

Seed priming with polyethylene glycol improved drought tolerance of late sown wheat by enhanced gas exchange attributes

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Abstract. Late sowing, especially in regions prone to drought, significantly hampers crop growth and yield. To address this, field experiments were conducted during the winter of 2021–2022 at Maru and Mushaqr in Jordan to evaluate the effects of seed priming agents as seed priming with water (hydropriming), polyethylene glycol (osmopriming), calcium chloride (osmopriming), and a control (unprimed) on physiological, phenological and yield traits of durum wheat (umqais variety) under normal and late sowing conditions. Results showed that Maru exhibited superior performance in physiology, growth, and yield attributes compared to Mushaqr. While late sown wheat demonstrated better water use efficiency, normal sowing conditions generally favored other yield components. Seed priming by polyethylene glycol (PEG) improved relative water content, stomatal conductance, and grain yield compared to other treatments. Mushaqr recorded higher grain spike⁻¹ and spike m⁻² under normal sowing, while PEG-primed seeds produced significantly higher 1,000-grain weight and harvest index. Notably, PEG-primed seeds improved grain yield and 1,000-grain weight, suggesting enhanced drought resilience under late sowing conditions. The study concludes that seed priming, especially with PEG, effectively improves drought tolerance in late sown wheat by enhancing photosynthetic activity, chlorophyll content (SPAD), and water retention. The findings indicate that PEG seed priming can effectively mitigate the negative impacts of late sowing, supporting its use as a practical strategy for improving wheat performance in semi-arid environments.

Key words: intrinsic water use efficiency, osmopriming, sowing date, stomatal conductance, yield components.

INTRODUCTION

Globally, wheat is among the most essential crop after maize and rice. It is a major dietary staple that withstands the growing global population (Faisal et al., 2023). Durum wheat (*Triticum durum* L.) contributes about five percent of global wheat production (Kobata et al., 2018). Besides, it is considered one of the most important cereals, usually grown in arid and semi-arid regions of the Middle East, including Jordan. However, food security in this region is primarily threatened by climate change, particularly drought (Munaweera et al., 2022). Future climate projections indicate that Middle Eastern

countries will experience rising temperatures and declining rainfall, with an expected increase of 1.3 °C in average temperatures and an 11% decrease in annual rainfall by 2050 (Tita et al., 2025). Given climate change challenges, the optimal sowing date is an effective and economical strategy for ensuring proper crop establishment and maximizing yield under dryland conditions (Samarah & Al-Issa, 2006; Serafin-Andrzejewska et al., 2021). Deviating from the recommended sowing schedule, whether advancing or delaying, can negatively affect yield potential of cereal crops throughout the growing season, and also expose them to drought and temperature stress (Liu et al., 2021). For example, Al-Issa (2001) found that sowing wheat one month earlier than the optimal time led to a yield reduction of 292 kg per hectare, whereas delaying sowing by one month resulted in an even greater reduction of 359 kg per hectare.

Recent research has highlighted the relationship between winter wheat yields and sowing dates across different regions (Kanapickas et al., 2024). The findings underscore the importance of regional factors when defining the optimum dates for sowing winter wheat. For instance, Ding et al. (2016) demonstrated that in the semiarid Loess Plateau of China, optimal sowing dates are significantly influenced by local precipitation patterns. Specifically, Christensen et al. (2017) demonstrated that optimal sowing dates generally result in higher yields, primarily due to improved resource utilization and enhanced nitrogen uptake. However, Liu et al. (2021) reported that delaying sowing dates led to reduced yields, primarily due to inhibited crop growth and decreased biomass production. The negative consequences of late sowing arise from environmental constraints such as unfavorable weather conditions during vegetative growth, shortened developmental phases, and elevated temperatures during critical stages like grain filling, which are detrimental to the photosynthesis rate (Garg et al., 2013; Liu et al., 2021). This combination of factors can impede grain filling, leading to reduced yield and quality (Fu et al., 2023). The decline in grain yield associated with postponed sowing dates often results from a shortened period leading up to anthesis, causing plants to enter the reproductive stage earlier and intercept less solar radiation (Maresma et al., 2019). Additionally, both the number of growth days and the overall growth duration of wheat are reduced when sowing is delayed (Ahmed & Fayyaz-ul-Hassan, 2015). As a result, the number of leaves and tillers is reduced (Yin et al., 2018). Thus, delayed sowing significantly impacts various growth parameters, including grain number per spike, 1,000-grain weight, dry matter accumulation, plant height, harvest index, and overall grain yield (Maresma et al., 2019).

Farmers in Jordan may delay wheat sowing until they are assured of sufficient rainfall or water availability. Late sowing can coincide with the onset of seasonal rains, which may improve germination and early growth. Typically, wheat sowing can be delayed until early February in Jordan. To address these challenges and improve wheat production in late-sowing situations, seed priming has emerged as a significant technique for enhancing drought tolerance (Hussein et al., 2017; El-Shazoly et al., 2025). Osmopriming (seeds soaked in osmotic solutions such as polyethylene glycol) and hydropriming (seeds soaked in water) are the most commonly used priming techniques (Singh et al., 2015; Aldahadha et al., 2024). Numerous researchers have previously reported enhancements in wheat grain yield resulting from seed priming (Singhal et al., 2019; Farooq et al., 2020; Mickky, 2022; Aldahadha et al., 2024). Moreover, Hosen et al. (2023) and Singh et al. (2023) recently investigated the impact of seed priming on wheat yield with different sowing dates. Their studies revealed that seed priming

enhanced wheat grain yield under late-sown conditions. However, limited information is available on the physiological performance of primed wheat seeds sown at different dates. The primary objective of this study was to evaluate the effects of different seed priming agents including polyethylene glycol (PEG), calcium chloride (CaCl_2), and water (hydropriming) on the physiological, phenological, and yield traits of durum wheat (*Triticum durum* L.) under two sowing dates (normal and late) across two distinct locations in Jordan (Maru & Mushaqr), which differ in rainfall and elevation. We hypothesized that late sowing would impose greater drought stress on wheat, particularly during critical growth stages such as anthesis, resulting in reduced physiological performance and yield. However, we expected that PEG osmoprimer would enhance gas exchange attributes (e.g., net photosynthesis, stomatal conductance), and mitigate yield losses, especially under late sowing and more drought-prone conditions.

