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**Irrigation-dependent effects of foliar salicylic acid on wheat growth, yield
and physiological responses**

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ABSTRACT

Freshwater scarcity is increasing reliance on deficit irrigation, which reduces crop productivity. Foliar salicylic acid is a low-cost means of alleviating water-stress damage, but its effectiveness across levels of water availability remains unclear. A greenhouse pot experiment evaluated wheat cultivar Zincol-16 under four foliar salicylic acid concentrations (0, 0.5, 1.0 and 1.5 mmol L⁻¹) and four irrigation regimes (40, 60, 80 and 100% of field capacity) in a factorial randomized complete block design with three replications. At 1.5 mmol L⁻¹, salicylic acid increased grain weight per pot by 8.1% under severe deficit (40% of field capacity) and by 25.9% under full irrigation, with plant height and spike length also responding most under full irrigation. In contrast, the same concentration raised relative water content by 18.5% under severe deficit but by only 6.7% under full irrigation, and lowered proline and malondialdehyde by 28.4 and 27.1% under severe deficit, where peroxidase, catalase and ascorbate peroxidase activities were also highest. Multivariate and path analyses indicated that water availability dominated trait variation and associated salicylic acid positively with growth and yield. Foliar salicylic acid therefore mainly protected plants under severe water stress but gave its largest yield gains under adequate irrigation. The 1.5 mmol L⁻¹ concentration was generally the most effective, although field validation is required.

Keywords: antioxidant enzymes; deficit irrigation; oxidative stress; phytohormone; salicylic acid

INTRODUCTION

Demand for freshwater is expected to surpass supply by 40% in the coming years, which places sustainable water management at the center of crop production planning. The use of fresh water is largest by agriculture, which uses about 75-80% of water withdrawal in many countries. Arid and semi-arid nations are under particular pressure, because climate change, rising temperatures, erratic rainfall, urban expansion, industrial demand and population growth are together intensifying water shortages (El-Hendawy et al., 2024). In response, deficit irrigation that supply water below full crop requirement has been promoted in these regions, since full irrigation is often not cost-effective despite its yield advantage. Deficit irrigation nevertheless disturbs a many of biochemical and physiological processes (Bhattacharya, 2021), including biomass accumulation, photosynthesis, nutrient balance, chlorophyll synthesis and water relations, and these disturbances translate into lower final yields. Reduced soil moisture also

restricts nutrient diffusion, lowering nutrient uptake and root biomass while altering mineralization and membrane permeability to cations. Operational strategies that moderate these penalties in crops such as wheat are therefore needed.

Wheat is among the most widely cultivated cereals worldwide and is consumed at high rates (Arzani and Ashraf, 2017). It occupies more than 220 million hectares globally, yields about 778 million metric tons annually and contributes some 10% of total agricultural value (Khan et al., 2020). The grain supplies approximately 9.4% protein, 1.8% fibre, 2.5% fat and 69% carbohydrate (Ahmad et al., 2022). Rising food demand linked with population growth underlines the crop's importance (Yanagi, 2024), and wheat production is projected to require a near doubling by 2050 (FAO, 2021). Over the past decade, water stress has continued to reduce wheat productivity, with reported yield losses approaching 50% (Nyaupane et al., 2024). Plants exposed to water deficiency produce signaling molecules like SA that is a phenolic phytohormone responsible for plant adaptation to different abiotic stresses. SA controls different metabolic and physiological responses, including transpiration, photosynthesis, water uptake, osmotic adjustment, stomatal regulation and defense signaling (Khalvandi et al., 2021; Yang et al., 2023). However, many genotypes may not produce enough SA to withstand severe water shortages. Exogenous SA application through seed treatment or foliar spraying can therefore increase SA availability and improve plant growth and yield under water-deficit conditions (Ghosh et al., 2021). Foliar application of SA has benefited several crops under water stress (Khan et al., 2003; Bidabadi et al., 2012), mainly by maintaining photosynthetic pigments and relative water content, strengthening antioxidant activity and improving nutrient-use efficiency. El-Nasharty et al. (2019) further reported that SA promotes systemic resistance to pathogens and increases plant tolerance to temperature extremes, drought and salinity. Thus, exogenous SA can activate the plant's natural defense mechanisms and improve its performance under stressful environmental conditions (Munsif et al., 2022a).

Although SA is generally recognized as improving plant tolerance to water deficit, few studies have investigated how different SA concentrations interact with progressively decreasing irrigation levels in wheat. Even fewer have determined whether SA is more beneficial under severe water deficit than under adequate water supply. We hypothesized that wheat responses to SA depend on the severity of water deficit and that biochemical protection and yield formation may respond differently. Therefore, this research aimed to: (i) quantify the effects of four SA concentrations on growth, yield, photosynthetic pigments, water status, oxidative-

stress indicators and antioxidant enzyme activities under four irrigation regimes; (ii) determine whether the effectiveness of SA changes systematically with water-deficit severity; and (iii) apply multivariate and path analyses to explore the statistical associations and putative pathways linking irrigation regime and SA concentration with wheat growth, physiology and yield.

Materials and methods

Experimental site, plant material and growing conditions

A pot experiment was conducted in the greenhouse of Amir Muhammad Khan Campus, Mardan, Faculty of Crop Production Sciences, The University of Agriculture, Peshawar, during the winter season of 2025–2026. The wheat cultivar Zincol-16 was obtained from the Cereal Crops Research Institute (CCRI), Pirsabak. Plastic pots measuring 20 cm in diameter and 30 cm in depth were used. Soil was passed through a 4-mm mesh to remove stones and pebbles, and each pot was filled with 5 kg of sieved soil. Before sowing, each pot received 400 mL of tap water. Fifteen seeds were sown approximately 2–3 cm deep in each pot on 15 November 2025. After successful emergence, the seedlings were thinned to five uniformly growing plants per pot. Fertilizers were applied at the recommended rates of 120 kg N, 90 kg P₂O₅ and 60 kg K₂O ha⁻¹, equivalent to 0.30 g N, 0.225 g P₂O₅ and 0.15 g K₂O per pot, respectively. Urea, diammonium phosphate and sulphate of potash were used as fertilizer sources. All phosphorus and potassium and half of the nitrogen were applied at sowing, while the remaining nitrogen was applied at the tillering stage. The plants were harvested at physiological maturity on 20 April 2026. The soil was described as silt loam, containing approximately 17.4% clay, 56.0% silt and 26.6% sand. It had a pH of 7.8, organic matter content of 0.54%, total nitrogen content of 0.22%, AB-DTPA-extractable phosphorus of 2.38 mg kg⁻¹ and AB-DTPA-extractable potassium of 117 mg kg⁻¹. Throughout the experiment, all pots were maintained weed-free, irrigated uniformly according to the treatment requirements and protected from rainfall.

Treatments and experimental design

Treatments were arranged as a two-factor factorial in a randomized complete block design with three replications, giving $4 \times 4 \times 3 = 48$ experimental units. The first factor was the irrigation regime, applied at 40, 60, 80 and 100% field capacity (FC). Irrigation treatments were initiated 20 days after sowing, following seedling establishment, and maintained until final harvest at

physiological maturity on 20 April 2026, i.e. 156 days after sowing (DAS); the irrigation treatments were therefore imposed for 136 days (20–156 DAS). pots were randomly positioned within each block at the beginning of the experiment and rotated weekly within their respective blocks. Field capacity was determined gravimetrically using three additional unplanted pots containing 5 kg of soil. The soil was slowly saturated with water, the pots were covered to minimize evaporation and allowed to drain freely for 48 h. Field capacity was calculated as:

$$\text{Field capacity (\%)} = \frac{M_{fc} - M_{dry}}{M_{dry}} \times 100$$

where M_{fc} is the mass of soil after saturation and 48 h of drainage, and M_{dry} is the oven-dry soil mass (g). The target mass of each experimental pot was calculated as the combined mass of the empty pot and dry soil plus 40, 60, 80 or 100% of the water retained at FC. Pots were weighed daily at approximately the same time, and water lost through evapotranspiration was replaced with tap water, assuming a water density of 1 g mL⁻¹. Thus, the assigned soil-moisture level was maintained gravimetrically throughout the treatment period.

