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RESEARCH

Evaluation of the Ameliorative Effects of Exogenous Herbal Saponin Application On Wheat (Triticum aestivum L.) Genotypes Under Drought Stress

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Abstract

Drought stress, namely water-deficit stress, is a major constraint on plant growth and productivity, particularly in rainfed agricultural systems. Saponins, a class of plant-derived secondary metabolites within the terpenoid group, are not directly involved in essential physiological processes but may contribute to plant responses to abiotic stress. However, their role in early-stage drought stress tolerance and the underlying physiological and biochemical mechanisms remains insufficiently understood. This study investigated the effects of foliar applied saponin (0%, 1%, 3%, and 5%) on two wheat cultivars with contrasting drought tolerance, Dağdaş 94 (tolerant) and Aldane (sensitive), under four irrigation regimes: no stress (NWS), light (LWS, 25%), moderate (MWS, 50%), and severe water stress (SWS, 75%). The greenhouse experiment followed a completely randomized design with three replications. Saponin had a significant effect on root length, while shoot growth in Dağdaş 94 improved with 1% saponin under NWS but was inhibited by 5% under SWS. Biomass production was generally unaffected by genotype or treatment, although the lowest values occurred at 3% saponin. Water use efficiency (WUE) increased with stress severity but was not influenced by saponin. Water stress substantially elevated hydrogen peroxide (H_2O_2) and malondialdehyde (MDA), confirming oxidative damage. Saponin modulated these effects depending on concentration and genotype. Notably, 5% saponin under SWS caused the greatest H_2O_2 and MDA accumulation in Aldane, while 1–3% saponin reduced MDA under MWS in both cultivars. Antioxidant enzyme activities (SOD, POD, APX) generally increased with stress and saponin, though 3% saponin limited POD induction in Dağdaş 94. Overall, moderate saponin concentrations (1–3%) improved antioxidant responses and reduced oxidative damage under water stress, highlighting its potential as a bioactive treatment to enhance drought resilience in wheat.

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Introduction

Drought is one of the most critical abiotic factors limiting crop production globally. The scarcity of water resources leads to substantial reductions in crop yield and quality (Du et al. 2013). As drought increasingly affects extensive agricultural regions, it possesses a significant threat to global food security (Liu et al. 2024b). Persistent or intermittent water shortages, particularly in arid and semi-arid regions, can be attributed to climate anomalies, elevated temperatures, declining cumulative precipitation, and the intensifying pressures of population growth, urbanization, and industrialization (El-Rawy et al. 2023). In response, many countries have implemented regulatory measures aimed at conserving water resources (Grafton et al. 2018). These include the installation of water meters in irrigation systems and the introduction of water pricing to limit agricultural water use and safeguard groundwater reserves, therefore, it is imperative to develop water-saving field strategy to reduce irrigation amount (Song et al. 2022). As a result, many farmers have adopted deficit irrigation strategies, which involve supplying water at levels below the crop's full evapotranspiration requirements (El-Hendawy et al. 2017).

Drought stress reduces the overall water potential in plants, including leaf water potential, leading to stomatal closure and inhibited growth. It adversely affects many physiological and biochemical processes that are typically stable under optimal conditions, with photosynthesis being among the most several impacted (Soliman et al. 2020). Nevertheless, plants have evolved diverse signaling pathways and adaptive responses to cope with drought and associated oxidative stress, including the accumulation of reactive oxygen species (ROS). These responses involve the activation of antioxidant defense systems, the accumulation of compatible solutes, and the synthesis of stress-related proteins (Ganiyeva et al. 2024). Consequently, exposure to deficit irrigation can substantially alter morphological, physiological, and biochemical processes, often culminating in significant yield reductions. In wheat (*Triticum aestivum* L.), the most widely cultivated cereal crop globally, drought-induced yield losses can exceed 50% (Nyaupane et al. 2024). Therefore, developing effective strategies to mitigate the adverse effects of limited water availability on wheat growth and productivity is of paramount importance. The efficiency of a plant's antioxidant defense system can be evaluated on its ability to accumulate compounds that scavenge free radicals (Jafarova et al. 2021).

Plant-derived bio stimulants, known for their antioxidant properties, have been reported to attract attention due to their potential role in enhancing plant defense mechanisms. Bio stimulants are defined by the European Bio stimulant Industry Council as substances and/or microorganisms that, when applied to plants or the rhizosphere, stimulate natural processes to enhance nutrient uptake, nutrient use efficiency, abiotic stress tolerance, and crop quality. However, the diverse origins and often poorly characterized nature of these substances complicate efforts to action and translate them into effective agronomic practices (Brown and Saa 2015; Carvalhais et al. 2013). Given recent advances, identifying beneficial allelopathic properties of plant-derived biochemicals may offer sustainable alternatives to synthetic agrochemicals in optimizing crop production systems. Among such compounds are saponins, which are secondary metabolites belonging to the terpenoid group. According to Szakiel et al. (2011), saponins are synthesized as part of plant defense mechanisms, contributing to enhance resistance against drought, salinity, and insect herbivory, as well as reinforcing structural integrity. Although not directly involved in essential physiological processes, saponins have surface-active properties that can alter membrane permeability in plant cells (Tiring et al. 2021). At low concentrations, saponins have been reported to mimic plant hormones, thereby promoting seed germination and enhancing growth and development. Conversely, higher concentrations have been shown to exert inhibitory effects on these processes (Mechshanova et al. 2024; Nguyen et al. 2020). While previous studies have shown that saponins can promote root development at low concentrations (Gülören 2021), enhance coleoptile growth (Durán et al. 2022), improve salinity tolerance (Yang et al. 2018), and increase drought tolerance through antioxidant activity (Wang et al. 2024), to date, no studies have investigated the effects of foliar-applied saponins on wheat exposed to water stress; therefore, this study hypothesizes that foliar application of saponins may enhance drought tolerance in wheat by modulating physiological and biochemical responses. Therefore, the present study aimed to evaluate the potential effects of foliar saponin application on the physiological and biochemical responses of wheat plants under various water stress levels.

Materials and Methods

Materials

In this study, two bread wheat varieties, Dağdaş 94 and Aldane, with different tolerance levels, were used. Dağdaş 94, recognized for its drought tolerance during early stages, was used as a drought-tolerance variety. In contrast,

Aldane, which has consistently shown below-average yields under drought conditions in previous studies, was selected as the drought-sensitive variety (Öztürk et al. 2014). The experiment was conducted in the greenhouse's facilities of the Faculty of Agriculture at Necmettin Erbakan University. A completely randomized design with a three-factor factorial arrangement and three replications was employed. The experimental treatments included two wheat genotypes, four different concentrations of plant-derived saponins referred to as Herbal Saponin Concentrations (HSC) (control: 0%, 1%, 3%, 5%), and four water stress levels (no water stress (NWS; full irrigation), light water stress (LWS; 25% water stress), moderate water stress (MWS; 50% water stress), severe water stress (SWS; 75% water stress)). The saponin solution was prepared from *gypsophila* root extract (Tito brand, Smart Chemistry Trade and Consulting Ltd., Izmir, Türkiye). According to the manufacturer's certificate of analysis, the extract was a liquid preparation with a pH of 5.47 and contained 4% saponin, 2.71% total sugars, 13.0% water-soluble dry matter, and 0.81% ash. Trace element levels were reported as 23.7 mg/L copper, < 5 µg/L arsenic, < 5 µg/L lead, < 5 µg/L mercury, and < 10 µg/L cadmium. Microbiological analysis indicated total bacterial counts of 7.2 × 10^5 cfu/mL and yeast-mold count of 4.4 × 10^5 cfu/mL, while fecal coliforms were not detected. Pots were prepared using a mixture of sand and garden soil at a 1:2 ratio. The field capacity and permanent wilting point values of the mixture soil were determined using pressure membrane and pressure plate.