MATERIALS AND METHODS

Locations study

Field experiments were conducted during the 2021–2022 growing season at two locations: Maru station, located in Irbid, northern Jordan (latitude $32^{\circ}35'4.7''$ N, longitude $35^{\circ}54'0.3''$ E, elevation 589 meters), and Mushaqr station, located in Madaba, central Jordan (latitude $32^{\circ}45'16.3''$ N, longitude $35^{\circ}48'1.5''$ E, elevation 796.3 meters). Average annual rainfall was 400 mm at Maru and 305 mm at Mushaqr. Both locations experience a Mediterranean climate, characterized by hot, dry summers. Chemical soil analyses for both sites are summarized in Table 1, and weather data are presented in Table 2.

Table 1. Soil characteristics of the experimental sites

Soil properties	Maru	Mushaqr
P (ppm)	11.9	12.5
K (ppm)	385.9	566.2
CaCO_3 (%)	2.6	18.2
Total N (%)	0.098	0.081
Organic matter (%)	1.23	0.83
PH	7.8	7.7
EC (dS/m)	0.64	0.91
Clay (%)	50.4	51.2
Silt (%)	37.9	35.6
Sand (%)	11.7	13.2
Texture	Clay	Clay

Treatments and experimental design

The field experiment was conducted using a randomized complete block design (RCBD) in a split-plot arrangement with three replicates. The main plots consisted of two sowing dates (normal and late sowing), while the sub-plots included various seed priming treatments. Data from both experimental sites were combined to determine whether significant differences existed between locations. Each location was treated as a separate experimental site, but data were also analyzed in

Table 2. Weather data during the growing seasons of 2021–2022 for both locations

Month	Maru		Mushaqr	
	Temperature (°C)	Rainfall (mm)	Temperature (°C)	Rainfall (mm)
Nov.	14.8	9	13.6	13.2
Dec.	9.6	103.5	8.3	57.4
Jan.	7.5	119	6.9	150.9
Feb.	8.4	62	7.5	29.2
Mar.	12.2	103	10.9	35.8
Apr.	17.1	3	15.7	0
May	20.8	0	19.5	0

a combined ANOVA framework to assess the overall effects. Location was included as a fixed factor, while Replication (block) was nested within location and treated as a random factor. Interactions among location, sowing date, and seed priming were tested to determine location-specific treatment responses. When significant interactions involving location were detected, means were further separated and analyzed within each location using one-way ANOVA.

In the laboratory of the National Agricultural Research Centre (NARC), wheat seeds were surface-sterilized using a 5% sodium hypochlorite solution for 10 minutes, followed by three rinses with distilled water, and then allowed to dry. The seeds were then primed for 12 hours at 24 °C using the following treatments: hydropriming with distilled water; osmopriming with polyethylene glycol (PEG6000; Merck, Germany) at an osmotic potential (Ψ_s) of -1.2 MPa; and osmopriming with a 1.5% CaCl_2 solution. Untreated seeds served as the non-primed (control) treatment. Seed priming was conducted by placing seeds on Petri dishes lined with double-layered Whatman No. 2 filter paper, moistened with 20 mL of the respective priming solution. For osmopriming, seeds were soaked in aerated solutions with low water potential, while hydroprimed seeds were immersed in water without aeration. After priming, the seeds were dried to near their original weight using forced air in a shaded area and stored at 5 °C until sowing. After priming, seeds were dried using forced air in a shaded area until they returned to their original pre-priming weight, as determined by weighing a representative seed sample before and after priming using a digital balance. The durum wheat variety (*Triticum durum* L.) used in this experiment was 'Umqais', provided by the Mushaqr Agricultural Research Center in Madaba, Jordan. This variety, with the pedigree *Um Rabi 5*, is one of the most widely cultivated in Jordan and was released in 2004 (Allozi & AlRawashdeh, 2014).

Crop management

The area of each main plot was 120 m² (5×24 m), while each sub-plot measured 10 m². Wheat seeds were sown at a rate of 12 g m⁻², with a row spacing of 17.5 cm and a planting depth of 7–10 cm. Seeds from the priming treatments were sown on December 14 and 15, 2021, as the normal sowing date, and on February 2 and 3, 2022, as the late sowing date, for the Maru and Mushaqr locations, respectively. These dates were selected based on local agronomic practices and rainfall patterns specific to each location. The crop had received 10 g m⁻² of diammonium phosphate (18% N and 46% P₂O₅) at the sowing time, then by 5 g m⁻² of urea (NH₂)₂CO (45% N) at the tillering stage. As this was a rainfed trial, no supplemental irrigation was applied. However, both sites were regularly monitored for pest and disease pressure. No chemical pest or disease control was necessary during the growing season due to the absence of significant infestations. Manual weeding, were performed uniformly across all plots.

Physiological traits

Relative water content (RWC) of the leaf was measured as described in detail by Aldahadha et al. (2012, 2019). A portable handheld photosynthesis system (CI-340, CID Bio-Science, WA, USA) was used to measure net photosynthetic rate (A), transpiration rate (E), and stomatal conductance (gs). Instantaneous water use efficiency (WUEi) was calculated as A/E, while intrinsic water use efficiency (WUEin) was calculated as A/gs.

Chlorophyll content was measured non-destructively using a SPAD 502 Chlorophyll Meter (Spectrum Technologies Inc., IL, USA). Physiological measurements were taken on the flag leaves at the anthesis stage (GS65), according to the Zadoks scale (Zadoks et al., 1974). In each plot, five flag leaves were randomly selected for gas exchange analysis. Phenological observations, such as days to 50% heading and physiological maturity, were visually scored on the same plots used for physiological and yield measurements, ensuring data consistency across traits.

