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Impact of salicylic acid priming on physiological, biochemical, and photochemical responses of *Zygophyllum fabago* under drought and high light stress

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Abstract

Although salicylic acid (SA) is known to increase plant tolerance to either drought or high light (HL), its effectiveness under their simultaneous occurrence remains unclear. Here, we examined the impact of SA seed priming (50 ppm) on growth, oxidative status, and chlorophyll *a* fluorescence in *Zygophyllum fabago* L. subjected to drought (withholding water for 20 days), HL (800 µmol m^{-2} s^{-1}) or their combination. All stress treatments, particularly the combined one, markedly reduced growth, whereas SA priming significantly increased shoot fresh and dry weight only under drought. Fast chlorophyll *a* fluorescence OJIP transients showed that drought, HL, and their combination enhanced the O–J phase, whereas SA-primed plants exhibited a slight attenuation of this rise. All stress treatments reduced phenomenological energy flux parameters and altered quantum yield for electron transport, but SA partially restored these parameters, bringing them closer to control values. The biplot of principal component analysis (PCA) indicated that under SA+Drought, higher antioxidant enzyme and phenylalanine ammonia-lyase (PAL) activities, along with increased phenolic and flavonoid contents, were key drivers of protection and growth maintenance under water stress. In contrast, under HL and combined Drought+HL, SA provided little protection, as shown by higher malondialdehyde (MDA), lower catalase (CAT) activity and maximum quantum yield of PSII (F_v/F_m), and no recovery of shoot dry weight. Overall, our findings highlighted the stress-specific nature of SA-induced tolerance and emphasized the need to assess exogenous protectants under multifactorial stress to predict their agronomic relevance.

Keywords: *Zygophyllum fabago*; Drought-High Light Combination; Salicylic Acid; OJIP Fluorescence; Antioxidant Defense; Water-Splitting Complex Activity

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Introduction

Drought is widely recognized as one of the most formidable environmental constraints, imposing severe restrictions on plant growth and yield worldwide (Munns & Gilliham, 2015; Liu et al., 2024; Sheuli et al., 2025). This stressor triggers a wide array of physiological dysfunctions and metabolic impairments, leading to the excessive accumulation of ROS (Habibi, 2020). Such oxidative bursts accelerate the degradation of chlorophyll, compromise the stability of membranes and photosynthetic proteins, and hinder photochemical efficiency by damaging photosystem II (PSII) and electron transport chains, thereby lowering yield potential (Raihan et al., 2025). In parallel, light intensity, spectral quality, and photoperiod critically modulate photosynthetic performance, morphogenesis, and secondary metabolism (Azizi et al., 2025; Cun et al., 2023). When light intensity becomes excessive, it disrupts the equilibrium between energy absorption and metabolic utilization, inducing photoinhibition and oxidative damage through ROS production. The overexcitation of PSII facilitates the formation of $^1O_2$ and the degradation of the D1 protein, while photosystem I (PSI) generates H_2O_2 and O_2^-, which together impair chloroplast homeostasis and electron flow (Didaran et al., 2024). The PSII reaction center is highly susceptible to damage across all light intensities; this protein is vital not only as a binding site for various cofactors but also for maintaining the conformational stability of PSII during its repair cycle (Ma et al., 2017; Su et al., 2014).

To counteract oxidative pressure during concurrent drought and HL exposure, plants have developed multifaceted adaptive strategies. These include the activation of enzymatic and non-enzymatic antioxidant systems (such as carotenoids, glutathione, ascorbate, and phenolics), hormonal modulation, and the accumulation of compatible solutes. Furthermore, sophisticated repair mechanisms exist to prevent the accumulation of damaged PSII subunits and mitigate stress-induced photoinhibition (Takahashi & Murata, 2008). A primary photoprotective response involves the dissipation of excess absorbed energy as heat; although this reduces absolute photosynthetic efficiency, it safeguards PSII reaction centers from irreversible oxidative damage. This thermal dissipation is closely linked to the xanthophyll cycle, comprising the interconversion of violaxanthin, antheraxanthin, and zeaxanthin, while secondary metabolites like flavonoids and anthocyanins provide supplementary light screening and antioxidative capacity (Kuczyńska et al., 2024; Araguirang & Richter, 2022). Beyond their protective utility, phytohormone-induced pigments also improve the nutritional quality of plant tissues (Gruda et al., 2025). Despite these innate defenses, physiological and proteomic responses to HL remain highly dynamic and are dictated by both light intensity and wavelength (Parrine et al., 2021). However, the integration of light signaling with hormonal pathways to maintain redox homeostasis and carbon fixation remains an unresolved frontier in plant science.

Since innate defenses are often insufficient under severe stress, contemporary research has focused on the exogenous application of protective molecules such as proline (Koc et al., 2024), nitric oxide (Wang et al., 2024), salicylic acid (SA) (Ali et al., 2022), and melatonin (Kaya et al., 2022). Among these, salicylic acid (SA) has emerged as a paramount regulator that fortifies antioxidant cascades and detoxifies ROS under various abiotic constraints (Kareem et al., 2019; Maghsoudi et al., 2020). The efficacy of SA in enhancing drought resilience has been documented in diverse crops, including rice, maize, wheat, and fig (Latif et al., 2016; Sharma et al., 2017), where it stabilizes photosynthetic activity and maintains osmotic balance (Paul et al., 2024). Under water deficit, SA acts as a critical signaling molecule that induces partial stomatal closure to minimize transpiration while preserving metabolic efficiency (Khan et al., 2015). It further bolsters defense by stimulating SOD, CAT, and APX activities and facilitating nutrient uptake (Urmi et al., 2023; Kumar et al., 2024). While evidence suggests that SA alleviates HL-induced damage by protecting the photosynthetic apparatus (Chen et al., 2016), its specific regulatory role in PSII protein stability and thylakoid phosphorylation under HL remains poorly understood.

Zygophyllum fabago L. (Syrian bean-caper) is a perennial herb typically inhabiting arid, nutrient-poor, and disturbed environments (Karimian et al., 2025). Although ecologically regarded as a facultative halophyte, controlled experiments have indicated a high sensitivity to salinity (Wang et al., 2020). In its natural habitat, *Z. fabago* frequently encounters the simultaneous pressures of drought and HL, yet its physiological responses to such combinations remain under-researched. While the species possesses inherent levels of stress tolerance, enhancing its capacity to maintain physiological homeostasis during extreme summer conditions is crucial. Although SA is known to improve tolerance to drought or HL individually, its effectiveness under their concurrent occurrence has not been established. Therefore, this study aimed to evaluate the physiological and

biochemical impacts of SA on the growth, PSII performance, and antioxidant machinery of *Z. fabago* under combined drought and HL stress, providing a novel assessment of SA-induced resilience in a multifactorial environmental context.

Materials and Methods

Plant material and treatments

Z. fabago seeds were sown in cylindrical plastic pots (15 cm diameter, 62 cm depth), with four seeds per pot. Each pot contained 16 kg of sandy loam soil characterized by a pH of 7.3, an electrical conductivity (EC) of 1.55 dS m^{-1}, and a field capacity (FC) of 23%. Basal fertilization consisted of 200 mg N kg^{-1} soil as NH_4NO_3, 50 mg P kg^{-1} soil, and 62.5 mg K kg^{-1} soil, both applied as KH_2PO_4, following the protocol by Habibi and Hajiboland (2013). Following emergence, seedlings were thinned to one per pot. Prior to treatment initiation, all plants were maintained at 95% FC by watering every 6-7 days. Sixteen weeks after sowing, when the seedlings had reached the final vegetative stage before the initiation of flowering, treatments were initiated, encompassing control (90-95% FC and 200-300 µmol m^{-2} s^{-1}), drought (no water and 200-300 µmol m^{-2} s^{-1}), HL (90-95% FC and 800-900 µmol m^{-2} s^{-1}) and salicylic acid (SA) applications. Water treatments (including well-watered and progressive drought-stressed treatments) were conducted at 112 days after sowing, and for the well-watered treatment, field capacity (FC) was maintained within the range of 90-95% throughout the experiment. Plants remained well-watered and acted as a control group. For the drought-stressed treatment (withholding water), FC decreased from 90% to 37% from 1 to 20 DAT. For SA priming treatments, *Z. fabago* seeds were soaked in aerated solutions of salicylic acid for 24 h. SA was dissolved in absolute ethanol, then added dropwise to water (ethanol/water: 1/1000 v/v) (Habibi, 2012).