Methods

A total of 96 pots were used in the experiment. Eight seeds were initially sown in each pot and subsequently thinned to three uniform plants per pot after emergence. To ensure adequate nutrient availability, fertilization was applied twice following sowing. Beginning at the three-leaf stage, a commercial soapwort extract (Tito brand), serving as the plant-based saponin source, was foliar-applied to both wheat cultivars in conjunction with the drought treatments. The extract was administered at a concentration of 7 g per application, with a total of five applications conducted at 7-day intervals. Soil moisture levels in the pots were monitored using the weighing method. Irrigation of the control pots was carried out when the total available water content declined by 45–55%, based on weight measurements (Yavuz et al. 2023). Other experimental treatments were irrigated on the same day as the control pots. Water stressed LWS, MWS and SWS treatments were watered with 75%, 50% and 25% of the water applied to the control pots, respectively.

Plants were harvested on the 64th day after sowing, following the completion of water stress and leaf treatments. Root and shoot measurements were recorded at harvest. Shoot length (SL) was defined as the distance from the root collar to the apical meristem, while root length (RL) referred to the length of the main root (Yu et al. 2022). Subsequently, the plants were oven-dried at 75 °C until a constant weight was achieved, and dry biomass (DB) was determined. The evapotranspiration (ET) was calculated according to the below equation:

$$ET = I - Dp \pm \Delta W$$

where: ET represents evapotranspiration (L), I is irrigation amount (L), Dp is amount of water leaking from the bottom of the pot (L), and ΔW is the change in water content of pot from the beginning to the end of the experiment.

Water Use Efficiency (WUE) was calculated using the following equation (Liu et al. 2024a):

$$WUE = DB/ET,$$

where: DB is the dry biomass (g), and ET is the evapotranspiration (L).

Fresh leaf samples harvested (0.5 g) were weighed, homogenized in 0.1% (v/v) trichloroacetic acid, and centrifuged at 12,000 × g for 15 min at 4 °C. The resulting supernatant was combined with 10 mM potassium phosphate buffer (pH = 7.0) and 1 M potassium iodide, and the hydrogen peroxide (H_2O_2) content was quantified spectrophotometrically at 390 nm. The H_2O_2 concentration was expressed as nmol/kg fresh weight (Yüksel 2024). MDA content, an indicator of lipid peroxidation, was determined using the 2-thiobarbituric acid reaction acidic and high-temperature conditions (Heath and Packer 1968). Absorbance was measured at 532 nm and corrected for non-specific turbidity at 600 nm. MDA levels were also expressed as nmol·kg^{-1} fresh weight.

SOD enzyme activity was determined by measuring the photoinhibition of NBT (nitroblue tetrazolium) at 560 nm in a spectrophotometer, according to Giannopolitis and Ries (1977). One unit of SOD activity was the amount of enzyme required to inhibit 50% of NBT photoreduction under assay conditions. POD activity was assessed by monitoring the increase in absorbance due to the oxidation of guaiacol at 470 nm, according to the protocol described by Shams et al. (2019). APX activity was quantified by measuring the decrease in absorbance at 290 nm, corresponding to the oxidation of ascorbate in the enzyme extract, as described by Murshed et al. (2008).

All experiments were conducted using a completely randomized design (CRD) with a three-factor factorial arrangement. Each treatment combination was replicated three times, with each replication consisting of five plants. Data was recorded and organized using Microsoft Excel

Table 1 ANOVA results of the traits studied.

Source of Variance	RL[1] (cm)	SL (cm)	DB (g)	WUE (g DM/kg H_2O)	SOD (EU/g FW)	POD (EU/g FW)	APX (EU/g FW)	MDA (nmol/kg)	H_2O_2 (nmol/kg)
	F values								
Genotype (G)	39.24***[2]	0.23	178.79***	46.11***	287.22***	955.84***	26.99***	431.67***	1.27***
Herbal Saponin Concentrations (HSC)	5.52**	8.06***	3.55*	1.04	192.96***	149.76***	8.63***	275.15***	2.13***
Drought (D)	5.37**	16.36***	5.90**	18.93***	298.30***	281.51***	24.80***	286.46***	1.04***
G × HSC	0.19	0.77	0.88	1.65	103.67***	52.20***	6.37***	11.23***	6.02***
G × D	0.41	4.01*	2.22	0.73	129.72***	62.90***	7.38***	20.53***	5.98***
HSC × D	0.34	0.98	0.26	1.19	81.30***	16.32***	1.22	66.04***	8.10***

[1]*RL* root length, *SL* shoot length, *DB* dry biomass, *WUE* water use efficiency, *SOD* superoxide dismutase, *POD* peroxidase, *APX* ascorbate peroxidase, *MDA* malondialdehyde, H_2O_2 hydrogen peroxide

[2]: *$p<0.05$.** $p<0.01$. *** $p<0.001$. Different lowercase letters in each column or row indicated significant differences at 0.05 level by the Duncan multiple comparisons

(Microsoft 365). The experimental design included three independent factors: (i) genotypes (G) representing two cultivars with differing drought tolerance; (ii) irrigation regimes (D), corresponding to different water stress levels; and (iii) herbal saponin concentrations (HSC). A three-way analysis of variance (ANOVA) was performed using IBM SPSS V. 22.0 software to evaluate the main effects and interactions among the independent variables. For post-hoc comparisons, Duncan's multiple range test was applied at a significant level of $p \leq 0.05$. To further explore the multivariate relationships among the measured traits and treatment groups, principal component analysis (PCA) was conducted.