Phenological and yield traits

Days to 50% heading (DH) were visually recorded as the number of days from seeding until the main spike emerged from the sheath of the flag leaf. Days to 50% physiological maturity (DM) were similarly determined by counting the days from seeding until the plants reached physiological maturity, indicated by the yellowing of the spikes. Plant height (PH) was measured from the soil surface to the top of the spike, excluding the awns. At harvest, 1 m² samples were hand-harvested, and shoots were categorized as either fertile (bearing spikes) or infertile (without spikes). For fertile shoots, spikes were separated at the collar, and straw fresh weight was recorded. All plant components were then dried at 80 °C for 48 hours, after which grain and chaff weights were measured. Thousand grain weight (TGW) was determined after removing broken grains. The total dry weight of infertile shoots was also recorded. The number of grains per spike was calculated as the average from 10 randomly selected spikes per plot. Biological yield (BY) was calculated as the sum of grain yield (GY) and straw yield. Harvest index (HI) was calculated as the ratio of total grain weight to total aboveground plant biomass.

Statistical analysis

Data were analyzed using three-way analysis of variance (ANOVA) with location, sowing date, and seed priming treatment. The combined ANOVA was performed across both locations using Statistix 8.1 software (Analytical Software, 2005). When significant interactions were detected ($P < 0.05$), simple effects were analyzed using one-way ANOVA within levels of the interacting factor, followed by Tukey's Honestly Significant Difference (HSD) test for mean separation. Significance threshold was set at $P < 0.05$ for all comparisons. For correlation analysis, Pearson's correlation coefficients were calculated to assess relationships between grain yield and physiological traits.

RESULTS

Main effect of location, sowing date, and seed priming on physiological traits

Maru had significantly ($P < 0.05$) higher RWC, SPAD, g_s, E, and A than Mushaqar (Table 3). For example, RWC at Maru was 9.8% higher, and g_s was 23.9% higher. Normal sowing resulted in significantly ($P < 0.05$) higher RWC, SPAD, g_s, E, and A by 15.2%, 4.3%, 29.8%, 17%, and 8.2%, respectively, when compared to late sowing. However, normal sowing had significantly ($P < 0.05$) lower WUE_i and WUE_{in} than late sowing (Table 3). Seed priming treatments significantly ($P < 0.05$) boosted some physiological traits. For example, seed priming with polyethylene glycol (PEG) resulted in increases in RWC, g_s, and A by 13.9%, 50.5%, and 42.5%, respectively, compared to

the control (Table 3). However, PEG treatment had significantly ($P < 0.05$) lower WUE_{in} than control (Table 3). Seed priming with PEG had significantly ($P < 0.05$) higher RWC and g_s than seed priming with CaCl₂ (Table 3).

Table 3. Main effect of location, sowing date, and seed priming treatments on some physiological parameters of wheat

Effect	RWC	SPAD	g _s	E	A	WUE _i	WUE _{in}
Location							
Maru	70.4 ^a	50.4 ^a	0.388 ^a	5.61 ^a	16.80 ^a	3.015 ^a	43.83 ^a
Mushaqr	64.1 ^b	45.0 ^b	0.313 ^b	4.72 ^b	13.97 ^b	2.952 ^a	46.16 ^a
<i>HSD (0.05)</i>	4.87	4.96	0.0638	0.585	2.65	0.653	14.17
Sowing date							
Normal	72.0 ^a	48.7 ^a	0.396 ^a	5.57 ^a	16.00 ^a	2.869 ^b	40.44 ^b
Late	62.5 ^b	46.7 ^b	0.305 ^b	4.76 ^b	14.78 ^b	3.099 ^a	49.55 ^a
<i>HSD (0.05)</i>	3.63	1.74	0.0129	0.326	0.897	0.122	4.108
Seed priming							
Control	62.6 ^d	44.9 ^c	0.277 ^d	4.42 ^c	12.41 ^c	2.810 ^a	46.29 ^a
Hydropriming	65.7 ^c	46.8 ^b	0.329 ^c	4.90 ^b	14.49 ^b	2.978 ^a	45.40 ^{ab}
CaCl ₂	69.3 ^b	49.2 ^a	0.378 ^b	5.55 ^a	16.97 ^a	3.072 ^a	45.48 ^{ab}
PEG	71.4 ^a	49.9 ^a	0.417 ^a	5.80 ^a	17.68 ^a	3.075 ^a	42.81 ^b
<i>HSD (0.05)</i>	1.58	0.90	0.0227	0.262	0.741	0.273	3.043

RWC: relative water content (%); g_s: stomatal conductance (mol H₂O m⁻² s⁻¹); E: transpiration rate (mmol H₂O m⁻² s⁻¹); A: net photosynthesis rate (μmol CO₂ m⁻² s⁻¹); WUE_i: instantaneous water use efficiency (mmol CO₂ mol⁻¹ H₂O); WUE_{in}: intrinsic water use efficiency (μmol CO₂ mol⁻¹ H₂O); HSD: honestly significant difference at $P < 0.05$ probability level using *Tukey's test*. Different letters within the same columns indicate significant differences.

Main effect of location, sowing date, and seed priming on phenological and yield traits

Maru location had significantly ($P < 0.05$) higher phenological and yield traits than Mushaqr (Table 4), except for DM and TGW. Specifically, PH, GY, and HI increased by 33%, 47%, and 10%, respectively at Maru when compared with Mushaqr. Normal sowing had significantly ($P < 0.05$) higher phenological and yield traits than late sowing. For example, normal sowing increased DM by 36%, spikes m⁻² by 41%, and GY by 75% (Table 4). Furthermore, seed priming had significantly ($P < 0.05$) higher phenological and yield traits than controls, except for PH, where no significant difference was found between hydropriming and controls. For instance, seed priming with PEG increased DM by 15%, spikes m⁻² by 22%, and GY by 36% compared to control (Table 4).