The concentrations of SA were chosen according to the effect of different SA (10, 50, 100, 200, 300, 400, 500, 600, 700 and 800 ppm) concentrations on *Z. fabago* seed germination as well as on seedling growth in a preliminary study, which showed that 50 ppm SA priming significantly promoted seed germination and seedling growth. The experiment was arranged with four independent pots serving as replicates for each treatment combination. Treatments consisted of high light (HL, 800-900 µmol m^{-2} s^{-1}), drought (withholding water for 20 days), SA seed priming (50 ppm), and their combination. The control treatment was 200-300 µmol m^{-2} s^{-1} without drought and SA seed priming. All plants were maintained in a controlled-environment growth chamber under the following conditions: day/night temperature of 25-35/18–21 °C, a 16/8 h light/dark photoperiod, relative humidity of 35–38%, and a daily photon flux density of 200–300 µmol m^{-2} s^{-1}.

Determination of plant biomass, proline and soluble sugars content

The third fully expanded, mature leaves from the shoot apex were harvested and used for the measurement of the studied parameters. Shoots and roots were carefully removed in order to determine dry weight (DW), and then dried for 48 h at 70 °C. For the latter analysis, samples were kept immediately in liquid N_2 until assay. For proline assay, leaf samples from each group were homogenized in 3% (w/v) sulphosalycylic acid at 4 °C, and the homogenate was centrifuged at 3,000g for 20 min. About 2 ml of extract was taken in a test tube, and to it 2 ml of glacial acetic acid and 2 ml of ninhydrin reagent were added. Absorbance of the red color developed was read at 520 nm against toluene on a UV-visible spectrophotometer. A standard curve was created using proline (Sigma). Soluble sugar concentration was determined according to the method described by Quentin et al. (2015). Briefly, leaf tissues were extracted with 2.5 mL of 80% ethanol in a water bath at 30°C for 2 h. The extracts were then centrifuged at 3,000 × g for 10 min, and the resulting supernatants were reacted with anthrone–sulfuric acid reagent. Absorbance was subsequently measured at 630 nm using a spectrophotometer. Glucose (Sigma) was used to prepare the standard calibration curve.

Determination of total chlorophylls and carotenoids

The concentrations of chlorophyll *a*, chlorophyll *b*, and total carotenoids in leaf tissues were quantified following pigment extraction in chilled acetone. Samples were kept in darkness at 4 °C for 24 h to ensure complete solubilization of the pigments, according to the procedure described by Lichtenthaler and Wellburn (1985).

Chlorophyll *a* fluorescence measurement

Chlorophyll a fluorescence parameters were measured on leaves between 09:00 and 11:00 h using a Pocket-PEA chlorophyll fluorimeter (Plant Efficiency Analyser, Hansatech Instruments Ltd., UK). Prior to measurement, leaves were dark-adapted for a minimum of 30 minutes. The JIP-test analysis was employed to quantify various phenomenological and biophysical parameters related to photosystem II (PSII) and photosystem I (PSI) function. Analysis of the polyphasic chlorophyll fluorescence rise (OJIP curve) provided insights into photosynthetic fluxes

(Strasser et al., 2004; Kumar et al., 2020). The JIP test is based on the rise in polyphasic fast chlorophyll a and is used for investigating the correlation between light-dependent reactions and chlorophyll *a* fluorescence. The O–J part of the fluorescence rise reflects the closure of some of the PSII reaction centers in response to the reduction of QA. The J–I part of the curve corresponds to the reduction of the secondary electron acceptor plastoquinone (PQ), and the I–P part is typically related to the reduction of electron transporters (such as NADP) of the PSI acceptor side. Specific parameters reflecting functional and structural alterations in PSII were calculated following established protocols (Kalaji et al., 2011), as detailed further in the subsequent sections.

F_o: Minimum fluorescence, when all PSII reaction centers (RC) are open.

F_m: Maximum fluorescence, when all PSII reaction centers are closed.

F_v: Variable fluorescence.

F_v/F_m: Maximum quantum yield of PSII.

F_v/F_o: Efficiency of the oxygen-evolving complex on the donor side of the PSII.

F_m/F_o: Maximum fluorescence normalized by minimum fluorescence.

V_j: Relative variable fluorescence at 2 ms (J-step), which refers to the number of closed RCs relative to the total number of RCs.

V_i: Relative variable fluorescence at 30 ms (I-step); that reflects the ability of PSI and its acceptors to oxidize reduced plastoquinone.

N: Turnover number: number of QA reduction events

S_m: Normalized total complementary area above the OJIP transient (reflecting multiple-turnover QA reduction events) or total electron carriers per RC.

ABS/RC: Absorption flux per RC; that reflects the proportion between chlorophyll *a* molecule amounts in fluorescence-emitting antenna complexes and the active reaction centers.

TR_o/RC: Trapped energy flux per RC.

ET_o/RC: Electron transport flux per RC.

DI_o/RC: Dissipated energy flux per RC.

ABS/CS: Absorption flux per cross section (CS); represents the amount of photon energy absorbed by the antenna associated with active and inactive reaction centres of PSII.

TR_o/CS_m: Trapped energy flux per CS.

ET_o/CS_m: Electron transport flux per CS.

DI_o/CS_m: Dissipated energy flux per CS.

RC/C_m: Amount of active PSII RCs per CS.

$ABS/CS_m = \approx F_o$: Absorbed photon flux per excited PSII cross section at time zero.

φP_o: Maximum quantum yield of primary photochemistry*;* that indicates the probability of trapping the energy of absorbed photons by PSII reaction centers.

φE_o: Quantum yield for the reduction of end acceptors of PSI per photon absorbed.

ψE_o: Probability (at time 0) that trapped exciton moves an electron into the electron transport chain beyond QA.

PI_{abs}: The performance index.

Assay of phenylalanine ammonia-lyase (PAL) activity and related metabolites

Phenylalanine ammonia-lyase (PAL) activity was assayed following the method of Zucker (1965). Fresh leaf samples were homogenized in 50 mM sodium phosphate buffer (pH 7.0) containing 2% (w/v) polyvinylpolypyrrolidone (PVPP), 2 mM EDTA, 18 mM β-mercaptoethanol, and 0.1% (v/v) Triton X-100. PAL activity was determined by monitoring the formation of cinnamic acid spectrophotometrically at 290 nm. One unit (U) of PAL activity was defined as the amount of enzyme required to produce 1 nmol of cinnamic acid per hour. Total phenolic content was determined according to the method of Velioglu et al. (1998), using gallic acid for preparation of the standard curve. The results were expressed as mg gallic acid equivalents (GAE) per gram of fresh weight (FW). Total flavonoid content was quantified using quercetin as the standard and expressed as mg quercetin equivalents (QE) per 100 g extract.