Results

Analysis of Variance

The results of the analysis of variance (ANOVA) for root length (RL), shoot length (SL), dry biomass (DB), water use efficiency (WUE), superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), malondialdehyde (MDA), and hydrogen peroxide (H_2O_2) are presented in Table 1. The analysis of variance revealed that the genotype had a highly significant effect on all parameters except SL ($p<0.001$). The application of plant saponin concentrations (HSC) did not significantly influence WUE but exhibited significant effects on the remaining variables at varying levels of significance ($p<0.05$, $p<0.01$, $p<0.001$). Drought stress (D) significantly affected all traits examined ($p<0.01$, $p<0.001$). The interaction between genotype and HSC had no significant effect on root length, shoot length, dry biomass, or water use efficiency. However, it significantly influenced biochemical and antioxidant parameters ($p<0.001$) (Table 1). The genotype and drought stress (G × D) interaction significantly affected SOD, POD, APX, MDA, and H2O2 ($p<0.001$), as well as SL ($p<0.05$), but did not significantly affect the remaining traits. The interaction between saponin concentrations and drought stress (HSC × D) was significant for SOD, POD, MDA, and H2O2 ($p<0.001$). Moreover, the three-way interaction (G × HSC × D) had a significant effect on morphological traits such as SL ($p<0.05$), and on key biochemical and antioxidant parameters including SOD, POD, MDA, and H_2O_2 ($p<0.001$). However, this three-way interaction had no significant effect on the other parameters (Table 1). These findings indicate that the effects of HSC applications vary depending on both drought severity and genotype.

Table 2 Mean comparison of herbal saponin source of the traits studied.

Herbal Saponin Concentrations (HSC)	RL (cm)	SL (cm)	DB (g)	WUE (g DM/kg H_2O)	SOD (EU/g FW)	POD (EU/g FW)	APX (EU/g FW)	MDA (nmol/kg)	H_2O_2 (nmol/kg)
0% (Control)	21.07^{a}	12.20^{ab}	0.90^{a}	0.63	79.68^{c}	7.55^{d}	1.98^{b}	0.69^{b}	0.63
1%	21.78^{a}	12.88^{a}	0.76^{ab}	0.58	75.73^{d}	10.64^{c}	1.47^{b}	0.56^{d}	0.58
3%	20.77^{ab}	11.68^{b}	0.64^{b}	0.53	82.55^{b}	11.89^{b}	1.73^{b}	0.59^{c}	0.53
5%	18.59^{b}	11.49^{b}	0.69^{ab}	0.52	84.33^{a}	12.57^{a}	2.61^{a}	0.73^{a}	0.52

*The means in a column with the same letter are statistically indistinguishable from each other ($p < 0.01$)

Table 3 Mean comparison of drought of the traits studied.

Drought (D)	RL[1] (cm)	SL (cm)	DB (g)	WUE (g/L)	SOD (EU/g FW)	POD (EU/g FW)	APX (EU/g FW)	MDA (nmol/kg)	H_2O_2 (nmol/kg)
SWS[1]	18.68^{b2}	10.95^{c}	0.55^{b}	0.75^{a}	84.59^{a}	14.67^{a}	3.04^{a}	0.75^{a}	1824.408^{a}
MWS	20.41^{ab}	11.84^{b}	0.74^{ab}	0.72^{a}	83.65^{a}	11.18^{b}	2.08^{b}	0.66^{b}	1665.825^{b}
LWS	21.51^{a}	12.41^{ab}	0.85^{a}	0.46^{b}	79.74^{b}	9.19^{c}	1.56^{bc}	0.58^{c}	1502.419^{c}
NWS	21.60^{a}	13.04^{a}	0.86^{a}	0.33^{b}	74.32^{c}	7.60^{d}	1.11^{c}	0.58^{c}	1187.580^{d}

[1]*SWS* severe water stress (75% water stress), *MWS* moderate water stress (50% water stress); *LWS* light water stress (25% water stress) and *NWS* no water stress (full irrigation)
[2]The means in a column with the same letter are statistically indistinguishable from each other ($p < 0.01$)

Comparison of Herbal Saponin Concentrations

When comparing the mean values of plant saponin concentrations (HSC) applied as foliar treatments, the greatest root length (RL) was obtained in the 1% HSC treatment (21.78 cm), which did not significantly differ from the control group. The shortest RL (18.59 cm) was recorded in the 5% HSC treatment, representing a 15% reduction. For shoot length (SL), the highest value was also observed in the 1% HSC treatment (12.88 cm), which was 5% higher than the control, while the lowest value was recorded at 11.49 cm in the 5% HSC treatment. Regarding dry biomass (DB), the control group exhibited the highest value (0.90 g), followed by the 1% HSC (0.76 g) and 5% HSC (0.69 g) treatments. The lowest DB value (0.64 g) was obtained from the 3% HSC treatment, which was 29% lower than the control. No statistically significant differences were observed in the water use efficiency (WUE) among the HSC treatments.

Analysis of biochemical and antioxidant activity parameters presented in Table 2 revealed that the 5% HSC treatment resulted in the highest values for SOD (84.33), POD (12.57), APX (2.61), and MDA (0.73), representing increases of 6%, 40%, 24%, and 5%, respectively, compared to the control. No significant differences in H_2O_2 accumulation were detected among the HSC treatments (Table 2).

Comparison of Drought Levels

Comparison of the mean values under the drought stress factor (D) indicated that the highest root length (RL), shoot length (SL), and dry biomass (DB) were recorded under NWS, whereas the lowest values were observed under SWS. A negative correlation was found between water availability and water use efficiency (WUE), with the highest WUE (0.75 g/L) observed at SWS and the lowest (0.33 g/L) under NWS. With respect to biochemical and antioxidant parameters, an increasing trend was observed in response to intensified drought stress. At SWS, mean values of SOD, POD, APX, MDA, and H_2O_2 increased by 12%, 48%, 63%, 23%, and 35%, respectively, compared to NWS (Table 3).

Physiological Traits

According to the ANOVA results presented in Table 1, significant differences in the means for shoot length (SL) were identified for both the G × D and G × HSC × D interactions ($p < 0.05$). Increasing drought severity in both Aldane and Dağdaş 94 genotypes resulted in reduction in SL compared to their respective controls. The highest SL for Dağdaş 94 was recorded under control conditions (NWS) at 13.31 cm, whereas the lowest SL was observed under the SWS treatment for the same genotype, at 10.25 cm. The LWS treatment for Aldane and the LWS and MWS treatments for Dağdaş 94 produced SL values statistically similar to those of the control groups, setting them apart from the more severely stressed treatments (Fig. 1).

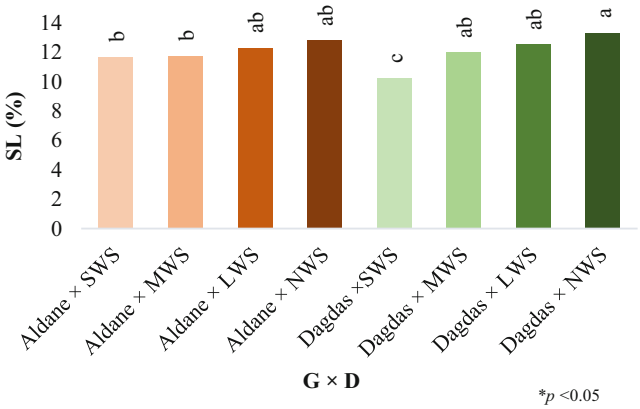

Fig. 1 The effect of drought on shoot length (SL) in two contrasting wheat genotypes, Aldane and Dağdaş 94

Evaluation of the interaction among genotype, herbal saponin concentration (HSC), and drought level revealed that the greatest SL was observed in Dağdaş 94 under full irrigation (NWS) with 1% HSC treatment, measuring 14.74 cm—an increase of 12.8% compared to its corresponding control (Dağdaş 94 × 0% HSC × NWS). Conversely, the lowest SL value was recorded under SWS in Dağdaş 94 treated with 5% HSC, with a mean of 8.93 cm, representing a 20.7% reduction compared to its control under the same drought level (Dağdaş 94 × 0% HSC × SWS) (Fig. 2). Under full irrigation (NWS), Aldane treated with 1% HSC exhibited a 7.6% increase in SL compared to its corresponding control (Aldane × 0% HSC × NWS). This treatment (Aldane × 1% HSC × NWS) yielded the highest SL value among Aldane treatments, reaching 14.27 cm, and was statistically distinct from the other groups. All other treatments fell within a similar significance range (Fig. 2).

