

Effects of drought priming at seedling stage on salt-tolerance physiology at flowering stage and subsequent seed setting of winter wheat

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Abstract: To explore cultivation techniques for improving winter wheat yield in saline-alkali soils, this study investigated the effects of seedling-stage drought priming on salt tolerance and related physiological mechanisms during later growth stages. The experiment was arranged in a completely randomised design. Three soil moisture levels – 40% (W1, severe drought), 60% (W2, mild drought), and 80% (W3, well-watered) of field capacity – were applied from emergence to jointing, followed by normal irrigation and saline irrigation at 1‰ (S1), 3‰ (S2), or 5‰ (S3) NaCl. Compared with W1 and W3, mild priming (W2) significantly reduced flag leaf malondialdehyde and sterile spikelets while increasing chlorophyll and seed-setting under saline irrigation ($P < 0.05$). Treatment efficacy followed $W2 > W3 > W1$ and diminished with increasing salinity ($S1 > S2 > S3$). At S1, W2S1 increased stomatal conductance, superoxide dismutase (SOD) activity, and the contents of betaine and plant brassins, grains per spike (19.5%), 1 000-grain weight, and yield per plant (34.8%) *versus* W3S1. At S2, W2S2 increased transpiration rate, stomatal conductance, SOD activity, and the contents of soluble sugar, plant abscisic acid, and plant gibberellins, grains per spike, 1 000-grain weight, and yield per plant (35.0%) *versus* W3S2. Even at S3, W2S3 maintained higher SOD activity, and higher contents of osmotic substances and plant hormones (plant brassins, plant abscisic acid, and plant gibberellins), grains per spike, 1 000-grain weight, and yield per plant than W3S3. It can be seen that this advantage in seed-setting per plant is attributed to the coordinated regulation of antioxidant enzymes, osmotic substances, hormones, and photosynthesis, effectively alleviating salt stress damage. In conclusion, mild drought priming at the seedling stage establishes a stress memory that is still detectable at 7 days after anthesis (early grain filling), enhancing salt tolerance through coordinated regulation of antioxidant enzymes, osmotic substances, hormones, and photosynthesis, ultimately improving seed-setting. These findings offer a practical approach for stabilising wheat production in saline-alkali soils.

Keywords: saline-alkali stress; antioxidant defense; photosynthetic characteristics; endogenous hormones; grain formation; soil salinity

Saline-alkali stress is a major ecological constraint that limits the sustainable development of dryland agriculture worldwide (Lao et al. 2024). In China, significant portions of land are saline-alkali, and

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their adverse impacts on the growth and yield of key crops such as wheat have become increasingly severe (Wang et al. 2022, Ju et al. 2023, Sarika et al. 2023). Wheat is the most important food crop in China, and stable wheat production is crucial for national food security (Zhang et al. 2024b). However, salt stress significantly suppresses wheat yield formation (Rio et al. 2022). Therefore, developing effective cultivation strategies for winter wheat in saline-alkali areas holds both theoretical significance and practical value for ensuring stable grain yields.

Various approaches to mitigate salt-induced damage have been investigated, and drought priming has gained considerable attention as an effective approach to enhance crop stress resistance. Previous studies have demonstrated that controlling water supply for 7–10 days during the seedling stage can significantly improve wheat drought resistance from the jointing to flowering stages, resulting in a notable compensatory growth effect (Xiao et al. 2014). Molecular studies indicate that moderate drought during early growth stages can establish a "stress memory" in crops. This memory enhances antioxidant enzyme activity, maintains ion homeostasis (e.g., K^+/Na^+ balance), and protects photosynthetic structures under subsequent stress through epigenetic mechanisms such as DNA methylation, histone modification, and small RNA regulation (Louis et al. 2023). Additionally, drought priming promotes the synthesis of abscisic acid (ABA) in plants (Yoshida et al. 2024), which plays a crucial role in the formation and recall of stress memory (Ping et al. 2019), synergistically improving the capacity of crops to cope with recurring stress.

Current research on drought priming-induced stress memory has primarily focused on its cross-adaptability to drought and extreme temperatures (Lou et al. 2021); however, its potential in alleviating salt stress remains understudied. Existing studies on salt stress have emphasised the use of exogenous hormones and optimised fertilisation strategies (Mushtap et al. 2021, Ali et al. 2023). This raises an important scientific question: under salt-stress conditions, can the defensive memory induced by drought priming at the seedling stage persist through the critical reproductive stage, the flowering period, and ultimately contribute to improved seed-setting performance?

To address this question, this study applied drought priming treatments to winter wheat at the seedling stage to investigate whether physiological responses to salt stress, such as those involving the antioxidant

system, are regulated by priming-induced stress memory when salt stress is applied at the flowering stage. Furthermore, this study elucidates how this memory effect influences floret fertility and assimilate partitioning to grains. The overall objective was to determine whether drought priming at the seedling stage effectively enhances salt tolerance during the flowering and grain-filling stages, thereby providing a novel theoretical basis and a practical approach for salt-tolerant, high-yield cultivation practices.

MATERIAL AND METHODS

Test treatment. A pot experiment was conducted in a rain-proof shelter at University using the winter wheat cultivar Qingmai 11. Each pot (20 cm in diameter and 20 cm in height) was filled with 10 kg of soil. The test soil was collected from a field experiment site in the Yellow River Delta. It is classified as a typical coastal Solonchak (FAO-WRB system) with a loamy-sand texture. Prior to sowing, the soil was thoroughly leached with fresh water three times to reduce salinity. The basal soil properties after this pretreatment were as follows: pH 7.3, salinity 0.93‰, cation exchange capacity 5.02 cmol_+/kg , carbonate content (as CaCO_3) 11.37 g/kg, organic carbon content approximately 2.26 g/kg, total nitrogen 0.60 g/kg, available phosphorus 20.04 mg/kg, and available potassium 198.03 mg/kg. The determination methods were as follows: pH was determined by the $\text{pH}_{\text{H}_2\text{O}}$ method (water-to-soil ratio 5:1); salinity was determined as water-soluble salt content by the oven-drying gravimetric method; cation exchange capacity was determined by the neutral ammonium acetate exchange method; carbonate was determined by the gasometric method; organic carbon was determined by potassium dichromate oxidation with external heating; total nitrogen was determined by the acid digestion-Kjeldahl method using an A33 continuous-flow analyser; available phosphorus was determined by the Olsen method (NaHCO_3 extraction followed by molybdenum-antimony-ascorbic acid colourimetry); and available potassium was determined by neutral NH_4OAc extraction followed by flame photometry. Analytical-grade urea (providing 0.90 g N) and analytical-grade monocalcium phosphate monohydrate (providing 0.56 g P) were applied as basal fertilisers; no potassium fertiliser was added. Forty seeds were sown per pot and subsequently thinned to 30 uniform seedlings after emergence. The ex-

Table 1. Experimental factors and levels

Factor	Level	Code	Description
Water regime (emergence-jointing)	severe drought	W1	40% of field capacity
	mild drought	W2	60% of field capacity
	well-watered	W3	80% of field capacity
Saline irrigation (jointing-maturity)	low salinity	S1	1‰ NaCl
	moderate salinity	S2	3‰ NaCl
	high salinity	S3	5‰ NaCl

periment was arranged in a completely randomised design with six replications.