Assay of antioxidative enzymes and related metabolites

Activity of enzymes was assayed in leaves harvested in the middle of the day. The activities of SOD (EC 1.15.1.1), CAT (EC 1.11.1.6) and APX (EC 1.11.1.11) were measured according to methods described elsewhere (Habibi, 2020). SOD activity was evaluated using the nitro blue tetrazolium (NBT) photoreduction technique as reported by Giannopolitis and Ries (1977), using the following buffer: 0.1 mM EDTA, 50 mM Na_2CO_3 pH 10.2, 13 mM methionine, 63 µM nitroblue tetrazolium chloride (NBT), 13 µM riboflavin. CAT activity was determined following a protocol adapted from Simon et al. (1974) using H_2O_2 as substrate. CAT activity is inferred from the decrease in absorbance at 240 nm, indicative of hydrogen peroxide (H_2O_2) content. The rate of lipid peroxidation was evaluated from the levels of MDA formed in a reaction medium containing thiobarbituric acid (Sigma) at 532 nm. MDA levels were monitored using a 1,1,3,3-tetraethoxypropane (Sigma) standard curve. H_2O_2 content analyses were evaluated according to the method of Velikova et al. (2000) based on the standard curve

of H_2O_2 (Sigma).

Statistical analysis

The experiment was arranged in a completely randomized design (CRD) with four independent replications. Analysis of variance (ANOVA) was performed to compare the data means, and the Tukey test ($P < 0.05$) was used to test for significant differences between means. The achieved data on Chl fluorescence were assessed using the PEA Plus ver. 1.10 software. Correlation analysis using principal component analysis (PCA) was performed to determine the relationship between parameters, and the results were visualised with a biplot graph settled from PC1 and PC2.

Results

Impact of salicylic acid on growth parameters under simultaneous drought and HL stress

Analysis of growth responses revealed that drought, HL, and especially their combined application imposed substantial negative effects on growth parameters (Table 1). We detected that the shoot fresh and dry weight of *Z. fabago* plants were decreased by exposure to drought, HL, and their combination—the seed priming of SA enhanced shoot fresh and dry weight in *Z. fabago* plants under drought-alone conditions. However, plant growth was not significantly influenced by SA application under HL alone and the drought+HL combination. Drought or HL alone and their combination resulted in an increase in the proline content compared to the control. Drought or HL alone and their combination significantly increased soluble sugar contents compared to control plants; however, soluble sugar contents were not significantly influenced by SA application under both normal and stressed conditions.

Table 1 Effect of SA application on fresh and dry weight (g plant^{-1}), proline (µmol g^{-1} FW) and soluble sugars (mg g^{-1} FW) contents in *Z. fabago* plants grown under drought or HL alone and their combination. Data of each row within each parameter indicated by the same letter are not significantly different (P<0.05, Tukey test). Values are the mean ± SD (n=4).

Treatment	Shoot FW	Shoot DW	Proline	Soluble sugars
Control	5.07±0.45 ^{a}	1.10±0.16 ^{ab}	10.2±2.10 ^{c}	10.9±1.25 ^{bc}
Drought	3.08±0.36 ^{cd}	0.50±0.20 ^{de}	27.0±2.90 ^{b}	16.3±1.53 ^{a}
HL	3.86±0.41 ^{bc}	0.71±0.11 ^{cd}	24.3±3.39 ^{b}	14.8±1.75 ^{a}
Drought+HL	2.10±0.50 ^{e}	0.25±0.13 ^{e}	27.1±2.00 ^{b}	15.6±1.08 ^{a}
SA	5.19±0.32 ^{a}	1.20±0.17 ^{a}	12.2±1.55 ^{c}	9.52±1.81 ^{c}
SA+Drought	4.52±0.29 ^{ab}	0.85±0.10 ^{bc}	38.3±3.05 ^{a}	14.7±1.60 ^{a}
SA+HL	3.90±0.32 ^{bc}	0.70±0.09 ^{cd}	23.0±2.10 ^{b}	15.0±1.17 ^{a}
SA+Drought+HL	2.82±0.24 ^{de}	0.41±0.08 ^{de}	24.1±3.20 ^{b}	13.74±1.01 ^{ab}

Effects of SA priming on leaf pigments and chlorophyll *a* fluorescence under drought, HL and combined stress

After 20 days of water stress, *Z. fabago* plants showed a significant decrease in both chlorophyll *a* and *b* contents; plants exposed to only HL stress could maintain chlorophyll contents at relatively high levels (Fig. 1). Exposure to drought and HL combination caused a marked reduction in chlorophyll contents. Plants treated with drought or HL alone and their combination exhibited levels of carotenoids similar to those of the controls. Furthermore, we found that SA application increased the contents of carotenoids when compared with non-SA-pretreated plants under drought and high light.

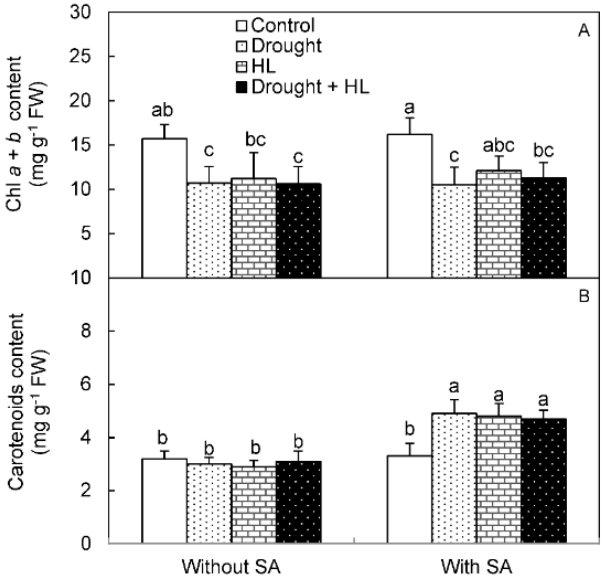


Fig. 1 Effect of SA application on Chl *a*, *b* and carotenoid contents in *Z. fabago* plants grown under drought or HL alone and their combination. Bars indicated with the same letter are not significantly different (P<0.05, Tukey test). Values are the mean ± SD (n = 4).

Although the maximum quantum yield of PSII (F_v/F_m) remained unchanged under drought or HL when applied individually, a pronounced decline was observed after 20 days of exposure to the combined stress (Fig. 2). SA priming did not alleviate this reduction. Both individual (drought or HL) and combined stress treatments markedly decreased the oxygen-evolving complex efficiency of PSII (F_v/F_o) and the overall photosynthetic performance index (PI_{abs}). However, SA application enhanced only the F_v/F_o parameter in plants subjected to water deficit, while no significant improvement was observed for the other fluorescence parameters.

Using fast chlorophyll *a* fluorescence (OJIP) kinetics, the polyphasic analysis showed that drought or HL alone and their combination caused increases in the O-J phases compared to control plants; however, the I-P phase displayed a marked decrease in fluorescence intensity relative to control plants under HL alone and drought+HL combination (Fig.3). In contrast, SA-treated plants exposed to drought or HL alone and their combination exhibited a slight decrease in the O-J phase of the fluorescence rise.