The second factor was SA concentration, applied at 0 (S0), 0.5 (S1), 1.0 (S2) and 1.5 mmol L⁻¹ (S3), equivalent to 0, 69.06, 138.12 and 207.18 mg L⁻¹, respectively, based on an SA molar mass of 138.12 g mol⁻¹. The SA solutions were prepared in distilled water and supplemented with 0.1% (v/v) Tween-20 as a surfactant. Foliar treatments were applied twice, at 30 and 40 days after sowing, using a hand-held sprayer. Each pot received 25 mL of the respective solution per application, distributed uniformly over the foliage during the early morning. Control plants were sprayed with an equal volume of distilled water containing 0.1% Tween-20. During spraying, pots were separated and the soil surface was covered to prevent spray drift and the entry of SA solution into the soil.

Growth and yield attributes

Plant height and spike length were measured on six randomly selected tillers and mature spikes per pot, respectively, and averaged to obtain one value per pot. Grains per pot were counted in full. Total grain weight per pot (g) was recorded on an electronic balance.

Photosynthetic pigments

Chlorophyll a, chlorophyll b and carotenoid concentrations were determined spectrophotometrically. Fresh leaf tissue (200 mg) was submerged in 8 mL of 80% (v/v)

acetone and held in darkness at -40°C for 48 h. Absorbance of the extract was recorded at 663.6, 646.6 and 440.5 nm, and pigment concentrations were calculated following Lichtenthaler (1987). The equations below give the pigment concentrations in the acetone extract (C , $\mu\text{g mL}^{-1}$):

$$\text{Chl a } (\mu\text{g mL}^{-1}) = 12.25 A_{663.6} - 2.55 A_{646.6}$$

$$\text{Chl b } (\mu\text{g mL}^{-1}) = 20.31 A_{646.6} - 4.91 A_{663.6}$$

$$\text{Carotenoids } (\mu\text{g mL}^{-1}) = 4.69 A_{440.5} - 0.267 (\text{Chl a} + \text{Chl b})$$

$$\text{Total chlorophyll } (\mu\text{g mL}^{-1}) = \text{Chl a} + \text{Chl b}$$

where A denotes absorbance at the subscripted wavelength. Pigment concentrations in the extract were then converted to a fresh-weight (FW) basis as:

$$\text{Pigment } (\text{mg g}^{-1} \text{FW}) = (C \times V) / (W \times 1000)$$

where C is the pigment concentration in the extract ($\mu\text{g mL}^{-1}$) calculated from the equations above, V is the total extract volume (8 mL), W is the fresh mass of leaf tissue extracted (0.2 g) and 1000 converts μg to mg . For example, an extract containing $10 \mu\text{g}$ chlorophyll a mL^{-1} corresponds to $(10 \times 8) / (0.2 \times 1000) = 0.40 \text{ mg g}^{-1}\text{FW}$. Total chlorophyll was calculated as the sum of chlorophyll a and chlorophyll b and expressed in the same units.

Relative water content and osmotic adjustment

Relative water content (RWC) was determined at 60 days after emergence and calculated as:

$$\text{RWC } (\%) = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

where FW is the fresh mass, TW is the fully hydrated or turgid mass, and DW is the oven-dry mass of the leaf sample, all expressed in grams.

Free proline was determined colorimetrically following Bates et al. (1973). Absorbance was measured at 520 nm against a reagent blank. Where the calibration equation $C = 36.2311 (A_{520} - A_{\text{blank}})$ expressed as C as μg proline in the assay aliquot, proline content was calculated as:

$$\text{Proline } (\mu\text{mol g}^{-1}\text{FW}) = \frac{36.2311(A_{520} - A_{\text{blank}}) \times \left(\frac{V}{a}\right)}{115.13 \times F}$$

where (V) is the total extract volume (mL), (a) is the extract aliquot used in the assay (mL), (F) is the fresh leaf mass (g), and $115.13 \mu\text{g } \mu\text{mol}^{-1}$ is the molecular-mass conversion factor for proline. Outcomes were reported as $\mu\text{mol g}^{-1}$ FW.

Oxidative stress markers

Malondialdehyde (MDA) was measured by the thiobarbituric acid assay as described by Taulavuori et al. (2001). Tissue was collected 60 days after emergence, weighed (100 mg), ground in liquid nitrogen and homogenized. The homogenate was suspended in 500 μL of 0.1% trichloroacetic acid (TCA) and centrifuged at $15,000 \times g$ for 10 min at 4 °C. A 100 μL aliquot of the supernatant was combined with 1.5 mL of 0.5% thiobarbituric acid in 20% TCA and incubated at 95 °C for 25 min. Samples were cooled on ice to 25 °C and absorbance was read at 532 and 600 nm; the reading at 600 nm was subtracted from that at 532 nm, and concentrations were obtained from a calibration curve of known MDA standards (Licaj et al., 2023).

Hydrogen peroxide (H_2O_2) was determined following Velikova et al. (2000). Fresh leaf tissue (0.5 g) was homogenized in 5 mL of ice-cold 0.1% (w/v) TCA and centrifuged at $12,000 \times g$ for 15 min at 4 °C. The supernatant (0.5 mL) was mixed with 0.5 mL of 10 mM potassium phosphate buffer (pH 7.0) and 1.0 mL of 1 M KI, vortexed and incubated for 60 min at 25 °C in darkness. Absorbance was measured at 390 nm. The reagent blank contained 0.1% TCA instead of extract, while a sample blank contained extract but water instead of KI to correct background absorbance. H_2O_2 standards of 0–1.0 mM prepared in 0.1% TCA were processed identically. Extract concentration was calculated as $C = (A_{390} - b)/m$, where (m) and (b) are the calibration-curve slope and intercept. H_2O_2 content was calculated as $(C \times V/W)$ and expressed as $\mu\text{mol g}^{-1}$ FW, where (V) is extract volume (5 mL) and (W) is tissue mass (0.5 g).

Antioxidant enzyme activities

Peroxidase (POD), catalase (CAT) and ascorbate peroxidase (APX) activities were determined by homogenising 0.1 g fresh leaf tissue in 1 mL of ice-cold 50 mM phosphate buffer (pH 7.8), followed by centrifugation at $10,000 \times g$ for 25 min at 4 °C. The supernatant was used for the enzyme and protein assays. Each assay was performed at 25 °C in a 3.0 mL reaction mixture containing 50 mM potassium phosphate buffer (pH 7.0) and 0.1 mL of enzyme extract, and absorbance changes were recorded for 3 min. POD was assayed with 20 mM guaiacol and 10 mM H_2O_2 at 470 nm ($\epsilon = 26.6 \text{ mM}^{-1} \text{ cm}^{-1}$; Chance and Maehly, 1955), CAT with 10 mM H_2O_2

at 240 nm ($\epsilon = 0.0394 \text{ mM}^{-1} \text{ cm}^{-1}$; Aebi, 1984), and APX with 0.5 mM ascorbate, 0.1 mM EDTA and 0.1 mM H_2O_2 at 290 nm ($\epsilon = 2.8 \text{ mM}^{-1} \text{ cm}^{-1}$; Nakano and Asada, 1981). Total soluble protein was determined by the Bradford (1976) method using bovine serum albumin as the standard. One unit (U) of activity was defined as the conversion of 1 μmol of substrate min^{-1} . Enzyme activity was calculated as:

$$\text{Volumetric activity } (\mu\text{mol min}^{-1}\text{mL}^{-1}\text{extract}) = (\Delta A / \Delta t \times V_r) / (\epsilon \times l \times v_a)$$

$$\text{Specific activity (U mg}^{-1}\text{protein)} = \text{Volumetric activity} / P$$

where $\Delta A / \Delta t$ is the absolute change in absorbance per minute, V_r is the reaction volume (3.0 mL), v_a is the volume of enzyme extract in the assay (0.1 mL), ϵ is the extinction coefficient ($\text{mM}^{-1}\text{cm}^{-1}$), l is the light path length (1 cm) and P is the protein concentration of the extract (mg mL^{-1}).