Table 4. Main effect of location, sowing date, and seed priming treatments on growth, yield and yield components of wheat

Effect	DH	DM	PH	GN	SN	BY	GY	TGW	HI
Location									
Maru	100 ^a	127 ^a	100 ^a	25 ^a	257 ^a	7.3 ^a	2.3 ^a	38.1 ^a	0.32 ^a
Mushaqr	89 ^b	121 ^a	75 ^b	21 ^b	203 ^b	5.4 ^b	1.6 ^b	36.8 ^a	0.29 ^b
<i>HSD (0.05)</i>	9.13	7.8	5.82	1.05	7.40	0.32	0.08	2.48	0.02

Table 4 (continued)

Sowing date									
Normal	110 ^a	143 ^a	109 ^a	25 ^a	269 ^a	8.0 ^a	2.5 ^a	39.1 ^a	0.31 ^a
Late	79 ^b	105 ^b	67 ^b	21 ^b	191 ^b	4.7 ^b	1.4 ^b	35.7 ^b	0.29 ^b
<i>HSD (0.05)</i>	3.58	5.37	3.49	0.51	8.94	0.20	0.07	1.27	0.01
Seed priming									
Control	88 ^d	115 ^d	82 ^b	21 ^c	204 ^d	5.8 ^c	1.6 ^d	36.1 ^c	0.27 ^c
Hydropriming	93 ^c	121 ^c	85 ^b	23 ^b	227 ^c	6.2 ^b	1.9 ^c	37.2 ^b	0.30 ^b
CaCl ₂	97 ^b	128 ^b	91 ^a	23 ^a	240 ^b	6.6 ^a	2.1 ^b	38.1 ^a	0.32 ^a
PEG	100 ^a	132 ^a	92 ^a	24 ^a	249 ^a	6.8 ^a	2.2 ^a	38.3 ^a	0.33 ^a
<i>HSD (0.05)</i>	2.02	3.14	4.30	0.50	6.49	0.29	0.07	0.55	0.01

DH: days to heading; DM: days to maturity; PH: plant height (cm); GN: grain number per spike; SN: spike number per meter square; BY: biological yield (ton ha⁻¹); GY: grain yield (ton ha⁻¹); TGW: 1,000-grain weight (g); HI: harvest index; *HSD*: honestly significant difference at $P < 0.05$ probability level using *Tukey's test*. Different letters within the same columns indicate significant differences.

Effect of interaction between location and sowing date on some physiological and yield traits

A significant ($P < 0.05$) interaction between location and sowing date was presented for A, SPAD, and WUE_{in} (Fig. 1), as well as a significant ($P < 0.05$) interaction including grains spike⁻¹ and spikes m⁻² (Fig. 2). In Maru, normal sowing increased A by 13.4% compared to late sowing, while in Mushaqr, the difference was not significant. This likely reflects Maru's higher seasonal rainfall, which may have supported stronger photosynthetic activity in timely sown crops (Fig. 1, A). Conversely, SPAD values increased significantly ($P < 0.05$) by 10.4% with normal sowing in Mushaqr, but not in Maru, indicating that light or nutrient limitations may have been more responsive to sowing time in the drier location (Fig. 1, B). Moreover, late sowing in Mushaqr significantly ($P < 0.05$) increased WUE_{in} by 34.8% compared to normal sowing, but not in Maru, suggesting adaptive stomatal regulation under more severe drought conditions (Fig. 1, C).

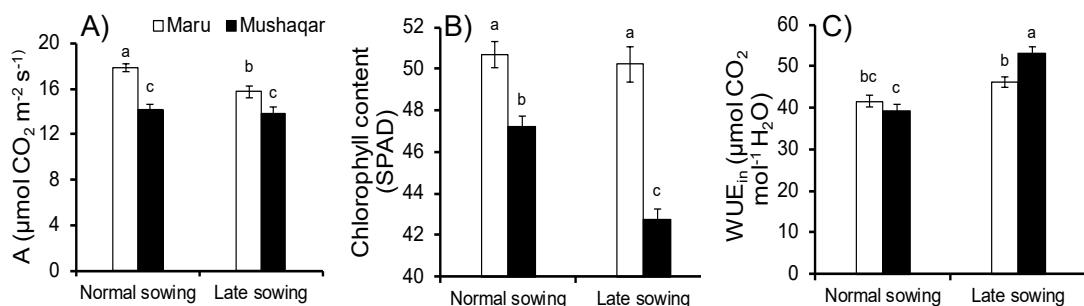


Figure 1. Location x sowing date interaction effect on (A) net photosynthetic rate, (B) total chlorophyll content by SPAD, and (C) intrinsic water use efficiency for wheat grown under seed priming treatments. Bars with the same letters are not significantly different, *Tukey's Range Test* at $P < 0.05$. Error bars show standard errors, $n = 3$.

In Maru and Mushaqr locations, normal sowing resulted in significant ($P < 0.05$) increases in grains spike^{-1} by 11.6% and 22.8%, respectively (Fig. 2, A), as well as significant increases in spikes m^{-2} by 28.7% and 57.4%, respectively, when compared to late sowing (Fig. 2, B).

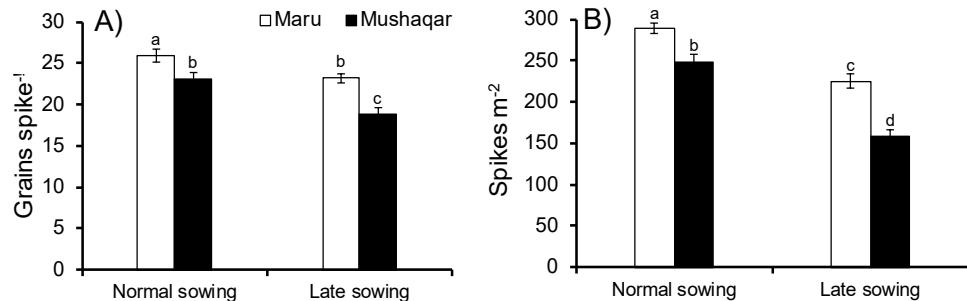


Figure 2. Location x sowing date interaction effect on (A) grain number per spike, and (B) spike number per meter square for wheat. Bars with the same letters are not significantly different, Tukey's Range Test at $P < 0.05$. Error bars show standard errors, $n = 3$

Effect of interaction between location and seed priming on some physiological and yield traits

In Maru location, seed priming with PEG significantly ($P < 0.05$) increased E by 5.5% compared to CaCl_2 , but not significant in Mushaqr (Fig. 3). Furthermore, E improved significantly ($P < 0.05$) by 34.8% in seeds primed with PEG in Maru, while in Mushaqr, E increased by 26.7% (Fig. 3).

