^{-2}. Three wheat seeds, from each variety and from each treatment of seed priming, were placed at a depth of 2-3 cm below the soil surface. Wheat seeds were sown on 28th January 2021. Plants were thinned to two seedlings per pot at the two-leaf stage one week after seedling emergence. Pots were supplied with NPK fertilizer on a weekly basis from the beginning of the tillering stage.

Drought treatments

Pots were regularly watered to field capacity twice per week during the vegetative stage and three times per week from the anthesis stage until maturity. However, drought was imposed by withholding watering for 7 days at either tillering (GS 22; D1) or anthesis (GS 65; D2) according to the Zadoks scale (Zadoks et al. 1974) on separate sets of plants, and compared with well-watered (WW) plants. Drought at the tillering stage was imposed from 31th March to 7th April 2021, while drought at the anthesis stage was imposed from 26th April to 3th May 2021.

Relative water content and physiological measurements

Leaf relative water content (RWC) was determined according to the method of Slatyer (1967) and as briefly described by Aldahadha et al. (2012). Transpiration rate (μg cm^{-2} s^{-1}) was measured with a portable steady state porometer (LICOR model LI-1600), while total chlorophyll content was determined non-destructively using a portable chlorophyll meter; SPAD 502 Chlorophyll Meter (Spectrum Technologies Inc., Plainfield, IL, USA) on the same leaf as RWC prior to excision at the beginning (Day 0) and one week after drought (Day 7) at either tillering or anthesis stages. Physiological measurements were made at midday between 12 and 2 p.m.

Growth and yield components

At the full maturity stage, the number of tillers and heads per plant were counted. The plants were harvested on 2nd June 2021 when they had reached their final maturity. The above-ground plant parts were harvested and separated into vegetative and head parts. The grains were separated from the heads by threshing, and grain weight was determined for each pot. The total dry weight of the shoots was determined after drying in an oven at 80 ºC for two days. The one thousand-grain weight was determined from the weight of 200 seeds per sample. Harvest index was calculated by dividing grain weight by total (grain plus shoot) weight.

Experimental design and statistical analysis

This experiment was performed in a factorial (4 x 4 x 3) completely randomized design with three factors: four wheat varieties, four treatments of seed priming, and three drought conditions. There were three replicates for each treatment. Data were analyzed for both the main and interaction effects by analysis of variance (ANOVA) using Statistix 8.1 (Analytical Software, 2005). When there were significant interactions, a one-way ANOVA was used, and means were separated by honestly significant differences (HSD) at a P value less than 0.05%.

Conclusions

Growth and yield of durum wheat were inhibited due to drought, with a higher reduction at the anthesis stage. An

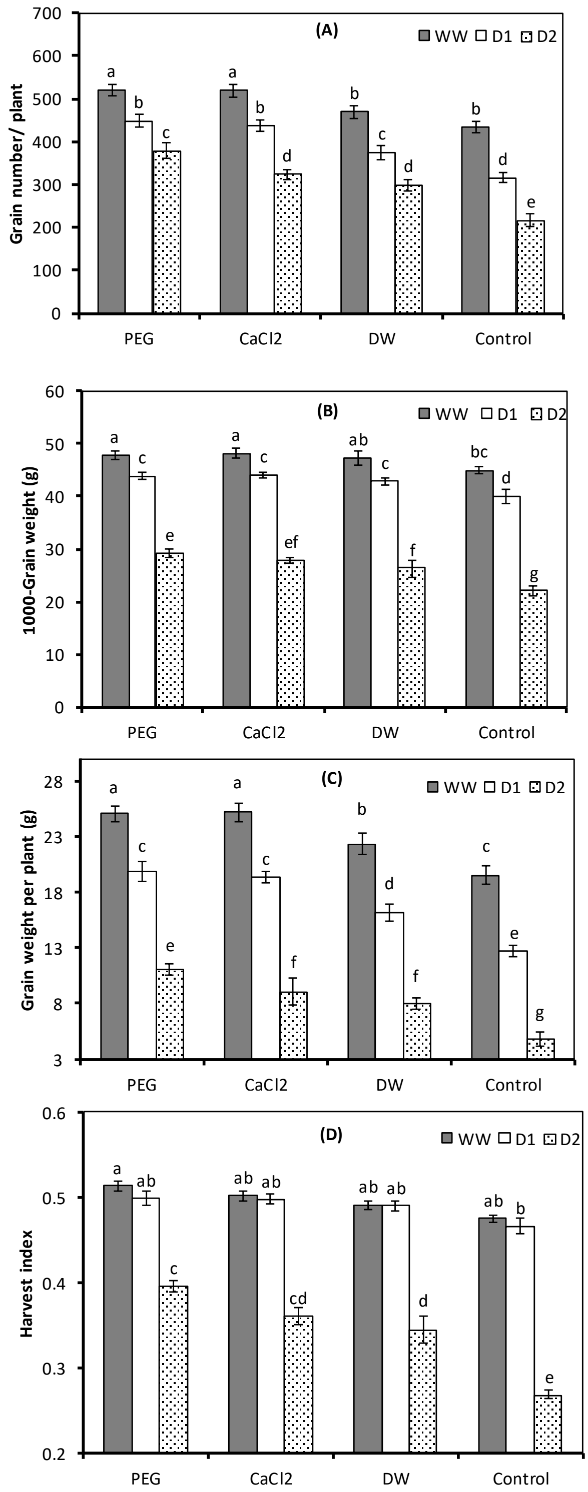

Fig 7. Interaction between seed priming and drought conditions for grain number per plant (A), 1000-grain weight per plant (B), grain weight per plant (C), and harvest index (D). Lines with the same letter are not significantly different at $p < 0.05$ using Tukey's test. Error bars show standard errors, n = 3.

alternative approach to alleviating the negative effects of water stress is through the application of pre-sowing seed priming. In this experiment, osmopriming and hydropriming improved some physiological attributes of wheat, which in turn increased growth and yield parameters. Overall, the highest grain weight was attained in var. Sham 1 under PEG priming compared with unprimed conditions, whereas the lowest improvement was for var. Hourani when seeds were primed with DW. Interestingly, seed priming performed much better at anthesis drought in terms of grain yield, possibly through enhancement of RWC and photosynthetic physiology. Understanding the mechanism of this interaction requires extra investigation. These findings provide support for further study of the interaction between drought and seed priming at the whole plant level under field conditions.

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