Statistical analysis

All analyses were performed in R version 4.6.1. Because irrigation and SA treatments were assigned independently to individual pots within each replication, the data were analyzed as a 4×4 factorial randomized complete block design, with irrigation, SA and their interaction as fixed effects and replication as a random block effect. Significant means were separated using Fisher's protected LSD test at $\alpha = 0.05$. Relationships among traits were examined using principal component analysis (PCA; 14 standardized traits, $n = 48$). Path analysis was performed in R by maximum-likelihood estimation on the 48 experimental observations. Water deficit was coded as $100 - \% \text{ FC}$ and SA as its concentration (mmol L^{-1}). Variables were standardized as z-scores, and equal-weight composites were calculated as the mean z-score of their constituents: oxidative stress (H_2O_2 , MDA), photosynthetic pigments (chlorophyll a, chlorophyll b, carotenoids), antioxidant enzyme activity (POD, CAT, APX) and growth and yield (plant height, spike length, grains and grain weight per pot); RWC and proline were single indicators. The model included paths from water deficit and SA to all six endogenous variables, from oxidative stress to pigments and from RWC to growth and yield; antioxidant enzyme activity was modelled as a parallel stress response to avoid collinearity (20 free parameters, 13 df). Because 48 observations (≈ 2.4 per parameter) fall below commonly recommended ratios (Jackson, 2003) and RMSEA is unreliable at small sample sizes (Kenny et al., 2015), the model was kept parsimonious and treated as exploratory; its coefficients are interpreted as statistical associations rather than causal effects (Arif and MacNeil, 2023). Direct, indirect and total

standardized effects were estimated, and model fit was assessed using χ^2 , CFI, RMSEA with its 90% confidence interval, and SRMR.

RESULTS

Growth and yield attributes

SA significantly influenced growth and yield across all irrigation regimes (Table 1 and Supplementary Table 1). Under 40% FC, plant height rose by 18.5%, from 53.6 cm in the control to 63.5 cm with S3, while at 100% FC it rose by 25.2%, from 60.8 to 76.1 cm. Spike length increased by 23.5% at 40% FC (6.5 to 8.1 cm) and by 33.9% at 100% FC (9.1 to 12.2 cm). Grains per pot increased by 9.9% at 40% FC (139 to 152) and by 7.4% at 100% FC (163 to 175). Grain weight per pot increased by 8.1% at 40% FC (4.50 to 4.87 g) and by 25.9% at 100% FC (4.50 to 5.67 g). For grain weight per pot the gain from S3 rose monotonically with water supply, from 8.1% at 40% FC through 13.3 and 23.0% at 60 and 80% FC to 25.9% at 100% FC. Plant height and spike length showed the same tendency, with the largest proportional gains at 100% FC. Grains per pot was the exception, responding similarly at all irrigation levels (4.0–9.9%).

Table 1. Growth and yield of wheat under four salicylic acid concentrations applied across four irrigation regimes.

Parameter	Irrigation (% FC)	Salicylic acid concentration (mmol L ⁻¹)			
		Control (0)	S1 (0.5)	S2 (1.0)	S3 (1.5)
Plant height (cm)	40	53.6 ± 1.67 h	53.6 ± 2.03 h	57.7 ± 2.12 g	63.5 ± 2.14 de
	60	59.9 ± 2.10 fg	63.8 ± 2.10 cde	62.4 ± 2.10 ef	63.3 ± 2.13 def
	80	61.7 ± 2.09 ef	66.6 ± 2.11 bcd	62.5 ± 2.11 ef	67.1 ± 2.08 bc
	100	60.8 ± 2.10 efg	63.5 ± 2.12 ef	69.7 ± 2.10 b	76.1 ± 2.11 a
	LSD (0.05)	3.5			
Spike length (cm)	40	6.5 ± 0.48 j	7.2 ± 0.40 ij	8.3 ± 0.48 fgh	8.1 ± 0.47 gh
	60	7.6 ± 0.48 hi	8.7 ± 0.44 fg	8.9 ± 0.49 ef	9.0 ± 0.47 def
	80	9.5 ± 0.39 cde	9.9 ± 0.48 cd	10.2 ± 0.44 bc	12.0 ± 0.48 a
	100	9.1 ± 0.48 def	10.9 ± 0.49 b	10.9 ± 0.48 b	12.2 ± 0.49 a
	LSD (0.05)	0.8			
Grains pot ⁻¹	40	139 ± 2.87 h	148 ± 2.96fg	149 ± 2.94 fg	152 ± 2.97 f
	60	146 ± 2.99 g	146 ± 2.90 g	152 ± 2.91 f	157 ± 2.94 e
	80	165 ± 2.88 cd	164 ± 2.72 d	170 ± 2.94 bc	172 ± 2.92 ab
	100	163 ± 2.92 d	170 ± 2.94 bc	167 ± 2.94 cd	175 ± 2.92 a
	LSD (0.05)	4.9			
Grain weight pot ⁻¹ (g)	40	4.50 ± 0.17 d	4.50 ± 0.17 d	4.57 ± 0.16 d	4.87 ± 0.21 bc

60	4.50 ± 0.17 d	4.73 ± 0.17 cd	4.57 ± 0.17 d	5.10 ± 0.17 b
80	4.50 ± 0.17 d	4.63 ± 0.19 cd	5.10 ± 0.19 b	5.53 ± 0.18 a
100	4.50 ± 0.17 d	5.10 ± 0.17 b	5.60 ± 0.17 a	5.67 ± 0.17 a
LSD (0.05)		0.28		

Means followed by the same letter within a parameter do not differ significantly at $p \leq 0.05$ according to the LSD test. LSD is the least significant difference for the irrigation $\times$ salicylic acid interaction. FC, field capacity. Values are means of three replications. $\pm$ is the standard deviation of three replications.

Photosynthetic pigments

Photosynthetic pigment concentrations varied significantly with both irrigation regime and SA concentration (Figure 1, Supplementary Table 1). The lowest chlorophyll a, chlorophyll b and carotenoid concentrations occurred at 40% FC, where S3 gave higher values than S1 and S2 although all values remained low. A more substantial increase appeared at 80% FC, where chlorophyll a and carotenoid concentrations under S3 were significantly higher than under S1 and S2, with chlorophyll b following the same pattern. These values did not differ significantly from those recorded at 100% FC, where S3 produced the highest concentrations of all three pigments. Pigment accumulation under S3 was thus superior across the irrigation gradient, and at 80% FC with S3 it matched the concentrations obtained under full irrigation. Total chlorophyll (chlorophyll a + b; Figure 1c) followed the same pattern, being lowest at 40% FC without SA and highest at 100% FC under S3; unlike chlorophyll a and b, however, total chlorophyll under S3 at 80% FC remained significantly lower than under S3 at 100% FC.