Biochemical Components

The interaction between varying concentrations of plant-derived saponin (HSC: 0%, 1%, 3%, and 5%) and two wheat genotypes (Aldane and Dağdaş 94) significantly influenced hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) levels ($p < 0.001$; Table 1). In Aldane, HSC treatments led to increases in H_2O_2 content relative to the control (Aldane × 0% HSC), with increases of 8.7%, 10.8%, and 11.0% observed for the 1%, 3%, and 5% HSC treatments, respectively. In contrast, in Dağdaş 94, the 1% HSC treatment reduced H2O2 levels by 2.4% compared to the control, while 3 and 5% HSC treatments increased H_2O_2 by 16.8 and 19.9%, respectively (Fig. 3a). Regarding MDA levels, Aldane exhibited a decrease under the 1% (14%)

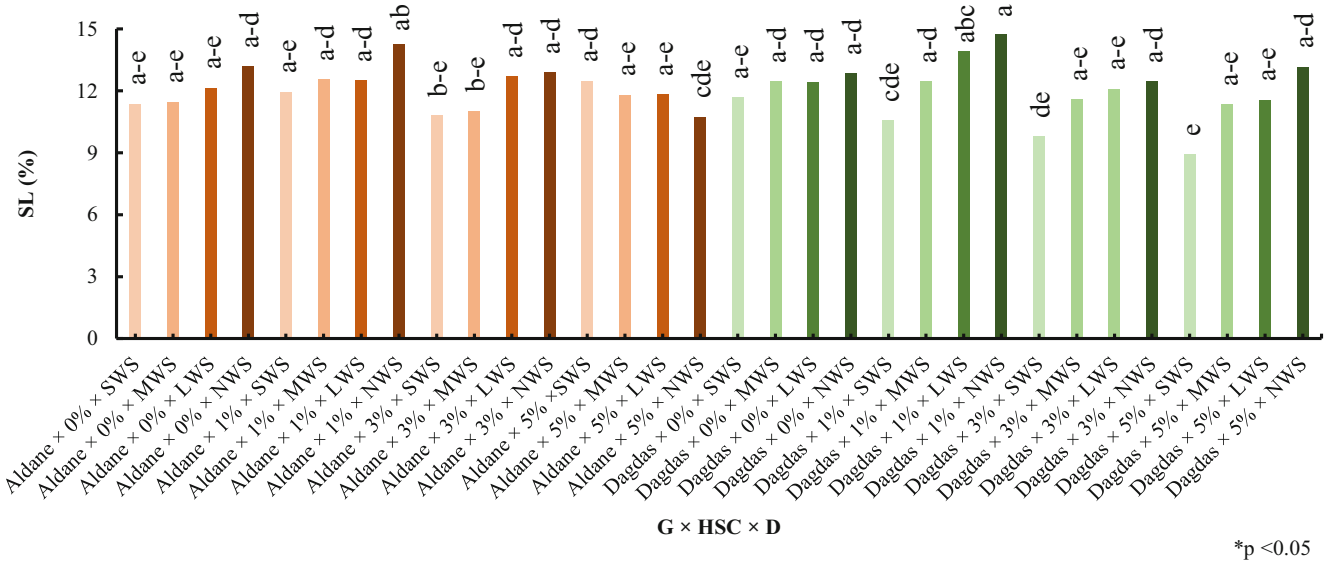

Fig. 2 Effect of genotype, herbal saponin concentrations and drought interaction on shoot length (SL)

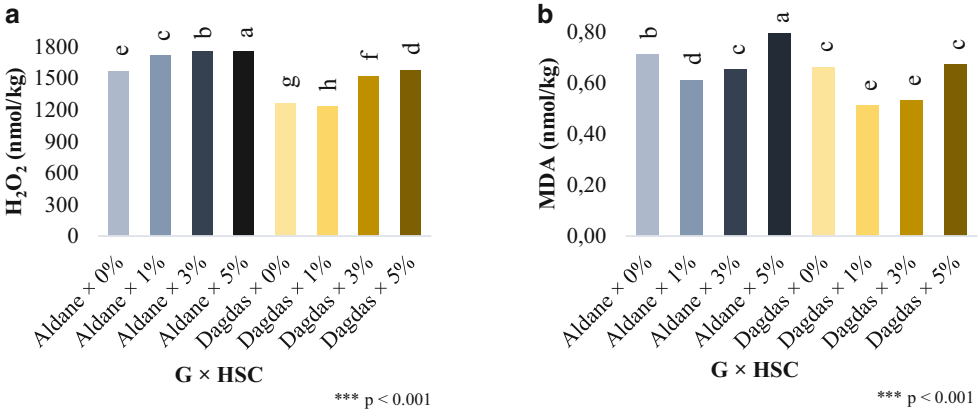

Fig. 3 Effect of herbal saponin concentrations on the **a** hydrogen peroxide (H_2O_2) and **b** malondialdehyde (MDA) in two contrasting wheat genotypes, Aldane and Dağdaş 94

and 3% (8.5%) HSC treatments compared to its control, whereas the 5% HSC treatment caused a 10.1% increase. In Dağdaş 94, the 5% HSC treatment resulted in MDA levels statistically similar to the control, while 1 and 3% HSC treatments reduced MDA content by 22.7 and 19.6%, respectively (Fig. 3b).

Genotype × drought level interactions also significantly affected H_2O_2 and MDA levels ($p < 0.001$; Table 1). Increasing drought stress in both genotypes led to elevated levels of H_2O_2 and MDA. The highest values for Aldane were observed under SWS, with 2031.805 nmol/kg H2O2 and 0.83 nmol/kg MDA. In contrast, the lowest values were recorded in Dağdaş 94 under NWS, with 1108.404 nmol/kg H_2O_2 and 0.54 nmol/kg MDA (Fig. 4a, b). Furthermore, significant effects ($p < 0.001$) were also observed for the interaction between drought levels and foliar-applied HSC concentrations on H_2O_2 and MDA levels (Table 1).