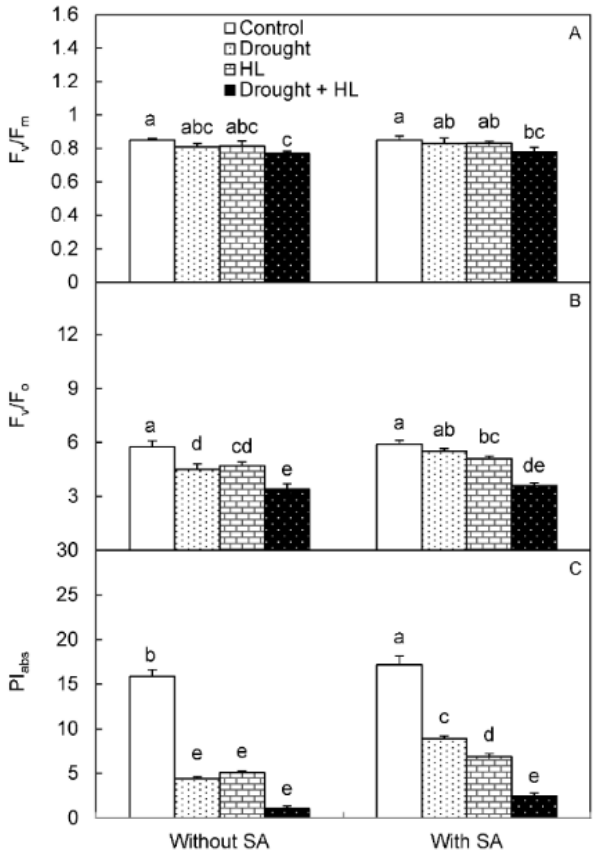


Fig. 2 Effect of SA application on the maximum quantum yield (F_v/F_m), oxygen-evolving complex efficiency of PSII (F_v/F_o) and the performance index of photosystems (PI_{abs}) in *Z. fabago* plants grown under drought or HL alone and their combination. Bars indicated with the same letter are not significantly different ($P<0.05$, Tukey test). Values are the mean ± SD (n = 4).

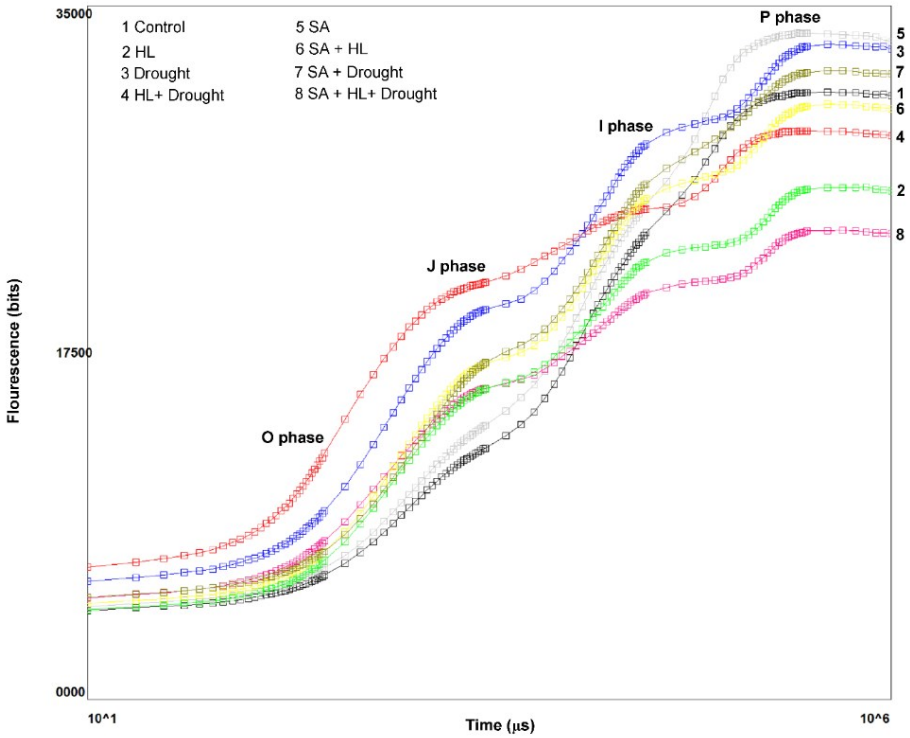


Fig. 3 Effect of SA application on the fast chlorophyll *a* fluorescence transient kinetics of *Z. fabago* plants grown under drought or HL alone and their combination.

We observed a slight increase in the values of V_j (relative variable fluorescence at J step) in leaves of *Z. fabago* plants under combined stress (Table 2). In addition, exposure to drought or HL alone and their combination caused a significant increase in the specific energy fluxes such as absorption flux per reaction center (ABS/RC) and trapped energy flux per reaction center (TR_o/RC) compared to the control (Table 2).

Table 2 Various technical fluorescence parameters of *Z. fabago* plants affected by SA under drought or HL alone and their combination. Data of each row within each parameter indicated by the same letter are not significantly different (P<0.05, Tukey test). Values are the mean ± SD (n=4).

Treatment	F_o	F_m	F_v	V_j	V_i	S_m	N	phi(P_o)	psi(E_o)	phi(E_o)
Control	4544±180 c	30677±985^b	26133±521^b	0.27±0.020^d	0.72±0.02 b	27.8±1.36 a	22.1±2.0^b c	0.85±0.01^a	0.72±0.05 a	0.61±0.1^a
Drought	5953±156 b	32987±1000^a	27034±563^b	0.47±0.022^b	0.81±0.03 a	28.6±2.3^a	26.5±1.4^a bc	0.82±0.02^a bc	0.52±0.06 b	0.43±0.21 ab
HL	4547±178 c	25849±952^c	21302±356^c	0.48±0.030^b	0.82±0.04 a	30.8±2.4^a	25±1.8^{abc}	0.82±0.03^a bc	0.51±0.04 b	0.42±0.11 ab
Drought+HL	6460±158 a	28703±900^b	22243±456^c	0.63±0.034^a	0.82±0.03 a	19.2±2.5^b	26.9±3.2^a b	0.77±0.01^c	0.36±0.05 c	0.28±0.13 b
SA	4778±174 c	33597±789^a	28819±412^a	0.27±0.025^d	0.7±0.02^b	28±1.96^a	22±2.4^{bc}	0.85±0.02^a	0.62±0.07 a	0.62±0.14 a
SA+Drought	5227±120 b	31743±852^a	26516±387^b	0.39±0.026^c	0.78±0.03 ab	29.6±3.10 a	21.4±2.2^c	0.83±0.03^a b	0.5±0.03^b	0.5±0.1^{ab}
SA+HL	4853±192 b	30029±963^b	25176±654^c	0.44±0.036^c	0.81±0.05 a	30±2.41^a	24±2.7^{ab}	0.83±0.01^a b	0.55±0.05 b	0.46±0.14 ab
SA+Drought+HL	5119±145 b	23683±911^d	18564±600^d	0.53±0.021^b	0.83±0.04 a	29±2.70^a	28.4±2.8^a	0.78±0.02^b c	0.46±0.04 bc	0.36±0.12 ab

Treatment	ABS/RC	TR_o/RC	ET_o/RC	RE_o/RC	ABS/CS_m	DI_o/CS_m	TR_o/CS_m	ET_o/CS_m	RE_o/CS_m
Control	0.93±0.12 b	0.79±0.11^b	0.57±0.02^a	0.21±0.05^a	30±2.3^{abc}	4544±145 d	26±1.8^a	18.8±2.3^{bc}	7103±185 b
Drought	1.12±0.15 b	0.92±0.13^b	0.48±0.03^b c	0.16±0.06^a	32±1.6^{ab}	5953±172 b	27±1.7^a	14±1.5^{bc}	4955±200 d
HL	0.98±0.14 b	0.8±0.14^b	0.41±0.04^c	0.14±0.04^a	26±2.5^b	4547±156 d	21±1.6^{bc}	11±1.0^c	3768±211 e
Drought+HL	1.8±0.16^a	1.4±0.12^a	0.51±0.02^a b	0.25±0.05^a	29±3.2^{abc}	6460±187 a	22±1.5^{bc}	80±5.6^a	3958±256 e
SA	0.9±0.18^b	0.77±0.15^b	0.56±0.03^a	0.23±0.03^a	33±1.5^a	4778±195 d	28±1.3^a	21±2.3^b	8584±274 a
SA+Drought	0.86±0.22 b	0.72±0.11^b	0.43±0.05^c	0.15±0.07^a	32±2.6^{ab}	5227±142 c	26±2.0^a	16±2.0^{bc}	5709±300 c
SA+HL	0.94±0.24 b	0.79±0.10^b	0.44±0.02^b c	0.15±0.06^a	30±3.7^{ab}	4853±108 c	25±1.9^{ab}	14±1.6^{bc}	4751±285 d
SA+Drought+HL	1.25±0.28 b	0.98±0.16^b	0.45±0.03^b c	0.16±0.03^a	24±3.0^c	5119±174 c	18.5±1.8^c	86±7.0^a	3140±264^f