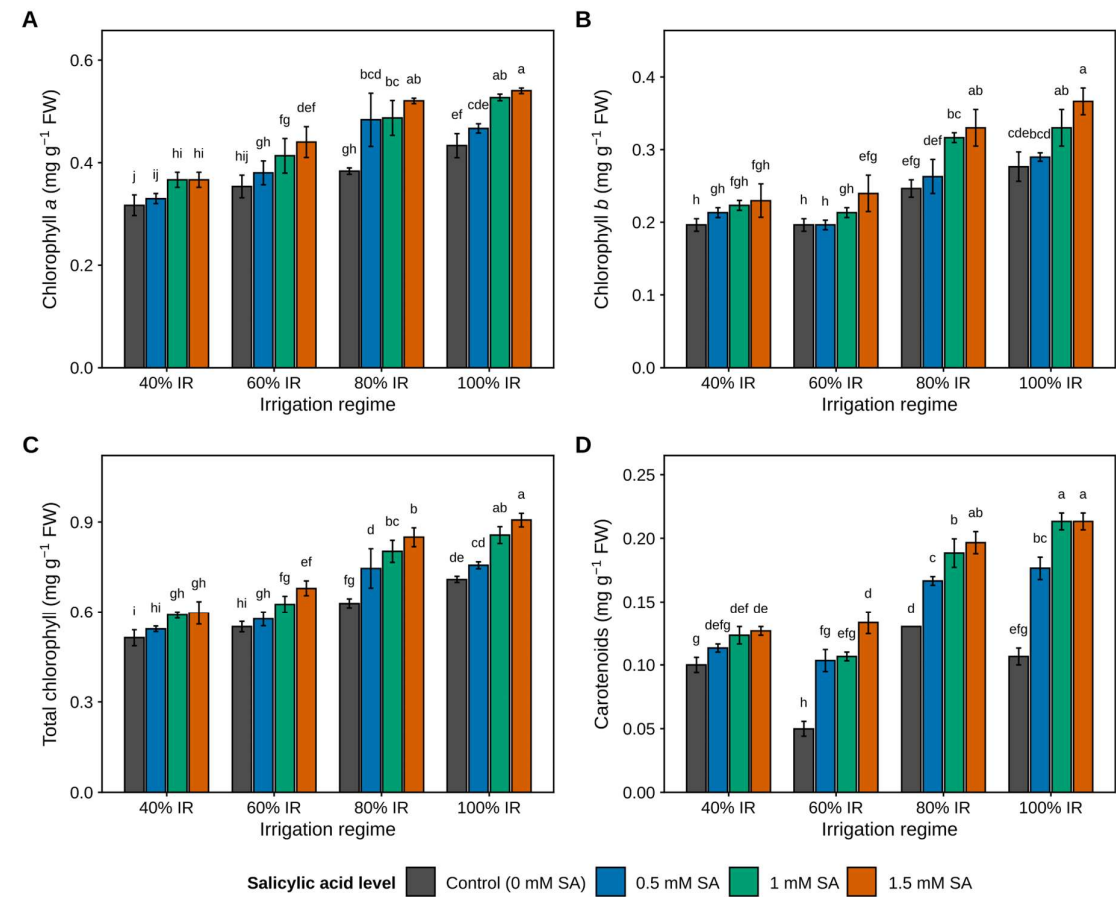


Figure 1. (a) Chlorophyll a, (b) chlorophyll b, (c) total chlorophyll (chlorophyll a + b) and (d) carotenoid concentrations (mg g⁻¹FW) of wheat under four salicylic acid concentrations across four irrigation regimes. Bars are means of three replications and error bars denote standard deviation.

Water status and osmotic adjustment

Relative water content was lowest at 40% FC at every SA concentration and increased with water supply (Figure 2a). Values at 80 and 100% FC were statistically similar, and RWC under S3 at 80% FC matched that obtained at 100% FC across all SA concentrations. In proportional terms the protective effect of SA on RWC was greatest where water was scarcest: S3 raised RWC by 18.5% at 40% FC, by 13.8% at 60% FC, and by only 6.9 and 6.7% at 80 and 100% FC. Proline concentration declined as both irrigation supply and SA concentration increased (Figure 2b). The highest values occurred at 40% FC, where S3 reduced proline by 28.4% relative to the untreated control; the corresponding reductions were 11.7, 16.9 and 17.8% at 60, 80 and 100% FC.

Oxidative stress markers

Hydrogen peroxide concentration fell significantly with increasing SA concentration and increasing water supply (Figure 2c). The highest values occurred without SA at 40% FC, and the lowest under S3 at 80 and 100% FC. Reductions achieved by S3 were 18.6% at 40% FC, 34.8% at 60% FC, 32.8% at 80% FC and 9.4% at 100% FC. Malondialdehyde followed the same overall pattern (Figure 2d): the highest concentration occurred at 40% FC without SA, and S3 lowered MDA by 27.1% at 40% FC, 23.1% at 60% FC and 20.0% at 100% FC, with no net change at 80% FC.

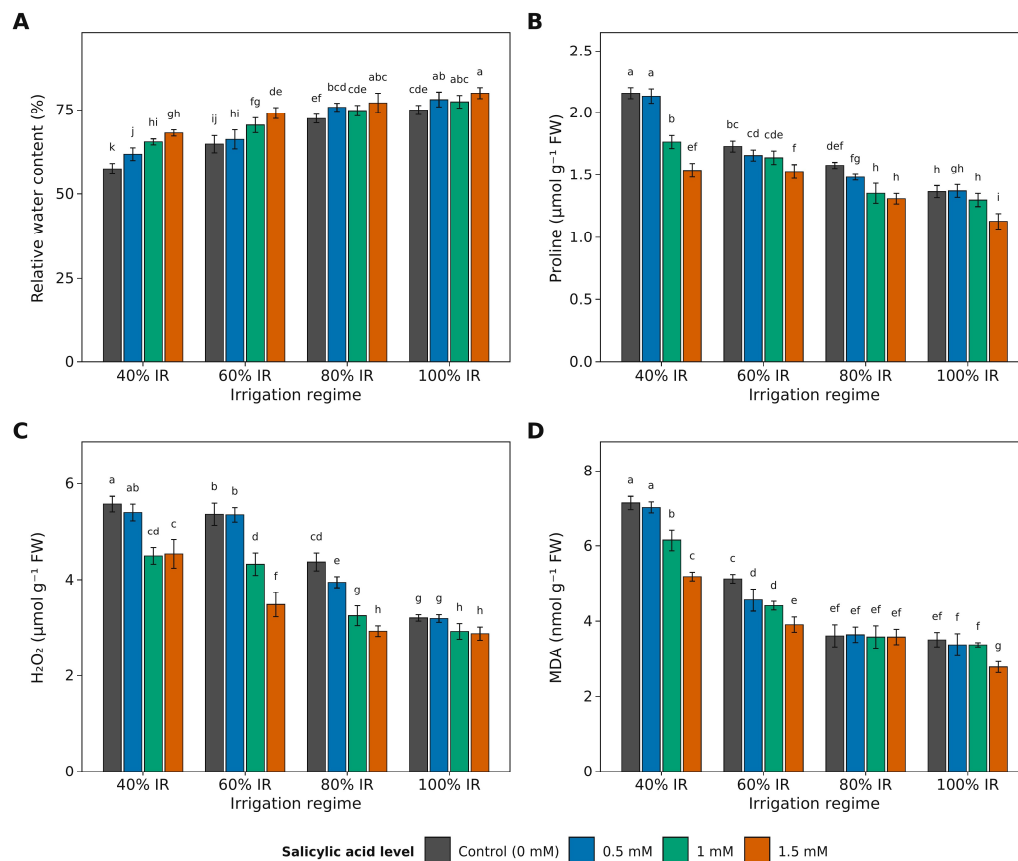


Figure 2. (a) Relative water content, (b) proline, (c) hydrogen peroxide and (d) malondialdehyde concentrations of wheat under four salicylic acid concentrations across four irrigation regimes. Bars are means of three replications and error bars denote standard deviation.

Antioxidant enzyme activities

Antioxidant enzyme activities (expressed as $\text{U mg}^{-1}\text{protein}$) responded to both factors (Figure 3, Supplementary Table 1). POD activity increased with SA concentration, with the highest activities under S2 and S3, and declined as irrigation supply increased, although SA maintained

activity above the control at every irrigation level (Figure 3a). CAT activity was highest at 40% FC under S3, and was higher and statistically similar under the remaining SA concentrations compared with the control (Figure 3c). APX activity was greatest under the two lowest irrigation regimes (40 and 60% FC), reaching a maximum under S3, and was lower at higher irrigation levels (Figure 3b). All three enzymes therefore peaked under the combination of severe deficit and the highest SA concentration.

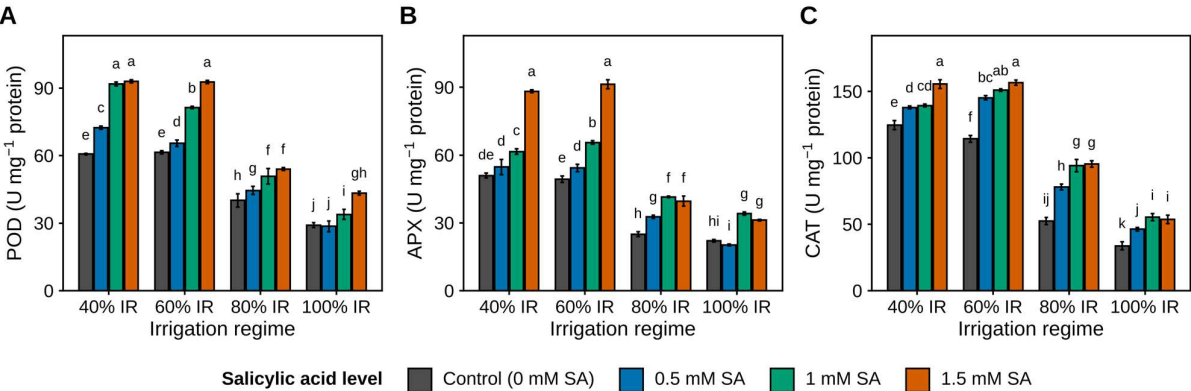


Figure 3. Activities of (a) peroxidase (POD), (b) ascorbate peroxidase (APX) and (c) catalase (CAT) in wheat under four salicylic acid concentrations across four irrigation regimes. Bars are means of three replications and error bars denote standard deviation. Activities are expressed as U mg⁻¹protein, where 1 U is the amount of enzyme converting 1 μmol of substrate per minute; protein was determined according to Bradford (1976).