In Mushaqr, seed priming with PEG significantly ($P < 0.05$) increased DH by 3.6% compared to seed priming with CaCl_2 , but not in Maru (Fig. 4, A). Furthermore, DH increased significantly ($P < 0.05$) by 9.3% with PEG-primed seeds in Maru, whereas, in Mushaqr, DH increased by 19.6% (Fig. 4, A). In Maru, seed priming with PEG, CaCl_2 , and water significantly ($P < 0.05$) increased spikes m^{-2} by 15.6%, 12.3%, and 8.1%, respectively compared to control (Fig. 4, B). In Mushaqr location, the increases in spikes m^{-2} were 31.6%, 25.4%, and 16.4% for seed priming with PEG, CaCl_2 , and water, respectively compared to control (Fig. 4, B). In Mushaqr, seed priming with water significantly ($P < 0.05$) increased TGW by 5.1% compared to the control, but not in Maru (Fig. 4, C). Moreover, the TGW improved significantly ($P < 0.05$) by 3.1% in PEG-primed seeds in Maru, while in Mushaqr, it increased by 9.3% (Fig. 4, C). In Mushaqr, seed priming with CaCl_2 significantly ($P < 0.05$)

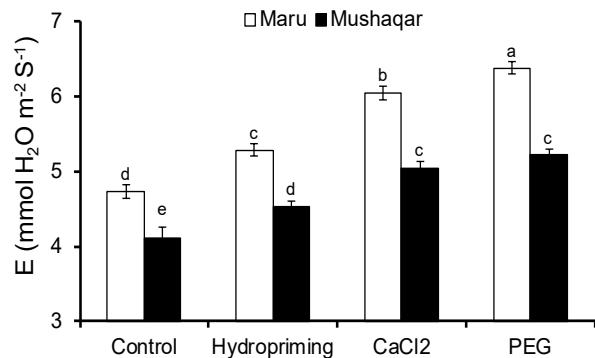


Figure 3. Location x seed priming interaction effect on transpiration rate (E) for wheat. Bars with the same letters are not significantly different, Tukey's Range Test at $P < 0.05$. Error bars show standard errors, $n = 3$.

increased HI by 7.8% compared to seed priming with water, but not in Maru (Fig. 4, D). Also, HI improved significantly ($P < 0.05$) by 13.5% in PEG-primed seeds in Maru, while in Mushaqar, HI increased by 28.9% (Fig. 4, D).

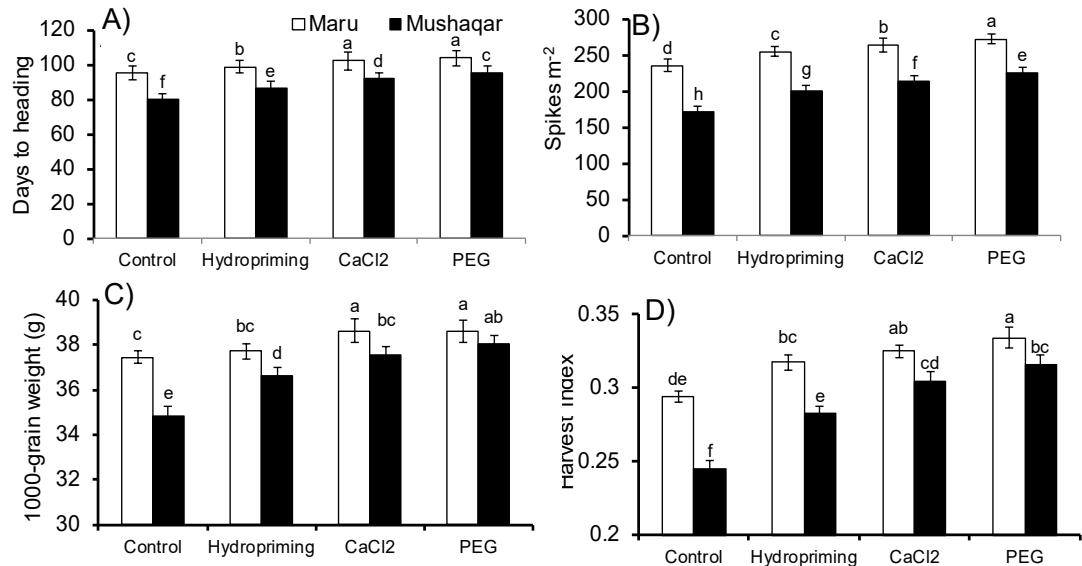


Figure 4. Location x seed priming interaction effect on (A) days to heading, (B) spike number per meter square, (C) 1,000-grain weight, and (D) harvest index for wheat grown at different sowing dates. Bars with the same letters are not significantly different, *Tukey's Range Test* at $P < 0.05$. Error bars show standard errors, $n = 3$.