Conversely, significant reductions were observed in phenomenological energy fluxes: mean absorption flux per cross-section (ABS/CS_m), trapped energy flux per cross-section (TR_o/CS_m), electron transport flux per cross-section (ET_o/CS_m), and RE_o/CS_m under drought or HL alone and their combination (Table 2). However, the dissipated energy flux per cross-section (DI_o/CS_m) exhibited a similar pattern to the specific energy flux parameters under stress conditions. In addition, φE_o (quantum yield for electron transport) and ψE_o (efficiency/probability that an electron moves further than QA) were dramatically influenced by combined stress (Table 2). However, when SA was applied, these stress-induced changes were significantly mitigated, with reductions in F_o, DI_o/CS_m, ABS/RC and TR_o/RC, compared to plants under stress alone. Thus, SA application under combined stress effectively modulated these parameters, bringing them closer to control values. Other parameters, such as N, Vi, ABS/CS_m, TR_o/CS_m, ET_o/CS_m, and RE_o/CS_m, were not significantly affected in either stress- or stress + SA-treated plants. Figure 4 exhibited principal component analysis within the chlorophyll *a* fluorescence-related attributes, showing that PC1 and PC2 were responsible for 61.53% and 21.14% of the total variance, respectively. In our study, the score plot clearly separated drought or HL alone and their combination treatments from control, SA, SA+Drought and SA+HL treatments along the first component, indicating that SA significantly affected the measured photochemical traits under drought or HL alone. The PC results clearly separated the different control, SA, SA+Drought and SA+HL treatments into one cluster, which was associated with parameters indicative of quantum yields and efficiencies (φP_o, ψE_o and φE_o), phenomenological energy flux per cross section (ABS/CS_m, TR_o/CS_m and RE_o/CS_m), F_m, F_v, F_v/F_m, F_v/F_o, PI_{abs}, and Chl *a*+*b* content. The second cluster belongs to Drought,

HL, Drought+HL, and Drought+HL+SA treatments and was characterized by an increase in markers of specific energy fluxes per reaction center parameters (ABS/RC and TR_o/RC), F_o, V_i, V_j, and N. Within the chlorophyll *a* fluorescence-related attributes, specific energy fluxes per reaction center parameters were negatively correlated with F_v/F_m and PI_{abs} parameters. Pearson correlation heat map among chlorophyll *a* fluorescence-related attributes is shown in the supplementary file (Supplementary Fig. 4).

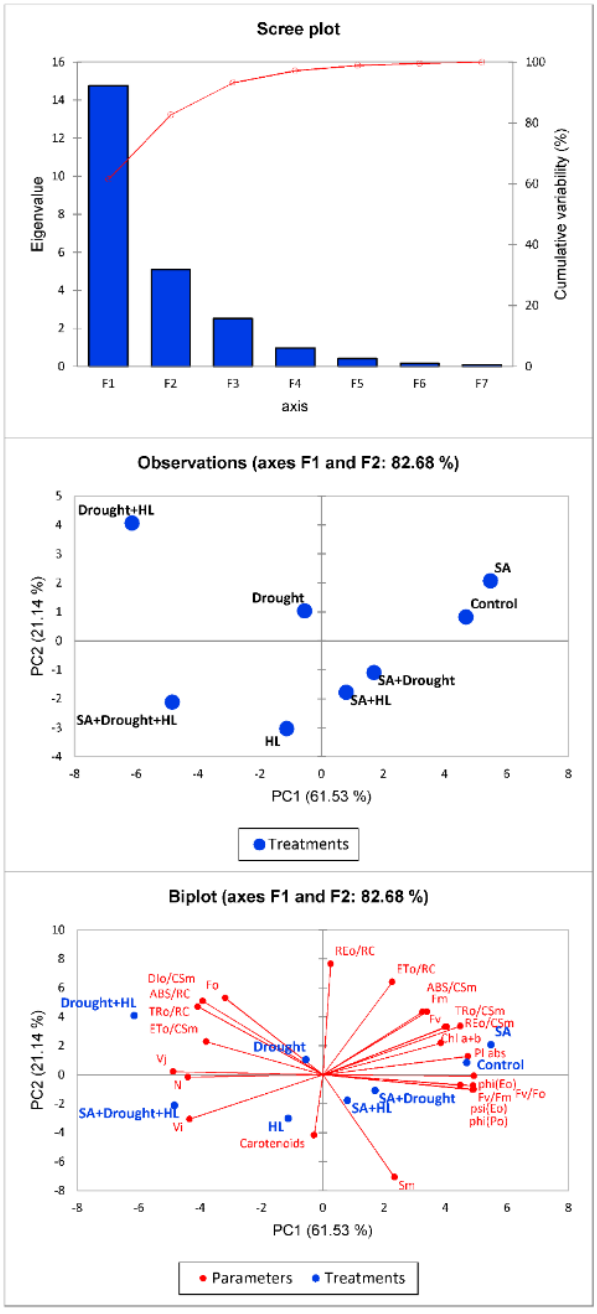
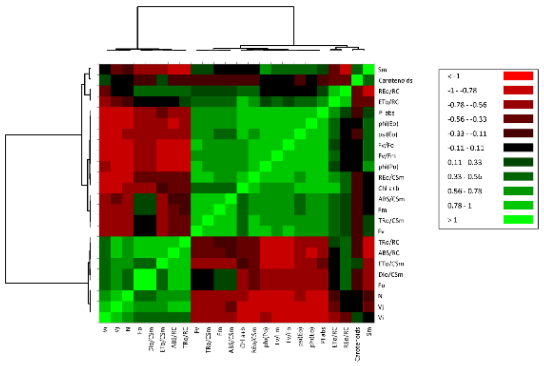


Fig. 4 PCA biplot showing the correlations between chlorophyll *a* fluorescence-related attributes of *Z. fabago* plants affected by SA under drought or HL alone and their combination. Control, SA, HL, drought, HL+drought, SA+HL, SA+drought, and SA+HL+drought indicated treatments. Chl *a*: *chlorophyll a* and Chl *b: chlorophyll b*.



Supplementary Fig. 4. Pearson correlation heatmap among chlorophyll *a* fluorescence-related attributes in *Z. fabago* plants.

Regulation of the enzymatic antioxidant system by SA priming in stressed *Z. fabago* plants

Under non-stress conditions, phenolic and flavonoid contents were not influenced by exposure to SA priming (Fig. 5). Phenolic and flavonoid contents were significantly enhanced by drought or HL alone, which was associated with a marked increase in PAL activity. In addition, under drought or HL alone, the content of phenolic and flavonoids was further increased by SA priming. In the present study, the contents of phenolic compounds and flavonoids as well as the activity of PAL were not significantly affected by stress combination under both -SA or +SA treatments.