Principal component analysis

Principal component analysis placed 83.8% of the total variance on the first two components, with PC1 accounting for 69.9% and PC2 for 13.9% (Figure 4). PC1 separated the irrigation regimes and ordered them along the water supply gradient. Grain weight per pot, grains per pot, plant height, spike length, chlorophyll a, chlorophyll b, carotenoids and RWC loaded positively on PC1, indicating their association with adequate water supply, whereas proline, H₂O₂ and MDA loaded negatively, reflecting their association with deficit. The antioxidant enzymes POD, APX and CAT loaded negatively on PC1 but carried a large positive loading on PC2, placing them almost orthogonal to the yield traits; enzyme induction and yield formation therefore varied along largely independent axes. Observations from 40% FC occupied the region of high stress markers and high enzyme activity, while those from 100% FC occupied the opposite region. Grouping by SA concentration produced a parallel but more compressed separation, with control observations displaced towards the stress-marker region and S3 observations towards the growth and pigment region.

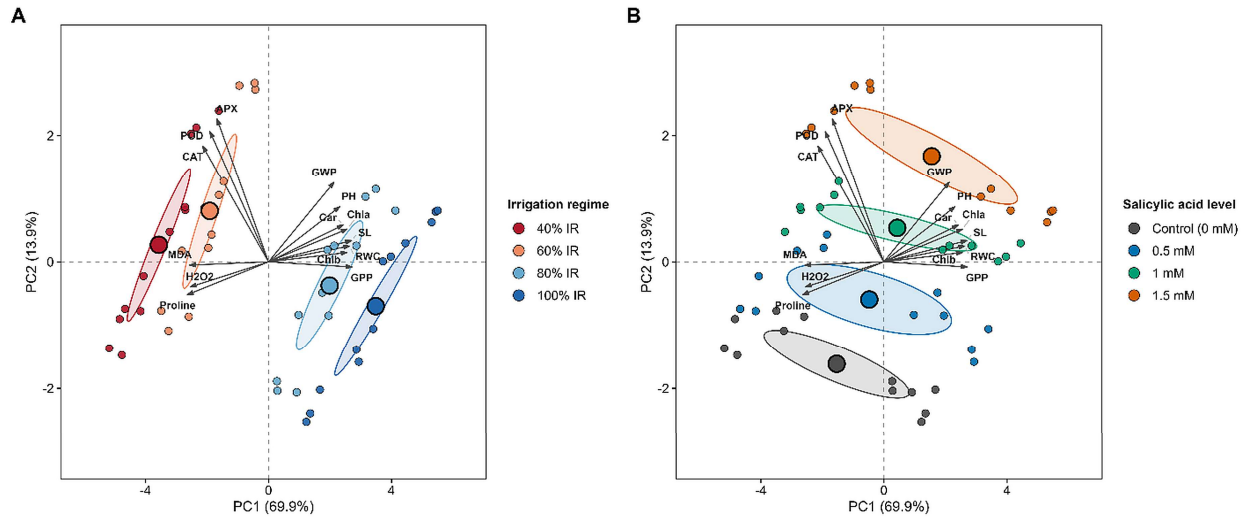
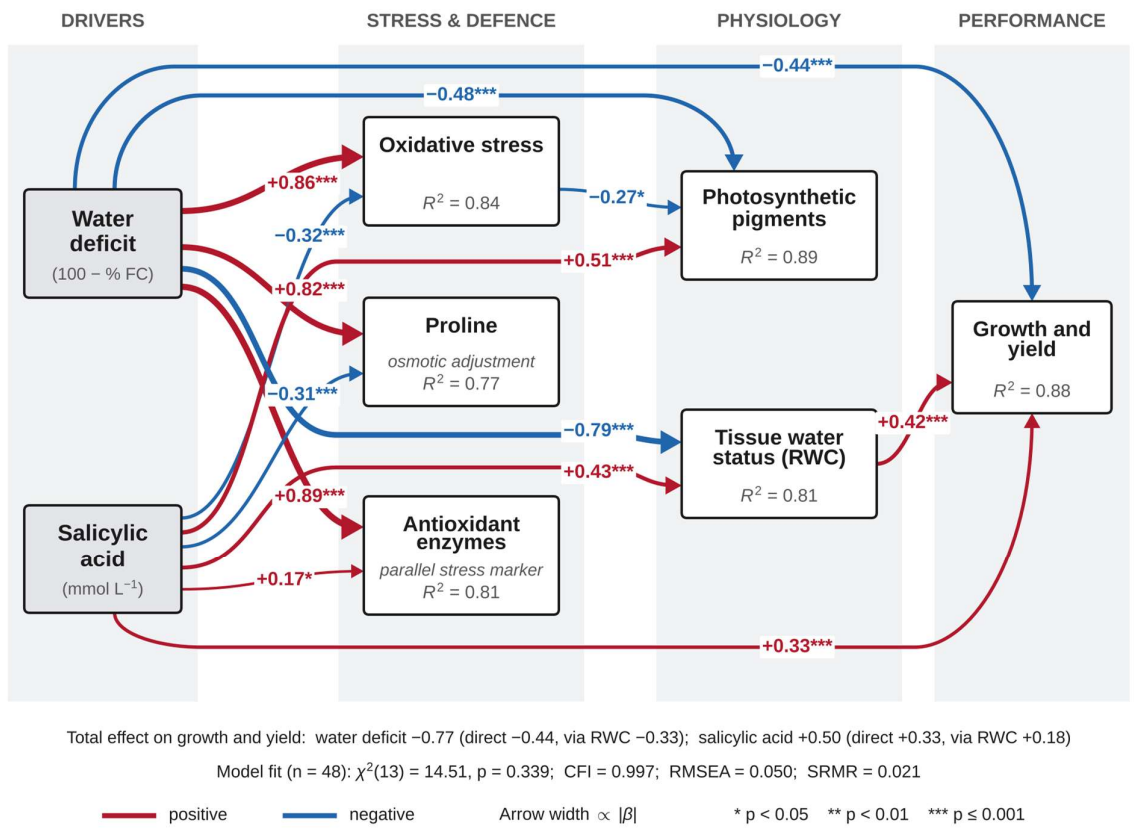


Figure 4. Principal component analysis biplots of 14 wheat traits ($n = 48$ observations; $PC1 = 69.9\%$ and $PC2 = 13.9\%$ of the total variance, 83.8% in total), with observations grouped by (a) irrigation regime and (b) salicylic acid concentration. Arrows are trait loadings, large symbols are group means and shaded areas are 95% confidence ellipses of the group mean.

Path analysis

A path model was fitted to the 48 experimental observations to examine the statistical pathways linking water deficit and SA concentration with growth and yield (Figure 5). The path model showed a good fit, $\chi^2(13) = 14.51$, $p = 0.339$, CFI = 0.997, RMSEA = 0.050 and SRMR = 0.021, although these indices have limited power at this sample size. The model explained 84% of the variance in oxidative stress, 77% in proline, 81% in antioxidant enzyme activity, 81% in relative water content (RWC), 89% in photosynthetic pigments and 88% in yield. Water deficit was positively associated with oxidative stress ($\beta = +0.86$, $p < 0.001$), proline ($\beta = +0.82$, $p < 0.001$) and antioxidant enzyme activity ($\beta = +0.89$, $p < 0.001$), while being negatively associated with RWC ($\beta = -0.79$, $p < 0.001$), pigment concentration ($\beta = -0.48$, $p < 0.001$) and yield ($\beta = -0.44$, $p < 0.001$). In contrast, SA was negatively associated with oxidative stress ($\beta = -0.32$, $p < 0.001$) and proline accumulation ($\beta = -0.31$, $p < 0.001$), was positively associated with antioxidant enzyme activity ($\beta = +0.17$, $p = 0.014$), and was positively associated with RWC ($\beta = +0.43$, $p < 0.001$), pigment concentration ($\beta = +0.51$, $p < 0.001$) and yield ($\beta = +0.33$, $p < 0.001$). Oxidative stress was negatively associated with pigments ($\beta = -0.27$, $p = 0.039$), whereas RWC positively predicted yield ($\beta = +0.42$, $p = 0.001$). The total standardized effect of water deficit on yield was -0.77 , comprising a direct effect of -0.44 and an indirect effect of -0.33 through RWC. The total standardized effect of SA was $+0.50$, with direct and RWC-mediated effects of $+0.33$ and $+0.18$, respectively. These effects are decompositions of

1 statistical associations within the specified model and do not by themselves demonstrate causal
2 mechanisms.