From emergence to tillering, three soil moisture regimes were maintained by adjusting soil water content to 40% (W1, severe drought), 60% (W2, mild drought), or 80% (W3, well-watered) of field capacity. Starting at the jointing stage (April 1), salt stress was applied through irrigation water with NaCl concentrations of 1, 3, and 5‰, and soil moisture was maintained at $\geq 75\%$ of field capacity. Although soil EC was not continuously monitored, salinity was imposed quantitatively through the same NaCl treatments, and all pots had the same initial soil salinity (0.93‰). Each treatment combination was replicated six times. A summary of the experimental design is provided in Table 1. Tap water was used for all experimental irrigation, and its water quality parameters are presented in Table 2.

Determination items, sample collection, and methods

Photosynthetic parameters. Chlorophyll *a*, chlorophyll *b*, and carotenoid contents in flag leaves were determined spectrophotometrically after extraction with 95% ethanol. Absorbance was measured at 663, 645, and 470 nm.

Photosynthetic parameters of flag leaves were measured 7 days after anthesis, a representative early grain-filling stage critical for grain setting, on clear days between 9:00 and 11:00 a.m. using an

LI-6800 portable photosynthesis system (LI-COR, Lincoln, USA). Measurements were conducted under the following conditions: photosynthetically active radiation of 1 000 $\mu\text{mol}/\text{m}^2/\text{s}$, CO_2 concentration of 385 $\mu\text{mol}/\text{mol}$, and a closed gas path.

Enzyme activities. Flag leaves sampled at the flowering stage were immediately frozen in liquid nitrogen and stored at -80°C until analysis. The activities of superoxide dismutase (SOD), peroxidase (POD), and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) were measured using commercial assay kits (SOD: Solarbio, BC0095; POD: Solarbio, BC01753587; Rubisco: Shanghai, MM-060302).

Osmotic solute contents. Soluble sugar, malondialdehyde (MDA), proline, and betaine contents in flag leaves collected at flowering were quantified using assay kits. Kits for soluble sugar, MDA, and proline were obtained from Solarbio (BC0295, BC0035, BC0025), and the betaine assay kit was sourced from Edison (ADS-F-QT006).

Hormone contents. Concentrations of brassinosteroids, abscisic acid, and gibberellin in flag leaves at flowering were measured using ELISA kits (Shanghai Tongwei, China; MM-012502, MM-3599202, MM-118502) according to the manufacturer's instructions.

Yield-related traits. At physiological maturity, the following yield components were recorded: grain number per spike, number of sterile spikelets per spike, grain weight per spike, and 1 000-grain weight.

Table 2. Water quality parameters of experimental water

	Nitrate (N, mg/L)	Chlorate (ClO_3^- , mg/L)	pH	Chloride (mg/L)	Sulfate (mg/L)	Total hardness (CaCO_3 , mg/L)	Total dissolved solids (mg/L)
Mean	1.80	< 0.0050	7.19	13.87	22.73	105.57	248.57
$\pm$ SD	± 0.26		± 0.06	± 2.40	± 2.11	± 16.82	± 56.30

Data represent water quality measurements obtained during the 7-month experimental period ($n = 7$). Chlorate was below the detection limit of 0.0050 mg/L. SD – standard deviation

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Statistical analysis

Statistical analysis was conducted using SPSS 20.0 (IBM, Armonk, USA). Two-way ANOVA was used to test the main effects of water regime (W) and salinity (S), and their interaction ($W \times S$). Duncan's multiple range test was adopted for post-hoc multiple comparisons, and statistical significance was set at $P < 0.05$. All graphs were produced with OriginPro 2022 (OriginLab, Northampton, USA).

RESULTS

Chlorophyll contents and proportions. Under the same irrigation water salinity level, the contents of chlorophyll *a*, chlorophyll *b*, and carotenoids were significantly higher in the W2 treatment compared to W1 and W3 (Figure 1). At 1‰ salinity, chlorophyll *a* content in W2S1 was significantly higher compared to W1S1 and W3S1 by 33.4% and 13.2%, respectively. Chlorophyll *b* content increased by

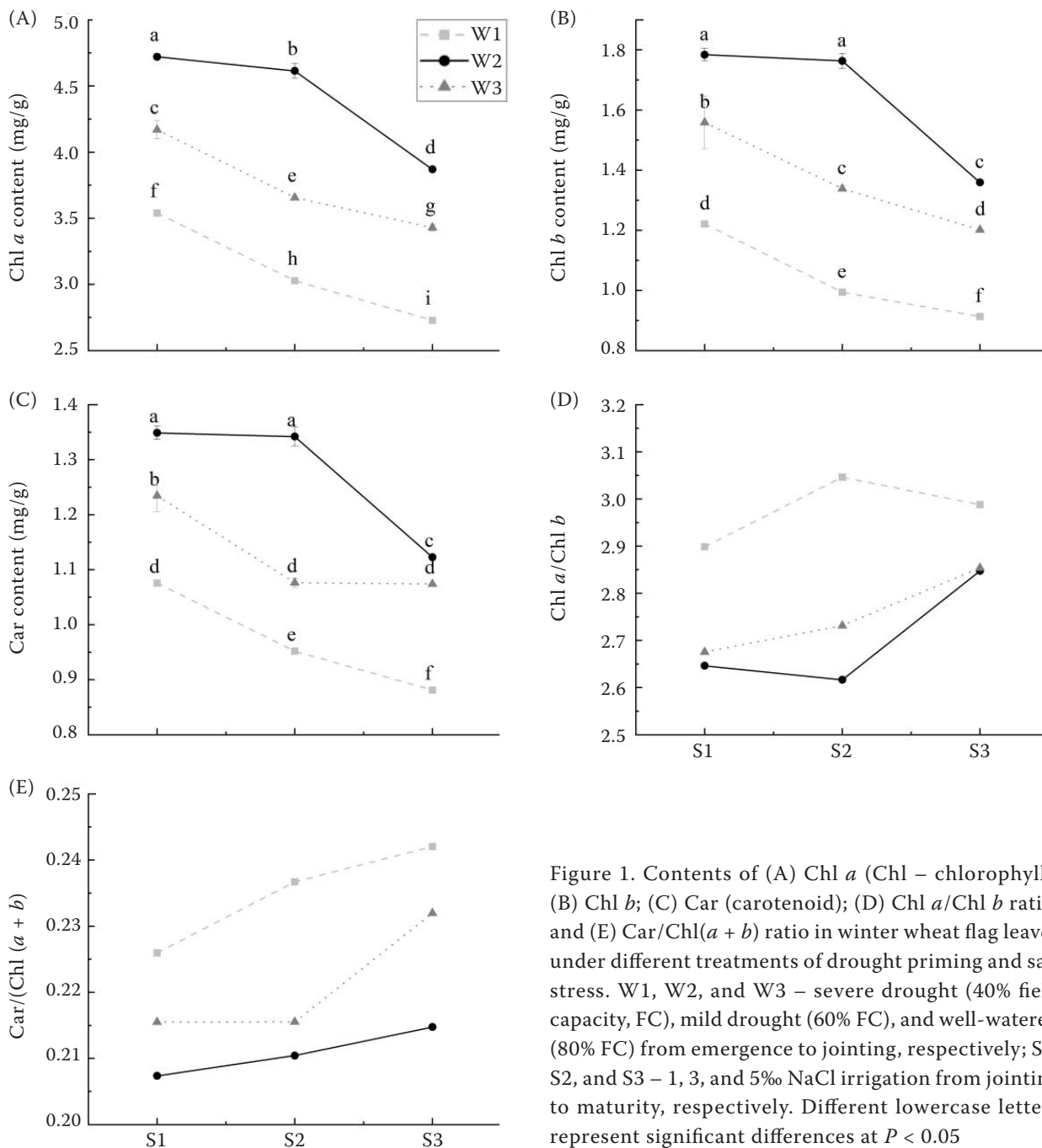


Figure 1. Contents of (A) Chl *a* (Chl – chlorophyll); (B) Chl *b*; (C) Car (carotenoid); (D) Chl *a*/Chl *b* ratio, and (E) Car/Chl(*a* + *b*) ratio in winter wheat flag leaves under different treatments of drought priming and salt stress. W1, W2, and W3 – severe drought (40% field capacity, FC), mild drought (60% FC), and well-watered (80% FC) from emergence to jointing, respectively; S1, S2, and S3 – 1, 3, and 5‰ NaCl irrigation from jointing to maturity, respectively. Different lowercase letters represent significant differences at $P < 0.05$