The lowest H_2O_2 content (1138.1 nmol/kg) was recorded in the control treatment (0% HSC × NWS), while the highest value (1908.6 nmol/kg) occurred under the 5% HSC × SWS interaction, representing a 40.4% increase. Across all irrigation levels, increasing HSC concentrations consistently led to elevated H_2O_2 levels compared to the 0% HSC treatments (Fig. 5a). For MDA, the lowest levels were observed in the 1% HSC × NWS (0.48 nmol/kg), 1% HSC × LWS (0.51 nmol/kg), and 3% HSC × LWS (0.51 nmol/kg) interactions. Conversely, the greatest MDA accumulation was found under the 5% HSC × SWS treatment, reaching 0.97 nmol/kg—an approximate 48.5% increase compared to the lowest value (Fig. 5b).

Cellular Antioxidants

The interaction between plant saponin concentrations (HSC) and wheat genotypes significantly influenced cellular antioxidant enzyme activities ($p < 0.001$; Table 1). Under the 1% HSC treatment, superoxide dismutase (SOD) activity decreased in both Aldane (8.5%) and Dağdaş 94

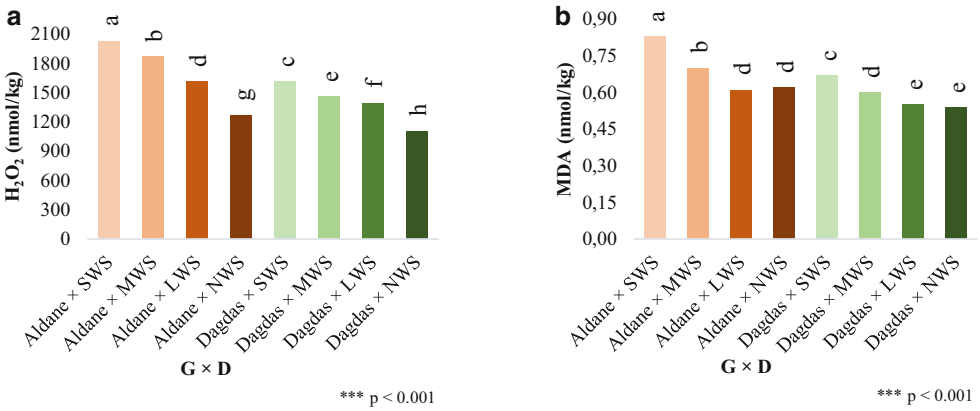

Fig. 4 Effect of drought on the **a** hydrogen peroxide (H_2O_2) and **b** malondialdehyde (MDA) in two contrasting wheat cultivars, Aldane and Dağdaş 94

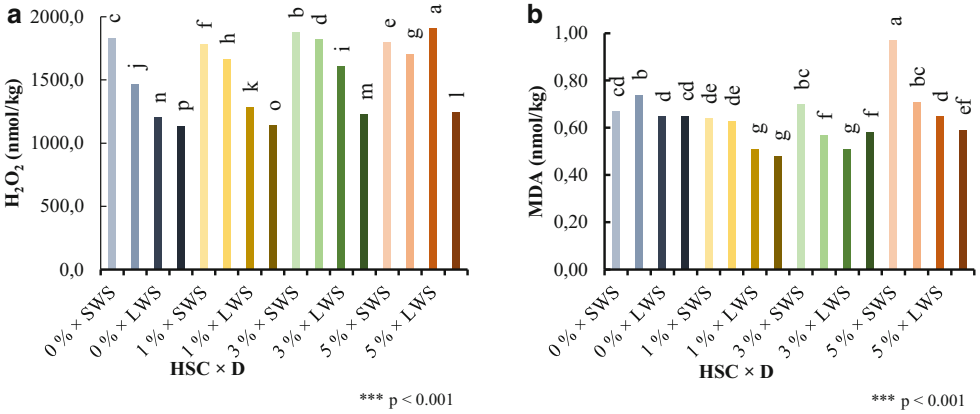

Fig. 5 Effect of HSC treatments on **a** hydrogen peroxide (H_2O_2) and **b** malondialdehyde (MDA) under drought conditions

(1.64%) compared to their respective controls. In contrast, the 3% HSC treatment increased SOD activity by 7.8% in Aldane, while SOD levels in Dağdaş 94 remained statistically comparable to the control. At the 5% HSC level, SOD activity further increased by 8.5% in Aldane and by 2.6% in Dağdaş 94 (Fig. 6a). Peroxidase (POD) activity showed a dose-dependent increase in both genotypes. In Aldane, POD activity significantly increased by 35.7%, 43.1%, and 43.6% in response to 1%, 3%, and 5% HSC treatments, respectively, compared to the control. Similarly, Dağdaş 94 exhibited moderate increases in POD activity of 13.1%, 20.1%, and 32.1% under the same respective HSC concentrations (Fig. 6b).

In Aldane, ascorbate peroxidase (APX) activity remained statistically similar across HSC treatments when compared to the control. The highest APX activity was observed in the control group (0% HSC), while the lowest was recorded with the 1% HSC treatment—a reduction of 35.3%. In Dağdaş 94, APX activity under 1 and 3% HSC remained comparable to the control, whereas the 5% HSC treatment induced a significant increase of 60.1% (Fig. 6c).

Antioxidant enzyme activities were also significantly affected by the interaction between drought stress treatments and genotypes ($p < 0.001$; Table 1). SOD activity exhibited a positive correlation with increasing drought stress. The highest SOD activities were observed at the most severe stress level (SWS) in Aldane (84.55 EU/g FW) and Dağdaş 94 (84.63 EU/g FW), with both genotypes falling within the same statistical significance group. Conversely, the lowest SOD activity (68.02 EU/g FW) was recorded in Aldane under full irrigation (NWS), representing a decrease of approximately 19.0% (Fig. 7a).

POD activity also increased with greater drought severity. The lowest POD activity was observed in Dağdaş 94 under well-watered conditions (NWS; 4.88 EU/g FW), while the highest value (20.38 EU/g FW) was recorded in Aldane under SWS, corresponding to a 76.1% increase (Fig. 7b). APX activity demonstrated a variable response depending on drought intensity. The lowest APX activities were observed under mild to moderate stress levels in both genotypes, which did not differ significantly from one another. However, the highest APX activity was found in Aldane under SWS, reaching 4.06 EU/g FW (Fig. 7c).