3
4 Figure 5. Path model of the associations of water deficit and salicylic acid concentration with wheat growth and
5 yield, fitted to the 48 experimental observations (16 treatment combinations $\times$ 3 replications). Values on arrows
6 are standardized path coefficients and values within boxes are the proportion of variance explained. Physiological
7 constructs are standardized composite indices as defined in Section 2.8. Arrows indicate the hypothesized
8 direction of paths; coefficients represent statistical associations, not experimentally demonstrated causal effects.

9 **DISCUSSION**

10 Salicylic acid (SA), applied in our experiment as four foliar concentrations across four
11 irrigation regimes, improved wheat performance at every water level tested, but which traits
12 benefited most depended systematically on how much water the crop received as the central
13 finding of this study is obtained against a backdrop of increasing water-scarcity pressure on
14 staple cereals (Khan et al., 2022). Improvements in plant height, spike length, and especially
15 grain weight per pot were largest under full irrigation, whereas protection of tissue hydration
16 and suppression of stress markers were largest under the most severe deficit. Grain weight
17 showed this contrast most clearly. S3 increased grain weight by only 8.1% at 40% FC but by
18 25.9% at 100% FC. In contrast, RWC increased by 18.5% at 40% FC and only 6.7% at 100%

FC, while proline and MDA also showed their greatest reductions under severe water deficit. These outcomes suggest that SA helps plants maintain water content and reduces oxidative damage when water is scarce. However, this protection cannot fully restore yield because grain production remains limited by the low water supply.

When sufficient water is available, SA can express its full beneficial effects on plant growth and grain filling. A comparable context dependence is evident elsewhere in the SA literature. Munsif et al. (2022b) reported a slightly greater SA-plus-K-induced increase in wheat grain yield under mild than under severe drought (41% versus 37%), suggesting that the protective benefit does not continue to increase as water deficit becomes more severe. Conversely, when SA acts mainly as a growth promoter, its greatest benefits may occur under adequate water supply. Waseem et al. (2006) found that SA promoted wheat growth under non-stress conditions but did not fully overcome drought-induced growth reductions, while Sharafizad et al. (2012) recorded the highest grain yield with 0.7 mM SA under non-stressed conditions. Reports that SA benefits are greatest under stress and reports that they are greatest under favorable conditions may therefore both be correct, depending on which trait class and irrigation range a given study happens to cover.

The increase in plant height under SA is consistent with improved stomatal regulation and reduced transpiration loss, which help maintain cell turgor and support elongation, as reported by Parveen et al. (2021) in wheat, and with SA-mediated modulation of aquaporins and hence water transport efficiency (Quiroga et al., 2018). Neither stomatal conductance nor aquaporin expression was measured in the present study, so these remain mechanisms proposed on the basis of the cited literature rather than conclusions demonstrated here. The increase in spike length, most pronounced under S3, may reflect the reported capacity of SA to enhance nitrogen, potassium and phosphorus uptake and to regulate source–sink balance and Rubisco activity (Khalvandi et al., 2021). Improvements in grain number and grain weight under SA at both limited and full irrigation are consistent with a reduction in oxidative load and a strengthened antioxidative defence. Under deficit, accumulation of reactive oxygen species damages cellular components and reduces reproductive success, and SA is reported to raise the activity of antioxidant enzymes that neutralise these species and protect cellular integrity (Khalvandi et al., 2021).

SA also influences hormone signalling, moderating the inhibitory effect of abscisic acid on grain filling and favouring assimilate flow towards the grain, and is reported to promote sucrose transport and conversion to starch (Chen et al., 2017). Reduced photosynthetic activity at 40% FC lowered pigment concentrations, although S3 afforded partial protection, raising chlorophyll contents relative to the control treatment, plausibly through enhanced antioxidant defense and upregulated chlorophyll biosynthesis (Kang et al., 2014). At 100% FC, S3 further stabilised chlorophyll pigments over the unsprayed control. The pigment response to irrigation and SA is consistent with the role of SA in regulating stress-responsive transcription factors such as WRKY and NAC (Erpen et al., 2018), which control photosynthesis-related genes, and parallels the improvements in chlorophyll reported by Aires et al. (2022) following foliar SA in tomato.

Among the stress indicators, the decline in RWC at 40% FC indicates severe water stress with consequent loss of turgor and impaired cellular function. S3 partly offset this decline, which is consistent with improved osmotic regulation, and the finding that RWC under S3 at 80% FC matched that at 100% FC suggests better leaf diffusive resistance under moderate deficit. This is in agreement with Munsif et al. (2022b) and Tayyab et al. (2020). Proline concentration fell rather than rose with SA application. Much of the literature reports the opposite, since proline commonly accumulates as an osmoprotectant under stress and the decline observed here is best interpreted as evidence that SA reduced the severity of the stress experienced by the tissue, thereby lowering the demand for osmotic adjustment (Nazar et al., 2015), and the parallel reductions in H_2O_2 and MDA support that reading. The interpretation nevertheless remains inferential in the absence of metabolite flux measurements. H_2O_2 and MDA were highest at 40% FC without SA and were reduced by SA, most strongly at S3, respectively. This is consistent with activation of POD, CAT and APX and consequent scavenging of reactive oxygen species as reported by Aldesuquy et al. (2018). Upregulation of chaperones and heat shock proteins and altered protein kinase activity have been proposed as the underlying mechanism (Nazar et al., 2015), and a protective effect of SA against drought-induced oxidative damage has been demonstrated repeatedly (Yousefzadeh Najafabadi and Ehsanzadeh, 2017; Wang et al., 2019).

The multivariate analyses reinforce this interpretation while adding an important caution. PCA separated full from deficit irrigation along PC1 and placed growth and pigment traits opposite the stress markers, confirming that water availability dominated the trait covariance structure.

Antioxidant enzymes were nearly orthogonal to yield traits, suggesting that enzyme induction and yield formation were not closely associated within the two-dimensional PCA space. In the path model fitted to the 48 experimental observations, most of the positive total standardized association between SA and growth and yield performance ($\beta = 0.50$) was attributed to the direct path ($\beta = 0.33$), with a smaller component ($\beta = 0.18$) operating statistically through RWC. These mediator coefficients are model-dependent associations; they are consistent with, but do not demonstrate, an RWC-mediated mechanism. Comparable wheat studies have shown that SA responses depend on water availability and that improvements in pigments, plant water status, antioxidant activity and yield are not uniform across increasing levels of water deficit (Munsif et al., 2022a; Mohammed et al., 2023). Under adequate water supply, SA may promote growth, grain filling and yield, whereas under severe water deficit its main contribution may be the maintenance of tissue hydration and reduction of oxidative damage, without fully restoring yield potential.

Several limitations should be acknowledged. This single-season pot experiment used one cultivar, and the restricted rooting volume may have altered plant growth and the severity of the imposed water deficit, limiting direct extrapolation to field conditions (Poorter et al., 2012; Moshelion et al., 2024). Superoxide dismutase, gas exchange, photosynthetic rate, water-use efficiency and assimilate partitioning were not measured; therefore, the proposed mechanisms remain hypotheses rather than demonstrated pathways. Moreover, because the path model included only 48 observations and collinear predictors, its mediator coefficients should be interpreted as model-dependent associations rather than established causal mechanisms (Arif and MacNeil, 2023). Accordingly, the direct and indirect paths reported here should be regarded as hypotheses to be tested in experiments that manipulate the proposed mediators, such as leaf water status, directly. In last, because 1.5 mmol L^{-1} SA produced the best response for most traits, the optimum concentration may lie beyond the tested range. Future field studies should therefore include multiple cultivars, broader SA doses and comparable moisture gradients.