46.1% and 14.5%, and carotenoid content by 25.4% and 9.3%, respectively, under the same conditions. Under 3‰ salinity, chlorophyll *a* content in W2S2 was significantly higher than in W1S2 and W3S2 by 52.4% and 26.2%, respectively. Chlorophyll *b* content also increased significantly by 77.4% and 31.8%, and carotenoid content increased by 41.0% and 24.7%, with all differences being statistically significant. At the highest salinity level (5‰), the W2S3 treatment exhibited significant improvements: chlorophyll *a* content was 41.9% and 12.9% higher than that in W1S3 and W3S3, respectively; chlorophyll *b* increased by 48.8% and 13.1%; and carotenoid content increased by 27.4% and 4.5%. Additionally, the proportion of chlorophyll *b* was higher in the W2S1 and W2S2 treatments, whereas chlorophyll *a* accounted for a larger proportion in W1S2 and W1S3. The W1S3 treatment also showed a relatively higher proportion of carotenoids.

Photosynthetic parameters. As shown in Table 3, at 1‰ salinity, no significant differences in the net photosynthetic rate (P_n) of flag leaves were observed among the W1S1, W2S1, and W3S1 treatments. However, the W2S1 treatment resulted in a significantly higher intercellular CO_2 concentration (c_i), exceeding W1S1 by 6.2%, and a notable increase in transpiration rate (T_r) by 70.6%. Furthermore, stomatal conductance (g_s) in W2S1 was 58.0% and 31.2% higher than in W1S1 and W3S1, respectively. At 3‰ salinity, the W2S2 treatment exhibited an 18.6% higher net photosynthetic rate than W1S2. Although c_i showed no significant differences among

treatments, T_r and g_s in W2S2 were significantly higher, by 81.3% and 73.3%, respectively, compared to W1S2. g_s was also 41.5% higher than in W3S2. Under 5‰ salinity, the W2S3 treatment led to significant increases of 71.0% in P_n and 6.9% in c_i relative to W1S3. Although no significant differences in T_r were detected among the treatments, the g_s of W2S3 was 36.5% higher than that of W1S3.

Enzyme activities. As shown in Figure 2, mild drought priming at the seedling stage (W2) effectively enhanced enzyme activities in flag leaves during the flowering stage under salt stress. At 1‰ salinity, the W2S1 treatment significantly increased Rubisco activity by 5.5% and POD activity by 23.4% compared with W1S1. Furthermore, SOD activity under W2S1 was 38.8% and 15.5% higher than that under W1S1 and W3S1, respectively. At 3‰ salinity, both W1S2 and W3S2 showed significantly lower Rubisco activity than W2S2. Compared to W1S2, W2S2 increased POD and SOD activities by 30.5% and 35.0%, respectively. Additionally, SOD activity in W2S2 was 10.8% higher than in W3S2. Under the highest salinity level (5‰), the W2S3 treatment significantly enhanced Rubisco activity by 5.0% and POD activity by 24.8% relative to W1S3. SOD activity was also significantly higher in W2S3, by 27.8% and 18.8%, compared to W1S3 and W3S3, respectively.

Osmotic substance contents. The contents of soluble sugar, proline, betaine, and MDA in flag leaves at the flowering stage were significantly influenced by both water regime and salt stress (Figure 3). At 1‰ salinity, the W2S1 treatment exhibited

Table 3. Effects of drought priming at the seedling stage on photosynthetic parameters of flag leaves of winter wheat at the flowering stage under salt stress

	Net photosynthetic rate ($\mu\text{mol}/\text{m}^2/\text{s}$)	Intercellular CO_2 concentration ($\mu\text{mol}/\text{mol}$)	Transpiration rate ($\text{mmol}/\text{m}^2/\text{s}$)	Stomatal conductivity
W1S1	18.0 ± 1.4^a	424.6 ± 5.2^{bc}	1.7 ± 0.6^c	54.0 ± 2.0^d
W2S1	18.7 ± 0.1^a	451.0 ± 7.0^a	2.9 ± 0.5^a	85.3 ± 2.1^a
W3S1	18.5 ± 0.3^a	434.0 ± 5.0^{ab}	2.0 ± 0.6^{abc}	65.0 ± 1.0^c
W1S2	15.6 ± 1.0^b	413.5 ± 7.4^{bc}	1.6 ± 0.1^c	44.9 ± 0.2^e
W2S2	18.5 ± 0.3^a	435.1 ± 4.9^{ab}	2.9 ± 0.2^{ab}	77.8 ± 1.8^b
W3S2	18.3 ± 0.5^a	428.1 ± 7.4^b	1.9 ± 0.1^c	55.0 ± 2.6^d
W1S3	10.7 ± 0.2^c	403.1 ± 1.4^c	1.5 ± 0.3^c	43.7 ± 2.2^e
W2S3	18.3 ± 0.8^a	430.9 ± 9.5^{ab}	2.0 ± 0.3^{bc}	59.2 ± 1.4^d
W3S3	17.6 ± 0.8^a	416.0 ± 2.0^{bc}	1.7 ± 0.3^c	53.3 ± 0.6^d

W1, W2, and W3 – severe drought (40% field capacity, FC), mild drought (60% FC), and well-watered (80% FC) from emergence to jointing, respectively. S1, S2, and S3 – 1, 3, and 5‰ NaCl irrigation from jointing to maturity, respectively. Different letters represent significant differences between treatments ($P < 0.05$)