Effect of interaction between sowing date and seed priming on some physiological and yield traits

In normal sowing, seed priming with PEG, CaCl₂, and water significantly ($P < 0.05$) increased RWC by 10.4%, 7.4%, and 2.7%, respectively compared to control (Fig. 5, A). In late sowing, seed priming with PEG, CaCl₂, and water increased RWC by 18.2%, 14.5%, and 7.7%, respectively compared to control (Fig. 5, A). Seed priming with PEG under late sowing did not significantly ($P < 0.05$) differ in RWC from unprimed seeds or control under normal sowing (Fig. 5, A). Moreover, seed priming with PEG significantly ($P < 0.05$) increased A by 4.7% compared to seed priming with CaCl₂ under normal sowing, while no significant difference was observed between seed priming with PEG and those with CaCl₂ under late sowing (Fig. 5, B). Seed priming with PEG increased A by 30.5% and 57.6% under normal and late sowing, respectively compared to control (Fig. 5, B). Seed priming with PEG significantly ($P < 0.05$) increased SPAD values by 1.9% compared to seed priming with CaCl₂ under normal sowing, but no significant difference was found between seed priming with PEG and those with CaCl₂ under late sowing (Fig. 5, C). SPAD values showed a significant ($P < 0.05$) increase of 11.2% and 10.9% in PEG-primed seeds under normal and late sowing, respectively compared to control (Fig. 5, C). In addition, seed priming with PEG significantly ($P < 0.05$) reduced WUE_{in} by 10.5% compared to the control under late sowing, while no significant difference was found between seed priming with PEG and the control under normal sowing (Fig. 5, D).

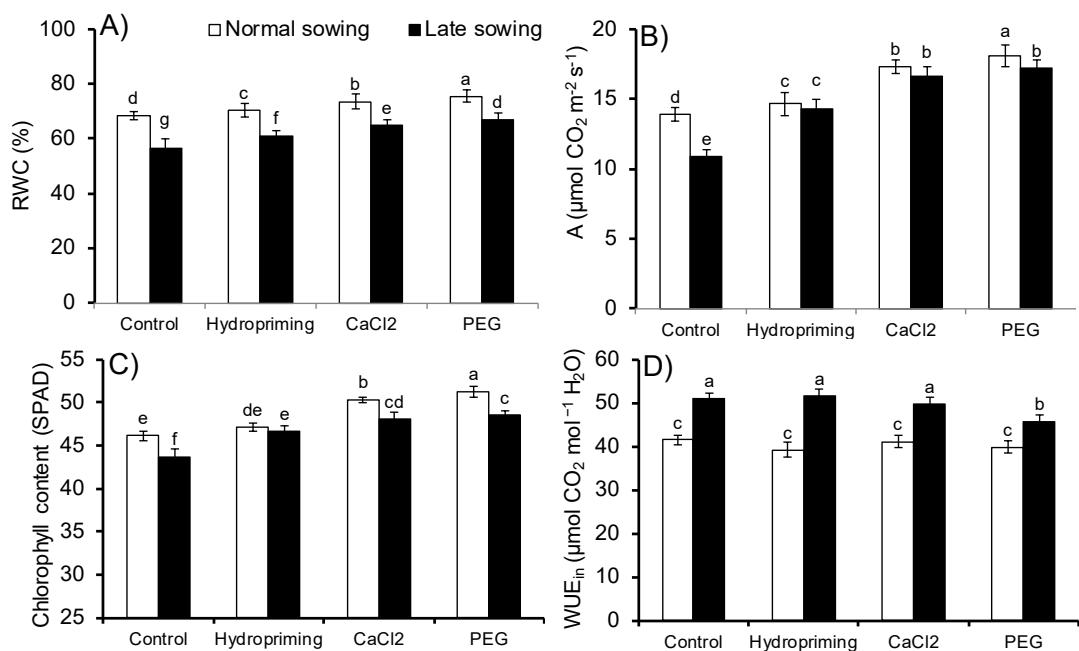


Figure 5. Sowing date x seed priming interaction effect on (A) relative water content, (B) net photosynthetic rate, (C) chlorophyll content by SPAD, and (D) intrinsic water use efficiency for wheat grown in both locations. Bars with the same letters are not significantly different, Tukey's Range Test at $P < 0.05$. Error bars show standard errors, $n = 3$.

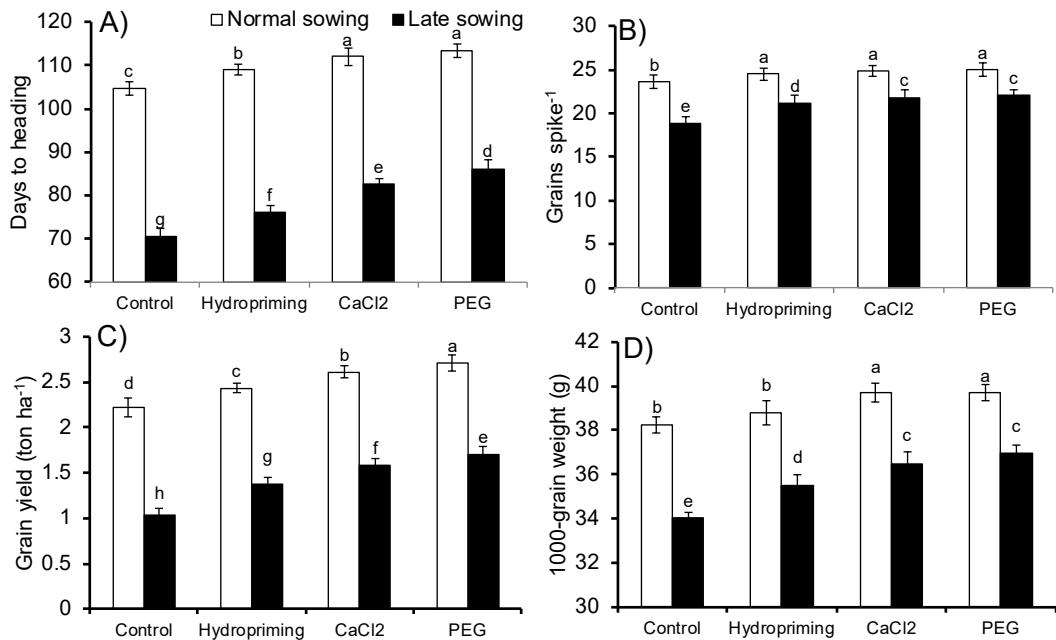


Figure 6. Sowing date x seed priming interaction effect on (A) days to heading, (B) grain number per spike, (C) grain yield, and (D) 1,000-grain weight for wheat grown in both locations. Bars with the same letters are not significantly different, Tukey's Range Test at $P < 0.05$. Error bars show standard errors, $n = 3$.