Multivariate Analysis

Principal Component Analysis (PCA) provided meaningful insights into the interrelationships among key traits and their contributions to overall variability under different treatments conditions. In the Aldane genotype, PCA ex-

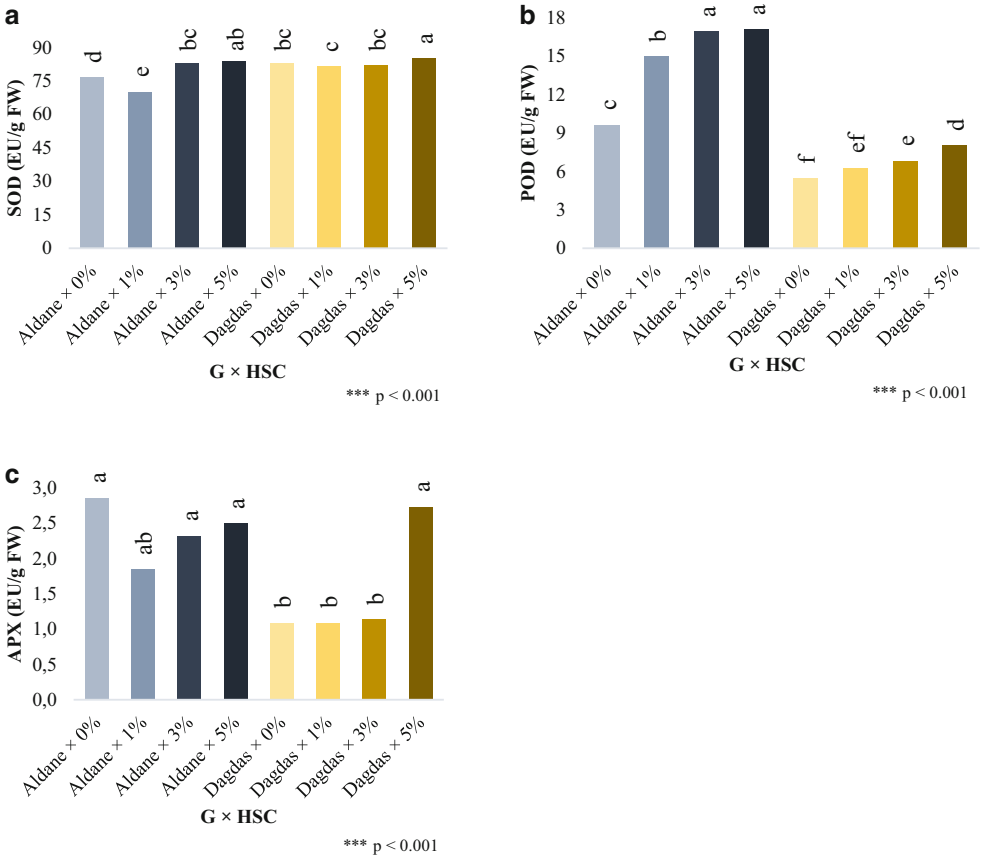

Fig. 6 Effect of HSC Treatments on **a** Superoxide Dismutase (SOD), **b** Peroxidase (POD), and **c** Ascorbate Peroxidase (APX) in Two Contrasting Wheat Cultivars, Aldane and Dağdaş 94

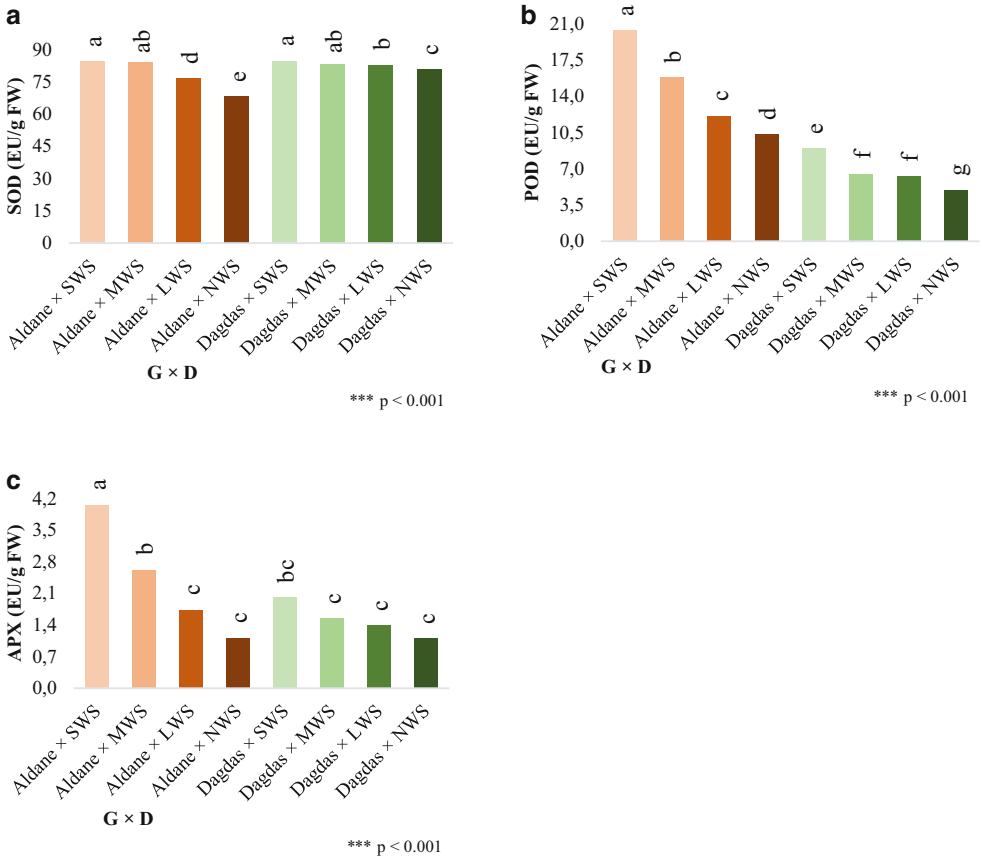

Fig. 7 Effect of drought stress on the **a** superoxide dismutase (SOD), **b** peroxidase (POD) and **c** ascorbate peroxidase (APX) in two contrasting wheat cultivars, Aldane and Dağdaş 94

Table 4 PC matrix for significantly contributing traits for Aldane and Dağdaş 94.

Drought (D) SWS[1]	Aldane		Dağdaş 94	
	PC 1	PC 2	PC 1	PC 2
RL	–0.38	–0.15	–0.35	0.33
SL	–0.30	0.61	–0.40	0.00
DB	–0.19	–0.39	0.01	0.82
WUE	0.31	–0.15	0.27	0.26
SOD	0.34	–0.40	0.41	0.14
POD	0.36	0.26	0.35	–0.07
APX	0.41	0.15	0.34	–0.23
MDA	0.26	0.42	0.32	0.27
H2O2	0.40	–0.09	0.36	0.00
Proportion of total variance (%)	52.07	14.47	55.69	15.65
Cumulative percent of variance (%)	52.07	66.54	55.69	71.34

plained 66.5% of the cumulative variance (PC1 = 52.1%, PC2 = 14.5%), while in Dağdaş 94, it accounted for 71.3% (PC1 = 55.7%, PC2 = 15.6%) (Table 4).

The analysis revealed that the examined traits could be classified into four distinct clusters, reflecting diverse responses to the applied treatments. The first principal component (PC1), which accounted for the largest portion of total variance, was positively correlated with six physiological and biochemical parameters: WUE, SOD, POD, APX, MDA, and H_2O^2. These traits tended to increase concurrently, suggesting coordinated enhancement of oxidative stress responses and antioxidant activity under stress conditions. Conversely, PC1 exhibited negative correlations with root length (RL), shoot length (SL), and dry biomass (DB), indicating an inverse relationship between stress tolerance indicators and growth-related parameters.