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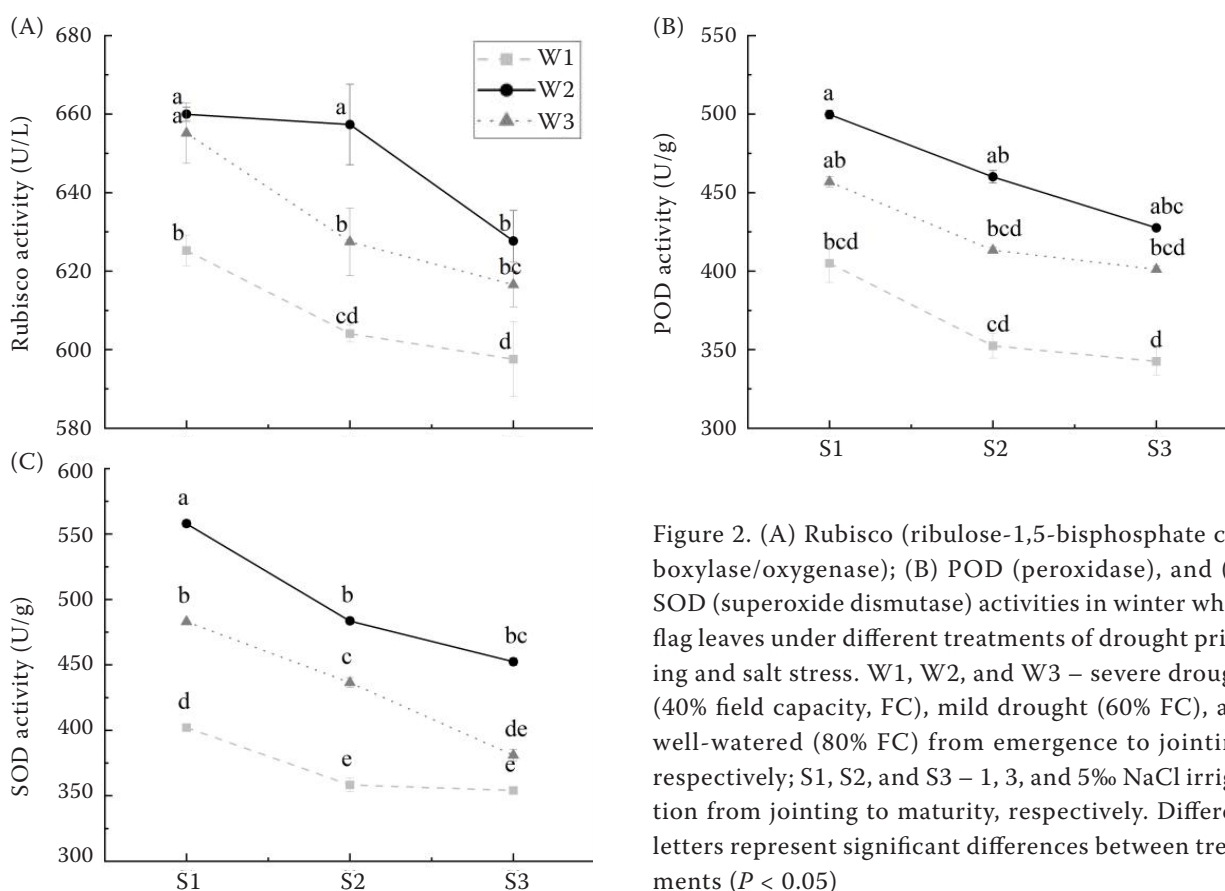


Figure 2. (A) Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase); (B) POD (peroxidase), and (C) SOD (superoxide dismutase) activities in winter wheat flag leaves under different treatments of drought priming and salt stress. W1, W2, and W3 – severe drought (40% field capacity, FC), mild drought (60% FC), and well-watered (80% FC) from emergence to jointing, respectively; S1, S2, and S3 – 1, 3, and 5‰ NaCl irrigation from jointing to maturity, respectively. Different letters represent significant differences between treatments ($P < 0.05$)

a 19.7% higher soluble sugar content than W1S1, and a 13.2% greater proline content. Betaine content was significantly increased by 95.0% and 32.1% compared to W1S1 and W3S1, respectively. In contrast, the MDA content under W2S1 was significantly lower than that of W1S1 and W3S1 by 31.2% and 18.8%, respectively. At 3‰ salinity, the W2S2 treatment showed significantly higher soluble sugar content (50.0% and 18.1% higher compared to W1S2 and W3S2), proline content (14.8% compared to W1S2), and betaine content (125.8% and 31.1% compared to W1S2 and W3S2). Its MDA content was 19.1% lower than in W1S2. Under 5‰ salinity, the W2S3 treatment resulted in more pronounced effects: soluble sugar content was 48.2% and 33.5% higher than in W1S3 and W3S3, respectively; proline content increased by 25.4% compared to W1S3; and betaine content rose by 145.6% and 47.9% relative to W1S3 and W3S3. The MDA content under W2S3 was 24.9% lower than in W1S3.

Hormone contents. Hormone levels in flag leaves were significantly influenced by the interaction between drought priming and salt stress (Table 4). At 1‰ salinity, the W2S1 treatment resulted in significantly

higher brassin content compared to W1S1 and W3S1 by 7.1% and 3.0%, respectively. Absciscic acid and gibberellin contents under W2S1 also significantly increased by 9.8% and 8.6%, respectively, compared to W1S1. At 3‰ salinity, the W2S2 treatment showed a 7.1% increase in brassin content compared to W1S2. Both ABA and gibberellin contents were significantly higher in W2S2 than in W1S2 (by 9.4% and 8.4%, respectively) and W3S2 (by 6.2% and 4.3%, respectively). Under 5‰ salinity, the W2S3 treatment maintained this trend, with brassin content being 5.3% and 3.7% higher than in W1S3 and W3S3, respectively. ABA content in W2S3 was significantly increased by 5.8% compared to W1S3, whereas gibberellin content was significantly higher than in both W1S3 and W3S3 by 8.0% and 7.2%, respectively.

Yield-related traits. As shown in Table 5, mild drought priming (W2) significantly improved yield-related traits under salt stress. At 1‰ salinity, the W2S1 treatment increased grains per spike by 37.4% and 19.5%, 1 000-grain weight by 51.5% and 12.9%, and grain weight per panicle by 108.1% and 35.0%, compared to W1S1 and W3S1, respectively, while reducing the number of sterile spikelets by 27.8%