Seed priming with PEG significantly ($P < 0.05$) increased DH by 4.4% compared to seed priming with CaCl_2 under late sowing, while no significant difference was found between seed priming with PEG and those with CaCl_2 under normal sowing (Fig. 6, A). Moreover, DH revealed a significant ($P < 0.05$) increase of 8.4% in PEG-primed seeds during normal sowing and an increase of 22.2% in late sowing (Fig. 6, A). Seed priming with PEG significantly ($P < 0.05$) increased grains spike $^{-1}$ by 4.3% compared to seed priming with water under late sowing, although no significant difference was found under normal sowing (Fig. 6, B). Seed priming with PEG increased grains spike $^{-1}$ by 5.8% and 16.8% under normal and late sowing, respectively compared to control (Fig. 6, B). In normal sowing, seed priming with PEG, CaCl_2 , and water significantly ($P < 0.05$) increased GY by 22.1%, 17.8%, and 9.8%, respectively compared to control (Fig. 6, C). These seed priming treatments also increased GY in late sowing by 65.9%, 54.7%, and 33.8%, respectively compared to control (Fig. 6, C). In normal and late sowing, TGW showed significant ($P < 0.05$) increases of 3.8% and 8.6%, respectively, in PEG-primed seeds compared to the controls (Fig. 6, D).

Correlation between grain yield and physiological traits

Grain yield (GY) showed a positive correlation with all measured physiological traits, except of WUE_i and WUE_{in} (Table 5). The strongest significant ($P < 0.01$) correlation was observed between GY and RWC ($r = 0.94$), followed by GY and g_s ($r = 0.87$), and then GY and E ($r = 0.83$). A significant positive correlation ($P < 0.01$) was found between A and the other physiological traits, except for WUE_{in} . The most significant correlation among the physiological traits was found between RWC and g_s ($r = 0.90$). Instantaneous water use efficiency (WUE_i) was positively correlated with all measured physiological parameters except for RWC and E. Furthermore, WUE_i showed a significant correlation only with A and WUE_{in} . However, WUE_{in} exhibited a negative correlation with all measured physiological parameters except for WUE_i . A highly significant ($P < 0.01$) correlation was found between WUE_{in} and RWC, E, and g_s (Table 5).

Table 5. Pearson's correlation coefficients between grain yield (GY) of wheat and other physiological parameters under two sowing dates and four seed priming conditions at two locations

	A	GY	RWC	SPAD	E	WUE_i	WUE_{in}
GY	0.67**						
RWC	0.75**	0.94**					
SPAD	0.75**	0.73**	0.71**				
E	0.82**	0.83**	0.86**	0.69**			
WUE_i	0.45**	-0.12	-0.03	0.20	-0.13		
WUE_{in}	-0.19	-0.67**	-0.62**	-0.37*	-0.43**	0.30*	
g_s	0.84**	0.87**	0.90**	0.73**	0.86**	0.12	-0.69**

**, * are significant at $P < 0.01$ and $P < 0.05$, respectively. A: net photosynthesis rate; RWC: relative water content; E: transpiration rate; WUE_i : instantaneous water use efficiency, WUE_{in} : intrinsic water use efficiency, and g_s : stomatal conductance.

DISCUSSION

Location effects

The present study highlights the significant impact of location on physiological (Table 3) and yield traits (Table 4) in wheat. The Maru location demonstrated a clear advantage over Mushaqar in both aspects. This improvement is likely due, in part, to the greater rainfall received in Maru, which experienced 39.4% more precipitation during the growing season (Table 2). Specifically, during the vegetative stage, wheat in Maru received approximately 114.2 mm and 103 mm more rainfall than in Mushaqar under normal and late sowing conditions, respectively. Mushaqar represents the drier regions of central Jordan, where water scarcity is common, while Maru is located in the northern region, which typically has better water availability. The increased water availability in Maru likely facilitated improved physiological responses and overall plant growth, both of which are critical for optimizing photosynthesis (Qiao et al., 2024). However, it is noteworthy that no significant differences were observed in instantaneous water use efficiency (WUE_i) and thousand grain weight (TGW) between the two locations, suggesting that these traits may be more influenced by crop management practices than by environmental conditions (Bani-Khalaf et al., 2024).

Sowing date effects

Normal sowing significantly outperformed late sowing in nearly all measured physiological, growth, and yield parameters of wheat (Tables 3 and 4). This aligns with the findings of Ma et al. (2018), who emphasized the importance of sowing timing in achieving higher physiological efficiency and yield potential in wheat. Under normal sowing conditions, the crop benefits from increased water availability, which enhances physiological responses and ultimately boosts both biomass and yield (Wu et al., 2023). In contrast, late-sown wheat exhibited a decline in photosynthetic rate, likely due to stomatal closure and reduced CO_2 diffusion, as plants experienced significant stress, particularly during anthesis. Our results showed that late sowing reduced the number of days to heading and maturity, decreased plant height, and ultimately lowered yield and its components. Similar findings were reported by Sial et al. (2005) and Hosen et al. (2023), who attributed the higher grain yield under normal sowing to the production of a greater number of heavier grains per spike.

In this study, the interaction observed between location and sowing date for some physiological and yield parameters (Figs 1 and 2) indicates notable variability in how these factors influence wheat performance. While normal sowing significantly improved net photosynthesis in Maru, such improvements were not observed in Mushaqar, suggesting that the higher rainfall in Maru played a critical role in maximizing the benefits of timely sowing. In contrast, normal sowing improved total chlorophyll content only in Mushaqar. The lack of a significant increase in chlorophyll content with sowing date in Maru could indicate that plants there are already optimized for their environment and are not limited by light capture. Furthermore, normal sowing resulted in greater percentage increases in grain and spike numbers in Mushaqar, approximately twice those observed in Maru compared to late sowing, suggesting that Mushaqar may benefit more from normal sowing conditions than Maru.