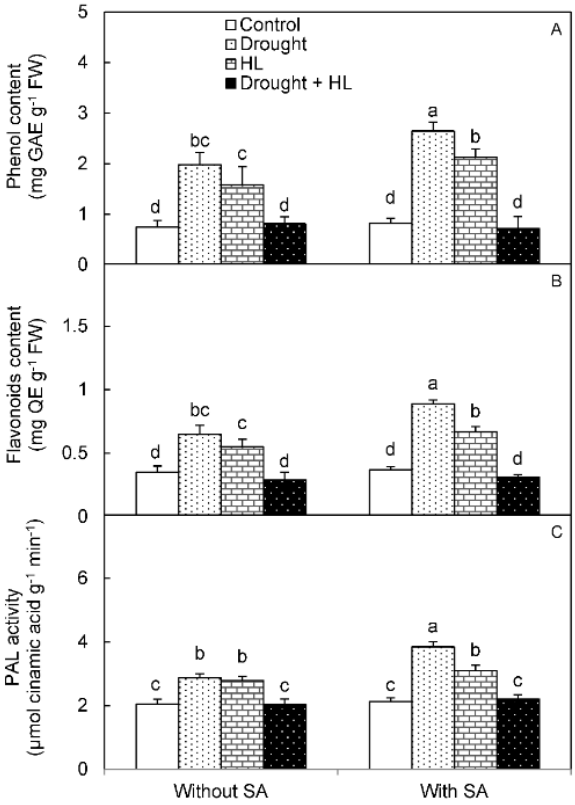


Fig. 5 Effect of SA application on the total phenol and flavonoid contents, and the activity of phenylalanine ammonia-lyase (PAL) in *Z. fabago* plants grown under drought or HL alone and their combination. Bars indicated with the same letter are not significantly different ($P<0.05$, Tukey test). Values are the mean ± SD (n = 4).

Significant changes in the activities of key defense enzymes, including SOD and CAT, were detected under drought or HL alone and their combination (Table 3). A significant increase in SOD activity was only detected under conditions of drought stress. Plants treated with drought alone and the drought+SA combination showed a significant increase in CAT activity compared to the control group (Table 3). In contrast, plants treated with HL and HL+Drought exhibited lower CAT activity compared to the control group. Under drought or HL alone and their combination, H_2O_2 and MDA contents were increased compared to the control; however, the increases in MDA content in the leaves of drought-stressed *Z. fabago* plants were markedly inhibited by SA priming. In contrast, the addition of SA resulted in increased levels of H_2O_2 as well as enhanced levels of MDA under HL alone and stress combination conditions.

Table 3. Effect of SA application on the activity of superoxide dismutase (SOD, U mg^{-1} protein), catalase (CAT, µmol H_2O_2 mg^{-1} protein min^{-1}), and the content of MDA (nmol g^{-1} DW) and H_2O_2 (µmol g^{-1} DW) in *Z. fabago* plants grown under drought or HL alone and their combination. Data of each row within each parameter indicated by the same letter are not significantly different ($P<0.05$, Tukey test). Values are the mean ± SD (n=4).

Treatment	SOD	CAT	H_2O_2	MDA
Control	2.20±0.32 ^{b}	5.12±0.32 ^{bc}	10.9±1.5 ^{d}	22.3±2.1 ^{c}
Drought	3.23±0.25 ^{a}	12.5±1.02 ^{a}	21.3±2.7 ^{c}	38.4±3.7 ^{b}
HL	2.02±0.11 ^{b}	2.35±0.84 ^{d}	22.6±3.0 ^{bc}	41.4±3.5 ^{b}
Drought+HL	1.81±0.23 ^{b}	3.34±0.71 ^{cd}	29.7±3.6 ^{a}	75.6±6.9 ^{a}
SA	2.17±0.12 ^{b}	6.12±0.34 ^{b}	11.0±1.2 ^{d}	20.3±1.5 ^{c}
SA+Drought	3.83±0.17 ^{a}	18.2±1.36 ^{a}	18.6±1.7 ^{c}	23.2±1.2 ^{c}
SA+HL	2.23±0.16 ^{b}	3.77±0.63 ^{cd}	21.7±2.3 ^{bc}	39.8±3.1 ^{b}
SA+Drought+HL	2.12±0.19 ^{b}	3.81±0.21 ^{cd}	27.6±2.8 ^{ab}	47.0±4.6 ^{b}

The PCA and correlation analyses within the growth and ionic parameters showed a clear distinction between PC1 and PC2, which accounted for a combined 92.06% of the total variability (Fig. 6). The PCA results indicated that PCA loading and score plot indicated that PC1 and PC2 were responsible for 48.21% and 43.85% of the total variance, respectively. The variables can be broadly categorized into three clusters. The control and SA treatments formed a tight cluster positioned along the positive axis of PC2, which was associated with parameters indicative of plant biomass (including shoot FW and shoot DW). The correlation analysis demonstrated that shoot biomass was significantly and negatively correlated with H_2O_2 content. The second cluster, which was proximate to the Drought, SA+Drought and SA+HL treatments, was characterized by markers of several antioxidant indicators, including increased levels of phenol, flavonoids, proline and the activities of PAL, SOD and CAT. In contrast, HL-, Drought+HL- and SA+Drought+HL-treated plants were distinctly separated from SA+Drought-treated plants due to significant

accumulation of MDA. Pearson correlation heat map among growth and antioxidant indicators has been included in the supplementary file (Supplementary Fig. 6).

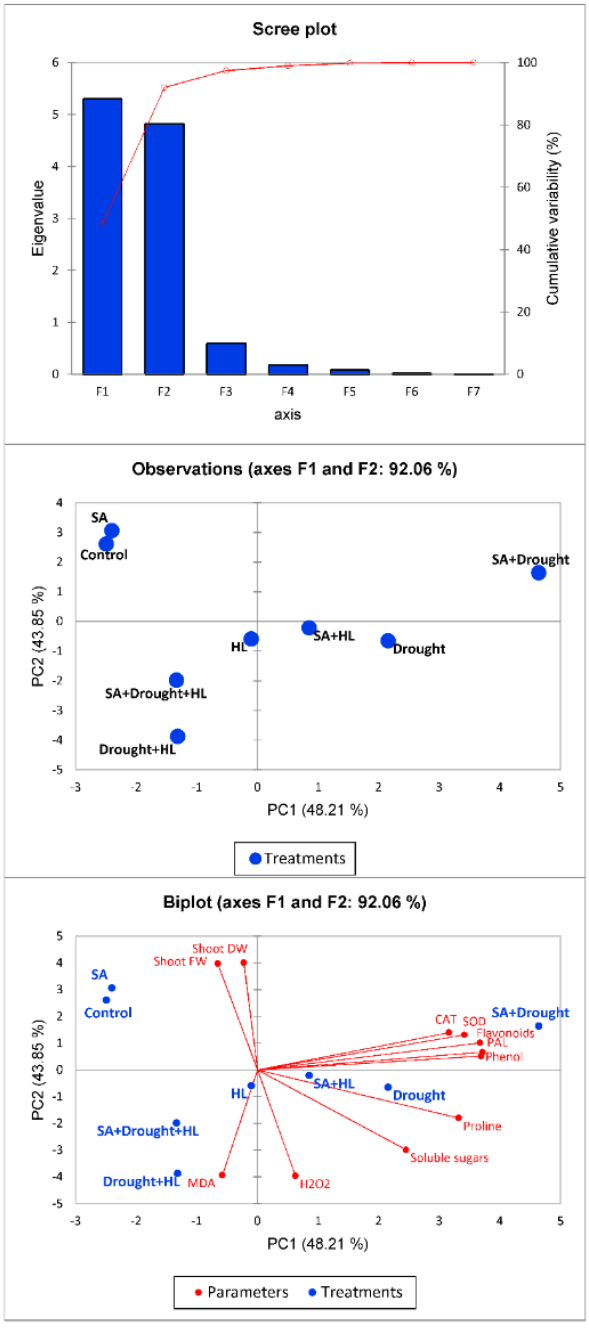
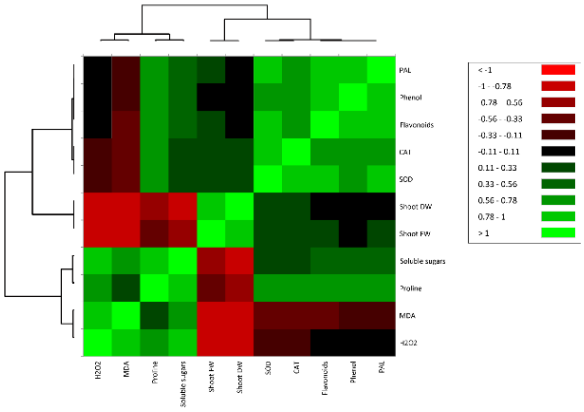


Fig. 6 PCA biplot showing the correlations between growth, phenolic and antioxidative indicators of *Z. fabago* plants affected by SA under drought or HL alone and their combination. Control, SA, HL, drought, HL+drought, SA+HL, SA+drought and SA+HL+drought indicated treatments. CAT *Catalase*, SOD *Superoxide dismutase*, H_2O_2 *Hydrogen peroxide*, MDA *Malondialdehyde*.