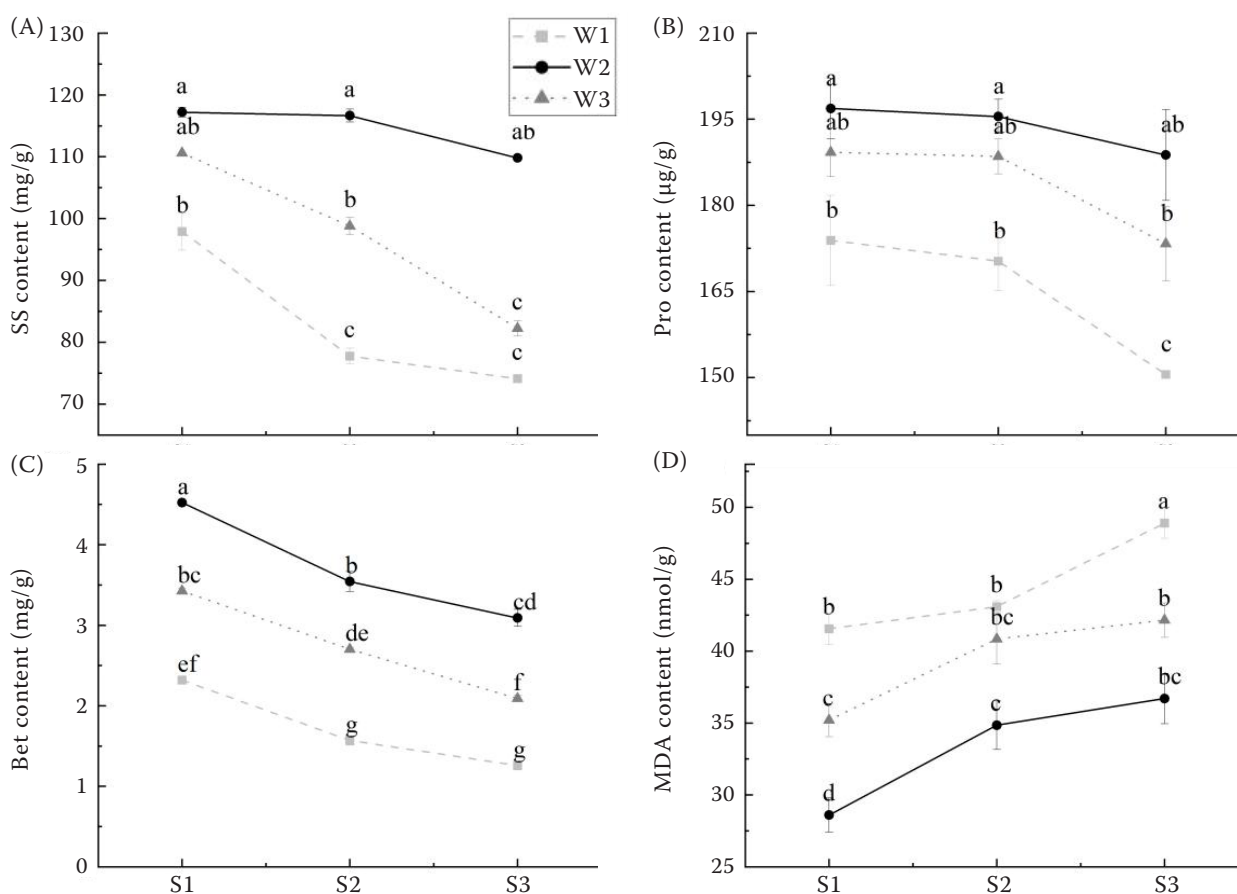


Figure 3. (A) SS (soluble sugar); (B) Pro (proline); (C) Bet (betaine), and (D) MDA (malondialdehyde) contents in winter wheat flag leaves under different treatments of drought priming and salt stress. W1, W2, and W3 – severe drought (40% field capacity, FC), mild drought (60% FC), and well-watered (80% FC) from emergence to jointing, respectively; S1, S2, and S3 – 1, 3, and 5‰ NaCl irrigation from jointing to maturity, respectively. Different letters represent significant differences between treatments ($P < 0.05$)

Table 4. Effect of drought priming at the seedling stage on hormone content in flag leaves of winter wheat under salt stress

	Plant brassin (ng/L)	Plant abscisic acid (μg/L)	Plant gibberellin (pg/mL)
W1S1	180.5 ± 0.4 ^c	340.1 ± 3.2 ^{cd}	543.6 ± 3.7 ^{bc}
W2S1	193.4 ± 1.8 ^a	373.3 ± 3.5 ^a	590.4 ± 4.6 ^a
W3S1	187.7 ± 2.4 ^b	367.8 ± 2.8 ^a	579.8 ± 5.8 ^a
W1S2	177.4 ± 2.6 ^c	337.4 ± 8.2 ^d	536.1 ± 9.7 ^c
W2S2	188.2 ± 0.4 ^b	369.0 ± 3.7 ^a	581.1 ± 3.0 ^a
W3S2	185.6 ± 2.5 ^b	347.6 ± 2.5 ^{bc}	557.2 ± 5.9 ^b
W1S3	176.6 ± 1.7 ^c	333.9 ± 2.2 ^d	533.3 ± 11.9 ^c
W2S3	185.9 ± 2.3 ^b	353.4 ± 2.3 ^b	576.0 ± 4.8 ^a
W3S3	179.2 ± 3.7 ^c	337.8 ± 4.1 ^d	537.2 ± 3.4 ^c

W1, W2, and W3 – severe drought (40% field capacity, FC), mild drought (60% FC), and well-watered (80% FC) from emergence to jointing, respectively. S1, S2, and S3 – 1, 3, and 5‰ NaCl irrigation from jointing to maturity, respectively. Different letters represent significant differences between treatments ($P < 0.05$)

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Table 5. Effects of drought priming on yield traits of winter wheat under salt stress

	Grain number per spike	Thousand seed weight (g)	Single ear seed weight (g)	Number of sterile spikelets
W1S1	42.3 ± 0.12 ^d	35.7 ± 0.13 ^f	1.5 ± 0.13 ^d	1.8 ± 0.14 ^b
W2S1	58.1 ± 0.11 ^a	54.1 ± 0.13 ^a	3.1 ± 0.14 ^a	1.3 ± 0.13 ^e
W3S1	48.6 ± 0.14 ^c	47.9 ± 0.12 ^c	2.3 ± 0.14 ^c	1.5 ± 0.32 ^d
W1S2	36.5 ± 0.08 ^f	33.5 ± 0.14 ^h	1.2 ± 0.15 ^e	1.9 ± 0.12 ^b
W2S2	52.4 ± 0.11 ^b	51.5 ± 0.10 ^b	2.7 ± 0.09 ^b	1.3 ± 0.07 ^e
W3S2	47.8 ± 0.13 ^c	42.1 ± 0.13 ^e	2.0 ± 0.10 ^c	1.6 ± 0.10 ^c
W1S3	32.4 ± 0.14 ^g	31.6 ± 0.14 ⁱ	1.0 ± 0.11 ^f	2.2 ± 0.19 ^a
W2S3	48.2 ± 0.06 ^c	47.5 ± 0.11 ^d	2.3 ± 0.13 ^c	1.5 ± 0.07 ^{cd}
W3S3	38.2 ± 0.05 ^e	34.4 ± 0.08 ^g	1.3 ± 0.11 ^e	1.9 ± 0.12 ^b

W1, W2, and W3 – severe drought (40% field capacity, FC), mild drought (60% FC), and well-watered (80% FC) from emergence to jointing, respectively. S1, S2, and S3 – 1, 3, and 5‰ NaCl irrigation from jointing to maturity, respectively. Different letters represent significant differences between treatments ($P < 0.05$)

and 13.3%. At 3‰ salinity, W2S2 significantly outperformed both W1S2 and W3S2, increasing grains per spike by 43.6% and 9.6%, 1 000-grain weight by 53.7% and 22.3%, and grain weight per panicle by 120.7% and 34.1%, respectively. The number of sterile spikelets was also significantly reduced by 31.6% and 18.8% compared to W1S2 and W3S2. Under 5‰ salinity, W2S3 maintained superior performance, with increases in grains per spike (37.4% and 19.5%), 1 000-grain weight (50.3% and 38.1%), and grain weight per panicle (123.6% and 74.2%) compared to W1S3 and W3S3, respectively, along with reductions in the number of sterile spikelets by 31.8% and 21.1%.

Two-way ANOVA of physiological and yield indices under drought priming and salt stress. Two-way ANOVA showed that both water regulation (W) and salt stress (S) had significant main effects on all measured indices ($P < 0.05$, Table 6). The $W \times S$ interaction was significant for most traits, including chlorophyll *a*, chlorophyll *b*, carotenoid, net photosynthetic rate, stomatal conductance, superoxide dismutase, peroxidase, ribulose-1,5-bisphosphate carboxylase/oxygenase, abscisic acid, gibberellin, betaine, malondialdehyde, soluble sugar, grain number per spike, 1 000-grain weight and grain weight per spike ($P < 0.05$). This indicates that the effects of seedling drought priming on these physiological and yield-related traits varied with the subsequent salt stress level; in other words, the priming-induced stress memory was expressed under salt stress, and its protective effect was modulated by salinity. In contrast, the $W \times S$ interaction was not significant for proline, intercellular CO₂ concentration, transpira-

tion rate, brassinosteroid and sterile spikelet number ($P > 0.05$), suggesting that the responses of these indices to salt stress were relatively stable and less affected by the seedling water regime. For transpiration rate, both W ($P = 0.037$) and S main effects were significant, but their interaction was not. Similarly, intercellular CO₂ concentration, brassinosteroid and sterile spikelet number exhibited significant main effects but non-significant interactions ($P = 0.656$, 0.192 and 0.804, respectively).