CONCLUSIONS

Full irrigation produced the best overall growth and yield, and foliar salicylic acid improved wheat performance at every irrigation regime tested, with 1.5 mmol L^{-1} the most effective concentration. The nature of the benefit, however, depended on deficit severity. Under severe

deficit, SA acted chiefly in a protective capacity, raising relative water content by 18.5% and lowering proline, malondialdehyde and hydrogen peroxide by 28.4, 27.1 and 18.6% respectively at 40% of field capacity, while the associated yield gain remained modest at 8.1%. Under full irrigation the same treatment delivered its largest yield response, increasing grain weight per pot by 25.9%. Salicylic acid should therefore be regarded as a means of limiting oxidative damage and preserving tissue hydration when water is scarce, and as a yield-enhancing input when water is adequate, rather than as a substitute for irrigation. These conclusions are drawn directly from the factorial experiment. The multivariate analyses, performed on the same 48 experimental observations, were consistent with them: PCA showed that water availability dominated trait variation, and the path model associated the SA response in growth and yield mainly with a direct path and partly with RWC. Because these multivariate results describe statistical associations rather than tested mechanisms, they should be regarded as hypothesis-generating. Field validation across seasons, cultivars and a wider concentration range, together with measurements of gas exchange and water use efficiency, is the logical next step.

CRediT AUTHORSHIP CONTRIBUTION STATEMENT

Waleed Iqbal: Conceptualization, Methodology, Investigation, Formal analysis. Uzair Ahmed: Methodology, Investigation, Formal analysis, Visualization, Writing – original draft. Muhammad Zahir Afridi: Writing – review & editing. Muhammad Ayaz: Writing – review & editing. Hamza Azeem Khan: Visualization, Writing – original draft.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing or financial interests.

ETHICS AND PERMIT APPROVALS

Not applicable.

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REFERENCES

- Aebi H. (1984). Catalase in vitro. *Methods Enzymol* 105: 121–126.
[https://doi.org/10.1016/S0076-6879\(84\)05016-3](https://doi.org/10.1016/S0076-6879(84)05016-3)
- Ahmad A., Aslam Z., Javed T., Hussain S., Raza A., Shabbir R., Mora-Poblete F., Saeed T., Zulfiqar F., Ali M.M., Nawaz M., Rafiq M., Osman H.S., Albaqami M., Ahmed M.A.A., Tauseef M. (2022). Screening of wheat (*Triticum aestivum* L.) genotypes for drought tolerance through agronomic and physiological response. *Agronomy* 12: 287.
<https://doi.org/10.3390/agronomy12020287>
- Aires E.S., Ferraz A.K.L., Carvalho B.L., Teixeira F.P., Putti F.F., de Souza E.P., Rodrigues J.D., Ono E.O. (2022). Foliar application of salicylic acid to mitigate water stress in tomato. *Plants (Basel)* 11: 1775. <https://doi.org/10.3390/plants11131775>
- Aldesuquy H.S., Ibraheem F.L., Ghanem H.E. (2018). Exogenously supplied salicylic acid and trehalose protect growth vigor, chlorophylls and thylakoid membranes of wheat flag leaf from drought-induced damage. *J Agric For Meteorol Res* 1: 13–20.
- Arif S., MacNeil M.A. (2023). Applying the structural causal model framework for observational causal inference in ecology. *Ecol Monogr* 93: e1554.
<https://doi.org/10.1002/ecm.1554>
- Arzani A., Ashraf M. (2017). Cultivated ancient wheats (*Triticum* spp.): a potential source of health-beneficial food products. *Compr Rev Food Sci Food Saf* 16: 477–488.
<https://doi.org/10.1111/1541-4337.12262>
- Bates L.S., Waldren R.P., Teare I.D. (1973). Rapid determination of free proline for water-stress studies. *Plant Soil* 39: 205–207. <https://doi.org/10.1007/BF00018060>
- Bhattacharya A. (2021). Effect of soil water deficit on growth and development of plants: a review. In: *Soil Water Deficit and Physiological Issues in Plants*, Springer, Singapore, pp. 393–488. https://doi.org/10.1007/978-981-33-6276-5_5

- 1 Bidabadi S.S., Mahmood M., Baninasab B., Ghobadi C. (2012). Influence of salicylic acid on
2 morphological and physiological responses of banana (*Musa acuminata* cv. 'Berangan',
3 AAA) shoot tips to in vitro water stress induced by polyethylene glycol. Plant Omics 5:
4 33–39.
- 5 Bradford M.M. (1976). A rapid and sensitive method for the quantitation of microgram
6 quantities of protein utilizing the principle of protein–dye binding. Anal Biochem 72:
7 248–254. [https://doi.org/10.1016/0003-2697\(76\)90527-3](https://doi.org/10.1016/0003-2697(76)90527-3)
- 8 Chance B., Maehly A.C. (1955). Assay of catalases and peroxidases. Methods Enzymol 2:
9 764–775. [https://doi.org/10.1016/S0076-6879\(55\)02300-8](https://doi.org/10.1016/S0076-6879(55)02300-8)
- 10 Chen T., Zhao X., Zhang C., Yang Y., Feng B., Zhang X., Fu G., Tao L. (2017). Application
11 of salicylic acid improves filling of inferior grains of rice during late maturity under
12 mild cold stress. Crop Sci 57: 2130–2142. <https://doi.org/10.2135/cropsci2016.11.0941>
- 13 El-Hendawy S., Mohammed N., Al-Suhaibani N. (2024). Enhancing wheat growth,
14 physiology, yield, and water use efficiency under deficit irrigation by integrating foliar
15 application of salicylic acid and nutrients at critical growth stages. Plants (Basel) 13:
16 1490. <https://doi.org/10.3390/plants13111490>
- 17 El-Nasharty A.B., El-Nwehy S.S., Abou El-Nour E.A.A., Rezk A.I. (2019). Impact of
18 salicylic acid foliar application on two wheat cultivars grown under saline conditions.
19 Pak J Bot 51: 1939–1944. [https://doi.org/10.30848/PJB2019-6\(19\)](https://doi.org/10.30848/PJB2019-6(19))
- 20 Erpen L., Devi H.S., Grosser J.W., Dutt M. (2018). Potential use of the DREB/ERF, MYB,
21 NAC and WRKY transcription factors to improve abiotic and biotic stress in transgenic
22 plants. Plant Cell Tissue Organ Cult 132: 1–25. [https://doi.org/10.1007/s11240-017-](https://doi.org/10.1007/s11240-017-1320-6)
23 1320-6
- 24 FAO (2021). Crop Prospects and Food Situation – Quarterly Global Report No. 4, December
25 2021. Food and Agriculture Organization of the United Nations, Rome, Italy.
- 26 Ghosh U.K., Islam M.N., Siddiqui M.N., Khan M.A.R. (2021). Understanding the roles of
27 osmolytes for acclimatizing plants to changing environment: a review of potential
28 mechanism. Plant Signal Behav 16: 1913306.
29 <https://doi.org/10.1080/15592324.2021.1913306>