Supplementary Fig. 6. Pearson correlation heatmap among growth, phenolic and antioxidative indicators in *Z. fabago* plants.

Discussion

Seed priming of salicylic acid increased plant biomass under drought stress

While *Z. fabago* plants have been widely recognized as tolerant to mild water stress (Reza Yousefi et al., 2020), we observed that severe water stress (for 20 days) caused significant biomass reduction. Drought stress leads to an overproduction of reactive oxygen species (ROS), which negatively affects crucial processes like photosynthesis, respiration, nutrient absorption, and osmotic balance (Lei et al., 2025). This ultimately restricts plant growth, its distribution, and overall yield (Khan et al., 2019). Our study confirmed that water scarcity significantly hinders plant growth, evidenced by reduced shoot fresh and dry biomass. Comparable decreases in biomass and shoot size under drought conditions have been documented in a range of crops, including rice (El-Beltagi et al., 2025), pea (Anwar et al., 2025), and tomato (Kurniawan et al., 2025).

Additionally, similar growth reductions under water stress have been documented across various plants, such as rice (Sohag et al., 2020; Singh et al., 2025). While the effects of individual drought and HL stresses on growth parameters have been explored, this study presents the first evidence of their combined impact. The data strongly suggested that growth reductions were considerably more severe when drought and HL stress occur simultaneously. In this study, SA priming helped counteract the harmful effects of drought, which led to noticeable improvements in growth traits, including increased dry biomass. The current study's outcomes are consistent with earlier research on pea (Anwar et al., 2025) and tomato (Kurniawan et al., 2025) plants, where SA application notably improved plant growth and

yield under water stress conditions. Interestingly, while drought or HL alone and their combination resulted in a significant rise in Z. fabago proline levels, adding SA externally further enhanced these endogenous proline amounts, especially under water stress alone conditions. This aligns with findings from El-Beltagi et al. (2025) in rice, Naservafaei et al. (2025) in *Lallemantia Iberica,* and Dakheel et al. (2025) in strawberry, who observed that SA application boosted proline levels in the leaves of seedlings when exposed to water stress. Previous research suggests that applying water stress can effectively hinder starch degradation and increase soluble carbohydrate contents (Naservafaei et al., 2025). Consistent with this, our data showed that drought or HL alone and their combination caused notably higher soluble carbohydrate contents compared with the control; however, SA was not effective in improving soluble carbohydrate contents in this study. Given that SA priming under HL alone and combined stress did not fully counteract the shoot dry weight decrease, we conclude that HL alone and combined stress had a different effect on growth compared to drought applied alone. These results indicated that SA plays a decisive role in enhancing shoot biomass in *Z. fabago* plants subjected to individual drought stress. However, SA was not effective in improving shoot dry weight under the HL alone and combined HL+Drought stress. Results revealed that seed priming alone was not sufficient to provide strong protection at the later vegetative stage, particularly under the more severe combined stress treatment.

SA mitigated the adverse effects of water and HL stress on PSII function

The organelles responsible for photosynthesis, chloroplasts, exhibit significant vulnerability to diverse environmental stressors (Polesi et al., 2019). It is well-documented that the synergistic or individual effects of water scarcity and HL intensity compromise chloroplast ultrastructural integrity and diminish total chlorophyll content, subsequently impairing photosynthetic performance (Wang et al., 2014). Our findings revealed a substantial decline in Chl *a* and Chl *b* levels in *Z. fabago* under drought conditions, suggesting that water deficit not only inhibits pigment biosynthesis but also accelerates their catabolism. Nevertheless, evidence indicates that the exogenous application of growth regulators can mitigate the degradation of chlorophylls and carotenoids, thereby enhancing plant resilience against adverse environments (Sardar et al., 2023). Consistent with this, our data showed that SA treatment raised carotenoid levels in HL- and drought-affected leaves. Carotenoids act as essential photoprotective agents and developmental signaling molecules when plants encounter a variety of biotic and abiotic stressors (Habibi, 2020). Therefore, their increased accumulation serves as an indicator that defense-related metabolic pathways have been activated to strengthen stress tolerance (Hafeez et al., 2024).

In our study, the enhanced levels of carotenoids likely played a key role in maintaining higher photochemical activity and providing superior photoprotection (Zhang et al., 2025). To assess PSII performance under the combined effects of HL, drought, and SA treatment, we utilized OJIP fluorescence transients, which provide insights into light-harvesting capacity and electron transport efficiency within PSII reaction centers. Our data indicated that drought, HL, and their combination accelerated the rise in fluorescence during the O-J phases. This suggested a bottleneck in electron transport beyond this stage, leading to restricted Q_A^- re-oxidation and an excessive accumulation of Q_A^- (Kalaji et al., 2016). The light-dependent O-J phase primarily reflects the antenna size and the functional connectivity between PSII reaction centers (Schansker et al., 2006).

Furthermore, drought and combined stress led to an increase in minimal fluorescence (F_o). Indeed, higher F_o values typically signify partial damage to PSII centers, which hampers electron transfer from QA to QB and reduces overall trapping efficiency. Because the D1 protein is a fundamental component of PSII, any elevation in F_o reflects its functional impairment. The maximum quantum yield of primary photochemistry (F_v/F_m) is a widely accepted metric for evaluating photosynthetic vitality and drought-induced physiological stress (Hasanuzzaman et al., 2017; Abdullaev et al., 2024). In this study, the lower F_v/F_m values recorded under combined stress highlighted a decline in photosynthetic efficiency, making the plants more susceptible to oxidative damage and long-term injury (Mohagheghian et al., 2025). Similarly, the reduction in the F_v/F_o ratio in this study confirmed that the interaction of water and HL stress significantly disrupted the photochemical electron transport system. The F_v/F_o ratio specifically describes the performance of the water-splitting complex on the donor side (Schreiber et al., 1995). This decline could result from the suppression of osmotic water uptake under stress (Fricke & Peters, 2002), as well as inhibited electron transport and phosphorylation pathways that ultimately decrease ATP production (Pereira et al., 2000).

Additionally, the affected F_v/F_o ratio may be linked to changes in unquenchable fluorescence

(F_o), which altered the energy transfer from the antenna complex to the reaction centers (DeEll et al., 2010). The ABS/RC ratio represents the total photons captured by chlorophyll molecules relative to the number of active reaction centers (RCs) (Rapacz et al., 2015). This metric is inherently influenced by the balance between active and inactive RCs; specifically, an increase in active centers leads to a proportional decline in the ABS/RC ratio. Furthermore, TRo/RC defines the maximum rate of exciton capture by the RC, which results in QA reduction. In the current study, the elevation of this ratio suggested that the entire QA pool has been reduced (Kalaji et al., 2014).