Correlations between physiological indices and seed-setting. Correlation analysis between physiological indices and seed-setting traits of winter wheat (Figure 4) indicated that endogenous hormones, antioxidant enzyme activities, and osmoregulatory substances in flag leaves were significantly positively correlated with seed-setting capacity. These beneficial physiological parameters also exhibited significant positive correlations with each other, suggesting synergistic regulatory effects. In contrast, MDA content and the number of sterile spikelets, both indicators of stress-induced damage, showed significant negative correlations with the favourable physiological traits. This indicates that oxidative damage and spikelet sterility impair normal physiological functions, thereby limiting yield formation.

DISCUSSION

Effects of drought priming at the seedling stage on photosynthetic indexes of winter wheat flag leaves at the anthesis stage under salt stress. Pre-anthesis drought stress typically reduces chlorophyll

Table 6. Results of two-way ANOVA for the effects of water regime (W), salinity (S), and their interaction (W × S) on physiological and yield traits of winter wheat

Measured indices	Main effect of water regulation (W)		Main effect of salt stress (S)		Interactive effect of W × S	
	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value
Chl <i>a</i>	3 616.794	< 0.01	1 368.239	< 0.01	64.530	< 0.01
Chl <i>b</i>	789.778	< 0.01	297.825	< 0.01	23.451	< 0.01
Car	1 340.225	< 0.01	551.745	< 0.01	64.251	< 0.01
P _n	36.686	< 0.01	72.666	< 0.01	22.004	< 0.01
c _i	24.250	< 0.01	39.093	< 0.01	0.618	0.656
T _r	3.969	0.037	16.707	< 0.01	1.165	0.359
g _s	196.362	< 0.01	546.543	< 0.01	29.797	< 0.01
SOD	3 777.851	< 0.01	1 759.844	< 0.01	103.788	< 0.01
POD	568.268	< 0.01	261.127	< 0.01	3.634	0.024
Rubisco	71.446	< 0.01	49.001	< 0.01	3.531	< 0.01
BR	20.172	< 0.01	55.586	< 0.01	1.706	0.192
ABA	49.039	< 0.01	110.699	< 0.01	8.502	< 0.01
GA	26.906	< 0.01	106.714	< 0.01	5.465	< 0.01
MDA	160.324	< 0.01	72.922	< 0.01	3.703	< 0.01
Bet	2 160.828	< 0.01	900.493	< 0.01	9.572	< 0.01
Pro	67.198	< 0.01	23.384	< 0.01	1.823	0.168
SS	1 232.759	< 0.01	495.279	< 0.01	73.340	< 0.01
GNS	19 359.905	< 0.01	47 354.243	< 0.01	762.087	< 0.01
TGW	9 971.150	< 0.01	46 481.077	< 0.01	1227.107	< 0.01
GWS	101.611	< 0.01	372.048	< 0.01	4.967	< 0.01
SSN	11.269	< 0.01	32.600	< 0.01	0.402	0.804

W – seedling drought priming treatment; S – subsequent jointing-stage salt stress treatment; W × S, interaction effect of water regulation and salt stress. *P* < 0.05 indicates significant difference, *P* < 0.01 indicates extremely significant difference. Chl *a* – chlorophyll *a*; Chl *b* – chlorophyll *b*; Car – carotenoid; P_n – net photosynthetic rate; c_i – intercellular CO₂ concentration; T_r – transpiration rate; g_s – stomatal conductance; SOD – superoxide dismutase; POD – peroxidase; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; BR – brassinosteroid; ABA – abscisic acid; Bet – betaine; GA – gibberellin; MDA – malondialdehyde; Pro – proline; SS – soluble sugar; GNS – grain number per spike; TGW – 1 000-grain weight; GWS – grain weight per spike; SSN – sterile spikelet number

content and photosynthetic parameters in winter wheat leaves (Wang et al. 2024). Although rewatering after seedling-stage drought can restore these physiological indices to normal levels (Lou et al. 2021), our findings reveal a more complex pattern. Under saline irrigation at 3‰ and 5‰, the net photosynthetic rate in the severe drought treatment (W1) did not return to normal levels after rewatering, whereas the mild drought priming group (W2) recovered effectively. Furthermore, the stomatal conductance of W2S2 was 41.5% higher than that of W3S2, indicating that the photosynthetic recovery of W2 depended not only on rewatering but also on maintaining stomatal conductance, thereby ensuring CO₂ supply under salt stress. This aligns with

previous reports and suggests that severe drought (40% field capacity) may cause substantial damage to the photosynthetic apparatus, preventing complete functional restoration.

Previous studies have shown that moderate drought priming promotes the accumulation of photosynthetic proteins and enhances Rubisco activity (Ashutus et al. 2024). Consistent with these findings, in this study, under 1‰ and 3‰ saline irrigation in our experiment, mild drought priming (W2) led to increased Rubisco activity. Thus, this suggests that stress memory established through mild drought priming at the seedling stage can enhance photosynthetic enzyme activity in winter wheat under low-to-moderate salt stress (1–3‰) at the flowering stage. However, under 5‰

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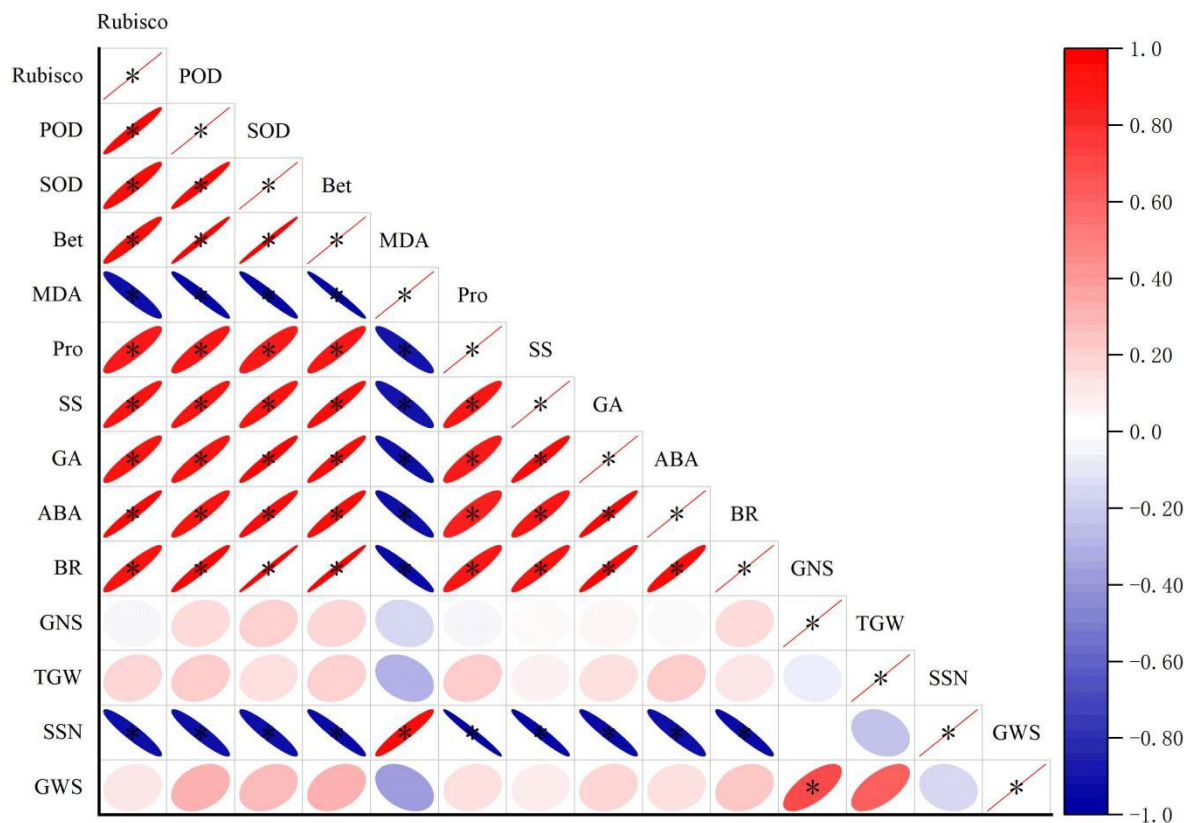