Treatment groups receiving NWS, LWS, and to some extent MWS were primarily associated with the negative loading of PC1, representing 52.07% of total variability in Aldane and 55.69% in Dağdaş 94. In Aldane, the highest values for morphological parameters (RL, SL, DB) were recorded in the 1% HSC—NWS group, while the 5% HSC—NWS group showed the lowest values. For Dağdaş 94, the highest RL, SL, and DB values were observed in the 0% HSC—MWS group, whereas the 1% HSC—NWS treatment resulted in the lowest averages (Fig. 8a).

As drought severity increased-particularly in the MWS and SWS groups—these treatments were associated with the positive loading of PC1, indicating elevated stress and antioxidant responses. In Aldane, the 5% HSC—SWS group exhibited the highest values for WUE, oxidative stress markers, and antioxidant enzyme activities. Similarly, in Dağdaş 94, the highest values for these traits were found in the 0% HSC—SWS group. In contrast, the 5% HSC—NWS group in Aldane and the 5% HSC—SWS group in Dağdaş 94 showed the lowest values for these parameters. Notably, in Aldane, the 0% HSC—MWS group, and in Dağdaş 94, the 3% HSC—MWS group demonstrated relatively lower oxidative and antioxidant values but maintained higher levels of morphological traits such as RL, SL, and DB. The second principal component (PC2) further differentiated treatment effects. In particular, the 1% HSC—MWS group in Aldane and the 3% HSC—LWS group in Dağdaş 94 were located within the negative loading of PC2, indicating the lowest overall performance within their respective treatment combinations (Fig. 8a, b).

Discussion

Numerous studies have demonstrated the impact of saponin-containing extracts on various growth parameters in crops such as wheat (Durán et al. 2022; Ganiyeva et al. 2024), soybean (Soliman et al. 2020), oat (Bljahhina et al. 2023), and barley (Ahmed et al. 2024). In the present study, the application of plant saponin concentrations (HSC) sprayed on leaves under drought conditions did not significantly influence root length in either wheat genotype. However, in the drought-tolerant Dağdaş 94 genotype, application of 1% plant saponin concentration with full irrigation levels resulted in an increase in shoot length compared to the control group. On the other hand, a 5% plant saponin concentration applied under 25% severe water stress conditions interacted negatively with the increased stress, suppressing shoot length in Dağdaş 94. As water potential decreases under drought conditions, leaf area is typically reduced to minimize transpirational water loss (Wang et al. 2017). Inadequate turgor maintenance under water-limited conditions can inhibit both cell division and expansion, ultimately limiting shoot growth (Hellal et al. 2018). In some studies that align with our data, the spraying of a 3% saponin-rich soybean stem extract on the medicinal plant *Peucedanum japonicum* Thunb resulted in an increase in shoot dry weight (Ulfa et al. 2015). In potato seedlings, treatment with a 5-ppm extract from mung bean and bean sprouts containing saponin resulted in increased shoot length compared to the control group (Jang et al. 2020).

In our study, the lowest dry biomass was observed in wheat plants treated with 3% HSC, whereas treatments with 1 and 5% HSC yielded dry biomass values comparable to the control. However, there were no statistically significant interactions between plant saponin concentrations, genotype, and drought conditions with respect to biomass accumulation. In a different study, Davidyants (2024) observed that foliar application of saponin-rich extracts at the heading stage in winter wheat increased leaf and spike dry weights,

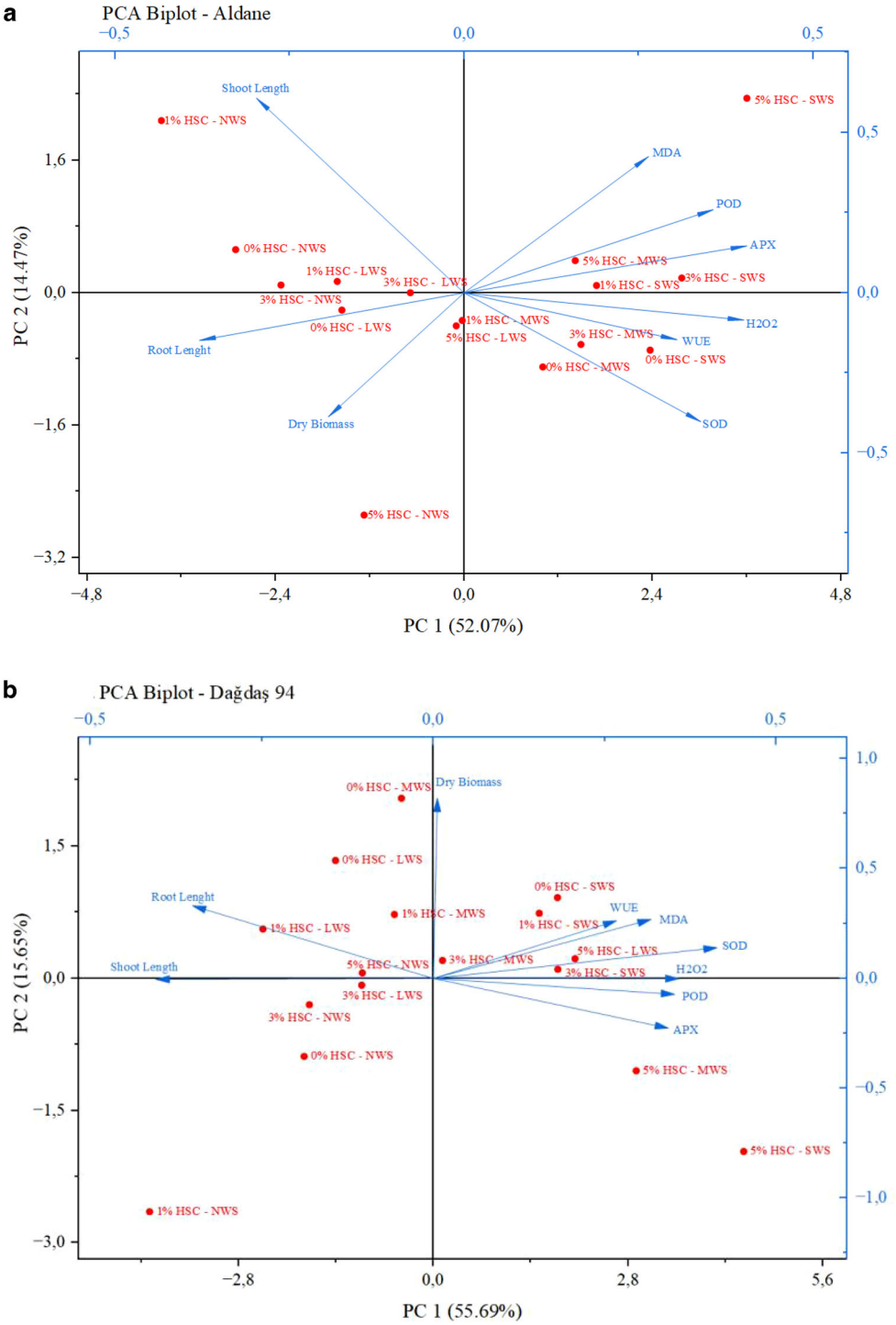

Fig. 8 The principal component biplots showing interrelationships of traits in **a** Aldane and **b** Dağdaş 94 across experimental treatments. Abbreviations are *RL* Root Length, *SL* Shoot Length, *DB* Dry Biomass, *WUE* Water Use Efficiency, *SOD* Superoxide dismutase, *POD* Peroxidase, *APX* Ascorbate Peroxidase, *MDA* Malondialdehyde, H_2O_2 Hydrogen peroxide

highlighting the importance of optimizing both timing and dosage of application alongside stress intensity.