Correlation analyses of chlorophyll *a* fluorescence attributes revealed that the improved photochemical efficiency observed in the SA+Drought treatment (evidenced by higher F_v/F_o and PI_{abs}) was negatively correlated with specific energy flux parameters, such as ABS/RC and ET_o/RC. Conversely, positive correlations were found with phenomenological energy fluxes per cross-section (ABS/CS_m, TR_o/CS_m, and RE_o/CS_m), underscoring their critical role in sustaining photosystem stability. Under drought, HL, and their combination, the observed reduction in ET_o/RC indicated a decline in the re-oxidation of reduced QA via electron transport within active RCs. Since this parameter primarily reflects the activity of functional centers, the decrease suggested a shift in the availability of active RCs. The performance index (PI_{abs}) serves as a comprehensive indicator of PSII's capacity to conserve absorbed light energy and facilitate electron flow through the photosynthetic chain (Strasser et al., 2004).

In this research, the significant decline in PI_{abs} under both stress conditions signified a reduction in functional PSII reaction centers and a compromised electron transport capacity (Kalaji et al., 2011). However, SA priming markedly improved both F_v/F_o and PI_{abs}, demonstrating the potential of salicylic acid to mitigate stress-induced photosynthetic suppression. As noted by Yan et al. (2024), PI_{abs} provides an integrative assessment of photosynthetic health by combining key metrics such as ABS/RC, φP_o, and φE_o. Exposure to drought and HL resulted in lower φP_o and φE_o values alongside an increased ABS/RC, suggesting an inefficient energy transfer from antenna pigments to RCs and a blockage of electron movement within PSII. Such inhibition often triggers photooxidative damage to thylakoid proteins, forcing plants to enhance energy dissipation as a photoprotective strategy (Tränkner et al., 2018). In line with this, DI_o/CS_m values rose significantly under stress, consistent with findings in cotton and oats (Li et al., 2022; Kappachery et al., 2024).

In contrast, SA supplementation effectively lowered ABS/RC while enhancing ψE_o, reflecting a more streamlined energy relay from light-harvesting complexes to the RCs (Li et al., 2022). Additionally, the combined stress significantly reduced S_m levels compared to control plants, indicating impaired electron transport through QA reduction and diminished energy fluxes (Akhter et al., 2021). Conversely, SA priming notably enhanced this parameter, suggesting its role in stabilizing electron transfer and restoring the balance of fluorescence transients (Li et al., 2022). Recent studies by Chen et al. (2020) have further demonstrated that SA can alleviate photoinhibition and strengthen photoprotection by dissipating excess energy, promoting the phosphorylation of PSII proteins, and preventing the disassembly of PSII super-complexes under HL stress. Moreover, according to Naservafaei et al. (2025) and Anwar et al. (2025), SA-treated plants not only maintained superior PSII photochemical activity under stress but also exhibited a more rapid recovery from photoinhibition once the stress was alleviated. Consistent with the above reports, SA increased carotenoid contents and optimized energy fluxes, which collectively fortified photosynthetic resilience and diminished the harmful effects of drought and HL stress on *Z. fabago* leaves. Results indicated that F_v/F_o can be more sensitive to drought and HL alone stress effects than F_v/F_m. This research highlighted the potential of SA priming as an effective tool for improving crop resilience to drought and HL alone stress; however, SA could not alleviate the detrimental effects of combined (Drought+HL) stress on photochemical energy fluxes.

SA priming was an alleviant for the oxidative stress effects caused by drought stress

It has been established that the accumulation of non-enzymatic antioxidants, including phenolic and flavonoid compounds, is intimately linked to the up-regulation of antioxidant enzymes such as SOD, CAT, and APX to mitigate ROS overproduction (Laxa et al., 2019; Hasanuzzaman et al., 2020; El-Beltagi et al., 2025). Consistently, our study demonstrated that phenolic accumulation in SA-primed plants under drought stress strongly correlated with elevated PAL, CAT, and SOD activities, suggesting that phenolics and flavonoids serve as primary agents in ROS scavenging. Such enhancements in total leaf phenols through SA application have also been reported in drought-stressed rice (El-Beltagi et al., 2025). Beyond non-enzymatic components, plants utilize a

sophisticated enzymatic network to neutralize excess ROS generated under adverse conditions (Mahawar & Shekhawat, 2019; Mahawar et al., 2024). Within this detoxifying system, SOD acts as the first line of defense by disproportionating superoxide radicals into H_2O_2, which is subsequently converted into water and oxygen by CAT (Khalvandi et al., 2021). Our results indicated that *Z. fabago* plants subjected to drought alone exhibited increased SOD and CAT activities, a response consistent with observations in rice (Koc et al., 2024) and wheat (Khalvandi et al., 2021).

Furthermore, SA priming further amplified the activities of these enzymes, aligning with findings in SA-treated tomato (Kaya et al., 2023) and winter wheat (Khalvandi et al., 2021). Notably, SA treatment led to a reduction in MDA concentrations under drought, implying that SA helps limit ROS buildup and safeguards membrane integrity from oxidative injury. Similar reductions in lipid peroxidation following SA application have been documented in water-stressed rice (Sohag et al., 2020). Interestingly, the simultaneous increase in H_2O_2 and antioxidant enzyme activity in the SA+Drought treatment suggests that H_2O_2 may function as a signaling molecule that triggers antioxidant responses, thereby preventing the formation of more hazardous ROS species like singlet oxygen and hydroxyl radicals (Wiciarz et al., 2018). Indeed, ROS (particularly H_2O_2) play a dual role in plant physiology, acting as metabolic signals at low concentrations but becoming harmful oxidants at high levels (Mardani Korrani et al., 2022; Samanta et al., 2024). However, the intricate interplay between SA and H_2O_2 in mitigating drought stress warrants further investigation.

In contrast, CAT activity was suppressed under HL and combined stress conditions, leading to a concurrent rise in H_2O_2 and MDA during Drought+HL stress. This indicated excessive ROS accumulation and severe oxidative damage to cellular structures (Rhaman et al., 2024; Liu et al., 2024). In this study, elevated ROS levels were associated with a decline in F_v/F_m, suggesting that the reduction in photosynthetic efficiency in *Z. fabago* is closely tied to oxidative disturbances, as previously observed by Azzabi et al. (2012). While SA successfully bolstered antioxidant capacity and PSII stability under individual drought stress, its protective role was markedly limited or absent under combined stress. This was evidenced by the suppressed CAT activity and elevated H_2O_2 and MDA levels, which coincided with reduced F_v/F_m under SA+Drought+HL conditions. The biplot of PCA revealed many significant factors, including enhanced activities of antioxidative enzymes and PAL as well as increased levels of phenol and flavonoid contents, as potent explanatory variables that were responsible for the induction of protective responses to cope with water stress in the SA+Drought treatment.

Conclusion

This study demonstrated that the efficacy of SA priming in *Z. fabago* was highly stress-specific. Although our findings highlighted the potential of SA priming, the duration of its efficacy requires further investigation. Future studies comparing seed priming with alternative strategies, such as foliar or repeated SA application, are essential to establish the long-term stability and practical viability of these treatments. Our findings indicated that SA serves as a decisive biostimulant under individual drought stress, where it significantly bolsters shoot biomass, optimizes photosynthetic energy fluxes, and enhances antioxidant defenses (e.g., elevated PAL activity, phenolic/flavonoid accumulation, and SOD/CAT activity). These physiological adjustments, as confirmed by PCA, effectively fortify the plant's resilience against water deficit. Conversely, SA priming showed limited protective capacity under HL stress and exhibited negligible efficacy under combined drought and HL conditions. Under the latter, the mitigation of photochemical damage, evidenced by reduced F_v/F_m and compromised electron transport, was insufficient, leading to significant oxidative stress (high H_2O_2 and MDA) and attenuated CAT activity. Consequently, while SA priming was a valuable strategy for enhancing drought tolerance, its ability to counteract growth inhibition and maintain photosynthetic stability is largely constrained by the complexity of multifactorial stress scenarios. Future research should focus on optimizing SA application protocols or exploring synergistic treatments to manage combined environmental stressors in xerophytic species better.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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