Figure 4. Correlation between physiological parameters and seed setting in winter wheat. Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; POD – peroxidase; SOD – superoxide dismutase; Bet – betaine; MDA – malondialdehyde; Pro – proline; SS – soluble sugar; GA – gibberellin; ABA – abscisic acid; BR – brassinolide; GNS – grains number per spike; TGW – 1 000-grain weight; SSN – sterile spikelets per spike; GWS – grain weight per spike. * $P < 0.05$

saline irrigation, no significant increase in Rubisco activity was detected, which differs from previous reports; however, this discrepancy may be explained by the possibility that at high salinity levels, the promotive effect of drought priming on Rubisco may be insufficient to counteract salt-induced damage, or that the physiological memory does not persist until the flowering stage.

Photosynthetic pigments, which participate in the primary reactions of photosynthesis, serve as indicators of plant photosynthetic capacity and physiological status (Yong et al. 2024). Chlorophyll *a* acts as a reaction-center pigment, primarily adapting to high-light environments and alleviating photoinhibition; chlorophyll *b* is mainly located in light-harvesting antenna complexes and is responsible for capturing light energy; and carotenoids absorb blue-violet light while providing photoprotective and antioxidant functions (Simkin et al. 2022, Li et al. 2025a). In this study, across all three salinity levels (1, 3, and 5‰), mild drought priming at the seedling stage (W2) in-

creased the contents of chlorophyll *a*, chlorophyll *b*, and carotenoids in flag leaves at the flowering stage, with the most pronounced effect observed on chlorophyll *b*. Moreover, the chlorophyll *b* content of W2S2 was 31.8% higher than that of W3S2. The increased proportion of chlorophyll *b* is beneficial for expanding the light-harvesting cross-section under salt stress, while increased carotenoids contribute to the xanthophyll cycle and ROS scavenging, thereby protecting PSII. Carotenoids were relatively less affected by the drought-salt interaction. Moreover, under the W2 treatment, the contents of all three pigments decreased with increasing salinity (W2S1 > W2S2 > W2S3).

The response of photosynthetic pigments to salt stress observed in this study differs from some previous reports. This discrepancy may be attributed to the memory effect of drought experienced at the seedling stage. Although it is well established that high salt stress inhibits chlorophyll synthesis and impairs photosynthesis (Li et al. 2024), findings regarding carotenoids are inconsistent. The increase

in carotenoid content observed in W2 treatments under moderate salinity suggests that drought priming may enhance photoprotective capacity, although the specific regulatory mechanism warrants further investigation.

Effects of drought priming at the seedling stage on antioxidant enzyme activity and osmotic substance content in flag leaves of winter wheat at the flowering stage under salt stress. Under stress conditions, plants accumulate reactive oxygen species (ROS) at elevated levels, which can cause oxidative damage. Antioxidant enzymes, such as SOD, mitigate oxidative damage by scavenging oxygen-free radicals (Rao et al. 2024). Consistent with these reports, the present study showed that the enhancement of SOD activity by mild drought priming at the seedling stage (W2) persisted until the flowering stage under 1–5‰ salinity, and the SOD activity of W2S3 was 18.8% higher than that of W3S3. Since SOD converts superoxide anions to H_2O_2 , which is subsequently scavenged by POD and other enzymes, the sustained increase in SOD activity helps reduce membrane lipid peroxidation. Its activity remained higher than that of the well-watered treatment (W3) at equivalent salt concentrations. In contrast, SOD activity in the severe drought treatment (W1) did not recover to the W3 level. Furthermore, although mild drought priming did not significantly enhance POD activity by the flowering stage, it maintained POD activity under salt stress at levels comparable to those under 1‰ salinity. These results suggest that mild drought priming at the seedling stage has a sustained positive effect on SOD activity until flowering, whereas its impact on POD activity is relatively limited or transient.

Soluble sugars and proline are key osmolytes that accumulate in plants under abiotic stress. Under drought or salt stress, soluble sugar content in wheat typically increases, thereby lowering cellular osmotic potential and improving stress tolerance (Ru et al. 2024, Chang et al. 2025, Li et al. 2025b). In this study, mild drought priming significantly increased soluble sugar content at the flowering stage under 3‰ and 5‰ saline irrigation, which helps to lower cellular osmotic potential, maintain turgor pressure, and preserve carbon sources for grain filling, indicating that its regulatory effect becomes more evident under moderate to high salinity.

Drought priming has also been reported to help plants maintain higher levels of proline and betaine, reducing osmotic potential and sustaining water

homeostasis, with similar effects observed under high-temperature and low-temperature stress (He et al. 2024, Schat et al. 2025). In the present study, mild drought priming at the seedling stage did not significantly increase proline content, suggesting that its regulatory effect on proline may be short-lived or masked by salt stress. In contrast, betaine concentrations increased under the mild drought priming treatment under 1‰ and 5‰ salinity, consistent with earlier findings (He et al. 2024), whereas no significant improvement was observed at 3‰ salinity. Notably, the betaine content of W2S3 was 47.9% higher than that of W3S3, while the MDA content was 24.9% lower than that of W1S3; betaine can stabilise enzyme structures and membrane systems, and the reduction in MDA indicates alleviated membrane lipid peroxidation, both of which jointly suggest that the priming memory still exerted osmotic protection and membrane protection functions at the flowering stage. The mechanism behind this inconsistent response requires further investigation.

Effects of drought priming at the seedling stage on hormone content in flag leaves of winter wheat at the flowering stage under salt stress. Previous studies on cross-stress priming and hormonal signal regulation have not extensively examined the role of drought priming in enhancing plant salt tolerance. Existing research has primarily focused on the functions of ABA and gibberellins (GAs). Expanding on this knowledge, the present study investigated the regulatory mechanisms involving brassinolide, ABA, and GAs under combined drought priming and salt stress conditions.