A parallel trend was observed between WUE values and drought intensity: WUE values increased with rising stress levels. However, foliar HSC applications did not significantly affect WUE values, which was largely influenced by genotype and drought level. Similar trends were reported by Alotaibi et al. (2023), who observed enhanced WUE in wheat under limited irrigation. Conversely, other studies have reported declines in WUE under drought conditions (Boutraa et al. 2010; Yong'an et al. 2010).

Our findings further revealed that drought stress, in combination with HSC treatments and genotype, significantly affected levels of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA), underscoring the oxidative damage induced by water deficit. Increased H_2O_2 and MDA levels

under drought are indicative of elevated reactive oxygen species (ROS) and lipid peroxidation, respectively. Mitochondria produce greater quantities of H_2O_2 during drought, and ROS such as H_2O_2 and superoxide radicals can trigger lipid peroxidation, which in turn may activate antioxidant defenses (Sultan et al. 2025; Tartoura 2010). Elevated MDA reflects cellular membrane damage and compromised membrane stability under stress (Ghaffari et al. 2019; Liang et al. 2021).

Under drought-induced oxidative stress, reactive oxygen species (ROS) can directly damage membrane lipids, leading to increased lipid peroxidation (Gorski et al. 1991). In the current study, HSC foliar applications under drought conditions significantly influenced biochemical responses in the drought-sensitive Aldane genotype. The highest MDA levels in Aldane were observed under 5% HSC treatment combined with severe drought (75%). Likewise, all HSC concentrations (1 and 3%) under severe drought also led to increased MDA compared to the control, reinforcing the role of MDA as a marker of oxidative stress (Hernández-Carlos et al. 2011). Interestingly, under moderate and well-watered conditions (MWS, LWS, and NWS), all HSC treatments reduced MDA levels in Aldane relative to their respective controls. In Dağdaş 94, the highest MDA content was recorded in the control under severe drought condition. However, under moderate drought conditions (MWS and LWS), 1 and 3% HSC applications reduced MDA levels compared to the untreated control. These findings suggest that lower concentrations of HSC helped maintain membrane stability under water-limited conditions in both genotypes. Rady et al. (2019) similarly demonstrated that foliar application of saponin-rich licorice root extract under salinity stress, which mimics drought-induced effects, reduced MDA in bean plants. Likewise, Pakhomova and Daminova (2020) found that triple applications of 0.05% ginseng root extract (Panax ginseng) to wheat plants and Sultan et al. (2025) in rice decreased lipid peroxidation activity (i.e., MDA levels), supporting the findings of our study.

Hydrogen peroxide (H_2O_2) levels were consistently higher in Aldane under well-watered conditions compared to Dağdaş 94. H_2O_2 content generally increased with drought severity in both genotypes. In Aldane, all HSC concentrations under drought stress led to increased H_2O_2 accumulation relative to the control, indicating that HSC might mimic or enhance stress signaling pathways. Similarly, treatment of grape cuttings with a triterpene compound like saponin (100 µg/mL) increased H_2O_2 levels (Rifai et al. 2018). These findings underscore the importance of optimizing the dose when applying such anti-stress agents, especially to sensitive genotypes.

In Dağdaş 94, foliar application of 1% HSC under light water stres (25%) and no stress slightly reduced H_2O_2 levels relative to the control. However, in the no stress conditions, the 5% HSC application increased H_2O_2 levels compared to all other treatments. Overall, these results suggest that HSC may stimulate antioxidant defense pathways and mitigate oxidative damage under drought conditions, particularly at lower concentrations. Treatments with 1 and 3% HSC proved most effective in alleviating biochemical stress markers, indicating a potential osmoregulatory role for HSC in enhancing drought resilience in wheat.

Drought stress disrupts various biochemical processes in plants, including respiration, photosynthesis, and enzymatic functions (Ors et al. 2021). Plants rely on a robust and intricate antioxidant defense system to mitigate ROS-induced damage. Among these, key enzymatic antioxidants SOD, POD, and APX play pivotal roles in detoxifying ROS under abiotic stress (Kusvuran et al. 2016). In the present study, antioxidant enzyme activities increased in response to drought severity, indicating a stress-adaptive mechanism. Foliar HSC concentrations also exhibited a dose-dependent trend, like the response observed under drought alone. However, previous studies have shown that saponin-rich treatments may induce phytotoxic effects at higher concentrations (Soliman et al. 2020). Under drought stress in particular, plants tend to enhance the production of SOD and POD enzymes to neutralize ROS (Dong et al. 2019). Consistent with this, in the relatively drought-tolerant Dağdaş 94 genotype, application of 3% HSC under moderate drought (50%) resulted in the lowest enhancement of antioxidant enzyme activity particularly POD compared to the control and other treatment groups (Fig. 8b). This suggests that under certain drought conditions, excessive HSC concentrations may not further enhance, and might even impair, the plant's biochemical defense capacity in some genotypes.

Conclusions

The findings of this study demonstrate that saponin application effectively promotes seedling development and enhances key physiological and metabolic responses in wheat subjected to early-stage drought stress. The observed improvement in drought tolerance was closely associated with increased antioxidant enzyme activity, elevated osmoprotectant accumulation, and the preservation of essential physiological functions. Notably, these positive effects were evident in both drought-sensitive and drought-tolerant wheat cultivars, underscoring the broad-spectrum efficacy of saponin in mitigating drought-induced physiological impairments. The results suggest that saponin holds considerable promise as a bioactive agent in agronomic strategies aimed at enhancing plant resilience under water-limited conditions. Furthermore, the positive responses observed in drought-tolerant genotypes highlight saponin's potential

to reinforce physiological stability, thereby contributing to improved crop performance under suboptimal moisture regimes. Future research should prioritize the elucidation of the molecular mechanisms underlying saponin-mediated drought tolerance, particularly through the investigation of stress-responsive gene expression networks. Additionally, long-term field trials are warranted to assess the impact of saponin application on yield stability and grain quality across various developmental stages, thereby validating its practical applicability in wheat production systems.

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Data availability All data supporting the conclusions of this article are included in this article.

Declarations

Conflict of interest A. Güleç, N. Yavuz, A. Türkoğlu, E.A. Yüksel, M. Armağan, K. Haliloğlu, D. Yavuz, A.A.L. Stansluos, G. Ağar and J. Bocianowski declare that they have no competing interests.

Ethical standards This article does not contain any studies with human participants or animals performed by any of the authors.

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