- 1 Jackson D.L. (2003). Revisiting sample size and number of parameter estimates: some
2 support for the N:q hypothesis. *Struct Equ Modeling* 10: 128–141.
3 https://doi.org/10.1207/S15328007SEM1001_6
- 4 Kang G., Li G., Guo T. (2014). Molecular mechanism of salicylic acid-induced abiotic stress
5 tolerance in higher plants. *Acta Physiol Plant* 36: 2287–2297.
6 <https://doi.org/10.1007/s11738-014-1603-z>
- 7 Kenny D.A., Kaniskan B., McCoach D.B. (2015). The performance of RMSEA in models
8 with small degrees of freedom. *Sociol Methods Res* 44: 486–507.
9 <https://doi.org/10.1177/0049124114543236>
- 10 Khalvandi M., Siosemardeh A., Roohi E., Keramati S. (2021). Salicylic acid alleviated the
11 effect of drought stress on photosynthetic characteristics and leaf protein pattern in
12 winter wheat. *Heliyon* 7: e05908. <https://doi.org/10.1016/j.heliyon.2021.e05908>
- 13 Khan M.A.U., Mohammad F., Khan F.U., Ahmad S., Raza M.A., Kamal T. (2020).
14 Comparison among different stability models for yield in bread wheat. *Sarhad J Agric*
15 36: 282–290. <https://doi.org/10.17582/journal.sja/2020/36.1.282.290>
- 16 Khan M.I.R., Poór P., Janda T. (2022). Salicylic acid: a versatile signaling molecule in plants.
17 *J Plant Growth Regul* 41: 1887–1890. <https://doi.org/10.1007/s00344-022-10692-4>
- 18 Khan W., Prithiviraj B., Smith D.L. (2003). Photosynthetic responses of corn and soybean to
19 foliar application of salicylates. *J Plant Physiol* 160: 485–492.
20 <https://doi.org/10.1078/0176-1617-00865>
- 21 Licaj I., Di Meo M.C., Fiorillo A., Samperna S., Marra M., Rocco M. (2023). Comparative
22 analysis of the response to polyethylene glycol-simulated drought stress in roots from
23 seedlings of “modern” and “ancient” wheat varieties. *Plants (Basel)* 12: 428.
24 <https://doi.org/10.3390/plants12030428>
- 25 Lichtenthaler H.K. (1987). Chlorophylls and carotenoids: pigments of photosynthetic
26 biomembranes. *Methods Enzymol* 148: 350–382. [https://doi.org/10.1016/0076-](https://doi.org/10.1016/0076-6879(87)48036-1)
27 [6879\(87\)48036-1](https://doi.org/10.1016/0076-6879(87)48036-1)
- 28 Mohammed N., El-Hendawy S., Alsamin B., Mubushar M., Dewir Y.H. (2023). Integrating
29 application methods and concentrations of salicylic acid as an avenue to enhance

- 1 growth, production, and water use efficiency of wheat under full and deficit irrigation
2 in arid countries. *Plants (Basel)* 12: 1019. <https://doi.org/10.3390/plants12051019>
- 3 Moshelion M., Dietz K.J., Dodd I.C., Muller B., Lunn J.E. (2024). Guidelines for designing
4 and interpreting drought experiments in controlled conditions. *J Exp Bot* 75: 4671–
5 4679. <https://doi.org/10.1093/jxb/erae292>
- 6 Munsif F., Farooq U., Arif M., Shah T., Jehangir M., Zaheer S., Akhtar K., Khan M.S.,
7 Ahmad I., Ahmad W., Ali S., Amir R. (2022a). Potassium and salicylic acid function
8 synergistically to promote the drought resilience through upregulation of antioxidant
9 profile for enhancing potassium use efficiency and wheat yield. *Ann Appl Biol* 180:
10 273–282. <https://doi.org/10.1111/aab.12731>
- 11 Munsif F., Shah T., Arif M., Jehangir M., Afridi M.Z., Ahmad I., Jan B.L., Alansi S. (2022b).
12 Combined effect of salicylic acid and potassium mitigates drought stress through the
13 modulation of physio-biochemical attributes and key antioxidants in wheat. *Saudi J*
14 *Biol Sci* 29: 103294. <https://doi.org/10.1016/j.sjbs.2022.103294>
- 15 Nakano Y., Asada K. (1981). Hydrogen peroxide is scavenged by ascorbate-specific
16 peroxidase in spinach chloroplasts. *Plant Cell Physiol* 22: 867–880.
17 <https://doi.org/10.1093/oxfordjournals.pcp.a076232>
- 18 Nazar R., Umar S., Khan N.A., Sareer O. (2015). Salicylic acid supplementation improves
19 photosynthesis and growth in mustard through changes in proline accumulation and
20 ethylene formation under drought stress. *S Afr J Bot* 98: 84–94.
21 <https://doi.org/10.1016/j.sajb.2015.02.005>
- 22 Nyaupane S., Poudel M.R., Panthi B., Dhakal A., Paudel H., Bhandari R. (2024). Drought
23 stress effect, tolerance, and management in wheat – a review. *Cogent Food Agric* 10:
24 2296094. <https://doi.org/10.1080/23311932.2023.2296094>
- 25 Parveen A., Ashraf M.A., Hussain I., Perveen S., Rasheed R., Mahmood Q., Hussain S., Ditta
26 A., Hashem A., Al-Arjani A.-B.F., Alqarawi A.A., Abd Allah E.F. (2021). Promotion
27 of growth and physiological characteristics in water-stressed *Triticum aestivum* in
28 relation to foliar-application of salicylic acid. *Water* 13: 1316.
29 <https://doi.org/10.3390/w13091316>

- 1 Poorter H., Böhler J., van Dusschoten D., Climent J., Postma J.A. (2012). Pot size matters: a
2 meta-analysis of the effects of rooting volume on plant growth. *Funct Plant Biol* 39:
3 839–850. <https://doi.org/10.1071/FP12049>
- 4 Quiroga G., Erice G., Aroca R., Zamarreño Á.M., García-Mina J.M., Ruiz-Lozano J.M.
5 (2018). Arbuscular mycorrhizal symbiosis and salicylic acid regulate aquaporins and
6 root hydraulic properties in maize plants subjected to drought. *Agric Water Manag* 202:
7 271–284. <https://doi.org/10.1016/j.agwat.2017.12.012>
- 8 Sharafizad M., Naderi A., Siadat S.A., Sakinejad T., Lak S. (2012). Effect of salicylic acid
9 pretreatment on yield, its components and remobilization of stored material of wheat
10 under drought stress. *J Agric Sci* 4: 115. <https://doi.org/10.5539/jas.v4n10p115>
- 11 Taulavuori E., Hellström E.K., Taulavuori K., Laine K. (2001). Comparison of two methods
12 used to analyse lipid peroxidation from *Vaccinium myrtillus* L. during snow removal,
13 reaclimation and cold acclimation. *J Exp Bot* 52: 2375–2380.
14 <https://doi.org/10.1093/jexbot/52.365.2375>
- 15 Tayyab N., Naz R., Yasmin H., Nosheen A., Keyani R., Sajjad M., Hassan M.N., Roberts
16 T.H. (2020). Combined seed and foliar pre-treatments with exogenous methyl
17 jasmonate and salicylic acid mitigate drought-induced stress in maize. *PLoS One* 15:
18 e0232269. <https://doi.org/10.1371/journal.pone.0232269>
- 19 Velikova V., Yordanov I., Edreva A. (2000). Oxidative stress and some antioxidant systems
20 in acid rain-treated bean plants: protective role of exogenous polyamines. *Plant Sci* 151:
21 59–66. [https://doi.org/10.1016/S0168-9452\(99\)00197-1](https://doi.org/10.1016/S0168-9452(99)00197-1)
- 22 Wang Y.Y., Wang Y., Li G.Z., Hao L. (2019). Salicylic acid-altering *Arabidopsis* plant
23 response to cadmium exposure: underlying mechanisms affecting antioxidation and
24 photosynthesis-related processes. *Ecotoxicol Environ Saf* 169: 645–653.
25 <https://doi.org/10.1016/j.ecoenv.2018.11.062>
- 26 Waseem M., Athar H.U.R., Ashraf M. (2006). Effect of salicylic acid applied through rooting
27 medium on drought tolerance of wheat. *Pak J Bot* 38: 1127–1136.
- 28 Yanagi M. (2024). Climate change impacts on wheat production: reviewing challenges and
29 adaptation strategies. *Adv Resour Res* 4: 89–107. https://doi.org/10.50908/arr.4.1_89

- 1 Yang H., Fang R., Luo L., Yang W., Huang Q., Yang C., Hui W., Gong W., Wang J. (2023).
2 Uncovering the mechanisms of salicylic acid-mediated abiotic stress tolerance in
3 horticultural crops. Front Plant Sci 14: 1226041.
4 <https://doi.org/10.3389/fpls.2023.1226041>
- 5 Yousefzadeh Najafabadi M., Ehsanzadeh P. (2017). Photosynthetic and antioxidative
6 upregulation in drought-stressed sesame (*Sesamum indicum* L.) subjected to foliar-
7 applied salicylic acid. Photosynthetica 55: 611–622. [https://doi.org/10.1007/s11099-](https://doi.org/10.1007/s11099-017-0673-8)
8 [017-0673-8](https://doi.org/10.1007/s11099-017-0673-8)