Seed priming effects

Seed priming, particularly with polyethylene glycol (PEG), significantly enhanced physiological parameters (Table 3), suggesting its effectiveness in mitigating drought stress, especially under late sowing conditions. Similarly, previous studies reported that PEG-based seed priming increased transpiration rates, total leaf chlorophyll, and relative water content (RWC) in wheat and other crops (Hussain et al., 2017; Abdolahi et al., 2018; Aldahadha et al., 2024). Our findings indicate that osmoprimer is more effective than hydropriming in enhancing certain physiological traits. This may be attributed to improved stress tolerance conferred by PEG (Zhang et al., 2015; Marthandan et al., 2020), or the potential role of CaCl_2 in stabilizing membranes under stress conditions (Hepler, 2005).

In this study, seed priming with PEG increased transpiration only in Maru when compared with CaCl_2 priming (Fig. 3). This could be attributed to better water availability in Maru, which allows the plants to respond more effectively to the osmotic adjustment benefits provided by PEG, along with improved leaf water status that enhances stomatal conductance and gas exchange. Moreover, PEG priming was more effective under late sowing than normal sowing in increasing relative water content (Fig. 5, A) and photosynthetic rate (Fig. 5, B), potentially enabling plants to better cope with stress (Mahboob et al., 2015; Aswathi et al., 2022). However, PEG priming significantly decreased intrinsic water use efficiency (WUE_{in}) under late sowing compared to unprimed seeds (Fig. 5, D). Although the PEG-primed plants exhibited higher photosynthesis and stomatal conductance, the proportional increase in stomatal conductance exceeded that of photosynthesis. This imbalance led to a reduction in intrinsic WUE. The photosynthetic rate is primarily regulated by stomatal conductance, although biochemical limitations also play a role (Chaves et al., 2009). In unprimed seeds, the concurrent reduction in stomatal conductance serves as a conservative strategy to enhance water use efficiency (Rouhi et al., 2007), supporting plant survival under water-limited conditions (Fuganti-Pagliarini et al., 2017).

Seed priming generally improved wheat growth and yield traits across different sowing dates, with PEG priming proving to be the most effective (Fig. 6). Recent studies by Aldahadha et al. (2024) and Tabassum et al. (2018) confirmed that seed priming with PEG or CaCl_2 resulted in higher yields compared to hydropriming. Osmoprimer seeds tend to absorb more water, promoting better stand establishment (Farooq et al., 2015). In this study, seed priming also improved the harvest index of wheat, which may be attributed to increased dry matter allocation to spikelets (Faisal et al., 2023). Moreover, seed priming led to a notable increase in grain yield under late sowing conditions, likely due to increased thousand grain weight (TGW) and a higher number of spikes. Therefore, implementing seed priming appears to be a viable strategy to mitigate yield losses typically associated with late sowing.

This study highlights the critical role of seed priming in enhancing wheat physiological traits, ultimately leading to increased grain yield. Our findings revealed a strong and significant positive correlation between grain yield and physiological traits (Table 5), particularly relative water content (RWC). These results are consistent with observations by Baloch et al. (2013) and Guizani et al. (2023). Higher RWC typically indicates better water availability within the plant, which is essential for maintaining cellular functions and supporting photosynthesis (Qiao et al., 2024). Among the

physiological traits, the most pronounced correlation was observed between RWC and stomatal conductance (g_s), aligning with the findings of Wang et al. (2024). Thus, wheat plants that maintain elevated RWC are likely to exhibit enhanced g_s , and conversely, those capable of sustaining higher g_s are better positioned to preserve RWC. Interestingly, our study found no significant relationship between grain yield and intrinsic water use efficiency (WUE) in PEG-primed seeds, or between grain yield and photosynthetic rate in hydroprimed seeds, suggesting a complex interplay of physiological mechanisms affecting yield under specific environmental conditions. Nonetheless, significant correlations were observed between grain yield and both transpiration rate and g_s across all seed priming treatments. This suggests that seed priming can effectively enhance grain yield by improving gas exchange and water utilization efficiency.

CONCLUSIONS

This study presents a novel multi-factorial field assessment of seed priming effects across two agro-ecological locations, two sowing dates, and multiple priming treatments. By integrating physiological, phenological, and yield traits, the research provides a comprehensive understanding of how seed priming modulates drought responses in durum wheat under realistic field conditions. This study underscores the pivotal role of seed priming, particularly osmoprimering with PEG, in mitigating the adverse effects of late sowing and drought stress on durum wheat under arid and semi-arid conditions in Jordan. The results revealed that osmoprimering significantly enhances key physiological parameters such as relative water content (RWC), net photosynthetic rate, and stomatal conductance, all of which are critical for improving wheat growth and yield. While normal sowing remains optimal for maximizing yield due to favorable water availability and longer growth duration, PEG-primed seeds demonstrated a strong capacity to alleviate the constraints associated with late sowing. Grain yield improvements with PEG priming were attributed to enhanced photosynthesis, improved gas exchange, and increases in both 1,000-grain weight and spike number, indicating superior drought resilience. While PEG priming generally improved photosynthetic activity and yield, it also resulted in a reduction in intrinsic water use efficiency (WUE_{in}) under drought conditions due to a proportionally greater increase in stomatal conductance than in CO₂ assimilation. The study also highlights significant interactions between location and sowing date, with the Maru site exhibiting better outcomes due to higher rainfall. These findings emphasize the importance of tailored crop management practices combining optimal sowing dates and advanced seed priming techniques to address climatic variability and ensure sustainable wheat production in arid regions. Future research should incorporate multi-season trials and explore genotypic variability to validate the consistency of seed priming effects. Additionally, further investigation into the underlying physiological mechanisms is needed, along with broader application of seed priming strategies to support global food security.

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