Previous studies have shown that drought priming can induce ABA synthesis, thereby promoting cell wall expansion and structural remodelling (Yoshida et al. 2024). In this study, the effect of mild drought priming (W2) at the seedling stage on ABA content in flag leaves at the flowering stage varied with salinity levels. Under 1‰ saline irrigation, ABA content in the W2S1 treatment was higher than in W1S1 but did not differ significantly from W3S1. In contrast, under saline irrigation at 3‰ and 5‰, ABA content in the mild drought priming treatment (W2) was significantly higher than in both the severe drought (W1) and normal irrigation (W3) treatments. Specifically, the ABA content of W2S2 was 6.2% higher than that of W3S2. Since ABA can induce antioxidant genes and regulate stomata, while GA and brassinosteroids help maintain photosynthesis and assimilate partitioning, these three hormones may synergistically enhance

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salt tolerance. These findings suggest that under low salinity (1‰), rewatering after mild drought priming can restore ABA content to normal levels, whereas under moderate-to-high salinity (3–5‰), the stress memory established by mild drought priming continues to influence hormonal regulation.

The effect of mild drought priming on gibberellin content in flag leaves followed a pattern similar to that of ABA. However, whether these hormones interact synergistically or antagonistically under such conditions remains unclear. Brassinolide, an efficient and broad-spectrum endogenous plant growth regulator, modulates various enzymes and hormones, thereby enhancing overall plant stress resistance (da Silva et al. 2024). The results of this study revealed that mild drought priming at the seedling stage (W2) significantly increased brassinolide content in winter wheat under salt stress at the flowering stage. At 3‰ salinity, brassinolide content reached levels comparable to those in the normal irrigation treatment (W3). This indicates that mild drought priming can establish a form of stress memory (Aboud et al. 2025), which subsequently influences hormonal responses under salt stress at the flowering stage and enhances the plant's physiological regulatory capacity.

Effects of drought priming at the seedling stage on winter wheat yield under salt stress. Salt stress

significantly inhibits crop growth and development, ultimately reducing yield (Wang et al. 2025). In the present study, yield stability of winter wheat under salt stress was improved through drought priming at the seedling stage, with the mild drought priming (W2) treatment demonstrating the most pronounced benefits. Under 1, 3, and 5‰ saline irrigation conditions, 1 000-grain weight, grains per spike, and grain weight per spike were consistently higher in the W2 treatment than in the well-watered control (W3). Moreover, the number of sterile spikelets in W2S2 was reduced by 18.8% compared with W3S2, which may be related to improved pollen viability and reduced floret degeneration due to better photosynthesis and hormone balance at the flowering stage. This improvement may be due to the priming-induced enhancement of the antioxidant system, which improved the plant's responsiveness to subsequent salt stress and thus reinforced salt tolerance and stabilised yield. The superior performance of W2 over W3 suggests that moderate drought priming induces a proactive stress defence strategy, whereas continuously well-watered plants lack such pre-adaptive capacity and are therefore more vulnerable to subsequent salt stress.

Furthermore, mild drought priming (W2) significantly reduced the number of sterile spikelets

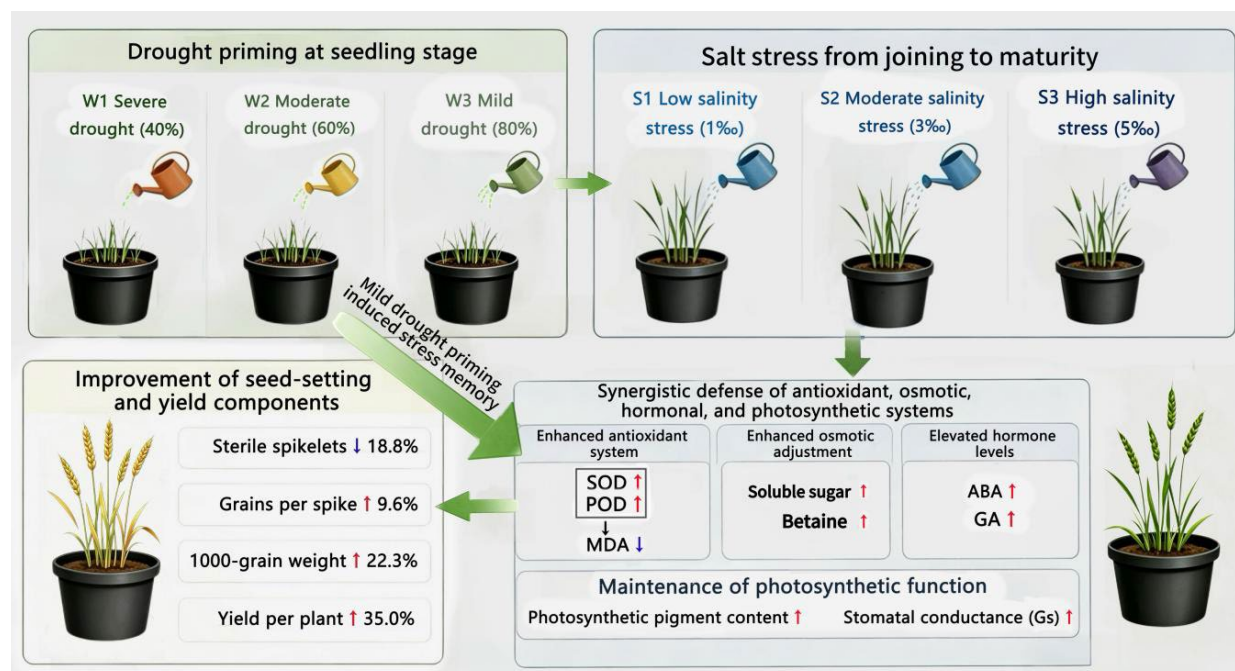


Figure 5. Mechanistic diagram of drought priming-induced stress memory, enhancing post-anthesis salt tolerance and yield in winter wheat. SOD – superoxide dismutase; POD – peroxidase; MDA – malondialdehyde; ABA – abscisic acid; GA – gibberellin

under salt stress. We hypothesise that this treatment improves seed-setting characteristics in winter wheat under saline conditions by enhancing key reproductive processes, such as pollen viability, leading to higher yield formation. These findings are consistent with those of Zhang et al. 2024a, who reported a yield-enhancing effect of drought priming in winter wheat. A unique aspect of this study is its focus on salt tolerance following rewatering after drought priming. The results provide further evidence that mild drought priming at the seedling stage effectively maintains yield stability under salt stress conditions.

In summary, this study demonstrates that mild drought priming at the seedling stage can establish a stress memory that is still detectable at 7 days after anthesis (early grain filling), effectively enhancing salt tolerance and improving seed-setting performance in winter wheat through the synergistic regulation of antioxidant enzymes, osmotic substances, and endogenous hormones (Figure 5). Several limitations should be acknowledged. First, this study was conducted with a single cultivar (cv. Qingmai 11) under pot conditions, and the results may not be fully transferable to field-grown crops or other genotypes. Second, although physiological memory effects were observed, the underlying molecular mechanisms (e.g., epigenetic regulation) were not addressed. Third, the beneficial effects diminished with increasing salinity, suggesting limited applicability under severe salt stress (> 5‰). Fourth, soil EC was not monitored, and photosynthetic parameters were measured only once, which limits the interpretation of actual root-zone salinity and the temporal dynamics of stress memory; future studies should include dynamic monitoring. Despite these constraints, our findings provide a practical reference for stabilising wheat production in saline-alkali soils *via* seedling-stage drought priming. Future studies with field validation, multi-genotype screening, and molecular investigations are needed to complement our findings.

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